Understanding the impacts of anthropogenic stressors on species, ecosystems, and fishing communities

Emma E. Hodgson

A dissertation
submitted in partial fulfillment of the
requirements for the degree of

Doctor of Philosophy

University of Washington
2017

Reading Committee:
Timothy Essington, Chair
Benjamin Halpern
Isaac Kaplan

Program Authorized to Offer Degree:
School of Aquatic and Fishery Sciences

University of Washington

Abstract

Understanding the impacts of anthropogenic stressors on species, ecosystems, and fishing communities

Emma E. Hodgson

Chair of the Supervisory Committee:
Professor Timothy Essington
School of Aquatic and Fishery Sciences

Anthropogenic modifications of marine environments result from a variety of activities and have effects across social and ecological dimensions. Humans inhabit linked systems, where our actions such as resource extraction, pollution and development influence species in both direct and indirect ways and feedback to influence the human communities dependent on living marine resources. In order to understand the consequences of our actions and develop strategies to plan for future environmental change, we need a diverse set of tools able to incorporate various levels of complexity. This necessitates the improvement and modification of existing tools, development of novel approaches and unique applications of methods from across fields. In this dissertation I address the ways in which we can use and improve existing tools in ecology to advance our understanding and management of marine resources. In the first Chapter I introduce a method to incorporate life stage specific responses to a stressor, ocean acidification,

to gain a broader understanding of population level vulnerability. In the second Chapter I extend this work to address ecosystem level change from ocean acidification in the California Current, using an ecosystem model to determine changes in biomass and fisheries catch. In the third chapter, I work to improve our understanding of how multiple stressors acting across life history can be magnified or mitigated, based solely on biological characteristics of populations. Finally, in the fourth Chapter I introduce ecologists and natural scientists to a broader understanding of research on risk in order to improve our methods for approaching ecosystem based fisheries management. My work spans ecological scales from populations to ecosystems and links between social and ecological systems.

Table of Contents

ACKNOWLEDGEMENTS

There are many people and organizations without which this thesis would not have been possible. To begin, I cannot fully express my gratitude to my supervisor and mentor, Tim Essington. Tim was the best supervisor I could have asked for; fundamentally he was my advocate, ensuring that I had opportunities to collaborate, present my work and stretch my thinking. But beyond that, Tim was instrumental in helping shape who I am as a scientist. He challenged me to think in new ways, to flounder and flail (like all students should sometimes), and he was always there to support me when I needed it. Tim is a brilliant writer, speaker, teacher and mentor, so thank you Tim for the last five years and for being my forever mentor.

I would also like to extend sincere gratitude to the rest of my committee. To Isaac Kaplan for his unwavering support of my work, for answering a million questions about the Atlantis model and for encouraging me to produce strong science. Thank you to Benjamin Halpern for being an incredibly welcoming mentor for the few months I spent in Santa Barbara, and for asking incredibly good, but challenging, questions; you pushed my thinking in new directions by ensuring that I could defend and justify my decisions. Thank you to Trevor Branch for encouraging me as a scientist and helping me brainstorm about my future directions as a scientist. And thank you to Terrie Klinger, my GSR, you are an inspiring scientist; thank you for being there to talk out ideas.

Funding for my work came from a variety of sources. Thank you to the School of Aquatic and Fishery Sciences, the National Science Foundation’s Graduate Research Fellowship Program, the National Science and Engineering Research Council (Canada) and the National Oceanographic and Atmospheric Administration’s Ocean Acidification Program.

I worked with many brilliant scientists throughout the course of my PhD. Particular thanks to Jameal Samhouri for the numerous meetings brainstorming and shaping my fourth chapter, and to Kristin Marshall for the close collaboration on the Atlantis model. In alphabetical order, thank you to many other researchers for your contributions, willingness to chat with me and/or sharing data and knowledge: Simone Alin, Edward Allison, Nathan Bennet, Nina Bednarsek, Ann Bostrom, Shallin Busch, Alison Cullen, Elizabeth Fulton, Nicolas Gruber, Chris Harvey, Albert Hermann, Steve Kasperski, Julie Keister, Jerry Leonard, Phil Levin, Nancy Lo, Paul McElhany, Jason Miller, Bill Peterson, Melissa Poe, Leif Rasmuson and Paul Reilly.

I would also like to thank the broader community of students and post docs at SAFS. Thank you to the Essington lab members, past and present, for their endless brilliance and support. You made the last five years fun and enlightening. I would like to thank, in particular, the five other women in the lab who I was with almost from start to finish (you know who you are); you are all brilliant and inspiring scientists. And thank you to other friends and colleagues in SAFS for making the last five years full of more than just research. SAFS is made up of an incredible group of students who all make this an incredible place to be.

Finally, thank you to the end of the earth and back to my friends and family. Being a graduate student is a rather crazy rollercoaster, and you all made it possible. To my friends in Seattle and other cities in North America, thank you for delicious food, letting me force you to play games, and for adventures in town, on the water, and out in the mountains. Thank you to my family, in particular my sister, my adorable nephew (who brings so much joy into this world) and to my three parents for your unwavering support and constant encouragement. And thank you, of course, to my incredible partner, Calder Cheverie. You are my rock and my home, here is to the end of long distance!

List of Figures

List of Tables

Introduction

Ecologists are increasingly recognizing that we live within linked social-ecological systems (SES), such that a change in one part of the system has the potential to influence other system components (Levins and Lewontin 1980, Liu et al. 2007). Human societies place a variety of pressures on marine ecosystems (Halpern et al. 2007), causing local species declines (Poloczanska et al. 2013, Purcell et al. 2013) up to whole ecosystem scale change (Kaplan et al. 2010). At the same time, human communities rely on marine resources for a variety of ecosystem services (Nelson et al. 2009), resulting in consequences for human communities when changes occur (Fernandes et al. 2016). With increasing pressure from human populations on ecosystems and potential feedbacks between system components (Holsman et al. 2017), the future is highly unpredictable (Schindler and Hilborn 2015). Therefore, to prepare for possible futures, it is essential to understand how anthropogenic actions affect individual species, the ecosystems they inhabit and in turn, the human communities dependent on these resources.

A growing body of research is providing scientists with an understanding of the responses of individual species to anthropogenic stress. Responses vary both in magnitude and form, at times with large differences between species even when responding to the same stressor (Hendriks et al. 2010, Kroeker et al. 2010). Stressors such as fishing, hypoxia, and ocean acidification can increase mortality (Diaz and Rosenberg 1995, Fletcher 2005, Fabry et al. 2008). But non-lethal impacts are also common, if not the norm. Decreases in growth have been observed as a result of low oxygen-levels and low pH waters (Landry et al. 2007, Clark et al. 2009, Adamack et al. 2012), as have behavioral changes that influence the ability to detect predators or find suitable habitat (Dixson et al. 2009, Munday et al. 2009).

A substantial portion of research has focused on the responses of individual species or life stages to stress, yet to fully understand the impacts of our actions, we need methods to place this information into a larger, more relevant ecological context. The effect of a single change may amplify or diminish when considered at the population level or within the food web (Crain et al. 2008). This introduces the importance of scale (Levin 1992); the scale of the information we have available and how it can be used to inform a more relevant management or ecological context. The process of scaling up available information can include: (i) incorporating individual life stage responses into understanding population consequences, (ii) including species responses in understanding food web impacts and ecosystem change, and finally (iii) understanding how species responses and ecosystem shifts impact human communities that depend on marine resources. This process of scaling up information from one level to a larger context requires tools that have the capacity for synthesizing information from multiple sources.

A suite of modeling tools is available to address these larger questions in ecology and management, ranging from data-limited, qualitative approaches to data-intensive, quantitative approaches. Qualitative and semi-quantitative methods include risk and vulnerability assessment to help understand the susceptibility of organisms to stressors like fishing (Fletcher 2005, Hobday et al. 2011), and more detailed food web models like loop analysis to address overall responses of different groups when one species responds to a stress (Melbourne-Thomas et al. 2012, Dambacher et al. 2015). Quantitative models have an extremely large range in scope, from single species approaches (Heppell 1998, Punt et al. 2014), to predator-prey interactions (Berryman 1992, Oken and Essington 2015) and food web or ecosystem models, for example Atlantis (Fulton et al. 2011), Ecopath and Ecosim (Pauly et al. 2000), and models of intermediate complexity (Plagányi 2007). Connecting species and food web changes to human interactions has been done with both qualitative models (Metcalf 2010) and large ecosystem models (Fulton et al. 2014a). The most appropriate tool to use depends on the question being addressed.

Here, I present four research chapters using a suite of tools to understand the impacts of human actions on species, ecosystems and human communities. The tools include risk and vulnerability assessment, population modeling, and ecosystem modeling. In two chapters I consider the impacts of a specific stressor—ocean acidification (OA). In the first Chapter I introduce a method to advance vulnerability assessment in a manner that explicitly considers how organism response changes with life stage—scaling single life stage vulnerability to a population level understanding. In the second Chapter I use the Atlantis ecosystem model to consider the ecological and economic impacts of ocean acidification across the California Current—scaling single species responses to ecosystem change. In the third Chapter I step away from investigating a specific stressor to consider the population impacts when stressors act on different life stages—again, scaling from life stage responses to population understanding. In this work, we provide the first theoretical basis for identifying species at risk of magnified effects from multiple stressors across life history. Finally, in the fourth Chapter I walk through a method for integrated risk assessment to improve our understanding of, and approaches to, ecosystem based fisheries management (EBFM)—combining information from social, ecological and economic metrics to approach system-level decision making.

Chapter 1

Extending vulnerability assessment to include life stages considerations[1]

Abstract

Species are experiencing a suite of novel stressors from anthropogenic activities that have impacts at multiple scales. Vulnerability assessment is one tool to evaluate the likely impacts that these stressors pose to species so that high-vulnerability cases can be identified and prioritized for monitoring, protection, or mitigation. Commonly used semi-quantitative methods lack a framework to explicitly account for differences in exposure to stressors and organism responses across life stages. Here we propose a modification to commonly used spatial vulnerability assessment methods that includes such an approach, using ocean acidification in the California Current as an illustrative case study. Life stage considerations were included by assessing vulnerability of each life stage to ocean acidification and were used to estimate population vulnerability in two ways. We set population vulnerability equal to: (1) the maximum stage vulnerability and (2) a weighted mean across all stages, with weights calculated using Lefkovitch matrix models. Vulnerability was found to vary across life stages for the six species explored in this case study: two krill – *Euphausia pacifica* and *Thysanoessa spinifera*, pteropod – *Limacina helicina*, pink shrimp – *Pandalus jordani*, Dungeness crab – *Metacarcinus magister* and Pacific hake – *Merluccius productus*. The maximum vulnerability estimates ranged from larval to subadult and adult stages with no consistent stage having maximum vulnerability across species. Similarly, integrated vulnerability metrics varied greatly across species. A comparison showed

---

[1] This work has been published:
Hodgson, E. E., T. E. Essington, and I. C. Kaplan. 2016. Extending Vulnerability Assessment to Include Life Stages Considerations. PLoS ONE **11**:e0158917.

that some species had vulnerabilities that were similar between the two metrics, while other species' vulnerabilities varied substantially between the two metrics. These differences primarily resulted from cases where the most vulnerable stage had a low relative weight. We compare these methods and explore circumstances where each method may be appropriate.

Introduction

Human activities are altering ecosystems across the globe at historically unprecedented rates. Predicting the consequence of these alterations for species, ecosystem structure and ecosystem resilience is essential to planning for the impacts of environmental change (Chapin et al. 1997, Clark et al. 2001). However, in many systems and for many species, there is a lack of data available to provide quantitative predictions of changing system states under new pressures (Dawson et al. 2011). For this reason, a variety of qualitative and semi-quantitative methods have been developed to guide decision makers about likely futures (Stobutzki et al. 2001, Fletcher 2005, Hobday et al. 2011). A common feature of many assessment tools is that they seek to evaluate the vulnerability of a species, ecosystem or human community to changing anthropogenic pressures (e.g., Hatton et al. 2006, Allison et al. 2009, De Lange et al. 2010, Teck et al. 2010). Vulnerability in this case is "the degree to which a system is susceptible to and is unable to cope with adverse effects" (McCarthy and (Eds.) 2001) and largely developed out of an interest in understanding linked human-ecological systems (Adger 2006). Three components are common to vulnerability assessments: *exposure, consequence from exposure* and *resilience* (Turner et al. 2003, Adger 2006, De Lange et al. 2010), which are used to assess *current* vulnerability of species or ecosystems to stressors (Halpern et al. 2008, Halpern et al. 2009) or to assess *future* vulnerability under stressors like climate change (Metzger et al. 2005, Allison et al. 2009).

To understand species vulnerability to new or existing stressors, we need to consider which life stages are likely to be vulnerable. For some stressors there is clearly an impact directed towards a single life stage (e.g., fishing of adults), while other stressors might affect multiple life stages (e.g., pollution or climate change). As vulnerability is a result of exposure to a stressor and the consequence of exposure, we may observe differences in life stage vulnerability due to varying degrees of stressor exposure and/or consequence. Many organisms exhibit distinct spatio-temporal distributions throughout their ontogeny (Bolten et al. 1998, Grantham et al. 2003), influencing the stressors they overlap with and possibly creating opportunities for natural avoidance of, or exposure to, stressors. Early life stages are often found to be particularly susceptible to chemical or physical stressors (Kurihara 2008, Baumann et al. 2011, Frommel et al. 2011, Hurst et al. 2013, Cripps et al. 2014) making their potential consequence high upon exposure. Consequently, vulnerability is likely to change through life (Small-Lorenz et al. 2013), and we need a way to identify the range in vulnerability across life stages and use that to inform population vulnerability.

For stressors that potentially impact species at multiple life stages, there is a major challenge in translating individual life stage vulnerabilities into a population vulnerability estimate. Population vulnerability could equal that of the most vulnerable life stage, or it could be some integration measure across the stages. If all life stages experience a similar vulnerability, then either approach will reach the same conclusion. However, if only one life stage experiences high vulnerability, and the rest experience low vulnerability, the implications of the stressor for the population is unclear. This is particularly the case if the most vulnerable stage is relatively unimportant from a demographic perspective (e.g., low reproductive value (Caswell 2001)). For example, in sea turtles the early life stages have a lower relative contribution to population growth and protecting later life stages is relatively more important (Crouse et al. 1987); however, for many species early life stages are more susceptible to stressors (Kurihara 2008, Frommel et al. 2014). This begs the question, "when does a highly vulnerable early life history stage translate into a highly vulnerable population?" Information provided by vulnerability assessment does not tell us how important each individual life stage is for the population or how the vulnerability translates to a quantitative change in a parameter value (e.g. survival, fecundity or growth).

Building on a rich history of risk and vulnerability assessment methodologies (Turner et al. 2003, Adger 2006, ISO 2009, De Lange et al. 2010, Gardali et al. 2012, Moyle et al. 2013) here we adapt semi-quantitative spatial vulnerability assessment to incorporate life stage considerations (Crouse et al. 1987, Caswell 2001), using the case study of ocean acidification in the California Current. An approach that explicitly and transparently addresses changing vulnerability as organisms move between environments and stages within their life cycle has been called for in the vulnerability assessment literature (Small-Lorenz et al. 2013). The California Current is a useful case study for these investigations as it is naturally prone to low pH and lower levels of aragonite saturation, with distinct spatial and seasonal patterns of pH (Gruber et al. 2012). This will likely make exposure change among life stages that inhabit diverse depth, longitudinal and latitudinal ranges, and we know from laboratory studies that responses from exposure to low pH vary between different life stages of an individual species (Kurihara 2008, Frommel et al. 2014).

We explicitly estimate vulnerability at all life stages for six species within the California Current. We then use these life stage vulnerability estimates to determine overall population vulnerability by comparing two metrics; the first metric assumes population vulnerability is equal to the vulnerability of the most vulnerable stage and the second integrates the vulnerabilities across all stages using a weighted approach. These two metrics were chosen because each might be useful in a different context. Using this process, we investigate the questions: (1) does vulnerability vary across life stages? (2) How do two these alternative approaches for evaluating population vulnerability compare when vulnerability does vary across stages? We use this exercise to reveal the benefits and limitations of these alternative approaches to confronting the challenge of life-stage specific vulnerability and determine vulnerability to ocean acidification for six ecologically and/or economically important species found in the California Current. Our method also directly assesses *confidence* in the vulnerability estimates (similar to the IPCC approach (Mastrandrea et al. 2010)), given the limited information we often have regarding particular stressor-response pairings (Halpern et al. 2008).

Methods

For six example species we calculated vulnerability across the main life history stages and used these estimates to determine population vulnerability. Stage vulnerability was the product of exposure to low pH and consequence from exposure (Figure 1.1), each having a score from 1-3 (similar to previous methods (Samhouri and Levin 2012)). Population vulnerability was calculated two ways: (1) we assumed population vulnerability was equal to the vulnerability estimate of the most vulnerable stage, and (2) population vulnerability was calculated as a weighted mean across all stages. In the latter approach, the weights were proportional to the relative importance of each stage for population growth rate, determined from stage-structured models developed for each species. Uncertainty was determined for each element included in the vulnerability estimates.

Using the case study of ocean acidification in the California Current, species were selected for assessment based on ecological importance, economic value, and/or presumed sensitivity to OA. OA sensitivity was based on distributions in low pH areas or demonstrated biological response to low pH. Species were also chosen to include a variety of taxonomic groups at different levels in the food web: pteropod, krill, shrimp, crab and fish (Table 1.1).

The study region was the US exclusive economic zone (EEZ) off Oregon and California in the California Current system. This section of the coast was chosen because of available model predictions of future ocean acidification levels (Gruber et al. 2012). The California Current is an eastern boundary current that receives water with high dissolved inorganic carbon during the upwelling season in both spring and summer, bringing low pH water into the shallow and nearshore environments (Feely et al. 2008, Gruber et al. 2012). Because the oceans absorb approximately one third of carbon emissions, ocean pH levels are declining globally (Caldeira 2003, Feely et al. 2004, Orr et al. 2005, IPCC 2014). For regions with naturally low pH such as the California Current, this can be particularly problematic because future declines may push pH beyond species' physiological tolerance thresholds (Fabry et al. 2008, Feely et al. 2008, Gruber et al. 2012). Moreover, this ecosystem exhibits wide seasonal variations in pH, which is relevant when considering exposure of life stages with distinct phenology that may coincide with or avoid low pH conditions.

Life Stage Vulnerability

pH model—Spatio-temporal projections of ocean pH were derived from the previously published Regional Ocean Model Systems (ROMS) model for the California Current (Gruber et al. 2012). ROMS is a dynamic, three-dimensional model, developed as a multi-purpose marine modeling system that has proved successful in marine environments (Haidvogel et al. 2008). The ROMS model used provides outputs on a 5 km^2 grid and uses present-day climatological boundary conditions, modifying only the carbon inputs to 2050 using the B1 and A2 IPCC pollution scenarios (Gruber et al. 2012). We used the outputs from the A2 highest emissions scenario for the year 2050, recognizing that this is a worst case scenario and allows us to assess the greatest possible vulnerability. The A2 scenario predicts 541 ppm partial pressure of CO_2 by the year 2050, increasing from 280 ppm in pre-industrial times (Gruber et al. 2012). This model is currently the most state-of-the-art for predicting oceanographic conditions in the California Current, resolving upwelling which is not well-resolved using the global scale models (Orr et al. 2005, Gruber et al. 2012). Although upwelling is well-resolved, we use model outputs at the monthly-average pH scale, which does not include natural pH fluctuations which occur on a much shorter time scale in the California Current (Hofmann et al. 2011). It is likely that inclusion of daily fluctuations would lead to species being exposed to lower pH values than those given by a monthly average, however, smaller scale exposure calculations are not within the scope of this paper.

To be consistent across the species included in this assessment, we used pH as the representative variable for acidification. Although aragonite saturation state may be more important for pteropods, using different variables for each species would require additional assumptions. Instead, we used pH as a proxy for aragonite saturation state to maintain consistency across species. The values of pH used to represent exposure (7.6-7.7) correspond to aragonite near or below its saturation state in the California Current, as it has been shown that a pH<7.75 is associated with aragonite saturation < 1.0 (Feely et al. 2008).

Mapping Distributions—Species distributions were mapped to address distinct spatial and temporal distributions throughout an organism's life. We created presence/absence maps for each month, species, and life history stage. We based these maps on survey data when available, or information collected through a literature review and consultation with experts. Most maps were created using the latter method. Each map was developed as a 2D polygon representing the presence of a species' life history stage for a given month of the year. We identified the deepest depth that the organism inhabits, and based exposure on pH levels at this depth. Because pH generally declines with depth, we were essentially calculating maximum potential exposure. Species distributions were assumed to remain the same between now and 2050. Although species distributions may shift in response to temperature and pH, we do not have the ability to precisely predict these shifts; we therefore make a simplifying assumption that distributions in 2050 will be roughly similar to those in present day. That is, our assessment of vulnerability is contingent on a stable spatial structure to populations.

Maps for Dungeness crab, pink shrimp, two krill species and pteropods were all developed using the literature review and expert consultation method. Preliminary distributions were determined using the literature. For most species (Dungeness crab, krill and pink shrimp), there was information on several life stages (adults, juveniles and eggs) to inform these distributional maps. For pteropods and the planktonic larval stages of these species, preliminary maps were based on limited information with high uncertainty. The preliminary map assumptions were then sent to experts for revisions, leading to final maps that were input into ArcGIS (version 10.2). Details on sources for all species maps can be found in Table A1 (Appendix A.1) and maps can be found in Figures Appendix A.11-38 (Appendix A.1).

We used survey data to describe distributions of Pacific hake. These data came from CalCOFI hake surveys during 1984-2012 (CalCOFI 2012), which contained data on egg and larval abundance at discrete survey locations. CalCOFI data were only used for years when greater than 500 individuals were collected, and we disregarded tows with fewer than 5 individual hake eggs or larvae. A convex hull was then created for monthly maps in ArcGIS. Note that we only mapped the distribution of Pacific hake eggs and larvae as there is no indication that adult teleost fish are impacted by OA. Therefore adult Pacific hake exposure and consequence were assumed to equal 1, the minimum level. This was reasonable given that there is little evidence of direct adverse consequences of OA adult stages of teleost fish (Melzner et al. 2009, Kroeker et al. 2010).

Calculating Exposure—To calculate vulnerability, we had to define conditions that would be considered high exposure (pH that produces maximum consequence). The pH experienced by each species' life stage was determined by overlaying life stage maps with pH predictions (Gruber et al. 2012) using ArcGIS. This produced a pH value for each 5 km^2 grid cell within the life stage's distributional range for each month of the year. Ultimately we were interested in generating a single exposure score to use in the semi-quantitative ranking of vulnerability, yet species are exposed to a gradient of pH levels. In other words, pH is a continuous variable and consequences of exposure to different pH values might also be continuous. Data needed to parameterize detailed, continuous stressor-response curves generally were not available. For this reason, we chose a simpler representation and an accompanying sensitivity analysis to measure vulnerability. We used a step function, assuming minimal adverse effects above a threshold pH level and maximum pH effects below the threshold (we tested the assumption of the shape of this 'threshold' curve against curves that take a more gradual sigmoidal shape – see Appendix A.2 for more information). We considered three threshold pH values to account for uncertainty: 7.6, 7.65, and 7.7 (Figure 1.2). These threshold pH values were chosen as they are the range within which negative consequences of pH are believed to occur, and are frequently used as the experimental 'low pH' value (Kroeker et al. 2010). While similar to stressor-response curves in environmental toxicology (Barnthouse 1992, EPA 1998), our stressor-response step functions were derived from assumed relationships rather than direct measurements.

Using the threshold approach, for each species' life stage, each grid cell within the distribution of that life stage was given a value of 0 or 1, indicating whether pH was above or below the threshold, respectively. This was done for all 12 months of the year (or for the months that life stage is found in the water column). We calculated the *percent exposure* to low pH as the percent of grid cells scored as a 1 (pH less than the threshold) out of all grid cells within the life stage's distribution throughout the year. Percent exposure was then translated into an Exposure value between 1-3 assuming that any percent exposure greater than 75% was considered *high exposure* (3), and values between 0% and 75% were linearly converted to values between 1-3 (Figure 1.2B). Although the relationship between percent exposure and the exposure score also involves potentially influential assumptions, these were necessary to simplify the framework and to focus on life-history-specific vulnerability. Previous authors have assumed similar relationships but have placed high exposure as anything above 50% (Williams et al. 2011). However, because in the California Current species are already experiencing pH around

7.6 (Feely et al. 2008), and our threshold pH of 7.6-7.7 is within the range of what some species may currently experience, we chose a higher end of >75% exposure to rank as 'high' exposure (3).

Consequence—The response of each organism to ocean acidification was determined through a combination of literature review and consultation with experts. For each species included in this analysis, we used the search engines Scopus, Web of Science and Google Scholar to identify papers on the species' response to low pH and low aragonite saturation. Research conducted on our species of interest was used when available; however for some species we used other species in the same genus. For Pacific hake, research on other teleost fishes was used. Additionally, we used recent unpublished investigations (see Appendix A.3) for the krill *Euphausia pacifica*.

Consequence was defined as whether the organism's life stage demonstrates an ability to tolerate exposure. We have used 'consequence' as opposed to the commonly used term 'sensitivity' (Adger 2006) since 'sensitivity' has numerous definitions depending on the field. In this paper we only use sensitivity in the sense of how assessment outputs depend upon input assumptions. There are a number of ways that organisms respond to ocean acidification: changing development times (Bechmann et al. 2011), increased or decreased survival (Dixson et al. 2009, Chambers et al. 2014), changes in calcification (Bednarsek et al. 2012) and changing response to predation (Dixson et al. 2009). As not all papers used the same experimental conditions or measured the same organismal responses, the purpose of this review was not to comprehensively assess whether increased developmental times are more or less detrimental to an organism than changes in survival. Rather, the review was used to determine more broadly whether lethal, sublethal or no effects were found for the study organism in response to OA.

Thus, the literature was used to categorize a life stage consequence (C) from low 1 to high 3 (see Table 1.2). We assigned consequence score 1 when all the evidence indicated that exposure had no impact on either development or survival. A consequence score 2 was assigned if evidence indicated moderate but sublethal effects, while a consequence score 3 was assigned if evidence indicated a strongly adverse impact (e.g., shell dissolution and clear increases in mortality). Most studies tested the response of organisms at pH values near to the threshold pH values we used to determine exposure (see Appendix A.3 Table A.3.1 for more information).

Stage Vulnerability— The vulnerability (V) of each life stage i was calculated multiplicatively: $V_i = (E_i) \times (C_i)$ similar to previous methods (Halpern et al. 2008), where E is exposure and C is consequence. Given values of E and C ranging between 1 and 3, the vulnerability for each life stage lies between 1 and 9. In the results we discuss the range in life stage vulnerability estimates within each species. Vulnerability range was calculated as the difference between the lowest and highest vulnerability estimates among all life history stages (note that since consequence and exposure are bounded by 1-3, Vulnerability is bounded by 1-9). We did not include *adaptive capacity* as a third axis to our vulnerability assessment (De Lange et al. 2010) because of the limited information available for the early life stages of most species in this assessment. Other authors have made a similar decision based on the inherent challenges in scoring adaptive capacity (Gardali et al. 2012).

Population Vulnerability

We calculated population vulnerability using two methods. First, we assigned population vulnerability equal to the maximum of the stage-specific vulnerability estimates. Second, we calculated a weighted mean, where weights were derived from summed elasticity values from population models (described below): $V_s = \sum_1^i w_{si} V_{si}$. Hereafter these two methods are referred to as: maximum stage vulnerability and integrated vulnerability.

Life History Models and Life Stage Weights— Stage-structured models were developed for five of the six species included in this analysis: pink shrimp, Dungeness crab, Pacific hake and two krill species *E. pacifica* and *T. spinifera*. A model was not developed for *L. helicina* due to a paucity of published data on the survival and durations of the life stages of this species; therefore we averaged vulnerability across life stages with equal weightings to produce the integrative metric. For *T. spinifera,* although a model was developed, most of the parameters used came from research on *E. pacifica* and as a result we concluded high uncertainty in model estimates. The models were developed according to standard methods in life history matrix modeling (de Kroon et al. 1986, Heppell et al. 2000, Caswell 2001, Morris and Doak 2002). For example, for a species with three life stages where only the final stage reproduces, the Lefkovitch matrix has the form:

$$\boldsymbol{A} = \begin{pmatrix} P_1 & 0 & F_3 \\ G_1 & P_2 & 0 \\ 0 & G_2 & P_3 \end{pmatrix}$$

where P_i is the probability of remaining in stage i from one time step to the next, G_i is the transition probability and F_i is the fecundity of life stage i. The two probabilities P_i and G_i were calculated as:

$$P_i = s_i - G_i$$

$$G_i = \frac{{s_i}^{d_i}}{\sum_{t=1}^{t=d} {s_i}^{t-1}}$$

where s_i is the daily survival rate and d_i is the duration of the ith life stage, defined as the total number of days that a species will remain in stage i. This equation is subject to the assumption that the population growth rate, $\lambda = 1$ (Caswell 2001). In this analysis, we were interested in the relative contribution to population growth that each life stage provides, not the 'true' population growth rate; thus, the assumption $\lambda = 1$ is appropriate. To ensure all models had a $\lambda = 1$, the matrix elements for each model were multiplied by a constant which varied between models (spanning 0.9714854-1.000133).

Survival rates and duration times for each stage were determined from the literature using published Lefkovitch matrices (Smith 1995, Bi et al. 2011), estimates from laboratory studies, or field based studies. Where possible, survival rates determined from field studies were preferred over laboratory estimates. Both methods result in limitations in the conclusion of true survival rates (for further discussion, see (Rumrill 1990)); however, field based estimates were chosen as they include all sources of natural mortality. For the krill model, we wanted to address the fact that eggs can develop into spawning sub-adults after 4-7 months (Harvey et al. 2010) which is dependent on the time of year when they are spawned (spring vs. summer; pers. comm. Julie Keister). We therefore include two 'types' for *E. pacifica* – early and late spawners, and calculated vulnerability separately for each type. However, results are only shown for the early spawning krill, as vulnerability was very similar for both types. Details on model parameters can be found in Appendix A.4.

We then used the elasticity of population growth rate to each of the matrix elements as the basis of assigning weights to life history stages. Elasticities for the matrix elements were calculated using $e_{ij} = \frac{a_{ij}}{\lambda}\left(\frac{\partial \lambda}{\partial a_{ij}}\right)$ (Caswell 2001), where a_{ij} are the elements of matrix A. Each life stage weight equaled the sum of e_{ij} for all non-zero elements of A for the ith life stage, i.e., w_i

$= \sum_j e_{ij}$. Elasticities indicate how a proportional change in any stage-specific survival, transition, or offspring production affects population growth rate, and therefore provides a basis to identify the stages over which changes in demographic rates are likely to have the largest population-level effect. They provide insight into which life stage may be most important for overall population growth.

Uncertainty

Uncertainty was assessed for both the exposure and consequence components of all life stages and combined to estimate overall population uncertainty. We used a semi-quantitative method because there was not sufficient information to quantify uncertainty more rigorously. The method estimates uncertainty in a similar manner to that used by the IPCC, scaling confidence to qualify the conclusions made (Mastrandrea et al. 2010). Uncertainty of each element was scored between 1-3, based on criteria defined *a priori* (Table 1.3) similar to consequence scores, where 1=low uncertainty and 3=high uncertainty. Uncertainty in exposure, Ue_i, was based on level of confidence in mapped distributions of each life stage i. Uncertainty in consequence, Uc_i, for each life stage was based on confidence in conclusions from studies for each stage i (uncertainty values and reasoning can be found in Appendix A.5). Total uncertainty for species s was calculated as the geometric mean of Ue_i and Uc_i for each life stage and summed using life history weights w_i:

$$U_s = \sum_1^i (\sqrt{Ue_i Uc_i}) w_i \ .$$

Results

Population distributions varied among life stages in time and space (latitude and longitude, and depth) and this variation led to different pH exposure through population life histories. For example, Dungeness crab adults inhabit a narrow band at the ocean bottom all months of the year (Figure 1.3). Because eggs are attached to females, eggs inhabit the same narrow band from October through March. In comparison, the larval stage is planktonic and is distributed in the upper water column further offshore (Figure 1.3). Consequently, adults and eggs have the highest exposure because pH is lowest along the bottom. Differences in exposure resulting from shifts in spatial distribution with age were found for all species (see Appendix A for maps), with pteropods as the exception. With limited detailed knowledge on their distributions, the pteropods were assumed to inhabit a similar spatial extent throughout their life history. Temporal variability was therefore more important than spatial variability in governing exposure differences for pteropod life stages.

Exposure scores were sensitive to the threshold pH value used (Figure 1.4), producing a wide range of exposure scores for each species' life history stage (Table 1.4). Changing threshold pH from 7.6 to 7.65 or 7.7 increased the median exposure from 1.54 to 3 (Figure 1.4). The high sensitivity to threshold pH levels was due to the fact that the ROMs model predicted many more pH 7.7 conditions than 7.6 conditions i.e. our threshold pH values spanned the edge of predicted future pH values. Because several studies indicate species begin responding within this range, the uncertainty about the precise threshold value produces a wide range of exposure scores across several species life history stages. This indicates that uncertainty in the value of the threshold pH has a large influence on the vulnerability and is a point of notable uncertainty.

Vulnerability estimates varied considerably across life history stages, due in equal parts to differences in exposure and consequence (Figure 1.5, A and B). To illustrate this variability across life history, we present results using threshold pH 7.65 (Figure 1.5). At the threshold 7.65, differences in vulnerability estimates across life stages of individual species ranged from 1.29 for Dungeness crab to 4.68 for the pteropods, with a mean difference of 2.96 across all species. Exposure and consequences scores within a life stage were often dissimilar, which produced a range of vulnerability estimates across life stages and species (Figure 1.5). In other words, many life stages had a moderate to low vulnerability estimate resulting from either high exposure paired with low consequence or the reverse (for example, Dungeness crab and pink shrimp adults and eggs, Figure 1.5A). In contrast, high scores for both exposure and consequence were not common for most species' stages—the pteropod species was the only species for which this occurred (e.g., the highest vulnerability estimates were for pteropod eggs and larvae, juveniles and subadults, Figure 1.5B). Pacific hake adults were the only stage to have both low exposure and low consequence, as a result of our assumption that adults are unaffected by low pH.

The relative importance of specific life stages differed across species, and these were reflected in distinct life stage weights (summed elasticity, Table 1.4). Adult stages were most important for pink shrimp, Dungeness crab, and Pacific hake (leading to weights 0.68-0.99, Table 1.4). These species are among the most long-lived of the species assessed, and each have relatively long-duration adult stages. Both krill species showed a more even distribution of weights across life stages from larvae through to adults, with slightly higher weights on the juvenile and sub-adult stages (adults: 0.09-0.35, juveniles and subadults: 0.3-0.35, Table 1.4). Krill are shorter lived, with a short adult duration and relatively longer larval, juvenile and subadult durations.

The stage with maximum vulnerability was not consistent across species (Figure 1.5C); ranging in value from 4.29-6.00 (with a mean of 5.64) using the pH threshold of 7.65. We had expected that larvae would be the most vulnerable stage for all species, because larvae tend to be more sensitive to low pH [22,23]; however, this expectation was not borne out. For some species, combinations of higher consequence with moderate exposure at the larval stage made this stage the most vulnerable (Dungeness crab, pink shrimp and Pacific hake). For others, consequence scores for the later life stages were as high or higher than early life stages and coupled with higher exposure rates, made the later life stages most vulnerable (pteropods and both krill species). Consequently, it is not possible to derive a generalization about which stage tends to be the most vulnerable.

Integrated vulnerability metrics varied greatly across species and were lower on average than the maximum stage vulnerability. Using the pH threshold of 7.65, integrated vulnerability ranged substantially: between 1.02 and 6.27 (with a mean of 4.18). Pacific hake had very low vulnerability, while vulnerability was moderately-low for Dungeness crab and pink shrimp, moderately high for both krill species and high for pteropods (Figure 1.5).

Comparing the two metrics, integrated and maximum stage vulnerability were quite similar for some species, while for others they varied substantially. The integrated metric was far lower than the maximum stage metric for three species (Dungeness crab, pin kshrimp and Pacific hake); in hake the difference was almost six-fold. For all three species, this difference was caused by low stage weights for the stage with the maximum vulnerability (larvae), so that high vulnerability in larvae was down-weighted in comparison to the lower vulnerability for later life stages. In contrast, for pteropods and krill, the two metrics were similar. For pteropods this similarity was due to similar vulnerability at all life stages, combined with equal weighting of stages. For the two krill species, the stages that were more vulnerable also tended to have higher life history weights. Thus, for half the species, when the high vulnerability stage was coupled with low stage weight, we found the choice of method profoundly governed the vulnerability estimate.

Considerable uncertainty was introduced by using a range in pH thresholds (Figure 1.5). Both the maximum stage and integrated metrics showed substantial ranges in value resulting from the pH thresholds of 7.6, 7.65 and 7.7, with the maximum stage metric having larger ranges for all species other than the krill *E. pacifica* (mean range of 3.14 for the maximum stage metric and 1.87 for the integrated). At the high end, pteropods had over a 5-point difference in vulnerability across pH thresholds, for both metrics. Pteropod vulnerability therefore ranged between moderate-low and high, depending on the threshold value used. In almost all cases, different vulnerability estimates would be reached depending on the threshold chosen.

All species had high uncertainty in either exposure or consequence but not both, leading to population uncertainties ranging from 1-3 (3 would be the maximum, if uncertainty in exposure and uncertainty in consequence were both 3; Table 1.4, Figure 1.6). Uncertainty in consequence was consistently high, as there was limited information on the response of species' life stages to OA; pteropods were the exception with low uncertainty in consequence, but high uncertainty in the other areas. By definition, uncertainty was closely related to the amount of previous research across a species' life stages; hence uncertainty in exposure, which was related to knowledge about life stage distributions, was low for most stages of Pacific hake, Dungeness crab and pink shrimp. These fishery species have known distributions, except for the larval stage of Dungeness crab and pink shrimp.

In some cases, the large source of uncertainty introduced from the three thresholds (range of y values in Figure 1.6) exceeds the uncertainty calculated directly for the exposure and consequence components (Figure 1.6). This was particularly noticeable for Dungeness crab, pink shrimp and Pacific hake, which had population uncertainty at the lower range (less than 2, Figure 1.6), but with large ranges in vulnerability resulting from different thresholds. In this case, the maximum stage metric ranged by over 3 points, greatly influencing the vulnerability conclusion. This was found because the thresholds used were on the lower end of pH values predicted in the ROMS model (Gruber et al. 2012), with many more values of pH predicted near 7.7 than there are at 7.6.

Discussion

Many anthropogenic stressors cover large spatial areas (Halpern et al. 2008, Halpern et al. 2009) and may interact with species at multiple points in their life cycle (e.g., pollution, temperature changes, hypoxic events), requiring that we find a way to assess organism vulnerability as it changes through life. The notion that response to environmental stressors changes through life is not new (Caswell 1996, Chaumot et al. 2002, Cripps et al. 2014), yet until now its relevance to applications of semi-quantitative vulnerability assessment had not been demonstrated. We propose a simple modification to a rich history of vulnerability assessment methods (Turner et al. 2003, Adger 2006, De Lange et al. 2010) that involves explicit consideration of exposure and consequence with life stage. This method resulted in clear changes through life in vulnerability to ocean acidification for all species in this assessment. Those stages with the highest consequence often had lower exposure, and vice versa, demonstrating the need to look at both concurrently. For example Pacific hake, Dungeness crab and pink shrimp larvae had high consequence with lower exposure, indicating that the distributions of sensitive planktonic larvae may naturally avoid the most harmful conditions, which for OA tend to be in the upper water column in offshore regions.

Translating life stage vulnerabilities into a single population level vulnerability estimate was sensitive to the method used. For species where the life stage that is most vulnerable also has the highest relative weight, the two metrics we used would be similar and either method could be employed (however, this was not found for most species in our assessment). In contrast, when the most vulnerable stage has a low relative weight, the single-stage and integrated metrics can vary substantially.

Using the maximum stage metric leads to a clear identification of which stage is most susceptible to a stressor, making it useful in certain circumstances. If the goal of the vulnerability assessment is to focus on an individual species to determine the most vulnerable stage or areas of high uncertainty, then this approach is appropriate. However, if the goal is to identify the most vulnerable species within a subset of species of interest, a common goal in these assessments (Fletcher 2005), then this approach may lead to false positives. Singling out the most vulnerable stage without factoring in the relative importance of that stage may lead to a high vulnerability estimate for a species that in fact will be minimally impacted. When considering a range of species, this may result in low priority species falsely being assigned as high priority, downgrading those that are in fact more vulnerable.

On the other hand, though it contains more information about all stages of a species, the integrated approach may lead to false negatives. In circumstances where the impact on the low weight stage is truly catastrophic, the impact on the population may very well be severe but this metric would negate the effect. If 100% mortality were imposed on a stage with low elasticity, we would not want to ignore this highly vulnerable stage. For this reason, both approaches are useful as together they better frame the range of vulnerability estimates for a species. We can return to our earlier point: when the two metrics agree, the assessment is clear. In cases where the two do not agree a more complicated model, for example including density dependence, may be needed to gain insight into the true impact of exposure and consequence for the population.

Our assessment highlighted the value of a detailed, stage-specific approach to judge vulnerability as functions of both exposure and vulnerability. For example, three species had considerable fisheries value: Pacific hake, pink shrimp and Dungeness crab. Of those three, none were found to have high vulnerabilities (1-6, depending on which metric was used), and each had low levels of uncertainty (Figure 1.6). Some of these species might have been judged to be vulnerable to OA if only consequence was considered. For example, a recent study (Miller et al. 2016) revealed high consequence of Dungeness crab larval exposure to pH 7.5, yet our study suggests that larval crab exposure to such low pH is relatively rare, and therefore the larval stage vulnerability score was low-moderate.

In comparison, the three holoplankton species in our assessment, pteropods and two krill, were found to have moderate to high vulnerability and uncertainty estimates on the higher end. The high uncertainty of the vulnerability estimate highlights the value of increasing our understanding of these species' vulnerability to ocean acidification. High uncertainty may mean that these species have true vulnerability levels that are higher or lower than those estimated. Krill are a critical component of marine food webs, and are a very important prey resource in the California Current (Miller et al. 2010), so additional knowledge of the distributions of early life stages and responses to pH will greatly enhance our assessment of krill vulnerability and therefore our understanding of the potential for broader ecological effects propagated through the food web.

Our assessment factored in uncertainty to help determine our confidence in the vulnerability estimates, but we found uncertainty to be unexpectedly large from the three pH thresholds used. Uncertainty in exposure and consequence can be used to help identify species for which we have limited biological knowledge. However, ranges in vulnerability estimates from the pH thresholds were frequently large, sometimes exceeding uncertainty estimates from exposure and consequence (Figure 1.6). The threshold pH is the value at which negative consequences of pH are believed to occur. We found that if the true threshold was 7.6, all species would have vulnerability below 5 (out of a maximum of 9) and be in the lower range of vulnerability estimates. In this case, the maximum stage and the integrated vulnerability metrics would be quite similar across the species, resulting in less challenge when deciding which metric is most appropriate. In contrast, if the threshold was 7.7, then we found very different vulnerabilities between metrics for some species, and higher overall vulnerability estimates. Clear identification of the appropriate pH threshold for each species would provide substantial insight into the true vulnerabilities of these species from ocean acidification. Additionally, true species vulnerability depends strongly on model predicted pH values and model uncertainty can be considerable and is best addressed by multi-model comparison (Cheung et al. 2016).

Because we used the oceanographic predictions from a previously published model (Gruber et al. 2012), our exposure mapping is based on monthly average pH levels and does not capture shorter duration pH levels that may impair species (Hofmann et al. 2011, Hofmann et al. 2014b). Research has shown that pH can range by 0.499 off Monterey Bay, California and by 0.397 off Point Conception, California within a 30-day period with pH ranging up to 0.35 within the span of days (Hofmann et al. 2011). Many organisms that already reside in these high fluctuating environments are likely adapted to cope with some level of fluctuation, but increased frequency of long-term extremes may cause harm (Thomsen et al. 2010, Hofmann et al. 2011, Hofmann et al. 2014b). Additionally, in the California Current, species are already experiencing pH around 7.6 (Feely et al. 2008), which is the predicted mean pH for global oceans in 2100 (Caldeira and Wickett 2005). Thus our threshold pH of 7.6-7.7 is within the range of what some species currently experience.

There are three key assumptions regarding species characteristics that warrant consideration. First, distributions were assumed to remain constant over the next 35 years. Given the minimal information available to map current distributions of all life stages, too many additional assumptions would be required to predict future distributions. Whether OA will cause distributional shifts is unknown. However, there is evidence that such shifts have already occurred in response to temperature (Sorte et al. 2010, Pinsky et al. 2013), suggesting that distributions will change but with a large unknown about the role that OA will play. Second, we did not account for the possibility of avoidance behavior. Avoidance behavior is even less well documented; however there is considerable evidence of species shifting distributions to avoid hypoxic conditions, including avoidance by larvae (e.g., Pihl et al. 1991, Diaz and Rosenberg 1995, Breitburg et al. 2003, Froehlich et al. 2014). Finally, in our assessment species were not assumed to have the capacity to evolve an adapted response to low pH (Hofmann et al. 2014a). Further refinement of the approach could involve addressing one of these assumptions.

In addition to threats from ocean acidification, these marine species will be experiencing warming oceans, hypoxia, point source pollution, and other stressors, all highlighting the importance of scaling up from single stressor studies to understanding cumulative impacts

(Halpern et al. 2009, Pinsky and Mantua 2014). Tight associations between variables need to be considered as they have been shown between naturally occurring temperature and pH values (Hofmann et al. 2014b), and between temperature with pCO_2 and with aragonite saturation (Reum et al. 2014). Although not within the scope of this work, the relative impact of stressors needs to be accounted for, as some are more influential than others. For example, temperature can have a stronger influence than OA (Arnberg et al. 2012). While in this study we advance methods in vulnerability assessment incorporating life stage considerations, there are important steps that remain to be taken towards cumulative impacts assessment.

Understanding and predicting species responses to environmental stressors is one of the fundamental questions in modern ecology (Williams et al. 2008, Dawson et al. 2011). Given the considerable resources required for quantifying population change, less data-dependent methods are valuable tools (Astles et al. 2006). Obtaining predictive power requires combining research from numerous approaches: physiological tolerance studies, behavioral studies, direct observation and population modeling (Dawson et al. 2011), but has also been argued to be likely not achievable (Schindler and Hilborn 2015). Consequently, the extensive level of effort needed to gain insights into possible futures is only warranted in cases where a species has some reasonable risk of exhibiting ecologically significant population-level effects. Vulnerability assessment is a critical point in the risk framework that can help direct management. Here we have introduced an approach that can help identify highly vulnerable stages and populations when the stressor being investigated is one which can influence species at multiple points in their life history.

Table 1.1 Species included in the vulnerability assessment. The reason for their inclusion and the life stages assessed.

Species ***Scientific and common names***	**Reasons for Inclusion**	**Life History Stages Included**
Pacific hake, *Merluccius productus*	$	Eggs, larvae and adults
Dungeness crab, *Metacarcinus magister*	$, S	Eggs, zoea larvae, megalopal larvae, juveniles and adults
Pink shrimp, *Pandalus jordani*	$	Eggs, larvae, juveniles and adults
Krill, *Euphausia pacifica*	E, S	Eggs, larvae, juveniles, subadults and adults
Krill, *Thysanoessa spinifera*	E, S	Eggs, larvae, juveniles and adults
Pteropod, *Limacina helicina*	S	Eggs, juveniles, sub-adults and adults

E = ecologically important, $ = economically valuable fishery species, S = known or presumed consequence from lower pH.

Table 1.2 Description of three consequences scores. Values range between 1-3 and were used to determine consequence from exposure to low pH.

Consequence	Category Description
1	Life stage demonstrates tolerance to exposure to low pH. Conclusion is based on direct experimentation on this or very closely related species, or based on known exposure patterns in sustained populations.
2	Life stage demonstrates some tolerance to exposure to low pH: evidence suggests limited, but not full, tolerance. Empirical evidence shows some effect, but effect size is moderate. Evidence may come from this or from a related species or similar life stage.
3	Life stage shows clear impact from exposure to low pH. This may be based on demonstration of direct effects on this or closely related species.

Table 1.3 Definitions used for uncertainty in exposure. Values from mapping distributions of species U_e and uncertainty in consequence U_c.

U_e	Definition
1	Low uncertainty in distribution: Map is based on multiple years of direct observations from surveys that span distributional range, distributions are consistent across years, or map is developed from conclusions found in numerous (3+) scientific papers and is supported by experts.
2	Moderate uncertainty in distribution: Distribution is based on minimal observations with some questionable accuracy of location or local conditions, full extent of distribution may not be precisely measured, or distribution is derived from model estimates
3	High uncertainty in distribution: Distribution is based on conclusions from few papers (1-2) with minimal spatial coverage requiring generalizations to determine coast-wide distributions, even with expert confirmation of best estimate.
U_c	
1	Low uncertainty in consequence conclusion: more than one study conducted directly on this species life stage, with agreement between studies
2	Moderate confidence in consequence conclusion: one study conducted on this species, more than one but with conflicting results, or study conducted on a species of the same genus or on same species but different life stage
3	High uncertainty in consequence conclusion: no studies directly on this species or any in the same genus, conclusions are on species in the same family

Table 1.4 Species specific values for consequence, exposure, life stage weights and the two uncertainty values.

Species	Life Stage	Consequence	Exposure pH=7.6	Exposure pH=7.65	Exposure pH=7.7	Life Stage Weight*	Uncertainty Exposure	Uncertainty Consequences
Dungness crab, *Metacarcinus magister*	Eggs	*1*	*1.67*	*3.00*	*3.00*	*0.16*	*1*	*3*
	Larvae	*3*	*1.03*	*1.43*	*2.09*	*0.03*	*3*	*2*
	Megalops	*3*	*1.00*	*1.39*	*1.98*	*0.03*	*3*	*3*
	Juveniles 1	*1*	*3.00*	*3.00*	*3.00*	*0.17*	*1*	*3*
	Juveniles 2	*1*	*3.00*	*3.00*	*3.00*	*0.21*	*1*	*3*
	Adult	*1*	*3.00*	*3.00*	*3.00*	***0.44***	*1*	*1*
Pink shrimp, *Pandalus jordani*	Eggs	*1*	*1.90*	*3.00*	*3.00*	*0.14*	*1*	*2*
	Larvae	*2*	*1.04*	*2.61*	*3.00*	*0.04*	*3*	*2*
	Juveniles	*1*	*1.89*	*3.00*	*3.00*	*0.27*	*1*	*3*
	Adult	*1*	*1.89*	*3.00*	*3.00*	***0.55***	*1*	*2*
Pteropod, *Limacina helicina*	Eggs & larvae	*3*	*1.04*	*2.24*	*3.00*	*0.25*	*3*	*2*
	Juvenile	*3*	*1.03*	*2.42*	*3.00*	*0.25*	*3*	*1*

	Subadult	*3*	*1.04*	*2.56*	*3.00*	*0.25*	*3*	*1*
	Adult	*2*	*1.04*	*2.42*	*3.00*	*0.25*	*3*	*2*
Pacific hake,	Eggs	*1*	*1.01*	*3.00*	*3.00*	*0.00*	*1*	*3*
Merluccius	Larvae	*2*	*1.06*	*2.15*	*3.00*	*0.01*	*1*	*3*
productus	Adult	*1*	*1.00*	*1.00*	*1.00*	***0.99***	*1*	*1*
Krill,	Eggs	*1*	*1.67*	*3.00*	*3.00*	*0.03*	*2*	*2*
Euphausia	Larvae	*2*	*1.02*	*1.37*	*1.83*	*0.27*	*2*	*2*
pacifica	Juveniles	*2*	*1.99*	*3.00*	*3.00*	*0.30*	*2*	*3*
Early-	Sub-adults	*2*	*2.35*	*3.00*	*3.00*	***0.32***	*2*	*3*
spawners	Adult	*2*	*2.13*	*3.00*	*3.00*	*0.09*	*2*	*3*
Krill,	Eggs	*1*	*1.71*	*3.00*	*3.00*	*0.028*	*2*	*3*
Thysanoessa	Larvae	*2*	*1.02*	*1.52*	*2.15*	*0.27*	*2*	*3*
spinifera	Juvenile	*2*	*1.74*	*3.00*	*3.00*	***0.35***	*2*	*3*
	Adult	*2*	*1.74*	*3.00*	*3.00*	***0.35***	*2*	*3*

*Bolded values in life stage weights column indicates the stage with the maximum importance for the species.

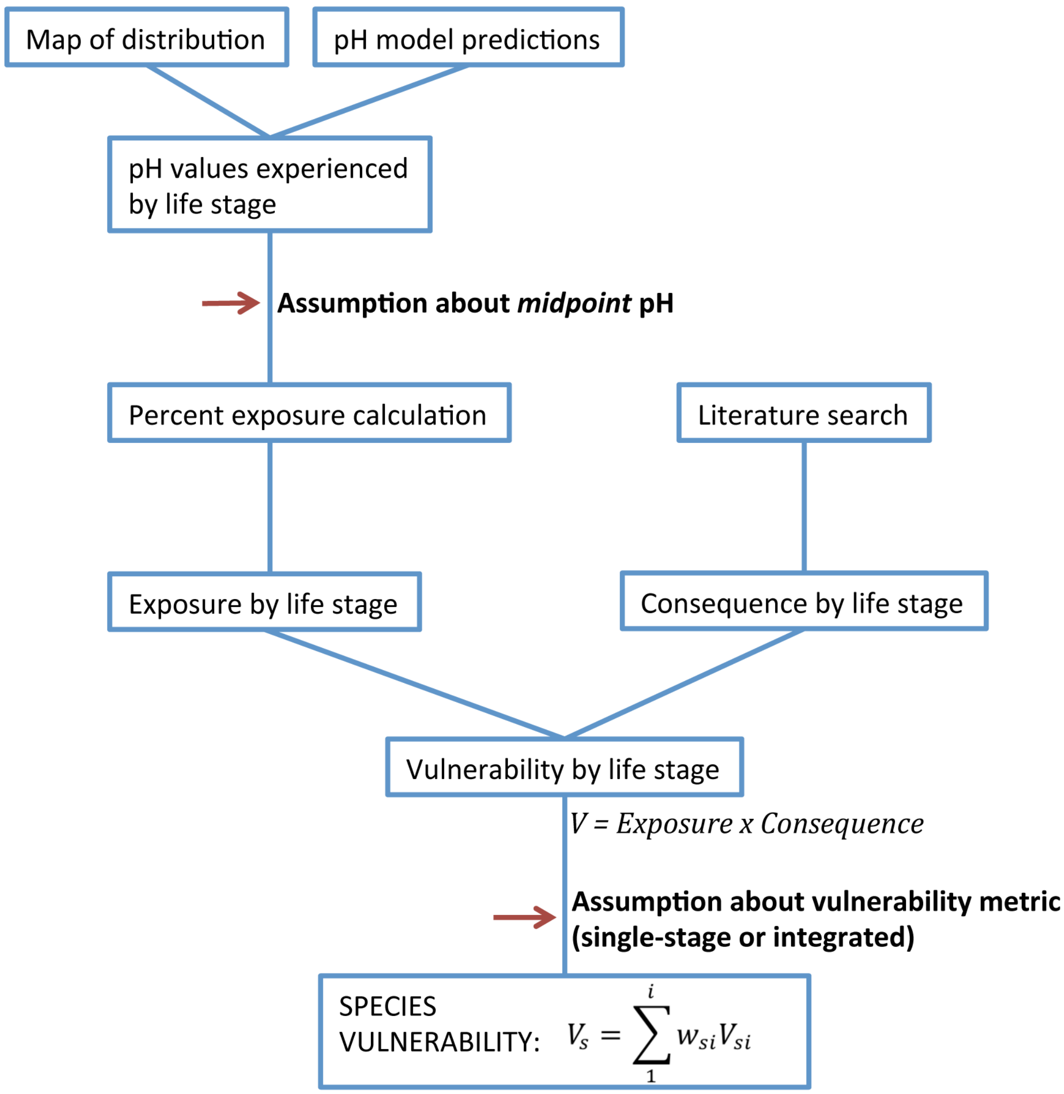

Figure 1.1 Conceptual diagram of vulnerability assessment components.

Diagram includes steps in the vulnerability assessment—exposure and consequence scores that determine stage vulnerability. Red arrows indicate key locations where assumptions are made in the final calculation.

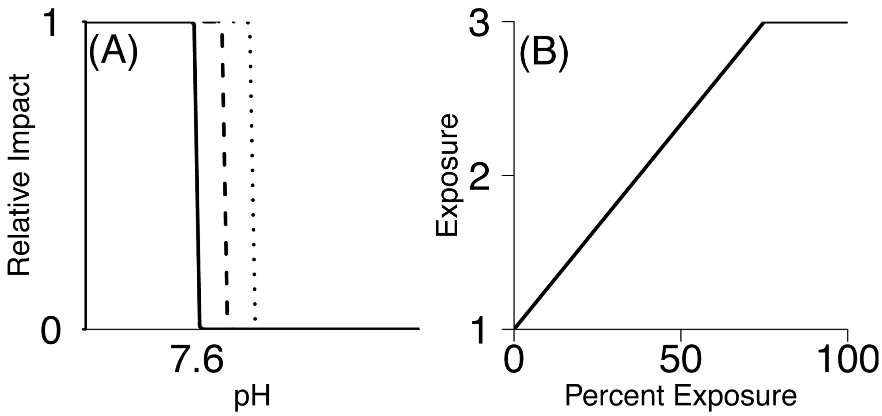

Figure 1.2 Method for translating pH exposure into exposure scores.

(A) Relative impact vs. pH for the three threshold values of 7.6, 7.65 and 7. (B) Scaling used to relate percent exposure to final exposure score.

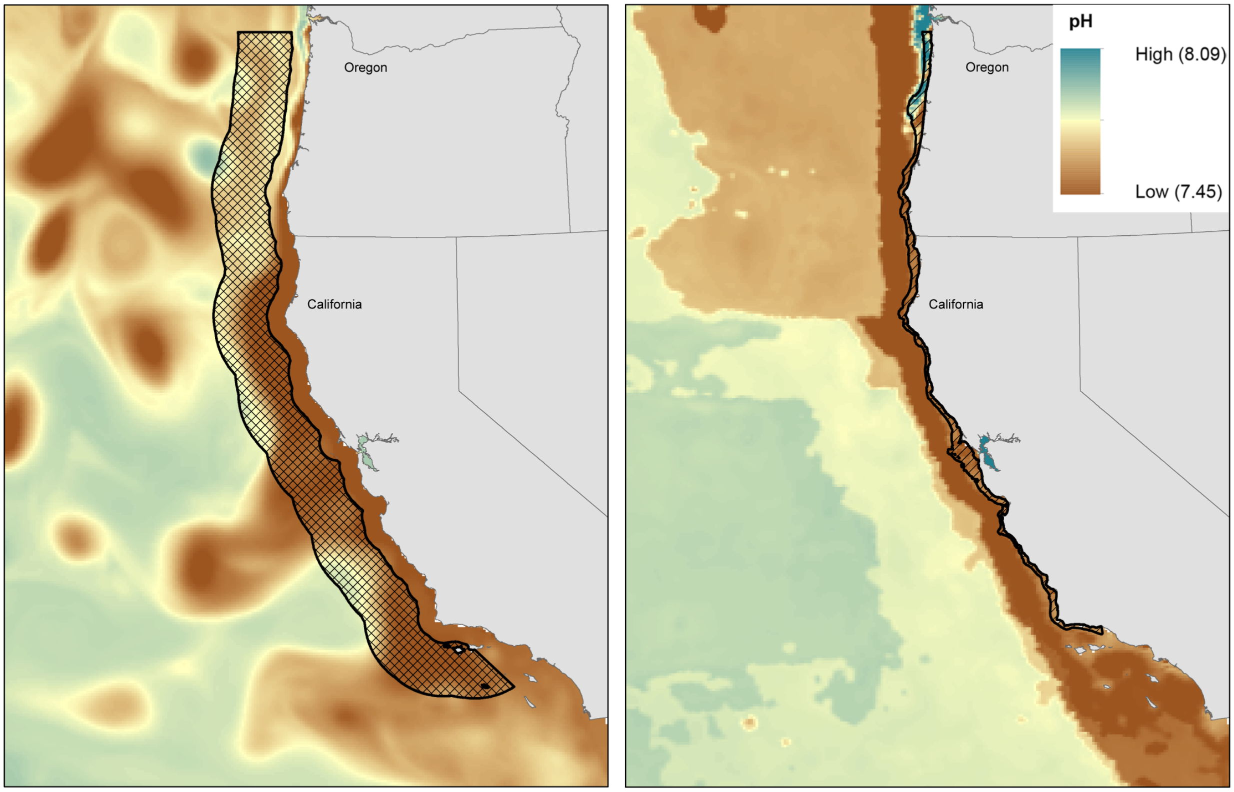

Figure 1.3 Dungeness crab larval, and egg and adult distributions with pH values for May 2050. (A) Larval distribution (checkered region with a black outline) with pH predictions at 70 m depth, and (B) adult and egg distributions (region identified with a black outline), with pH predictions along the sea floor.

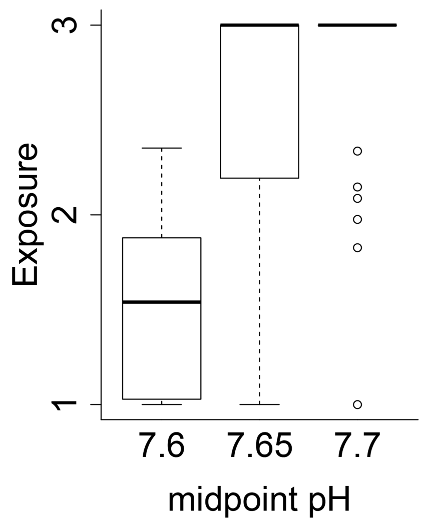

Figure 1.4 Comparison of exposure scores when using different mid-point pH values.

Across all species and life stages.

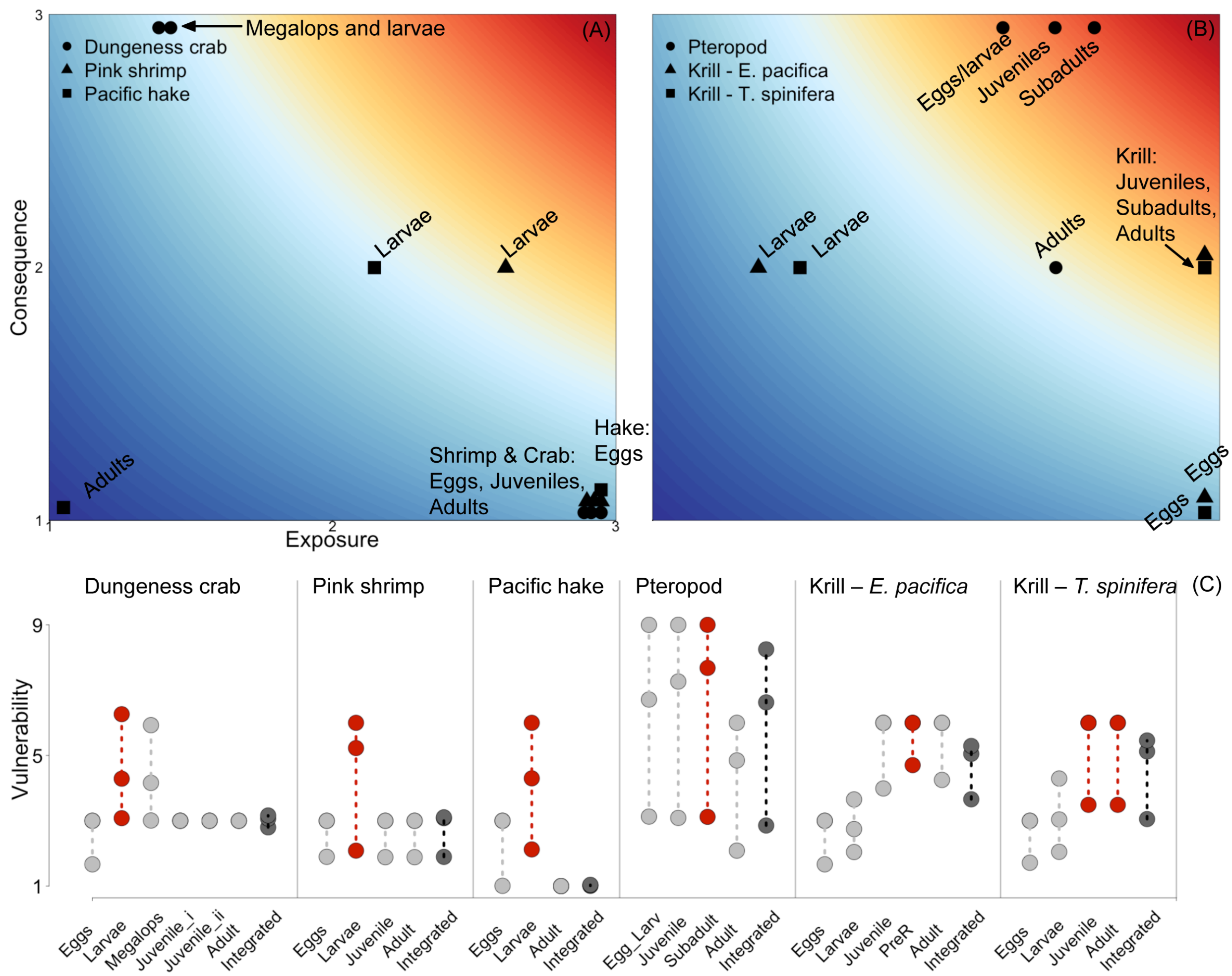

Figure 1.5 Vulnerability plots for six species assessed.

(A) Exposure and consequence scores calculated with critical pH 7.65 for: crab, shrimp and hake. (B) Exposure and consequence scores calculated with critical pH 7.65 for the three planktonic species. (C) Total vulnerability across all life stages with red indicating the single life stage with maximum vulnerability and dark grey indicating integrated vulnerability. Circles and connecting lines represent the range in vulnerability estimates across the three threshold pH values 7.6, 7.65 and 7.7.

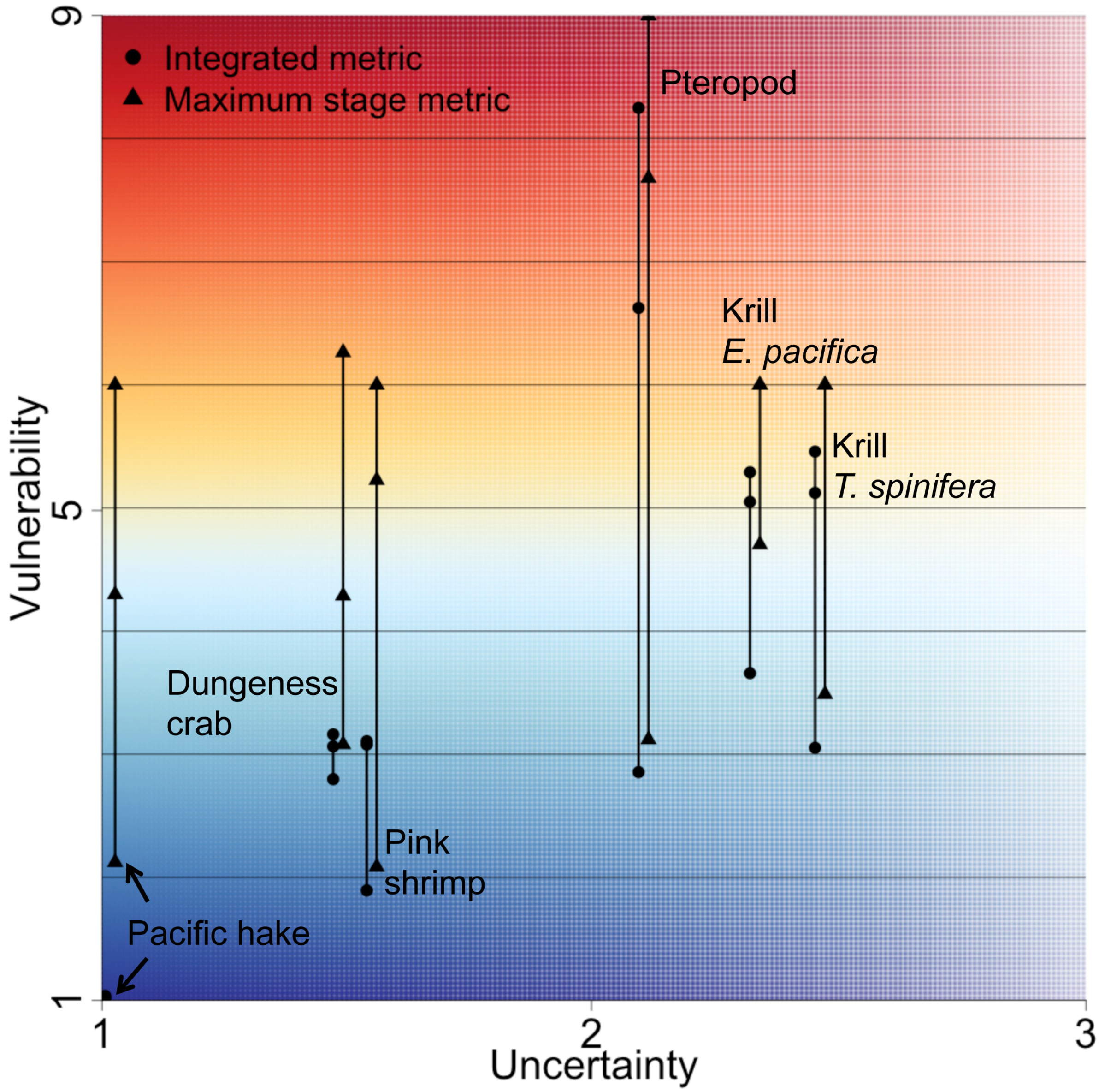

Figure 1.6 Vulnerability and uncertainty combined.

Vulnerability shown as both integrated (circles) and maximum stage (triangles) plotted against uncertainty. Species vulnerabilities range due to critical pH values between 7.6, 7.65 and 7.7.

Chapter 2

Spatially variable ocean acidification and its consequences in the California Current: interactions between oceanography, food webs, and fishing communities

Abstract

Marine ecosystems are experiencing rapid changes driven by anthropogenic stressors which, in turn, are affecting the human communities that rely on living marine resources. One such stressor is ocean acidification, with the potential for substantial biological and economic effects. Most research on ocean acidification has focused on the responses of an individual species or life stage. Yet, understanding how changes scale up from individual species to whole ecosystems, and to the services they provide, is critical to managing fisheries and setting research priorities. Analyses that measure ecosystem impacts are often conducted at a larger spatial scale than is relevant for management. Here we present a unique investigation focused on ecosystem impacts of ocean acidification in the California Current with spatial resolution that is relevant for stakeholders and managers. Using an ecosystem model in combination with oceanographic projections and an economic input-output model, we quantified biological responses in six regions from Vancouver Island, Canada to Baja California, Mexico and economic responses at 17 ports on the US west coast. Outputs show that declines in species biomass tend to be larger in the southern region of the model, but the largest economic impacts on revenue, income and employment occur from northern California to northern Washington State. The economic consequences are primarily driven by declines in Dungeness crab from loss of prey. Given the substantive revenue provided by the fishing industry on the west coast, the results from this scenario could have implications for communities, researchers and managers.

Introduction

The oceans are experiencing warming, acidification, eutrophication, and other changes that are modifying marine ecosystems (Halpern et al. 2008, Ekstrom et al. 2015); these modifications have consequences for human communities that rely on living marine resources. Much of the research focused on the impacts of novel stressors has investigated the responses of individual species (Crain et al. 2008, Darling and Côté 2008, Przeslawski et al. 2014). However, understanding how these changes scale up to impact ecosystems and ecosystem services, such as fisheries catch, is critical to setting research priorities and making strategic marine resource management decisions. Ecosystem scale research has begun to identify broad geographic regions most at risk from these modifications of the environment (Kaplan et al. 2010, Ainsworth et al. 2011, Cheung et al. 2011, Barange et al. 2014). However, impacts on human communities often depend on localized ecological change, making it critical to understand the fine scale shifts occurring (Ekstrom et al. 2015).

Species and stressors are heterogeneous in space and time, creating spatial and temporal variation in how marine populations are impacted by individual stressors. Because people benefit from a distinct set of species, variations in impacts across space or time can have socio-economic consequences at the same scale. Thus, methods to understand ecosystem change and its socio-economic consequences need to include oceanographic conditions at high resolution, the response of the ecosystem to those conditions and the dependencies of local human communities on marine resources (Allison et al. 2009).

Ocean acidification (OA) is a stressor with both spatial and temporal variability that has the potential to restructure marine systems (Griffith et al. 2011, Branch et al. 2012, Le Quesne and Pinnegar 2012, Marshall et al. 2017). Both calcifying and non-calcifying species have been shown to respond directly to changing pH (Branch et al. 2012, Kroeker et al. 2013, Busch and McElhany 2016). Ocean carbonate chemistry varies globally (Orr et al. 2005, Friedrich et al. 2012) and some regions are more at risk from OA than others because of a natural occurrence of low pH water from upwelling that is expected to be exacerbated by the effects of OA (Feely et al. 2016). These include eastern boundary currents like the California Current large marine ecosystem (Feely et al. 2008, Gruber et al. 2012).

The California Current is an upwelling system with high spatial variability in oceanographic conditions (King et al. 2011) and seasonally low pH in nearshore environments (Feely et al. 2008, Gruber et al. 2012). Upwelling occurs in spring and summer, bringing up low pH waters that create a temporal window of exposure to low pH that is expected to worsen with OA (Hauri et al. 2013). Latitudinally, the California Current can be divided into three regions (King et al. 2011). The region North of Cape Blanco (in southern Oregon) is defined by strong winter storms and substantial freshwater inputs. The region between Cape Blanco and Point Conception (northern California) experiences the strongest upwelling. The region south of Point Conception is characterized by weaker winds, weaker upwelling and dampened seasonality. Feely et al. (2016) report the lowest surface pH in the central region and a model by Hauri et al. (2013) projected this region to have the most variable pH levels (range = 7.85 to 8.15; s_{pH}=0.1) and the lowest surface pH most months of the year. Though species in this system may have adapted to these heterogeneous conditions (Pespeni et al. 2013), the natural occurrence of low pH waters can be problematic because future declines may push pH beyond species' physiological tolerance thresholds (Fabry et al. 2008, Feely et al. 2008, Gruber et al. 2012). The oceanographic heterogeneity will likely lead to variability in ecosystem changes.

The California Current supports a diverse food web and a multi-million-dollar fishing industry. The direct ex-vessel revenue from fisheries in the US portion of the ecosystem is worth over $450 million (PacFIN 2013). Fisheries catches are localized in time and space (Kaplan et al. 2013b). For instance, fisheries in Washington State are dominated by Dungeness crab (*Metacarcinus magister*), sardine (*Sardinops sagax*), Pacific hake (*Merluccius productus*), and shrimp (family Pandalidae), while ports off southern California catch market squid (*Doryteuthis opalescens*), mackerel (family Scombridae), sardine, anchovy (*Engraulis mordax)* and nearshore urchins (*Mesocentrotus* spp.) (PacFIN 2013). Given the variability of target species and total landings between ports in the California Current (Kaplan et al. 2013b) and heterogeneity of oceanographic conditions (King et al. 2011, Hauri et al. 2013, Feely et al. 2016), changes in catch from ocean acidification are likely to vary regionally. Basin-wide impacts have been projected in the California Current (Kaplan et al. 2010, Marshall et al. 2017), the southeastern Australia marine ecosystem (Griffith et al. 2011) and for four countries in the UK (Fernandes et al. 2016). To our knowledge, no work has estimated how OA may impact fisheries at finer spatial scales, such as the port-level.

Here we present a case study investigating spatial impacts of ocean acidification on species and fisheries in the California Current. We employ oceanographic predictions from a Regional Oceanographic Modeling System (ROMS) model forced by an earth system model (ESM2M) under climate scenario RCP8.5, an Atlantis end-to-end marine ecosystem model (Fulton et al. 2011), and an economic input-output model (Leonard and Watson 2011). This combination of approaches was used to project the state of the ecosystem in the 2060s, to identify species and communities potentially at risk, and therefore where future research and management focus is needed. Our specific focus is on the spatial patterns of ecosystem changes that might occur, and the consequences of these changes for port revenue, income and employment in US west coast communities.

Methods

Overview

We used an ecosystem model to investigate the impacts of ocean acidification in the California Current and consequences for fishing communities along the US west coast. Outputs generated by a ROMS provided physical forcing for the Atlantis ecosystem model for the present and 50 years in the future. Outputs from Atlantis were then passed to an economic input-output model developed for the west coast of the US (IO-PAC; Leonard and Watson 2011). Because the IO-PAC model and high-resolution revenue data were only available for the US portion of the model, we focused our economic analysis on the US west coast (i.e., excluding Canada and Mexico). We focused on the 17 US port groups on the outer coast (excluding Puget Sound) used by the Pacific Fisheries Information Network (PacFIN) to aggregate data and avoid issues of disclosure of confidential information (Table 8-1 of Appendix A in PFMC 2004). For all 17 port groups we simulated changes in catch, revenue, income and employment.

Summary of Atlantis model

We used the spatially explicit end-to-end ecosystem model Atlantis (Fulton et al. 2011) to simulate food web dynamics and fisheries. Atlantis represents ecosystem dynamics with three components: (i) an oceanographic sub-model (ii) an ecology sub-model and (iii) a human dynamics sub-model (Fulton et al. 2004a, Fulton et al. 2004b). Extensive documentation of the

Atlantis modeling framework, for both the California Current and other ecosystems, can be found in previous publications (Fulton et al. 2004a, Fulton et al. 2004b, Kaplan et al. 2010, Kaplan et al. 2013a). Thus, we briefly summarize the most recent version of the Atlantis model developed for the California Current (Marshall et al. 2017), including all three sub-models, highlighting changes we made explicitly to investigate spatial impacts of OA.

The physical domain of the Atlantis model is represented by polygons, which are defined by depth ranges and by longitudinal and latitudinal breaks. Our model includes 88 spatial polygons that span the entire domain of the California Current, from the north extent of Vancouver Island, Canada and south to Punta Eugenia, Baja California, Mexico. Longitudinal polygon boundaries were based on bathymetry with breaks at 50m, 100m, 200m, 550m and 1200m and then finally at the 200 nautical mile Exclusive Economic Zone (EEZ) (Figure 2.1). These breaks were chosen based on a mixture of bathymetric and biological information (representing: nearshore shelf, deeper shelf, shelf/slope break; see Appendix S1 in Marshall et al. 2017). Depth ranges of boxes within the model match the depths used to define bathymetric breaks.

Oceanographic model

The Atlantis model was forced with oceanographic outputs from an implementation of ROMS version 3.7 (Haidvogel et al. 2008, Moore et al. 2011) with biogeochemistry, configured to predict oceanographic conditions (currents, pH, oxygen, temperature, salinity and nutrients) for the present decade (2011-2020) and 50 years in the future (2061-2070). The two decade-long runs were used as opposed to creating a full time series of downscaled oceanographic conditions between 2011-2070 because the latter was too computationally intensive The model has 10x10 km horizontal grid resolution, includes tidal dynamics, and uses global model outputs from the NOAA Geophysical Fluid Dynamics Laboratory (GFDL) ESM2M model (Dunne et al. 2012, Dunne et al. 2013) to derive surface forcing, initial conditions, and boundary conditions for the two decades simulated. The climate scenario used was RCP8.5, which assumes continuation of present emissions trajectories. The two time periods were run independently. In each case the first year of the decade (January 1st 2011 and 2061, respectively) was initialized through interpolation of the global ocean simulation results (the ESM2M/TOPAZ simulation, scenario RCP8.5). This higher resolution model was developed because upwelling is not well resolved with global scale models (Orr et al. 2005) and upwelling plays an important role in the development and spatial extent of OA in the region. It is important to note that these models do not represent nearshore environments (inshore of 50 meters) with high resolution, thus do not represent land-based run-off as a contributor to OA. Previous models for the southern California Current have found expected pH levels of around 7.8 in nearshore surface waters by 2050, with heterogeneity in space (by latitude and depth) and seasonally (Gruber et al. 2012). Thus pH levels in this model are expected to be in a similar range. Further details on the ROMS implementation can be found in Marshall et al. (2017) and the associated appendices.

Two sets of oceanographic conditions were used to force Atlantis; oceanographic outputs for a single year, 2013 or 2063, were extracted from the decade-long runs. The single year of oceanography was then looped 100 times in the ecological model to achieve quasi-equilibrium ecological conditions. Looping a single year as opposed to the 10-year oceanographic simulations helped control for inter-annual variability in ocean conditions.

Ecological model

The Atlantis modeling framework is a C++ code base that simulates multi-species ecosystem dynamics in a spatial framework, using a simple forward-difference integration scheme typically on 12-hour time-steps (Fulton et al. 2004a, Fulton et al. 2004c, Horne et al. 2010). Atlantis is spatially explicit, with vertebrate numbers-at-age and weights-at-age tracked per polygon and invertebrates modeled as biomass pools per polygon. The model simulates processes including primary production, growth and reproduction, trophic dynamics, movement/migration, and habitat interactions within each polygon and depth layer. These processes can be directly impacted by environmental conditions such as pH, temperature, oxygen and water flux from ROMS or other oceanographic forcing. Predator-prey dynamics allow diet switching, predator starvation, and declines in predator weight-at-age if prey decline in abundance.

The most recent California Current Atlantis model includes 82 functional groups representing detritus (2 groups), primary producers (6 groups), benthic and pelagic invertebrates (25 groups), fishes (36 groups), marine mammals (10 groups) and seabirds (3 groups). This model is an update of the Marshall et al. (2017) model, which was developed to better represent groups that respond to low pH, including: pteropods, Dungeness crab, coral, coccolithophores and market squid. All biological parameters used in the model reported in this manuscript, such as recruitment, mortality, diets and distributions, were the same as those used in Marshall et al. (2017), save for a few changes discussed below.

We made slight modifications to the model parameterization used by Marshall et al. (2017). In that model, 11 groups declined to low biomass levels towards the end of the baseline simulation with no OA and no fishing. Similar challenges with persistence in complex ecosystem models have been reported by others (Gaichas et al. 2012, Thorpe et al. 2015) and are a substantial challenge in large multi-species models. Two of those functional groups are key invertebrate fishery species: pandalid shrimp and market squid. Market squid in particular is a highly important fishery species in Southern California (making up over 50% of the biomass of catch for 5 ports in 2013). Thus, with our focus on the spatial effects of OA on fisheries catch, we modified parameter values for five groups. We made slight modifications to feeding efficiency parameters for Dungeness crab, nearshore sea urchins and an epibenthic predatory invertebrate group comprised of sea stars and large predatory snails. Both feeding efficiencies and quadratic mortality rates were modified for market squid and pandalid shrimps.

With these modifications thirteen groups still declined to low biomass levels (<2% starting biomass) in this version of the model. These included: deep demersal fish, deep small rockfish, Pacific ocean perch (*Sebastes alutus*), Arrowtooth flounder (*Atheresthes stomias*), large demersal predators, large pelagic predators, Chinook salmon (*Oncorhynchus tshawytscha*), small demersal sharks, pelagic sharks, nearshore sea urchins, epibenthic predatory invertebrates, large phytoplankton and coccolithophores. Though the groups declining made up 17% of the functional groups in the model, they represented 2% of vertebrate biomass and <1% of consumer biomass in the model and accounted for 7.5% of 2013 US west coast catch. With our primary focus on effects on fisheries catch, the declining groups were not expected to greatly impact outputs, though future modeling efforts can work to increase persistence across groups. As noted, persistence is notoriously challenging in large multi-species models (Gaichas et al. 2012, Thorpe et al. 2015). Additionally, crangon shrimp were found to have unrealistic increases in biomass and were removed from economic analyses (they accounted for 0.1% of 2013 catch).

Fisheries parameterization

Fishing mortality for each functional group was set at a constant rate (e.g., 0.05 yr^{-1}) such that the catch (tons) in the first year of the model would match the 2013 catch data from PacFIN. Our US catches were allocated spatially to 17 port groups (hereafter called 'ports') along the coast, with one additional fishery in each of Canada and Mexico (Figure 2.1). Spatially explicit fishing mortality rates per port (or country) and functional group were then applied as constant fishing rates (see Appendix B.1). This assumes no management responses or shifts in fishery behavior in the future; while obviously unrealistic, this allows for consideration of OA effects clear of confounding socioeconomic dynamics which would make attribution incredibly difficult. US vessels were assumed to have access to coastal (nearshore) areas within 200km of the homeport (the main city in the port), and equal access to areas offshore to 1200m depth. Canadian and Mexican fishing mortality rates were applied equally to all Canadian and Mexican areas in the model domain, respectively.

Though our Atlantis model projects port-level catches, each of these ports has catch from a mix of vessel types (Table 2.1, originally derived from Leonard and Watson (2011)). These vessels types have distinct target species, economic characteristics, and subsequent vulnerabilities to ocean acidification. Therefore, Atlantis port-level catches were allocated to the vessel types based on the proportion of catches per vessel type reported in 2013. We report results for 10 vessel types that primarily harvest groups well represented by Atlantis biomass dynamics; nine other vessels types depend substantially on species that are poorly represented in the base Atlantis simulations (i.e., functional groups that do not persist) and these were aggregated into a 'generic' coast-wide fishery.

The catch (tons) landed at each port was converted to total revenue, using 2013 price per pound data (PacFIN 2013). Prices were found for each functional group at the resolution of vessel type and port. These prices were multiplied by biomass to find total revenue by: (1) vessel type at each port and (2) functional group at each port.

Input–Output models, IMPLAN, and IO-PAC

We used an Input-Output (IO) model (Leontief 1951) to investigate changes in income and employment resulting from changes in ex-vessel fisheries revenue. Here, and in previous work (Kaplan and Leonard 2012), we use IO models to capture direct, indirect, and induced effects. Direct effect refers to the change in production, such as impacts at the level of the vessel. Indirect effect refers to secondary activity caused by changing input needs of directly affected industries (e.g., changes in fleet revenue may cause a decline in output from shipyards that service those vessels). Induced effects are caused by changes in household spending from additional income generated by direct and indirect effects.

The Northwest Fisheries Science Center's input-output model for Pacific Coast fisheries (IO-PAC) was designed to estimate the gross changes in economic contributions and economic impacts resulting from policy, environmental, or other changes that affect fishery harvest (Leonard and Watson 2011). The IO-PAC was constructed by customizing Impact Analysis for Planning (IMPLAN) regional input-output (IO) software (IMPLAN, MIG Inc. Hudson Wisconsin).

Development of IO-PAC included customizing IMPLAN with an addition of 19 commercial fishing vessel types. The present application used a version of IO-PAC that was developed to include the 17 ports in the Atlantis model and the subset (10) of the 19 fishing vessel types for which spatial catches were tracked (Table 2.1). Economic impact estimates in IO-PAC include the effects of changes in fish harvest on income and employment by harvesting vessels and processors, at the scale of port and vessel type.

There are three major assumptions of IO-PAC: (1) Supply of outputs is not constraining. An increase in demand, such as demand by the fishing sectors for engine maintenance, is always met by an increase in supply for the commodity or service demanded. (2) Prices of commodities, such as processed fish, and factors of production, such as diesel fuel, are fixed, and here are denominated in 2013 dollars. (3) There is no substitution in either production or consumption, which means that a fishery sector will always require the same set of inputs (diesel, ice, etc.) to land a dollar's worth of fish. Similarly, households always purchase the same set of commodities in the same proportions.

Responses to pH

For this analysis, 10 functional groups were assumed to respond directly to pH. Groups were chosen based on a review of 393 papers on sensitivity of species in temperate oceans to carbon chemistry and a tailoring of species sensitivity estimates to the California Current (Busch and McElhany 2016) (Table 2.1). These were the same 10 groups affected by pH in the *Cumulative* scenario in Marshall et al. (2017). Functional group sensitivity was translated into species response through parameterizing pH-induced mortality (additional to any linear or quadratic mortality). All response curves were parameterized such that there was no pH-induced mortality above pH 8.0, and mortality linearly increased with declines in pH. The rate of decline (slope of the curve) was set such that the most sensitive group experienced a 10% total annual mortality rate for one unit change in pH (from 8.0 to 7.0). All other functional groups' pH response slopes were scaled against that group, using scaling parameters provided by Busch and McElhany (2016). Marshall et al. (2017) tested output sensitivity to this 10% mortality rate using alternative mortalities and found the direction of impact of species responses were largely insensitive to higher mortality rates.

Two sets of oceanographic outputs were used to run three Atlantis scenarios, isolating the effects of pH. As noted in the oceanographic modeling section, we used a single year of oceanographic output and ran it on loop in the Atlantis model to achieve quasi-equilibrium over a 100-year period. The three Atlantis scenarios included: two baselines using 2013 and 2063 oceanography (referred to as *2013Baseline* and *2063Baseline*), where no species responded to pH, and a third run with 2063 oceanography where species responded to pH (referred to as *2063pHmortality)*. We calculated the effect size for each functional group as the difference in biomass for the scenario with 2063 conditions with and without pH mortality turned on (*2063pHmortality* and *2063Baseline*, respectively), standardized by the biomass predicted in the 2013 runs (*2013Baseline*). Marshall et al. (2017) used a similar biomass metric. Biomass values used were an average over the final 10 years of the 100-year model run, representing quasi-equilibrium values under the oceanographic conditions used. Although biological responses to changes in temperature and oxygen levels are expected to be substantial (Shaffer et al. 2009, Barange et al. 2014, Fernandes et al. 2016), they were not the focus of our analysis.

Revenue changes were calculated at the finest resolution of functional group by vessel type and port, multiplying biomass by price:

$$R_{i,j,k,r} = P_{i,j,k} B_{i,j,k,r} \quad \text{[eq.1]}$$

where $R_{i,j,k,r}$ is functional group revenue calculated directly as the total biomass landed at the port, $B_{i,j,k,r}$, multiplied by the price, $P_{i,j,k}$, for group *i,* at port *j* for vessel type *k* and for model run

r (where the run can be *2013Baseline, 2063Baseline* or *2063pHmortality)*. We investigated revenue outputs at three scales, 1) total port revenue (*RP*), 2) revenue by port and vessel type (*RF*), and 3) revenue by port and functional group (*RS*). The effect size on revenue was calculated in the same way as for biomass, the difference between revenue under 2063 conditions with and without pH mortality, standardized by 2013 revenue.

We report changes in biomass and revenue only for effect sizes greater than |0.2|. This is the convention with large ecosystem models, which are best used to reveal large vulnerabilities rather than fine-grained projections (Fulton et al. 2011, Fulton et al. 2014b, Collie et al. 2016) and because a difference of less than 20% would be lost in the observation noise of most ecosystem processes.

Further economic analysis was performed using multipliers from the IO-PAC model, to consider direct, indirect and induced effects on income and employment. Multipliers for fisheries revenue and processor effect at each port were used. For example, income effects for a single port, j, were the product of revenue outputs by vessel type, k, and port, and the two multipliers:

$$I_{j,r} = \sum_{j=1}^{j=17} RF_{j,k,r} \ (M_{I,D,j} + M_{I,P,j}) \qquad \text{[eq.2]}$$

where $M_{I,D,j}$ is the economic multiplier for revenue for income at port j and $M_{I,P,j}$ is the multiplier for the processor effect on income at port j. The employment produced, $E_{j,r}$, was calculated the same way, using $M_{E,D,j}$ and $M_{E,P,j}$. The effect size on income and employment was calculated as the difference between scenarios in 2063 and standardizing by *2013Baseline*. Not all ports have processors, thus some ports only had $M_{I,D,j}$ and $M_{E,D,j}$.

Results

Changes in Biomass

Demersal functional groups were most affected by changes in pH. Sixteen functional groups experienced biomass effect sizes of 0.20 or greater. Affected groups included invertebrates and demersal fishes (Figure 2.2). We categorize functional groups according to three classes of response: functional groups with substantial changes (magnitude > 0.2)) that varied regionally, groups with substantial but spatially consistent changes, and groups with no substantial change (< |0.2|). We focus on functional groups with regional variability, and then briefly touch on the last two classes.

Invertebrates consistently had spatially variable responses (besides pandalid shrimp; Figure 2.2). For species directly responding to pH the variation was largely driven by local pH values. On average, pH was lowest between central California and Vancouver Island, though some benthic groups experienced pockets of very low pH in the south (Figure 2.2). Species exposure to pH was dependent on where along the bottom they were found, the bathymetry range, and the pH in that region. Dungeness crab experienced the lowest pH in Canadian waters, whereas benthic herbivorous grazers and bivalves both experienced the lowest pH in southern California. As a result, species responses to lower pH values do not consistently match what might be expected from observation (Feely et al. 2016) that the lowest pH and most severe effects would occur between northern California and Oregon. Rather, effects were often more substantial in the southern portion of the model, with the size of response scaling with the slope of their pH mortality curve (Table 2.1). Notably, the crab group (all crabs excluding Dungeness) had heterogeneous responses across space, likely due to low biomass (near 7% of starting biomass) creating higher sensitivity to small differences between 2013 and 2063. Declines in benthic herbivorous grazers, bivalves, deposit feeders and benthic carnivores were not only from direct effects of changing pH, but also from indirect food web effects via changes in predator-prey dynamics (Appendix B.2, Table B.2.1).

Other invertebrates not directly responding to declines in pH also exhibited variable response along the coast, resulting primarily from changes in predator and prey biomass levels. Groups with indirect declines—meiobenthos, gelatinous zooplankton, microphytobenthos and black corals—all responded in limited geographical regions (southern portion of the model), with meiobenthos and gelatinous zooplankton experiencing changes in predation. Indirect biomass increases resulted from release from predation for two groups not directly responding to pH, pandalid shrimp and microzooplankton.

Dungeness crab were a unique case. They were parameterized to respond directly to declines in pH, but the realized impact resulted almost entirely from indirect effects of changes in prey availability (Appendix B.2, Table B.2.1). This impact was most substantial off of Oregon and northern California, but also led to declines in Dungeness crab biomass off Canada and Washington State. Ninety percent of the Dungeness crab biomass in the model is in these northern regions, and we did not see the same substantial declines of Dungeness crab in southern regions.

Five functional groups exhibited consistent changes across space. These groups where four declining fish groups (Petrale sole *Eopsetta jordani*, Dover sole *Microstomus pacificus*, cowcod *Sebastes levis*, and deep large rockfish) and the increasing pandalid shrimps group (Figure 2.2). The four fish groups declined due to decreases in prey abundance that were substantial enough to create a consistent effect across all six regions. All four fish groups consumed benthic invertebrates that declined: benthic herbivorous grazers, bivalves and crangon shrimp (crangon shrimp is not shown in Figure 2.2, but declined in biomass by 19% across the entire model domain). Pandalid shrimp are preyed upon by both Dover sole and deep large rockfish in the model, fish biomass declines may have caused release from predation on pandalid shrimp, making increases constant in space.

Groups that did not respond > |0.2| included four of the functional groups parameterized to respond directly to declines in pH (mesozooplankton, pteropods, shallow benthic filter feeders and crangon shrimp), as well as pelagic fishes, mammals, sharks and seabirds. It is likely that for groups parameterized to respond to pH that did not change substantially, a combination of high productivity and release from predation were able to counteract direct effects from induced mortality.

Spatial Economic Impacts

Projected future revenue from catch in our base scenario (*2013Baseline*) mostly matched recent revenue composition for 2013 from the PacFIN records, with several differences driven by biomass trends in the simulations (Appendix B.3, Table B.3.1). For most ports (15 of 17) the functional groups comprising the majority of simulated projected revenue were unchanged from 2013 revenue data (Appendix B.3, Table B.3.1). However, port revenue from sablefish (*Anoplopoma fimbria*) and Pacific hake was consistently lower in the future projection than in 2013 landings data. Atlantis projections for North Coast, WA, Fort Bragg, CA and San Diego, CA did not realistically represent 2013 landings, as all three ports have substantial amounts of landings of species that became less abundant in Atlantis simulations. Simulated revenue per port (ratio of simulated revenue to revenue from PacFIN) ranged from 0.4 – 1.48 (mean 1.07, SD 0.39, Appendix B.3, Table B.3.2). Simulated revenue was lower than baseline records at ports between Crescent City and San Francisco, CA due to lower realized Dungeness crab abundance in those regions. Projected future revenue was higher than 2013 records in the southern California ports highly dependent on market squid, which were projected to increase in biomass over the course of the simulation.

Of the 16 major fishery target groups (i.e. groups which comprise 90% of model port revenue), one quarter had a substantial change in revenue ($RS > |0.2|$) in response to projected pH (Figure 2.3). Indirect food web effects drove these changes. Declines in revenue were dominated by declines in Dungeness crab, with effect sizes between -0.42 and -1.0+ at the nine U.S. ports north of Fort Bragg, CA. All other revenue effects (for two fishes and pandalid shrimp) were spatially consistent, because the three functional groups had homogeneous changes in the model. A number of ports experienced an increase in revenue from pandalid shrimp (consistently a 0.3 effect size). Seven ports experienced an effect size of -0.27 from declines in Petrale sole, some in the southern region (Figure 2.3). Three ports in Oregon and Northern California experienced declines in revenue from Dover sole with an effect size of -0.39.

Substantial port-level revenue changes ($RP > |0.2|$) occurred at ports north of Fort Bragg, CA, that had a large proportional reliance on Dungeness crab and flatfish (Figures 2.3 & 2.4). The most substantial declines occurred where there was both large reliance on Dungeness crab (> 50% of revenue), and where crab biomass declined most severely (Oregon and Northern California). Tillamook experienced the largest decline in revenue due to Dungeness crab. which made up 97.3% of revenue in *2013Baseline*. For comparison, in PacFIN Dungeness crab made up 86.3% of revenue for Tillamook in 2013 (Appendix B.3, Table B.3.1). Some ports experienced relief from Dungeness crab declines with increases in pandalid shrimp revenue (most notably for Coos Bay, Oregon with equivalent reliance on Dungeness crab and pandalid shrimp, Appendix B.3, Table B.3.1). Though Dover and Petrale sole both declined, neither had a strong influence on port-level revenue changes, as they made up a smaller proportion of port revenue (5.0-8.5% and 4.0-19.8% reliance on Dover and Petrale sole, respectively). The eight ports that did not experience declines greater than |0.2| nonetheless experienced modest declines in catch and revenue (Appendix B.4, Table B.4.1).

Income and employment impacts of OA reflected revenue impacts at the port-level, with the effect on employment often more exaggerated than the effect on revenue and income (Figure 2.4). For example, Crescent City revenue and income declined by 0.58 and 0.59 respectively, while employment declined by 0.71 (Appendix B.4). Newport had similar amplification of effects. In comparison, changes in income almost matched changes in revenue.

Parsing port-level revenue to vessel type suggests that nine of the ten vessel types will experience a decline > |0.2| in at least one port (Figure 2.5). The widespread impacts across vessel types reflects the fact that each vessel type fishes for many species throughout the year, thereby enhancing the likelihood that the catch composition of any single vessel type will include one or more species that is adversely affected by OA. For instance, hake trawlers, sablefish fixed gear vessels and crabber vessels all catch a mixture of species, with Dungeness crab making up a substantial proportion of revenue in our model. With Pacific hake and sablefish both declining over the 100-year simulations, hake trawlers and sablefish fixed gear vessels had a higher proportion of Dungeness crab than might be expected. Nonetheless, in Oregon and Washington (from Brookings north), these three vessel types and large trawlers show the strongest impacts of ocean acidification, despite crabber vessels experiencing some relief from increases in pandalid shrimp. In the south, Diver vessels experienced declines from a variety of species (Appendix

B.3, Table S3.3), though with nearshore urchins biomass declining to low levels, these declines are not as realistic.

Discussion

Though increasing focus has been placed on understanding the economic consequences of climate change (Cooley and Doney 2009, Barange et al. 2014, Punt et al. 2014, Falkenberg and Tubb 2017), or the resulting vulnerability of species and human communities (Ekstrom et al. 2015, Hare et al. 2016), such work is frequently at a larger spatial scale than is relevant for stakeholders and managers. In order to identify research and management priorities, higher resolution information is needed. Here, our modeling framework used high spatial resolution to project regionally varying biological and economic impacts of ocean acidification within the California Current. Though a number of functional groups were projected to respond (both positively and negatively), the model projects that the largest economic impacts may occur for central and northern west coast ports that rely on demersal species for a large portion of fisheries catch, in particular Dungeness crab. Short of immediate global actions to dramatically reduce CO_2 emissions, highly vulnerable ports and fisheries will need to consider resilient responses such as establishment of marine reserves, reductions in nutrient loading (Washington State Blue Ribbon Panel on Ocean Acidification 2012), or an emphasis on robust management, flexible and diversified fisheries, and increased monitoring (Pinsky and Mantua 2014, Schindler and Hilborn 2015).

The Atlantis model is best suited to questions of strategic management and exploration of ecosystem dynamics (Fulton et al. 2011). We use the model in the spirit of scenario analysis, a common approach used by businesses and organizations to explore possible future pathways with a recognition that there are large uncertainties when projecting forward in time (Postma and Liebl 2005, Amer et al. 2013). Thus, we used the Atlantis approach to explore one possible future to identify vulnerable species and ports that warrant scientific and management focus. The geographic variability of impacts resulted from the high resolution in the three components of our modeling framework: the ROMS model, the spatially explicit ecosystem model, and the spatially resolved fishing revenues used in an IO model. Additional scenarios, either through different models, different configuration of this same model, or other types of scenario assessment will more fully scope vulnerable species and communities (Peterson et al. 2003).

Indirect food web effects that varied with space reflect the complex predator-prey interactions and detailed species distributions that the Atlantis model can represent. Large-scale analyses of the effects of climate change frequently include either food web dynamics (Ainsworth et al. 2011, Barange et al. 2014), or high spatial resolution (Cheung et al. 2010, Cheung et al. 2011, Fernandes et al. 2016), but not both. Atlantis provides the ability to consider spatially variable indirect food web effects from changing oceanographic conditions. This high spatial resolution has often not been fully utilized in previously published Atlantis analyses that have summarized findings at a coarser resolution (Kaplan et al. 2010, Fulton 2011, Griffith et al. 2011, Marshall et al. 2017). Atlantis has been used to inform strategic management questions related to climate change, for instance in Australia (Fulton et al. 2011, Fulton and Gorton 2014) and while some users within management agencies there may directly utilize some of the finer scale information, existing publications tend to remain at the broad spatial scale.

Model outputs presented here confirm results from Griffith et al. (2011) suggesting that demersal species are most at risk from OA. Griffith et al. (2011) found substantial indirect impacts of OA on demersal fishes, including demersal sharks, shallow macrozoobenthos, cephalopods and benthic filter feeders. In the California Current Kaplan et al. (2010) found very strong indirect effects on flatfish, namely English sole, yellowtail rockfish and arrowtooth flounder. Unlike Kaplan et al. (2010), where most of the indirect effects appeared to be on demersal fishes, Marshall et al. (2017) and this paper found strong indirect effects on Dungeness crabs. These differences in model outcomes are not unexpected, given that the Kaplan et al. (2010) and the present model had different functional group structures. In contrast to the demersal community, consumers in the pelagic community (pelagic fishes, marine mammals and seabirds) experienced only small indirect effects in our model, consistent with previous results.

Our work and that of Marshall et al. (2017) highlights the importance of integrating vulnerability information for an individual species from a variety of methodologies to understand potential impacts across ecological scales, from physiological to population responses. For instance, previous work on Dungeness crab has provided mixed results regarding OA. Lab studies have shown that lowered pH reduces larval survival and slows development rates (Miller et al. 2016). In contrast, a population vulnerability assessment integrating across life stages showed that the overall population may have low vulnerability, even with high larval vulnerability (Hodgson et al. 2016). Here, we see that although direct effects from pH-induced mortality are insubstantial in our model, indirect food web effects (loss of prey) made Dungeness crab populations quite vulnerable. That declines in fishery revenue are so dependent on this species warrants future attention on details of Dungeness crab vulnerability and vulnerability of their primary prey resources.

Finally, the variability in ecological impacts was driven in part, by the oceanographic model (ROMS) which captures species' exposure to low pH. There are a number of methods simpler than a computationally intensive downscaled ROMS, however, each alternative method has limitations. For instance, initial insights into the ecosystem impacts from OA using Atlantis employed a uniform mortality rate, for groups assumed to be impacted by declines in pH (Kaplan et al. 2010, Griffith et al. 2011). Alternatively, direct use of global circulation models (GCMs) is possible but has limited utility in the California Current because they currently do not resolve upwelling regions from eastern boundary currents (Gruber et al. 2012) nor tidal forces on the continental shelf (Ådlandsvik and Bentsen 2007). Thus, using these models directly for projections of OA in the California Current is not yet ideal. Statistical downscaling is an alternative option, but is limited in the number of oceanographic variables produced and assumes that relationships between current climate conditions (correlations between oceanographic variables) hold under future climate conditions, which may or may not occur (Ekström et al. 2015). Given these varying limitations, ROMS was used here as it provides high-resolution outputs that resolves upwelling and includes numerous oceanographic parameters.

Uncertainties and Limitations

Though model complexity is useful in providing higher resolution outputs, it also introduces uncertainty (Cheung et al. 2016). A number of elements regarding model uncertainty, as defined by Hawkins and Sutton (2009) and Cheung et al. (2016) were addressed in Marshall et al. (2017), thus we focus on uncertainties as they pertain to influencing spatial impacts of OA.

The ROMS model used for present day and future oceanographic predictions was forced by a single realization of a global earth system model (GFDL ESM2M) run under a single emissions scenario (RCP 8.5). Both of these simplifications warrant addressing in future efforts, though were not within the scope of our analysis. Future work would benefit from downscaling of multiple realizations and multiple global earth system models to quantify both intrinsic and model uncertainty related to physics and biogeochemistry. Additionally, approaches should consider alternate emissions scenarios (Hawkins and Sutton 2009, Hollowed et al. 2009).

In our Atlantis ecosystem model, a substantial structural uncertainty was the representation of vertebrate spatial movements. Vertebrate biomass was distributed using prescribed seasonal shifts, with the exact daily distribution interpolated linearly from one season to the next. More complex movement patterns have been applied in some other Atlantis models (Fulton et al. 2014), including effects such as thermal tolerances, but previous experience has shown that these add substantially to model calibration. Consequently, we used prescribed seasonal movement, an effective handling for large model domains under historic conditions, but limits the evolution of spatial variability in future projections. There are two potential consequences of our approach. If a vertebrate functional group only experiences a decline in one region (e.g., -0.6 off Washington state), that effect will be smoothed out across all regions such that (1) our understanding of the variation in localized impacts would be reduced, and (2) there is the potential for fewer impacts to exceed our reporting threshold effect size of $> |0.2|$.

Predator diet compositions are notoriously challenging to estimate (Baker et al. 2014), and in Atlantis there is an additional complexity that diets evolve dynamically from initial parameterization based on shifts in prey abundance. For example, realized Dungeness crab diets were simplified and consisted of mostly bivalves, benthic herbivorous grazers and Dungeness crab (which are known to cannibalize (Fernández 1999)). With decreases in two of their main prey resources, cannibalism increased, likely driving declines in biomass (Figure 2.2). However, it is possible that this was a simplification of true crab diets, making them more sensitive to changes in the model then they would be to changes in the natural environment.

In the economic analysis we assumed fixed prices from present day through to the 2060s and did not include substitution between fisheries inputs (fisheries always use the same amount of diesel, food, etc. per dollar of revenue). These are both characteristics of IO models (Seung and Waters 2006) which have been used previously for moderate future forecasts (15 years; Kaplan and Leonard, 2012), and long-term forecasts over 50 years (Fernandes et al. 2016). Though these are both substantial assumptions, there is presently no alternative for analyzing port-level outputs for the US west coast. In the future, long term projections of economic responses may be better forecasted with techniques such as a Computable General Equilibrium (CGE) model (e.g., Finnoff and Tschirhart 2003) which factors in changing prices and input substitutions. We note that IO model estimates of impacts on employment and income did not substantially differ from changes in revenue (Figure 2.5); our economic outputs are most useful for identifying ports with higher relative vulnerability.

In addition to these primary limitations are a few key biological assumptions. We looked at ocean acidification as a single stressor, when it is well established that the California Current experiences a variety of anthropogenic impacts (Halpern et al. 2008). Thus future analyses would benefit from investigating cumulative effects, particular regarding temperature which is highly correlated to observed pH (Reum et al. 2014). Our work assumes pH only impacts mortality, though additional physiological processes have been included in other recent modeling efforts (Fernandes et al. 2016). Finally, we do not include the evolution of species responses or changes in species distributions given future climate conditions, and both of these are possible, if not likely (Cheung et al. 2010, Sunday et al. 2011, Lohbeck 2012, Pinsky et al. 2013).

Conclusions

Ocean acidification has the potential to restructure marine ecosystems and impact human communities dependent on marine resources (Le Quesne and Pinnegar 2012, Ekstrom et al. 2015)). With changes expected to vary across space and time it is critical to understand projected effects in order to prioritize research and make strategic management decisions. Though the economic consequences may be severe (Cooley and Doney 2009, Punt et al. 2014, Cooley et al. 2015), there has been limited research to quantify the impacts, especially at a high spatial resolution. The California Current is already experiencing the consequences of regional variations in pH, with evidence of pteropod shell dissolution (Bednaršek et al. 2014) and loss of revenue and jobs in the oyster industry (Washington State Blue Ribbon Panel on Ocean Acidification 2012, Ekstrom et al. 2015). Here we identify functional groups that may increase or decrease in response to declines in pH within the region, and the ports most vulnerable to these changing conditions. Dungeness crab in particular is a major fishery resource on the US West Coast, with projected declines that could trigger substantial economic impacts. This warrants further research and adaptive management approaches from state and tribal agencies in the face of these climatic changes.

Table 2.1 U.S. west coast vessel types.

As categorized by IO-PAC, with the designation use in this model: “Spatial” if the catch from the fleet was tracked by each port and “Generic” if the fleet’s catch was lumped into the generic coastwide fishery.

IO-PAC Fleet	**Atlantis Designation**
Pacific whiting trawler	Spatial
Large groundfish trawler	Spatial
Small goundfish trawler	Spatial
Sablefish fixed gear	Spatial
Other groundfish fixed gear	Spatial
Pelagic netter	Generic
Migratory netter	Generic
Migratory liner	Generic
Shrimper	Spatial
Crabber	Spatial
Salmon troller	Generic
Salmon netter	Generic
Other netter	Generic
Lobster vessel	Generic
Diver vessel	Spatial
Other, more than 15K	Generic
Other, less than 15K	Generic

Table 2.2 Ten functional groups directly responding to pH.

Showing the species making up each group, their relative survival scalar (proportional mortality for one unit decline in pH), realized pH exposure in the *2063pHmortality* scenario. Effect size for each species (E_i) was calculated for the whole model domain weighted by biomass within each polygon, and the min and max effect across regions. Effect sizes stronger than |0.2| are bold.

Functional Group Name	**Example species**	**Relative survival scalar**	**Realized Exposure**	**OA effect size: mean (min, max)**
Benthic herbivorous grazers	sea urchins (*Allocentrotus fragilis*), snails	0.1	7.670	**-0.74 (-0.80, -0.55)**
Mesozooplankton	copepods	0.099	7.726	-0.07 (-0.16, -0.04)
Bivalves	bivalves	0.089	7.768	**-0.29 (-0.42, -0.24)**
Pteropods	thecosome pteropods	0.081	7.714	-0.09 (-0.16, -0.05)
Crabs	crabs (excluding Dungeness crab)	0.070	7.669	**-0.09 (-0.82, 0.99)**
Shallow benthic filter feeders	tunicates, sponges	0.055	7.770	0.11 (0.07, 0.13)
Crangon shrimp	shrimps (excluding pandalids)	0.045	7.745	-0.19 (-0.19, -0.19)
Dungeness crab	Dungeness crab	0.041	7.770	**-0.47 (-1+, -0.03)**
Benthic carnivores	polychaetes,	0.039	7.805	**-0.23 (-0.24, -0.16)**

	nematodes			
Deposit feeders	amphipods, isopods	0.037	7.658	**-0.27 (-0.35, -0.17)**

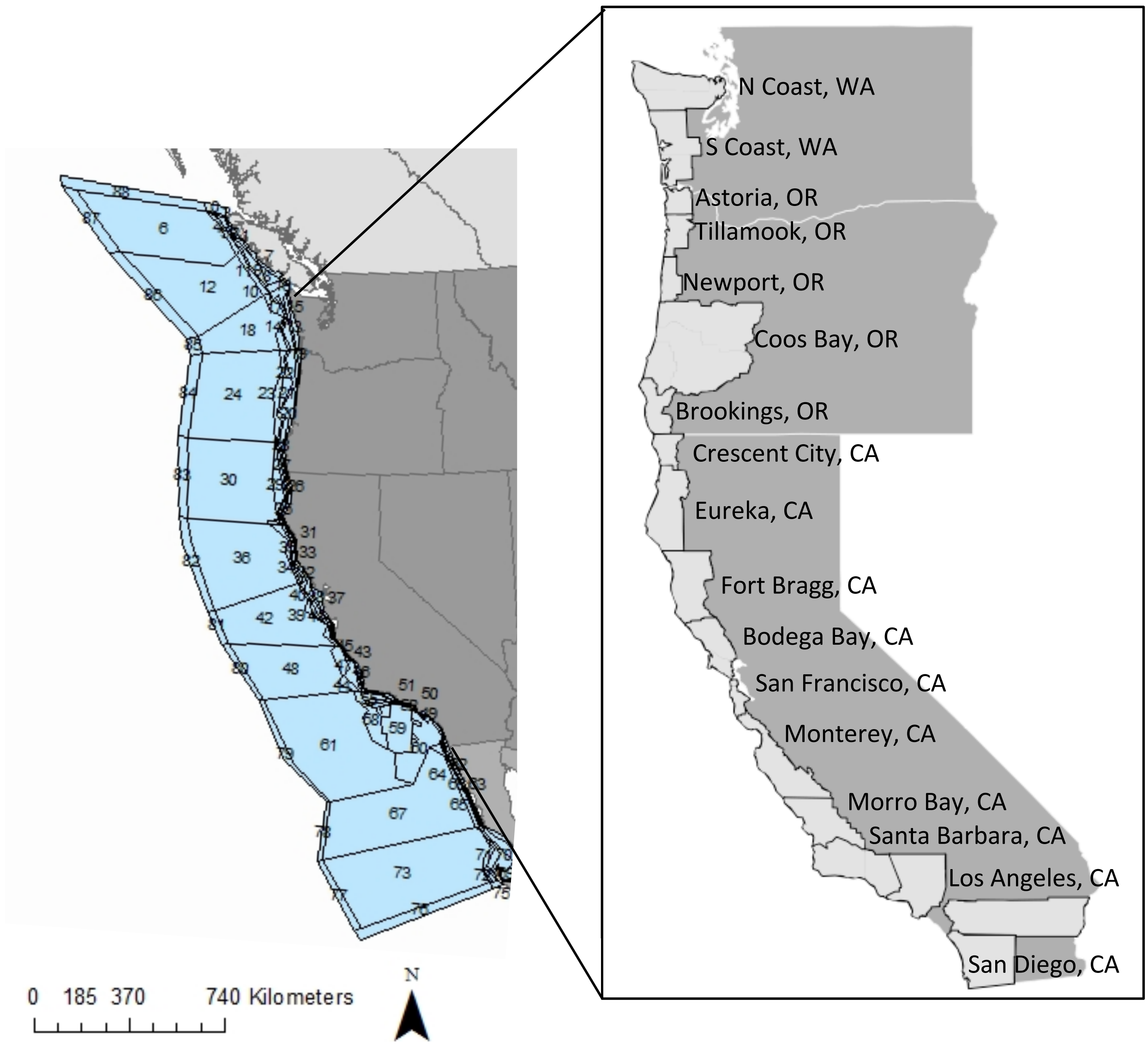

Figure 2.1 Atlantis polygons showing entire model domain.

Ports are identified in the inset for US West Coast ports only.

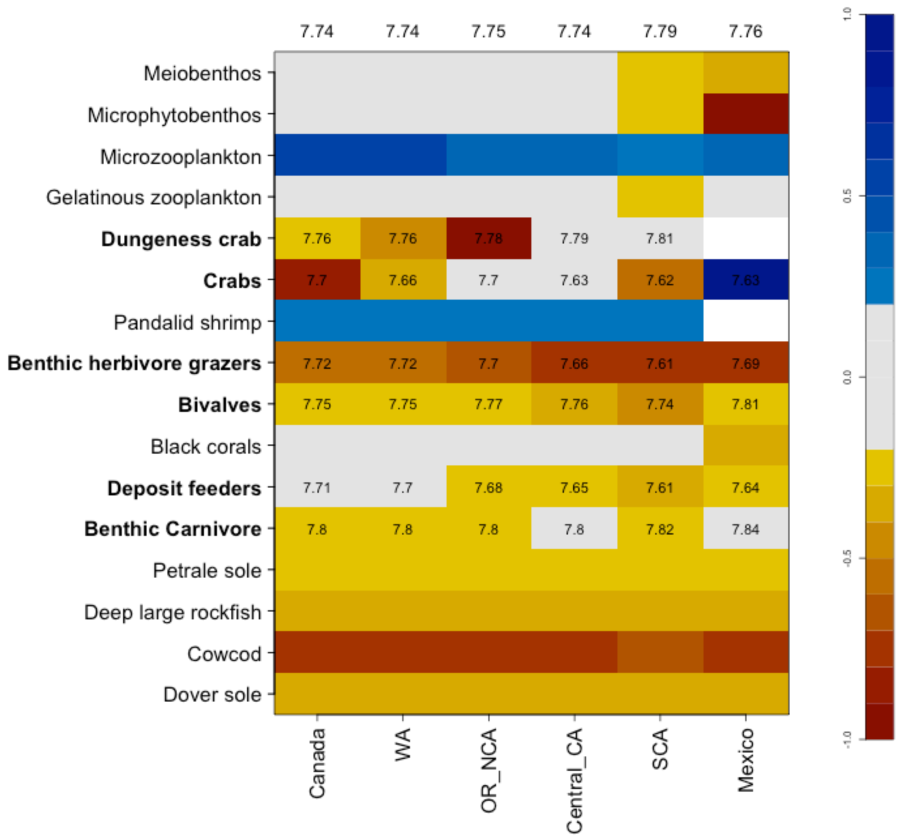

Figure 2.2 Change in biomass for species found to have >|0.2| change in biomass.

Changes <|0.20| are grey, and changes >|0.20| (either positive or negative) are colored according to the color bar. White indicates that there is no biomass for the specified functional group in the region (i.e., there are no Dungeness crab and pandalid shrimp off of Mexico). Numbers along the top of the plot indicate the mean change in pH within the region (averaged across all depths and months). Changes greater than 1.0 are possible due to the response metric which standardizes the decline in biomass (numerator) by *2013Baseline* (denominator), and in some cases the 2013 baseline had lower biomass than the *2063Baseline*. Realized exposure to pH is provided for groups responding directly to pH, exposure is the weighted mean pH species experienced in their realized distributions in the model, weights were the relative biomass experiencing each pH.

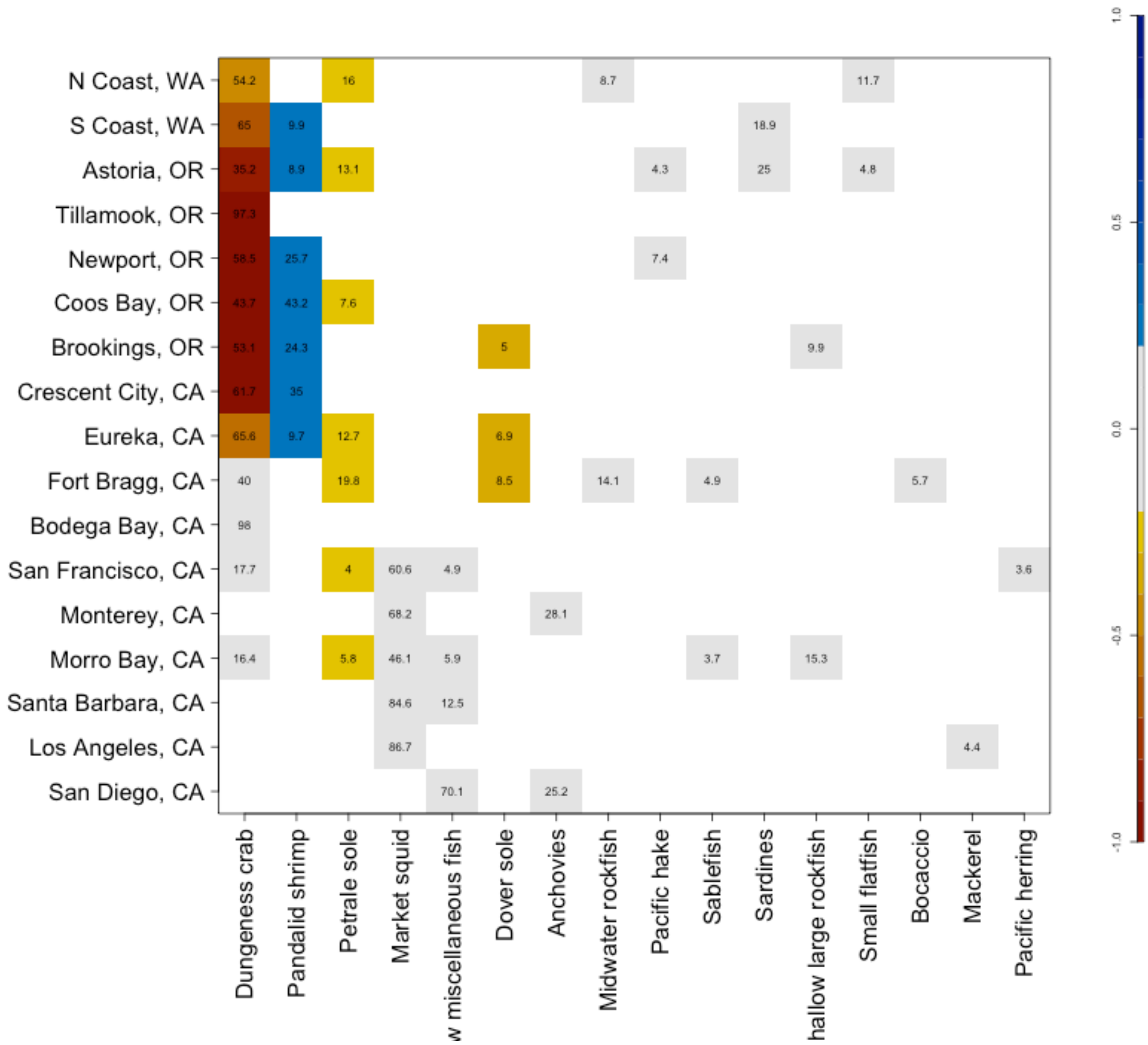

Figure 2.3 Functional groups making up over 90% of fisheries revenue by port.

Any species on the y-axis which was part of the groups making up 90% of revenue for each port has a square, where the number in the square signifies the proportion of revenue from that functional group in the model. The squares are then colored according to change in biomass from our response metric, legend provided.

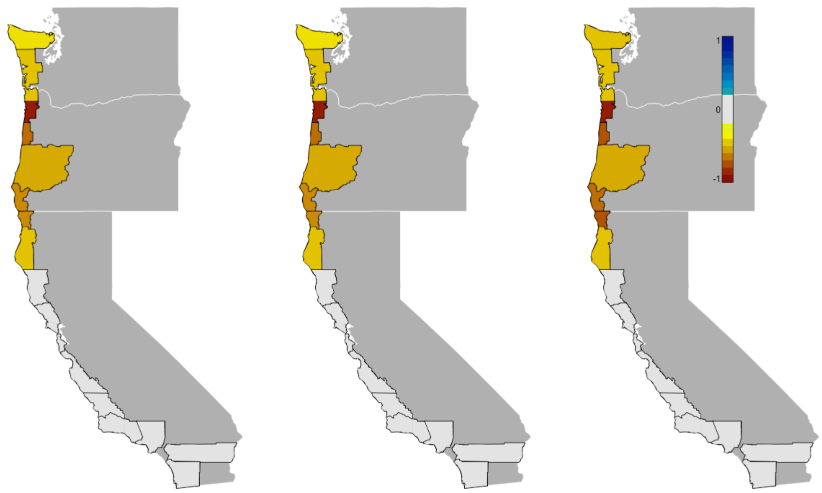

Figure 2.4 Change in biomass of revenue, income and employment by port.

Shown as revenue (A), income (B) and employment (C). Changes with an absolute value less than 0.20 are grey, and changes greater than 0.20 (either positive or negative) are colored according to the color bar binned by 0.10. Port groups are labeled in Figure 2.1, from north to south, the names are: North Coast WA, South Coast WA, Astoria, Tillamook, Newport, Coos Bay, Brookings, Crescent City, Eureka, Fort Bragg, Bodega Bay, San Francisco, Monterey, Morro Bay, Santa Barbara, Los Angeles, San Diego.

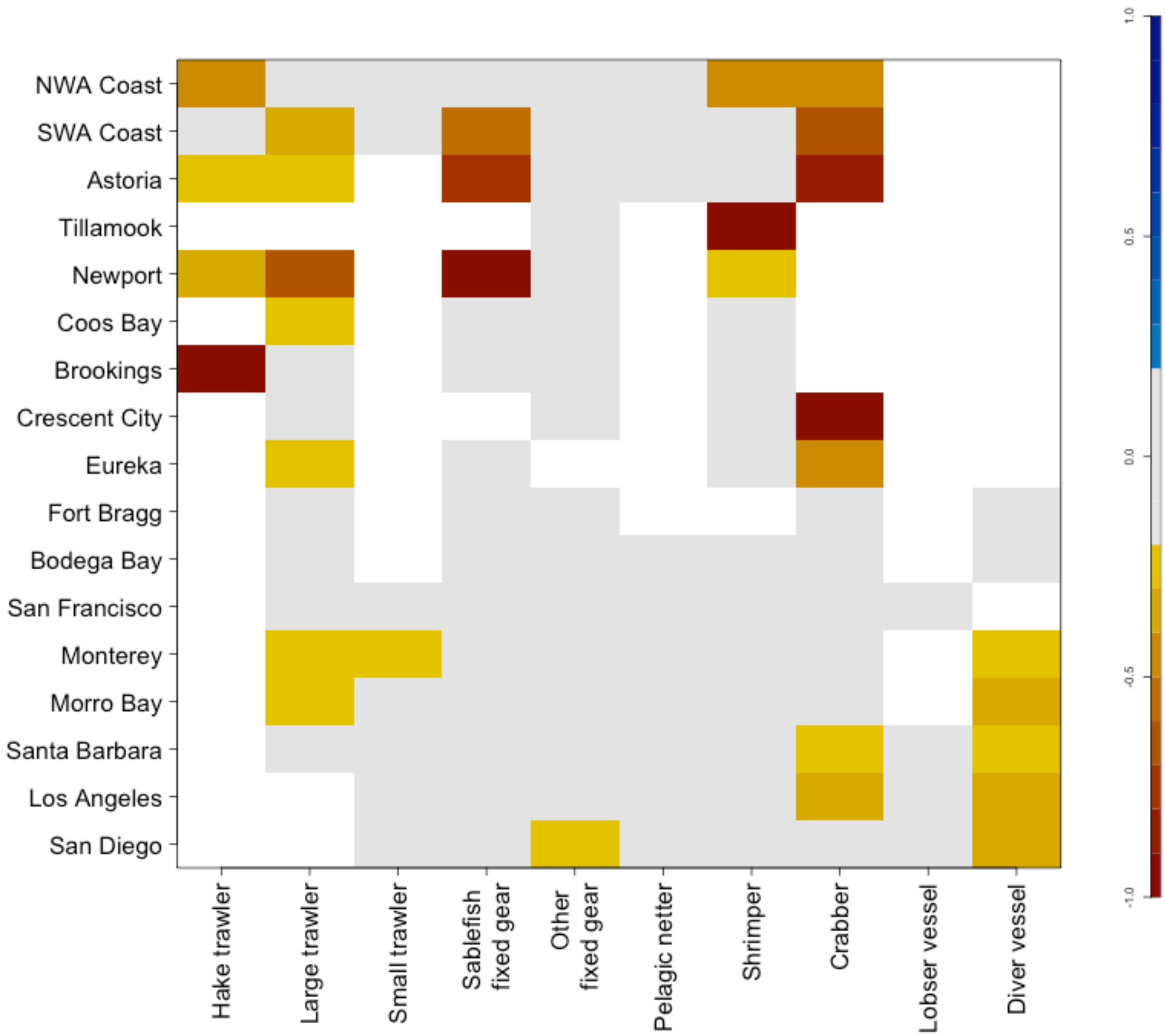

Figure 2.5 Change in fleet specific revenue driving port level revenue changes.

Changes with an absolute value less than 0.20 are grey, and changes greater than 0.20 (either positive or negative) are colored according to the color bar binned by 0.10. White indicates that the fleet did not land any species at the identified port in 2013.

Chapter 3

Density dependence governs when population responses to multiple stressors are magnified or mitigated[2]

Abstract

Population endangerment typically arises from multiple, potentially interacting anthropogenic stressors. Extensive research has investigated the consequences of multiple stressors on organisms, frequently focusing on individual life stages. Less is known about population-level consequences of exposure to multiple stressors, especially when exposure varies through life. We provide the first theoretical basis for identifying species at risk of magnified effects from multiple stressors across life history. By applying a population-modeling framework, we reveal conditions under which population responses from stressors applied to distinct life stages are either magnified (synergistic) or mitigated. We find that magnification or mitigation critically depends on the shape of density dependence, but not the life stage in which it occurs. Stressors are always magnified when density dependence is linear or convex, and magnified or mitigated when it is concave. Using Bayesian numerical methods, we estimated the shape of density dependence for eight species across diverse taxa, finding support for all three shapes.

---

[2] Manuscript in review:
Hodgson, E.E., T.E. Essington and B.S. Halpern. (In review). Density dependence governs when population responses to multiple stressors are magnified or mitigated. Ecology, manuscript ID: ECY17-0215

Introduction

A critical challenge for ecologists in the Anthropocene is understanding and predicting how populations and species will respond to novel stressors in their environment. This challenge is pronounced because most populations are exposed to multiple stressors (Wilcove et al. 1998, Halpern et al. 2008, Vorosmarty et al. 2010). Common stressors include habitat loss, exploitation, climate change, invasive species, and pollution (Richter et al. 1997, Wilcove et al. 1998, Dulvy et al. 2003, Venter et al. 2006). These stressors influence a variety of biological processes, including survival (Dulvy et al. 2003, Fabry et al. 2008), growth (Eeva and Lehikoinen 1996, Kruitwagen et al. 2006), reproduction (Jobling et al. 1996, Swift and Hannon 2010) and behavior (Munday et al. 2009). Though we have accumulated extensive knowledge about the impact of individual stressors, or two and sometimes three stressors, on different species (Crain et al. 2008, Vanhoudt et al. 2012, Przeslawski et al. 2014), our knowledge is largely based on studies that measure the direct responses of individual life stages (such as response of hatching success to low oxygen and pH (DePasquale et al. 2015)). We have a very limited understanding of population level consequences of exposure to multiple stressors, particularly when stressors act on different life stages.

Because both stressors and species' habitat use often vary in time and space, exposure to anthropogenic stressors varies across life history stages (Kingsolver et al. 2011, Salice et al. 2011). This is particularly true for highly migratory species (Webster et al. 2002, Ratikainen et al. 2008), though is also the case for species inhabiting diverse habitats throughout ontogeny. For example, terrestrial species such as migratory birds, ungulates and butterflies (Webster et al. 2002, Radchuk et al. 2013); freshwater species with complex life cycles that spend part of their life in the water and part on land (e.g. some amphibians (Salice et al. 2011)); and marine species that undergo large distributional shifts (e.g., whales, salmon, tuna; see also Table 3.1). Thus, most species are likely to experience exposure to different stressors throughout their life cycle (Webster et al. 2002, Hodgson et al. 2016). This can have population implications since the timing of stress within life history can impact population responses (Jonzen and Lundberg 1999, Liz and Ruiz-Herrera 2016).

Interactions between stressors may be exhibited in an additive, mitigated (antagonistic) or magnified (synergistic) manner (Darling and Côté 2008, Przeslawski et al. 2014), with existing approaches only beginning to address how they interact at the population level. Lab, mesocosm and field based methods to study multiple stressors have focused on effects on individuals through impacts on physiology or behavior (Darling and Côté 2008, Vanhoudt et al. 2012). However, understanding the impacts in a population context requires framing their influence on demographic rates (Caswell 2001). Existing work has begun to bridge these two approaches (e.g., Anderson's vitality; (Anderson 2000)) and a rich body of literature exists on the utility of elasticities across a range of model types (linear and nonlinear) to determine parameter influence and the sensitivity of the model to different perturbations (Caswell 2001, Caswell 2008). What is lacking is a general understanding of how stressors acting simultaneously on different life stages will interact at the population level.

Ultimately, predicting the consequences of multiple stressors on a population requires understanding where, and to what degree, density-dependence occurs. Stress on early life stages, especially if the stressor acts prior to density dependence, often has less of a population impact than stress on later life stages (Shuter 1990, Punt et al. 2014, Shelton et al. 2014, Punt et al. 2015). Additionally, compensatory density dependence can mitigate the impacts of a single stressor (Moe et al. 2002, Schipper et al. 2013) or even multiple stressors (Power 1997). Certain forms of density dependence or model structure can lead to higher equilibrium population sizes when survival is lowered, the 'hydra effect' (Abrams 2009, Liz and Ruiz-Herrera 2016). Thus, at the population scale the role and form of compensatory mechanisms in mitigating or exacerbating multiple stressor impacts needs to be understood if we are to comprehend how multiple stressors influence populations (Power 1997).

In this paper we identify the role that the timing and shape of the density dependence function play in making populations prone to magnification or mitigation of multiple stressors. We ask the question: is the interaction between two stressors consistently mitigated by density dependence, or are there circumstances where density dependence can also magnify the interaction? In particular, our focus is on how different shapes of the density dependence function influences population outcomes. To determine if our findings have broad relevance across different types of species, such as ungulates, birds, fishes and insects, we conducted an empirical analysis of density dependence to ask whether the types of density dependence that lead to magnified population responses are common.

Population Models

We used a generalized two-stage population model that could represent a variety of species, with a model framework borrowed from the rich history of stage-structured population modeling (Cushing 1998, Caswell 2001). To allow us to draw findings based on its mathematical properties, we included only two explicit life stages, a non-reproductive stage (early life history and/or juvenile) and a reproductive stage. The timing of events in life history influences the scale of population response (Jonzen and Lundberg 1999, Ratikainen et al. 2008), thus we explore two versions of this model, each with density dependence occurring at a different point in the life cycle. The basic model format used for both models is

$$\mathbf{N}(t+1) = \mathbf{A}_{\mathbf{N}(t)}\mathbf{N}(t) \tag{1}$$

where the projection matrix $\mathbf{A}_{\mathbf{N}(t)}$ is dependent on the population vector **N**(t) that contains abundance of stages N_1, non-reproductive stage, and N_2, adults.

Population Model 1: Density dependence prior to stage 1

In the first model we explore the case where stressors influence survival after the stage where density dependence occurs. The following projection matrix satisfies these properties

$$\mathbf{A}_{\mathbf{N}(t)} = \begin{pmatrix} 0 & f(N_2) \\ s_1 & s_2 \end{pmatrix} \tag{2}$$

where, stages 1 and 2 each have survival rates, s_1 and s_2 respectively. The function $f(N_2)$ represents the per capita production of stage 1 individuals by adults. The function is compensatory, meaning that it is a strictly decreasing function of N_2, i.e., $\frac{df(N_2)}{dN_2} < 0$. The equilibrium adult density, $\tilde{N}_2$, satisfies the following condition

$$f(\tilde{N}_2) = \frac{1-s_2}{s_1}. \tag{3}$$

This means that $\tilde{N}_2$ is defined by the inverse function

$$\tilde{N}_2 = f^{-1}\frac{1-s_2}{s_1}. \tag{4}$$

To simplify notation, we refer to the ratio $(1-s_2)/s_1$ from eqn 3 as x, and the inverse function $f^{1}(x)$ as $g(x)$, thus $\tilde{N}_2=g(x)$. Because this is a discrete time model, it can exhibit unstable dynamics (May 1976, Abrams 2009). Using standard first-order Taylor approximation around equilibrium density, we find that the model will be dynamically stable (no limit cycles) provided that $\left.\frac{df(N_2^*)}{dN_2^*}\right|_{\tilde{N}_2^*} \geq \frac{s_2 - 2}{s_1}$ where N_2^* is adult density standardized to units so that $\tilde{N}_2$=1.

Our interest is in comparing the change in $\tilde{N}_2$ in response to reductions in s_1 and s_2 when effects are additive to the realized change. If the combined reduction in $\tilde{N}_2$ is greater than the sum of reductions when each stressor is reduced individually (i.e., additive effects), then effects are defined as magnified (synergistic). Changes smaller than expected under the additive hypothesis are defined as mitigated (antagonistic).

We first determine the expected change when effects are additive. To do this, we use a second order Taylor approximation to express the change in population size from a reduction in survivorship Ds_i (where Ds_i is negative). Thus the change in $\tilde{N}_2$ (D$\tilde{N}_{2\,\mathrm{D}s_i}$=$\tilde{N}_2(s_i$+D$s_i)$-$\tilde{N}_2(s_i)$) from a change in either s_1 or s_2 (Ds_i) equals

$$\Delta \tilde{N}_{2\Delta s_i} \approx \frac{\partial g}{\partial s_i}(s_1, s_2)\Delta s_i + \frac{1}{2}\frac{\partial^2 g}{\partial s_i^2}(s_1, s_2)\Delta s_i^2 \qquad (5)$$

where the partial derivatives represent the local slope and shape at the original equilibrium. The additive population effects from changes in both s_1 and s_2 is the sum:

$$(\Delta \tilde{N}_{2\Delta s_1} + \Delta \tilde{N}_{2\Delta s_2}) \approx \sum_{i=1}^{2}\left[\frac{\partial g}{\partial s_i}(s_1, s_2)\Delta s_i + \frac{1}{2}\frac{\partial^2 g}{\partial s_i^2}(s_1, s_2)\Delta s_i^2\right]. \qquad (6)$$

We compare this to the actual D$\tilde{N}_2$, where the multi-variable Taylor expansion is

$$\Delta \tilde{N}_{2\Delta s_1 \Delta s_2} \approx \sum_{i=1}^{2}\left[\frac{\partial g}{\partial s_i}(s_1, s_2)\Delta s_i + \frac{1}{2}\frac{\partial^2 g}{\partial s_i^2}(s_1, s_2)\Delta s_i^2\right] + \frac{\partial}{\partial s_1}\left[\frac{\partial g}{\partial s_2}\right](s_1, s_2)\Delta s_1 \Delta s_2 . \qquad (7)$$

Therefore, the difference between the additive (D$\tilde{N}_{2\,\mathrm{D}s1}$+D$\tilde{N}_{2\,\mathrm{D}s2}$) (eqn 6) and the realized D$\tilde{N}_{2\mathrm{D}s1\mathrm{D}s2}$ (eqn 7) is:

$$(\Delta \tilde{N}_{2\Delta s_1 \Delta s_2} - (\Delta \tilde{N}_{2\Delta s_1} + \Delta \tilde{N}_{2\Delta s_2})) = \frac{\partial}{\partial s_1}\left[\frac{\partial g}{\partial s_2}\right](s_1, s_2)\Delta s_1 \Delta s_2 . \qquad (8)$$

We solved for this expression by substituting the derivatives of $\frac{\partial x}{\partial s_1}$, $\frac{\partial x}{\partial s_2}$ and $\frac{\partial}{\partial s_1}\left[\frac{\partial x}{\partial s_2}\right]$ giving the following (for full Taylor expansion and stability analysis see Appendix C.1)

$$\Delta s_1 \Delta s_2 \frac{1}{s_1^2}\left[\frac{dg(x)}{dx} + \frac{1-s_2}{s_1}\frac{d^2 g(x)}{dx^2}\right]. \tag{9}$$

This is the critical term that determines overall effects from two stressors. If the sign of this term is negative the effects are magnified and if positive the effects are mitigated, additive effects occur when this term is zero.

The joint effect on $\tilde{N}_2$ of changing juvenile and adult survivorship depends on the local shape (linear, concave, convex) of the density dependent function at equilibrium. We reveal this by defining conditions under which eqn 9 is positive or negative. Because *g(x)* is the inverse function of $f(N_2)$, we can define the first and second derivatives of *g(x)* based on $f(N_2)$. First note that because $\frac{dg(x)}{dx} = \frac{1}{(\frac{df(N_2)}{dN_2})}$, the sign of $\frac{dg(x)}{dx}$ is dependent on the sign of $\frac{df(N_2)}{dN_2}$; since $\frac{df(N_2)}{dN_2} < 0$, then $\frac{dg(x)}{dx} < 0$ for all *x*. Thus, there is a tendency towards a magnification of the response based on the first term, $\frac{dg(x)}{dx}$. For example, in the case of linear density dependence, the second derivative $\frac{d^2 g(x)}{dx^2}$ is zero and the stressors would be magnified (Figure 3.1B). To determine the sign of $\frac{d^2 g(x)}{dx^2}$ for cases with non-linear density dependence, note that it has the same sign as $\frac{df(N_2)}{dN_2}$ because of the following relationship

$$\frac{d^2 g(x)}{dx^2} = -\frac{\frac{d^2 f(N_2)}{dN_2^2}}{(\frac{df(N_2)}{dN_2})^3}. \tag{10}$$

We see that the sign of the second derivative at $\tilde{N}_2$ is critical in determining whether multiple stressors are magnified or mitigated. If the density dependent function $f(N_2)$ is locally convex (negative second derivative) near $\tilde{N}_2$, there is an even larger magnification of decline in $\tilde{N}_2$ with joint change in survivorships than the linear case (Figure 3.1C). In contrast, if the function is locally concave (positive second derivative) near $\tilde{N}_2$, magnification will be lessened, or even reversed to produce mitigated effects (Figure 3.1D). Thus, magnification or mitigation depends solely on the shape of the curve at equilibrium, i.e., the local shape of the density dependence function. Clearly, given the same f(0) and $\tilde{N}_2$, the slope $\left.\frac{df(N_2^*)}{dN_2^*}\right|_{\tilde{N}_2^*}$ will be more negative if $f(N_2)$ is locally convex, so is less likely to be dynamically stable. But provided that this slope exceeds s_2-$2/s_1$, then the convex density dependent shape will produce stable results and amplifying responses to multiple declines in survivorship.

In addition, the shape of density dependence also dictates the overall magnitude of response to single stressors. Figure 3.1 illustrates that for locally concave density dependence a smaller reduction in survivorship of either s_1 or s_2 is needed to produce a reduction in N_2 equivalent to either the linear or convex case. That is, a shallow slope of $f(N_2)$ near $\tilde{N}_2$ means a small change in survival produces a larger change in $\tilde{N}_2$ than is found in the linear or convex cases.

Because mitigation can only happen with concave functions, we explore whether common concave functions have sufficient curvature to produce mitigated effects. We use two simple versions of common classes of functions: the exponential family, $f(N_2)=ae^{-NB}$, and the polynomial fraction family, $f(N_2)=1/(a+bN)$. For each we solve for equilibrium density and substitute the actual derivatives of the density dependence functions into the portion of eqn 9 that determines the sign of the effect. We find that for the exponential family the term eqn 9 equals 0, i.e., effects are always additive. In contrast, we find that for the polynomial family eqn 9 is proportional to $1/(b(1-s_2)^2)$, i.e., effects are mitigated.

Population Model 2: Density dependence between stages 1 and 2

In the second model we explore the case where density dependence occurs between the two stages affected by stressors. The following projection matrix satisfies this property

$$\mathbf{A}_{\mathbf{N}(t)} = \begin{pmatrix} 0 & s_0 \\ f(N_1) & s_2 \end{pmatrix} \tag{11}$$

where s_2 is survival and s_0 now refers to fertility. In this case stability depends on the condition $\frac{df(N_1^*)}{dN_1^*}\Big|_{\tilde{N}_1^*} \geq \frac{s_2-2}{s_0}$, where N_1^* is the density of the non-reproductive stage standardized to units so that $\tilde{N}_1$=1. With the reproductive value is in the denominator, the right side of the equation is more likely to be a small negative number making the condition harder to meet. Thus, this model is more likely to exhibit unstable dynamics. We use similar steps to find that $\tilde{N}_2$ satisfies the following condition

$$f(s_0\tilde{N}_2) = \frac{1-s_2}{s_0}, \tag{12}$$

such that

$$\tilde{N}_2 = \frac{f^{-1}(\frac{1-s_2}{s_0})}{s_0}. \tag{13}$$

We define the term $(1-s_2)/s_0$ as y and the inverse function $f^{-1}(y)$ as $g(y)$, so that now $\tilde{N}_2=g(y)/s_0$. We can see there is a difference here between the first and second population models, with the extra term s_0^{-1} in our equilibrium expression for $\tilde{N}_2$. To simplify notation even further, we define $\tilde{N}_2=g(y)/s_0=h$ and as before use the Taylor expansion to calculate the realized

$\Delta\tilde{N}_{2\Delta s0\Delta s2}$, but this time in terms of h. The difference between the additive and realized effects, $(\Delta\tilde{N}_{2\Delta s_0\Delta s_2}-(\Delta\tilde{N}_{2\Delta s_0}+\Delta\tilde{N}_{2\Delta s_2}))$, is now dictated by $\frac{\partial}{\partial s_0}\left[\frac{\partial h}{\partial s_2}\right](s_0,s_2)\Delta s_0\Delta s_2$ from the multi-variable Taylor expansion (for the full Taylor expansion see Appendix C.1). We solve using $\frac{\partial y}{\partial s_0}$, $\frac{\partial y}{\partial s_2}$ and $\frac{\partial}{\partial s_0}\left[\frac{\partial y}{\partial s_2}\right]$, which gives us

$$\Delta s_0\Delta s_2\frac{1}{s_0^3}\left[2\frac{dg(y)}{dy}+\frac{1-s_2}{s_0}\frac{d^2g(y)}{dy^2}\right]. \tag{14}$$

We have a similar circumstance as in our first model, where the sign of this term depends on the first and second derivatives of the density dependence function at the initial equilibrium. As before, a locally convex or linear functional form at the equilibrium will always produce magnified effects and a concave functional form can produce mitigated effects. However, in this case a locally concave function has to have stronger curvature to produce mitigated effects because the first derivative, which is always negative and produces the tendency for magnification, is now multiplied by two. Thus, this model has a stronger tendency for magnified effects (further explanation in Appendix C.2).

We repeat our test of two example functional forms of concave density dependence to explore whether common concave functions have sufficient curvature to produce mitigated effects. We find that for the exponential family the sign is always negative because $\frac{1}{s_0^3}\left[2\frac{dg(y)}{dy}+\frac{1-s_2}{s_0}\frac{d^2g(y)}{dy^2}\right]$ is proportional to $-s_0/(b(1-s_2))$, i.e., it is always negative so produces magnified effects. For the polynomial family we find that $\frac{1}{s_0^3}\left[2\frac{dg(y)}{dy}+\frac{1-s_2}{s_0}\frac{d^2g(y)}{dy^2}\right]$ equals 0, i.e., additive effects.

Empirical Evidence for Different Shapes of Density Dependence

Given the influence of the local shape of density dependence at equilibrium on dictating model outcomes from two stressors, we evaluated whether there is biological support for the different shapes used. That is, we were interested in determining whether populations in nature exhibit shapes that are locally convex and would thereby be prone to magnify effects of multiple stressors. We collated data on density dependence in survival rates for 8 species consisting of insects, birds, fish, and ungulates. With these eight species, we provide examples with which to explore whether there is support for different local shapes of density dependence. These examples do not provide general conclusions about the density dependent relationship for each species or type of species.

For each dataset we determined the probability that the shape of density dependence was convex at population sizes from N=0 to the maximum N (N_{max}) observed for that population. To do this we fit a flexible sigmoid density dependence function (eqn 15), as it can produce locally linear, convex, or concave shapes:

$$f(N) = \frac{y_{max}}{(1 + e^{(k(N - N_{inf}))})} \tag{15}$$

where a_{max} is the survival rate at N=0, N_{inf} is the inflection point of the curve, and k is the steepness of the function. y_{max} is set to:

$$y_{max} = a_{max}(1 + e^{-kN_{inf}}) \tag{16}$$

to ensure that the intercept of the function $f(N=0)$ is a_{max}.

The inflection point is critical in the sigmoid function (the point at which the curve is momentarily linear and changes from being convex to concave). If a population is to the left of the inflection point, it experiences convex density dependence. If a population is to the right of the inflection point it experiences concave density dependence. Because we were interested in measuring the probability that the function is locally convex we used a Bayesian estimation procedure as that is the only method that allows for a direct calculation of the probability that $f(N)$ is convex for different values of N. Maximum likelihood and other methods in frequentist statistics do not allow for outputs that provide probabilities of different parameter estimates. The maximum likelihood approach is more relevant in circumstances where the researcher is interested in determining which functional form is most supported by the data. However, that was not our intent. Rather, we were interested in the posterior probability that the local shape of the density dependence function might take on a convex form, thus determining the biological relevance of our population model findings.

We extracted data on density dependent survival for individual life stages for eight species. These examples were chosen from the literature because they provided data on the relationship between the density of individuals of a particular life stage and the survival rate based on that density. Frequently data are provided on population size in relation to the population size in the previous year, however such data do not provide stage-specific insights. The examples were also chosen to cover a range of species types, but they were not intended to provide general conclusions about the shapes of density dependence for these species. Species included fishes *Oncorhynchus nerka* (Peterman 1978) and *Coryphopterus glaucofraenum* (Forrester 1995), insects *Lasioderma serricorn* (Bellows 1981) and *Operophtera brumata* (Hassell et al. 1976), birds *Colinus virginianus* (Guthery et al. 2000) and *Larus melanocephalus*

(Marvelde et al. 2009) and ungulates *Ovis canadensis* (Festa-Bianchet et al. 2003) and *Connochaetes taurinus* (Owen-Smith 2006). A variety of species were chosen to demonstrate the importance of this relationship across species types.

Bayesian statistics require the use of a likelihood function to compare predicted values given a set of parameter values to the data. The data (probability of survival) range between 0 and 1, thus our likelihood function was the beta distribution, which is continuous and restricted to 0-1. The beta distribution is defined by parameters α and β (note that these parameters are different from those in the population modeling section). Our aim was to ensure that the mean of the beta distribution for each data point, N_i, would equal the predicted value at N_i so we defined the parameter a such that: $a_i = b f(N_i)/(1-f(N_i))$.

We used weakly informative priors for β, a_{max}, N_{inf}, and k. All priors were defined by uniform distributions: $b \sim U(e^{-1}, e^{50})$, $a_{max} \sim U(0,1)$, $N_{inf} \sim U(\overline{N} - 6\ range(N), \overline{N} + 6\ range(N))$, $k \sim U(0, k_p)$. a_{max} has the biological range of [0,1] as survival cannot be outside that range. The range of N_{inf} has the potential to strongly influence posteriors if too restrictive (forcing the inflection point to occur within too narrow of a range). Therefore, we allowed N_{inf} to range greatly based on the median ($\overline{N}$) of the data and the range in the data (*range(N)*) multiplied by a constant. We tested different values for that constant to find the value at which point the model outputs became insensitive. This occurred when the prior was between $\overline{N} \pm 5 range(N)$ and $\overline{N} \pm 6 range(N)$; we therefore chose 6 as the constant to be more conservative. k can be thought of as the slope of the function and therefore influences the rate of change in survival with a change in population density. The maximum slope comes from the first derivative of $f(N_{inf})$, thus to find an upper limit on k (k_p) we found the k value that would cause no more than a 10% change in survival with a 10% change in density, assuming a y_{zero} at 1.0 and that the maximum slope occurs at the median ($\overline{N}$) of the data. The 10% rate of change was chosen as a limit primarily to prevent a density dependence relationship from taking on a *threshold* shape, as we believed such a shape is implausible (and generally was not supported by the data). We tested different restrictions on *k*, namely a 50% change in survival with a 10% change in *N*, which is a substantial change since survival is bounded between 0 and 1. For all data sets, the larger bounds on *k* made the outputs more likely to be convex, though they also resulted in stronger support for a threshold relationship. Prior values for *Ninf* and *k* for all data sets can be found in Table 3.2.

The model runs were performed using Just Another Gibbs Sampler (JAGS) version 4.2.0 (for example code see Appendix C.3), run using the R packages rjags (Plummer 2016) and R2jags (Su and Yajima 2015). Convergence was evaluated using trace plots, posterior density plots and the Gelman-Rubin convergence statistic (Gelman and Rubin 1992). We ran 4 chains for 500,000 iterations, with a burn-in period of 100,000 and thinning every 100th iteration, giving 4,000 posterior parameter estimates per chain for a total of 16,000 posterior parameter estimates. The chain length, burn-in period and thinning rate were chosen to ensure model convergence, which was supported by the output Gelman-Rubin statistics.

We found support for both locally convex and locally concave density dependence within the eight datasets (Figure 3.2). We calculated the proportion of model outputs at each value of *N* with a negative second derivative (probability of being convex) to determine support for each shape. Two datasets had high probabilities of being convex for all values of population size from N=0 to N_{max} (Figure 3.2F and G). A third dataset showed moderate support for a locally convex shape at smaller population sizes (Figure 3.2E). However, there is high uncertainty about the shape of the function at small population sizes because of the absence of data in that region. Regardless of this uncertainty, they do indicate that the local shape at low densities could plausibly be different from that at high densities. Two datasets did not show strong support for one shape over others, as the two were highly variable, making many possible shapes of the density dependence function fit the data equally well (Figure 3.2D and H). Neither had a probability far off from 50% of being concave or convex along the range of population sizes. Finally, three data sets were firmly concave along the range of N with very low probabilities of being convex from N=0 to N_{max} (Figure 3.2A-C).

Discussion

We demonstrated that both the shape of the density dependence function and the timing of when density dependence occurs strongly influence population consequences from two stressors. The convex and linear functional forms consistently lead to a magnification of impacts, while the concave functional form can lead to a mitigation or magnification depending on the strength of the curvature. That is, mitigation happens when density dependence exerts stronger effects at low population sizes than at high population sizes. Density dependence is known to dampen population response to stress (Power 1997, Salice et al. 2011, Schipper et al. 2013); however, to our knowledge, this is the first demonstration of the role density dependence plays in magnifying population response to multiple stressors at different stages. Considering that many species experience different stressors throughout their life history (Kingsolver et al. 2011, Flockhart et al. 2015), our findings are broadly applicable to a wide range of species and populations.

Population effects are most likely to be magnified when stressors act on stages before and after density dependence, counteracting the common finding that early life stages are less important from a demographic perspective. For instance, an early life history stage may be exposed to one stressor, undergo a density dependent transition, and then be exposed to a second stressor. This could occur with salmon which may experience density dependence early in life history (Sharma et al. 2005) and are exposed to multiple climate stressors both early and late in life (Healey 2011). In these cases, our results suggest that mitigation is far less likely than magnification. This result is somewhat counterintuitive because in both density independent and density dependent models, early life stages often have a lower reproductive value and survival rate, thus a smaller population contribution (e.g., Crouse et al. 1987). When considering population-level impacts, the response of an early life stage to a stressor has to be more severe than the response of a later life stage to produce a comparable outcome. In density dependent models, this is in part from the compensatory process counteracting declines of stages before density dependence (Shelton et al. 2014, Punt et al. 2015). Thus, existing frameworks may down-weight the role of early life stages in population processes, whereas our results show that early life stage sensitivity to stressors makes it harder to mitigate against stressors occurring before and after density dependence. This has important implications because early life stages are often those more sensitive to environmental stressors (Kurihara 2008).

Most of the frequently used functional forms of density dependence are concave (Ricker 1954, Beverton and Holt 1957, Bellows 1981), but assuming these relationships by default (i.e., in absence of supporting data) could lead to erroneous predictions of population responses to multiple stressors. Our Bayesian analysis provided biological support for both locally concave and convex shapes (Figure 3.2), indicating that no single shape is overwhelmingly prominent. The incorrect specification of functional forms of density dependence in models will have two effects. First, the magnitude of population level effect will be incorrect, as concave relationships have larger responses to any single stressor. Second, the propensity for magnification of effects will be incorrect for reasons outlined above. Detecting the density dependence relationship is challenging (Freckleton et al. 2006), but is critical to understanding interactions between stressors.

Though understanding population level effects from multiple stressors is clearly important (Harley et al. 2006), there has been is limited use of population models to this end. When they are applied, they are often of limited scope – models are either density independent so that only consequences on population growth rate can be measured (Kjaer et al. 1998, Dobson and Randolph 2011) or models only include stressors acting on one demographic process (Schipper et al 2013). One exception to these generalities is Power et al (1997), who explored the interactions between stressors acting on growth and mortality, finding magnified reductions in abundance of 0+ and 1+ individuals when both stressors occur. This study used a Ricker (exponential family) density dependence function, which controlled survival between the egg to 0+ stage and the 0+ to 1+ stage. Our findings give broader context to this finding, as we reveal that exponential family density dependence does not have sufficient curvature to reverse the magnifying effects of multiple stressors.

Our modeling approach provides a general framework to predict circumstances where different population outcomes will occur; empirical validation of this prediction is not yet achievable. Empirical measurements are naturally complex. Measuring population response to stressors on different life stages requires isolating population impacts from changes in each stage individually and then in combination. Though an ideal measurement to achieve, the complexity is at present prohibitive. Models are useful in these contexts as they provide heuristics and identify the key information needs for improving predictions (Starfield 1997).

Here, we considered a case with a number of biological simplifications. Stressors were assumed to be independent, they were assumed to act on single demographic processes, there were no carry-over effects, stressors did not impact the density dependent relationship directly and density dependence occurred at one life stage. Many of these assumptions have been discussed in previous literature. Stressors are not necessarily independent (some conditions are more likely to occur together, e.g., correlated temperature and pCO_2 levels (Reum et al. 2014)). It is also known that stressors influence a mixture of population processes including growth (Pichavant et al. 2001), behavior (Munday et al. 2009) and maximum population size (Salice et al. 2011). There is both biological and theoretical support for carry-over effects as a stress on one stage may result in higher vulnerability of a subsequent stage (Ratikainen et al. 2008, Fischer and Phillips 2014, Liz and Ruiz-Herrera 2016) or transmission between generations (Beckerman et al. 2002). Finally, stressors may impact density dependence directly (Sharma et al. 2005, Salice et al. 2011) and density dependence may occur at multiple life stages (Ratikainen et al. 2008).

Though our findings provide a general framework for when we would expect population consequences to be magnified or mitigated, the framework specifically relates to changes near the equilibrium. Using a Taylor approximation only provides an estimate the shape of a curve locally. Population impacts will not be properly estimated for large changes in survival in cases where the density dependence function is concave and convex in different regions. Even in this simplistic approach, density dependence was found to play a very strong role in dictating model outcomes. But further exploration of the role of density dependence and overall population responses in more complex situations is warranted.

We employed an approach that relies on measurement of equilibrium population size, yet equilibrium population size can be unstable. Two model characteristics contribute to unstable equilibria. First, stability depends on the slope of the curve representing N_{t+1}~N_t at equilibrium, where a steeper slope indicates a higher probability for instability (May 1976). This instability may be more likely with convex density dependence, as it exhibits a steeper slope at equilibrium, given the same f(0) and $\tilde{N}_2$. Second, delayed density dependence makes unstable dynamics more likely (Crone 1997). Population model 2 is similar to a single-stage model exhibiting delayed density dependence, thus this model is more likely to be unstable. We found this to be the case since the inequality contains the reproductive value in the denominator and the slope only has to become a small negative number before instability will result. However, it is important to note that population growth rates of many species are too low to create this instability in nature (Shelton et al. 2013).

Cumulative effects assessment has become a common part of environmental impact assessments. Population models offer a key tool for better understanding the impacts of multiple stressors, both by providing a mechanistic understanding and helping predict future responses under changing human pressures. Defining the shape of the density dependent relationship has always been a critical part of developing a population model, and we demonstrate that this is equally important in the context of cumulative effects. We contribute to the growing literature addressing the role of density dependence and model structure on population responses to stress (Jonzen and Lundberg 1999, Ratikainen et al. 2008, Abrams 2009). The choice of the model in and of itself dictated population outcomes, where effects from two stressors can be magnified at the population level. Moving forward, there is a natural opportunity for population models to be used more extensively for questions of cumulative effects assessment. Our results provide the guidelines and techniques for how to do this wisely.

Table 3.1 Examples of species with different stressors across stages of their life cycle.

Species	**Common Name**	**Species Type**	**Life Stages Impacted**	**Explanation**	**Citation**
Danaus plexippus	Monarch butterfly	Insect	Multiple: egg through to adults	Migratory species with different stressors in different habitats (milkweed decline in the United States and climate change and deforestation in Mexico).	Flockhart et al. (2015)
Oncorhynchus nerka	Sockeye salmon	Fish	Multiple: egg through to adults	Migratory species with changing temperatures and weather patterns influencing different life stage processes.	Healey (2011)
Melospiza melodia	Song sparrow	Bird	Juveniles and adults	Weather (temperature and precipitation) as a stressor having different influences on juvenile and adult survival rates.	Dybala et al. (2013)
Connochaetes taurinus	Wildebeest	Ungulate	Adults at different points in their	Migratory species with exposure to hunting pressure during	Thirgood et al. (2004)

			migration	unprotected portions of their migration route.	
Gastrophryne carolinensis	Eastern narrowmouth toad	Amphibian	Egg production and juvenile and adult survival	Species with complex life history, experiencing habitat loss (decreasing carrying capacity) and survival impacts from toxin exposure.	Salice et al. (2011)

Table 3.2 Parameter values and Bayesian priors.

Data set	**Species name**	**Species type**	N_{inf} **prior**	k_p
Bellows (1981)	*Lasioderma serricorn*	Insect	[-6082.66, 6179.95]	0.042
Hassell et al. (1976)	*Operophtera brumata*	Insect	[-1356.83, 1405.02]	0.087
Peterman (1978)	*Oncorhynchus nerka*	Fish	[$-1.15\text{x}10^8$, $1.37\text{x}10^8$]	$1.84\text{x}10^{-7}$
Forrester (1995)	*Coryphopterus glaucofraenum*	Fish	[-488.88, 531.12]	0.10
Owen-Smith (2006)	*Connochaetes taurinus*	Ungulate	[-53320.00, 63920.00]	$3.80\text{x}10^{-3}$
Festa-Bianchet et al. (2003)	*Ovis canadensis*	Ungulate	[-651.64, 960.58]	0.013
Marvelde et al. (2009)	*Larus melanocephalus*	Bird	[-7027.54, 7912.72]	0.0046
Guthery et al. (2000)	*Colinus virginianu*	Bird	[-616.54, 2622.91]	0.002

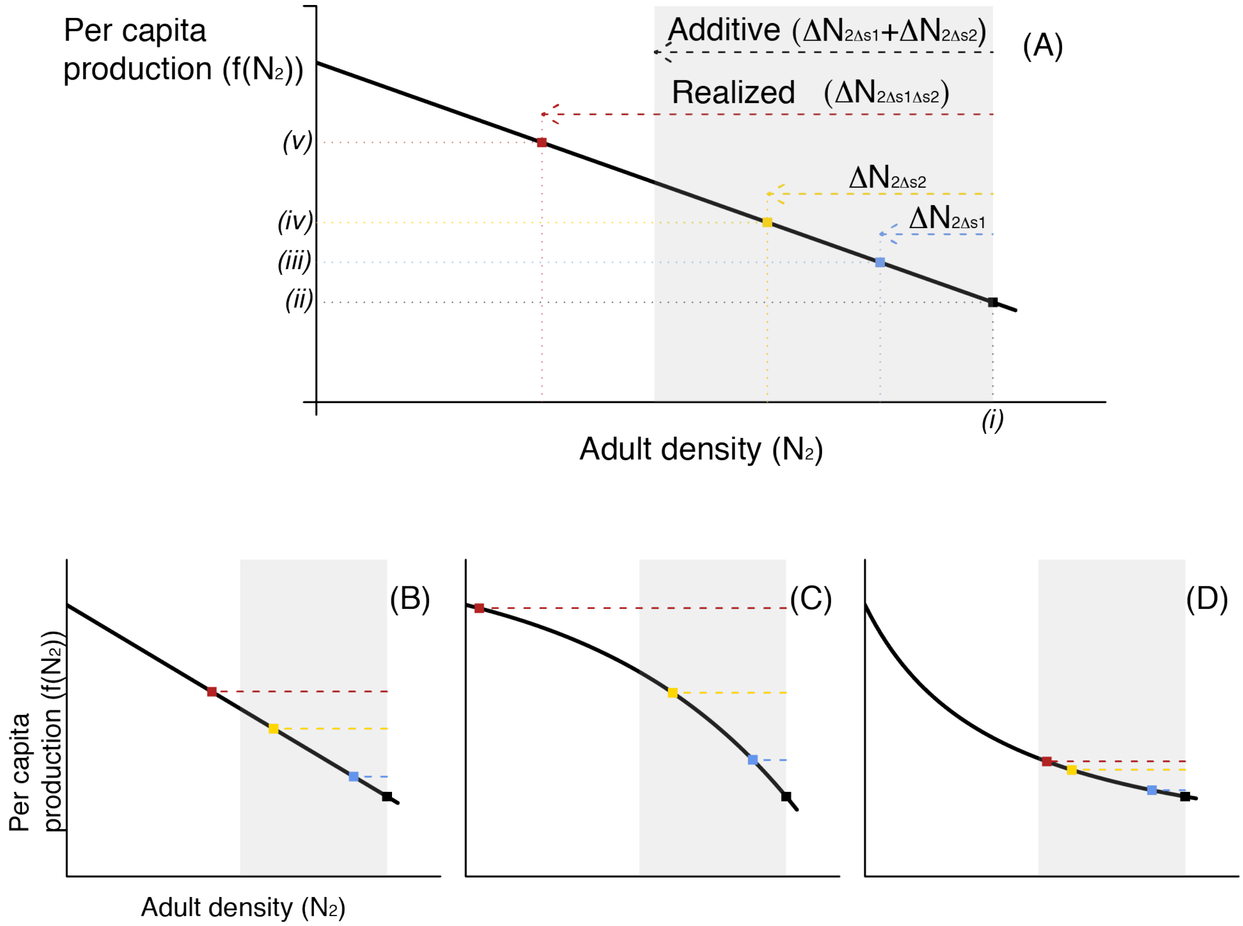

Figure 3.1 Visual representation of cumulative impacts.

Impacts on $\tilde{N}_2$ from reduction in in s_1 (blue point and line), s_2 (yellow point and line) and on both stages (red point and line), compared to the expected effect under the additive null hypothesis (grey band). A linear form was used for demonstration purposes, with hypothetical impacts (A). Realized impacts using all three forms of density dependence, parameterized to have matching points at $f(0)$ and $f(\tilde{N}_2)$ are shown, linear (B), convex (C) and concave (D). Values for Δs_1 and Δs_2 were found for all three functional forms that caused the same expected additive effect on $\tilde{N}_2$ (see Appendix S4 for details). This expected additive effect (grey band) can be compared to the realized effect (red line), where a mitigated (magnified) effect occurs when the realized effect is at a larger (smaller) $\tilde{N}_2$ than the additive effect.

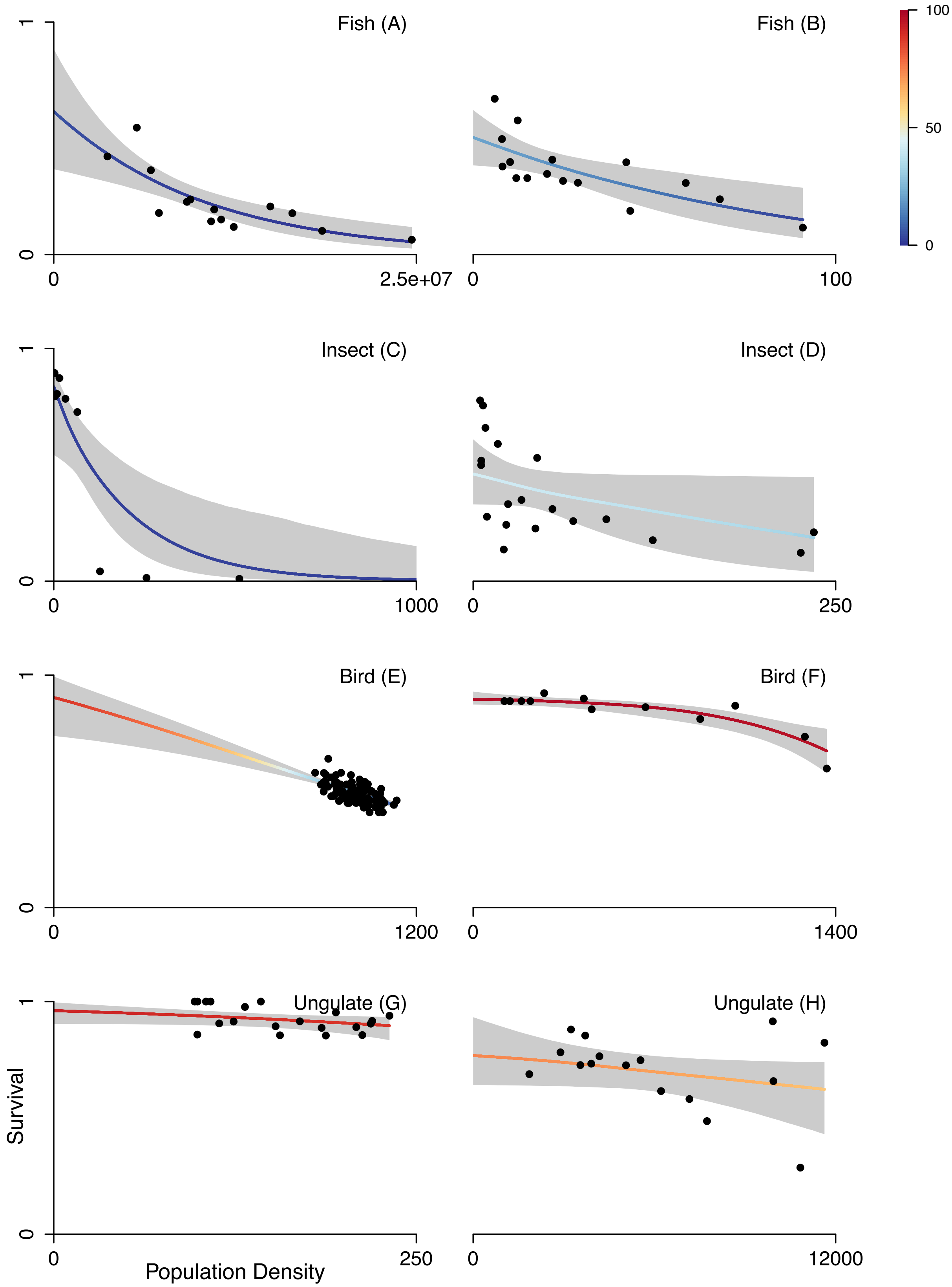
Fish (A)
Fish (B)
Insect (C)
Insect (D)
Bird (E)
Bird (F)
Ungulate (G)
Ungulate (H)
Survival
Population Density
0
1
2.5e+07
100
1000
250
1200
1400
12000
50

Figure 3.2 Fitted survivorship as a function of population density for eight species. Lines are the median, and line color is the probability of a convex curve at each population density (see legend). Grey polygons represent the 95% credible interval for the median. Species included our four different species types: fishes (A) *Oncorhynchus nerka* (Peterman 1978) and (B) *Coryphopterus glaucofraenum* (Forrester 1995), insects, (C) *Lasioderma serricorn* (Bellows 1981) and (D) *Operophtera brumata* (Hassell et al. 1976), birds (E) *Colinus virginianus* (Guthery et al. 2000) and (F) *Larus melanocephalus* (Marvelde et al. 2009) and ungulates (G) *Ovis canadensis* (Festa-Bianchet et al. 2003) and (H) *Connochaetes taurinus* (Owen-Smith 2006).

Chapter 4

Towards integrated risk analysis for ecosystem based fisheries management[3]

Abstract

Fisheries and marine management increasingly recognize the importance of considering the social, ecological, and economic spheres in decision-making processes. Approaching decisions from this perspective immediately presents potential tradeoffs among system components. Fisheries management has traditionally used performance metrics in a benefit-tradeoff framework, yet this approach ignores the potential losses to the system, and the metrics used do not necessarily capture non-economic social consequences often hard to quantify. Risk-tradeoffs are an alternative method that can be used to factor in both losses and gains to different system components, in addition to uncertainty in outcomes. However, risk is fundamentally a multi-disciplinary concept with nuanced approaches across many fields. In order to work towards an integrated risk framework, natural scientists would benefit from having an understanding of different disciplinary approaches to risk analysis. Here we present a brief history of risk research across disciplines in the ecological, economic and social sciences. We then introduce a number of factors critical to consider when working towards an integrated approach, such as issues of scale, stakeholder involvement and equity.

---

[3] This work would not have been possible without the substantial contributions from participants in a risk workshop held at the University of Washington on *risk across disciplines*. The final manuscript to be submitted for publication will include the authorship of the workshop participants and contributors (ordered alphabetically): Edward Allison, Nathan Bennett, Ann Bostrom, Alison Cullen, Timothy Essington, Stephen Kasperski, Phil Levin, Melissa Poe, and Jameal Samhouri.

Introduction

Managers and researchers are turning towards more holistic approaches to fisheries resource management and conservation as recognition of the limitations of single species approaches has developed. Broadly, there is a growing understanding that humans live in linked social-ecological systems (Liu et al. 2007, Ban et al. 2013, Koehn et al. 2013) where a single management strategy may provide a benefit to one component of the system and a loss to another (Holsman et al. 2017). Decisions have social, ecological and economic implications that are often not accounted for using current frameworks that tend to consider a limited number of outcomes, without factoring in connections within the system. In response, there are a growing number methods that work to consider all components within marine systems. They are broadly referred to as ecosystem approaches to management; where we use the term “ecosystem based fisheries management” (EBFM) here (Pikitch et al. 2004, Smith et al. 2007, Fulton et al. 2014a). However, our understanding of how to successfully implement EBFM, and factor in all parts of the system, is still limited (Dichmont et al. 2013).

Fundamentally EBFM requires a holistic approach that considers tradeoffs in losses and gains to different parts of the same system. Traditionally fisheries management has used a benefit-tradeoff framework, often employing performance metrics such as the ratio of current biomass to maximum sustainable yield (Hall and Mainprize 2004, Plagányi et al. 2013). Yet focusing on benefits does not address both the losses and gains, nor does it necessarily factor in uncertainty in outputs. In comparison, a risk approach includes both elements (Fischhoff et al. 1984, Aven and Renn 2009, Mahmoudi et al. 2013). “Risk refers to uncertainty about and severity of the consequences (or outcomes) of an activity with respect to something that humans value” (Aven and Renn 2009). This definition factors in two critical components: a particular outcome from an action taken, and the uncertainty with regards to that outcome. Thus, the risk-tradeoff approach, or integrated risk assessment, is ideally suited for EBFM where there is high uncertainty in system response and outcomes (Carpenter 1995, Burgman 2005, Aven and Renn 2009).

The challenge in moving towards integrated risk assessment is that the concept of risk has distinct bodies of research in the ecological, economic and social sciences (Renn 1998), where these disciplines often operate in isolation from each other. As noted by Hoffmann (2011) "[t]he way we have organized and talked about risk analysis over the past 30–35 years has made it more difficult for us to develop effective interdisciplinary risk assessment". The lack of integrated risk assessment may, therefore, be due to a lack of fully understanding different disciplinary approaches to the same core concept. In fisheries research there are established methods for risk analysis, which are focused primarily on the *ecological* components of the system (Fletcher 2005, Hobday et al. 2011, Fletcher 2014). This narrow interpretation of risk may impede a more holistic framework.

To achieve an integrated framework, natural scientists need a broader understanding of risk research in the social sciences and to develop a holistic framework to capture the required elements. Specifically, natural scientists must first have an understanding of the basic definitions of, and approaches to, risk across disciplines. One needs to define: what does 'risk' mean to the ecological, economic and social spheres? And how does one assess risk to these three components? We then need to consider the larger context, of what needs to be considered in moving towards a more integrated framework. That is, if we recognize that we are operating in a connected, social-ecological system, what are the core elements that need to be considered in an integrated approach?

Here, we document these two building blocks necessary to develop an integrated approach to risk analysis. To provide a foundation for natural scientists to broaden their understanding of risk, we briefly review risk research across the ecological, economic and (non-economic) social sciences. Then, we discuss a set of elements that are critical to consider in the process of moving towards an integrated approach. In this work, we build on recent work that has begun along these lines with publications providing documentation for natural scientists to better understand approaches in other fields (Armsworth and Roughgarden 2001, Bennett et al. 2017, Spalding et al. 2017).

Risk Across Disciplines

We provide an overview on approaches to risk in the three fields of ecological, economic and (non-economic) social sciences. This is not intended to be an exhaustive review, but rather to provide ecologists with initial insights into approaches and theories in the respective disciplines. As each of the fields has a multitude of sub-disciplines, with different approaches to risk, we have limited the range of topics to those the authors found most relevant to EBFM. In both the economic and social sciences sections, we end with an overview on how the approaches have already been integrated with fisheries research.

It is important to note that risk management process frequently involves a set series of steps, where each of the three disciplines in the TBL have largely focused on different components within the process. For example, the ISO 31000 outlines three phases within risk management (Figure 4.1; (ISO 2009)): (1) establishing the context, (2) performing risk assessment (identifying what is at risk and assessing that risk), and (3) risk treatment and management (the final decision making) (ISO 2009). Both risk communication, and monitoring and review in this case are intended to be a constant part of the process (ISO 2009). In other frameworks they may be their own phase within risk management (Hoffmann 2011).

Risk in the ecological sciences

Ecological risk assessment (ERA) has its roots in hazard and disaster management (Adger 2006) and ecotoxicological hazard and risk (De Lange et al. 2010), but has been applied to a wide range of contexts for populations, species and ecosystems (Stobutzki et al. 2001, Fletcher 2005, Adger 2006, Astles et al. 2006, Hatton et al. 2006, Astles et al. 2009, De Lange et al. 2009, De Lange et al. 2010, Teck et al. 2010, Samhouri and Levin 2012, Chen et al. 2013). Much of the research on ERA developed as a result of legislation requiring risk assessment as part of the management process. In the United States the passing of the National Environmental Policy Act (NEPA) established the requirement for risk assessment and in 1983 the National Research Council published what is referred to as the Red Book, *Risk Assessment in the Federal Government* (NRC 1983, Hoffmann 2011). The initial approaches developed were referred to as the risk-hazards assessment framework (Eakin and Luers 2006, De Lange et al. 2010).

Natural scientists tend to focus on *risk assessment*, the middle step in the risk management process outlined above. Methods have been developed ranging from qualitative risk assessment approaches (Harding 1998, Astles et al. 2006, Fletcher 2014) to highly quantitative (Punt and Walker 1999, Stobutzki et al. 2001, Zhou and Griffiths 2008), where each method is applicable in different contexts (see methods reviewed in (Barnthouse 1992, Burgman 2005, Hobday et al. 2011, Chen et al. 2013)). The outputs from this work may or may not be factored into management decision-making. One of the common themes of risk assessment across these ecological approaches is that risk assessment is assumed to be objective, often without explicit consideration of who defines what is important and what 'high risk' means (Freudenburg 1988, Renn 1998, 2008a). Overall, these methods bear strong similarity to human health risk assessment, which is also intended to be objective and quantitative (Renn 1998, 2008a). This group of methods has been referred to as *technical risk assessment* (Renn 1998, 2008a).

Risk in economics

Approaches to risk in the economic sciences are highly diverse, with some lines of research that bear the closest similarities to the approaches used in natural sciences. We break down economic approaches into three streams of research: (a) methods for performing risk assessment, (b) behavioral economics and understanding human decision-making under uncertainty, and (c) use of economic analyses in risk treatment and management. The first stream of research in the economic sciences is similar to technical risk assessment approaches in the ecological sciences. These include general methods such as insurance and actuarial risk determination (Zinn and Taylor-Gooby 2006, Renn 2008a), financial credit risk (Chen et al. 2016), and specific methods such as risk from catch variability in fisheries (Kasperski and Holland 2013). In these circumstances risk is frequently assessed as to how it will be experienced by a person, institution or industry.

Human decision making under uncertainty and risk is largely investigated through expected utility theory (EUT) and non-expected utility models (Starmer 2000). The idea in EUT is that people will make decisions to maximize their satisfaction (Renn 1998). Non-expected utility models resulted from inconsistencies in how well empirical evidence supported utility theory (Starmer 2000). These approaches take a step beyond technical risk assessment allowing for inclusion of non-monetary factors in risk decision making (Renn 2008a), by recognizing the role that human behavior plays. This field of research comes from behavioral economics where the initial focus was on determining universal laws of decision-making (Zinn and Taylor-Gooby 2006). Human behavior comes into play at multiple stages in the risk management process.

Finally, the formal mechanism through which economic considerations have been factored into risk management traditionally is through cost-benefit analyses (Williams and Thompson 2004, Yasui 2005, Hoffmann 2011). In this way, outputs from risk assessment are fed into a cost-benefit analysis that is used in the phase of risk treatment and management (Williams et al. 2008). For example, risks to human health from a proposed development project may be factored into subsequent cost-benefit analyses for the project that are used to make the final decision. The intention behind this approach is to keep "economic interests" out of the risk assessment process (Hoffmann 2011). However, authors have argued that for a fully integrative approach, economic factors should be explicitly considered within the ecological or human health risk identification and assessment, not just at the final management stage (Williams et al. 2008, Hoffmann 2011). This is in part because human economic status may actually influence health risks (particularly through likelihood of exposure), which is not factored in when economic factors are only considered post hoc (Hoffmann 2011).

Connections to fisheries—In the context of fisheries, economic considerations are consistently factored into decision-making, whether formally or informally. Thus they are the first step towards expanding from just ecological priorities in EBFM (Bradshaw et al. 2001). The ability to more easily tradeoff economic and ecological considerations may result from being able to compare them using the same unit of dollars (Vanclay 2004, Chan et al. 2012). Combination approaches in the marine sciences include ecosystem services (Chan et al. 2012), using ecological and economic objectives in a decision framework (Lane and Stephenson 1998) and factoring in fisher behavior into management scenario analysis (Wilen et al. 2002, van Putten et al. 2012).

Risk in the non-economic social sciences

From a social science perspective, risk research is largely focused on trying to understand how people (individuals and groups) think about, respond to, and make decisions regarding risk. Thus there are strong connections to behavioral economics focused on individual decision-making processes (Zinn and Taylor-Gooby 2006). Generally, the approaches to risk in the social sciences are further removed from the applications of risk research in the natural sciences. In the social sciences, risk analysis is not considered without also considering risk perception and risk communication (Freudenburg 1988, Fischhoff 1995, Bostrom 2014). Risk is studied from numerous disciplinary perspectives including psychology, sociology and anthropology (Zinn and Taylor-Gooby 2006, Renn 2008a). Broadly, the psychological approaches try to understand individual decision making processes (with connections to behavioral economics), where sociological and anthropological approaches try to understand larger cultural perceptions of risk (Zinn and Taylor-Gooby 2006, Renn 2008a). Zinn and Taylor-Gooby (2006) pose the juxtaposition "[s]ociological theories approach risk questions mainly from the opposite direction to psychologists and economists, moving from societal institutional structures to the levels of the individual, rather than the other way about".

Research in psychological risk assessment (and behavioral economics), for example, has informed our understanding of four categories of human biases that influence risk perception (Kahneman and Tversky 1979, Renn 1998, 2008a). First, *availability*, events that come more easily to mind are thought to be more probable. Second, *anchoring effect*, where a person is influenced by previous information received (information received earlier has a larger effect) and the perceived importance of that information. Third, *representativeness*, where an individual is more influenced by events they have experienced than by information based on probabilities. Fourth, *avoidance of cognitive dissonance*, where information that challenges part of a belief system will be down played.

In addition to the study of human perceptions of, and decision making in response to, risk there are also methods that are employed to *assess* risk to the social parts of the system. One example is social impacts assessment (SIA; (Vanclay 2004)), a form of risk assessment (Mahmoudi et al. 2013). SIA "is [the process of] analysing, monitoring and managing the social consequences of development" (Vanclay 2003). SIA involves the narrative approach, understanding what individuals perceive as risks from a management decision, including aspects that can and cannot be easily quantified. Social impacts can be incredibly diverse; individuals may be concerned that a particular management decision could have implications for elements such as their health and wellbeing, their property rights and/or their culture (Vanclay 2003).

Connections to fisheries—Within marine management and conservation, there has been a growing focus on pushing the field to recognize the importance of including social considerations within linked social-ecological systems (Liu et al. 2007, Ban et al. 2013, Koehn et al. 2013, Kittinger et al. 2014). However, these methods often focus on identifying the social aspects of the system that can be more easily quantified, such as access to fishing, recreation, and aquaculture (Koehn et al. 2013, Kittinger et al. 2014), rather than the narrative elements included in SIA. What is not easily accounted for currently are the cultural aspects of the system (Chan et al. 2012), and potential losses, such as loss of life-style, self-determination and traditional practices (Turner et al. 2008, Biedenweg et al. 2016). This is an active area of research documenting the non-economic and non-objective measures of connections people and communities hold to their natural resources (Turner et al. 2008, Satterfield et al. 2011).

Key considerations in moving towards an integrated approach

Beyond considering differences in the disciplinary approaches to risk, it is important to recognize some of the complexities in the broader context when considering all three components of the system. In a workshop setting, a number of critical factors to consider were identified, which we discuss here.

Engagement (stakeholders)

Natural resource management involves a variety of actors who have a stake in the resource in question (Grimble and Wellard 1997, Beierle 2002). For risk analysis, those actors or stakeholders are defined as "socially organized groups who are or will be either affected by or have a strong interest in the outcome of the event or activity from which the risk originates" (Renn 2008b). They can be individuals, groups, organizations, or government bodies, and often have different uses for the same or a related resource (Grimble and Wellard 1997). Identification of and engagement with stakeholders is a key component of establishing the context for risk analysis (Figure 4.1). Each stakeholder will bring different perspectives and interests. Incorporating these differences can lead to an improved understanding of the system and what is at risk from a proposed policy or management decision (Grimble and Wellard 1997, Hermansson 2012). For example, stakeholders may identify cultural aspects of the system not addressed in traditional impact assessment frameworks (Satterfield et al. 2011).

When it comes to risk management, stakeholders can be involved in a number of steps in the process. These include identifying *what* is at risk, the most appropriate management strategy(ies) to consider, and the best form(s) for risk communication. In this way, stakeholders can be a part of conflict-resolution (Renn 2008b) and ideally the process will lead to “socially best” policies (Grimble and Wellard 1997). Though some would argue that stakeholder involvement may lead to worse decision making, the evidence suggests this is not the case (Beierle 2002). There are many existing decision making formats for stakeholder involvement (Linkov et al. 2007, Gregory et al. 2012), and there are well established methods for identifying who the stakeholders are in the system (Renn 2008b). Critical to integrated risk assessment is the involvement of stakeholders.

Scale

Just as scale is widely considered a key factor in ecological research (Levin 1992), scale is critical in risk assessment. There are three important factors when considering the scale of an assessment: unit of analysis (or summary statistic; (Fischhoff et al. 1984)), spatial scale, and temporal scale. Within the ecological context the unit of analysis frequently ranges between individual organisms, populations, species and communities. For consideration of the social dimensions, units can similarly range between individuals, households, industries, communities (of place or of practice, defined by social channels), states or entire countries. Units of analysis, however, may be even more specific, such as death per hour from exposure to a particular stressor (Fischhoff et al. 1984). Consideration must be taken to determine what unit(s) of analysis is most appropriate for the question at hand. For example, a large scale analysis could use an average across populations, but this metric may conceal issues of distributions of risk within and between populations (Hermansson 2010). See below our discussion of *Equity*.

Stakeholder engagement may help in the process of identifying the most appropriate units to use, and it may often be the case that multiple units of analysis need to be assessed in order to quantify risk fully.

Defining the spatial and temporal dimensions requires setting boundaries to understand what elements are exogenous and endogenous to the system. This can also relate to framing human uses of the system across space and time (Kittinger et al. 2014). Determination of the spatial scale is a common component in environmental impact assessments (Hegmann et al. 1999, LNG 2016), and similar boundaries can be placed on a management decision framework. Temporal scale is important for considering how risks may be displaced to future generations (Hampel 2006) or determining appropriate discount rates for risks expected to occur in the future (Baram 1979).

Choices of scale are equally important for risk assessment, risk treatment, and risk communication. While the examples above focus primarily on how scale intersects with risk assessment, risk treatment will clearly be influenced by which elements are considered endogenous and therefore malleable, versus exogenous and out of the control of those charged with management. Similarly, risk communication must clearly delineate factors that are outside of the control of managers versus those that can be manipulated. For example, Washington State has identified that while controlling global emissions that lead to ocean acidification is not within the scope of state management, the state can work with national and international bodies to reduce carbon emissions, while addressing issues of local adaptation and remediation (Washington State Blue Ribbon Panel on Ocean Acidification 2012).

Equity

Closely linked to the question of scale is the distribution of risk across and within human and ecological communities; the element of equity (Zimmerman 1993). Management decisions do not impact all individuals and populations in the same manner. At both the social and ecological scales, groups may experience different levels of exposure to hazards across space and time (Boer et al. 1997, Shapiro 2005, Hodgson et al. 2016), and may have different fundamental vulnerabilities to that exposure (Arquette et al. 2002, Allison et al. 2009). For example, evidence suggests that certain socio-economic groups are more likely to experience exposure to toxic chemicals (Boer et al. 1997). As well, some populations may be more vulnerable due to existing exposures to other stressors. In marine systems species are experiencing numerous simultaneous impacts (Halpern et al. 2009, Maxwell et al. 2013) that may increase their overall vulnerability to new stressors. Frequently risk assessments use statistics based on majority populations – such as results from male subjects or particular socio-economic communities – or averages across groups (Hermansson 2005, Hermansson 2012). These majority metrics may obfuscate the fact that some subjects are at high risk. Hermansson (2012) notes that essential to an understanding of risk assessment is knowing "who is exposed to the risk, who benefits from it and who makes the decisions" and we would add, how the unit of analysis influences those conclusions. Therefore, when considering risk level for any metric used, how the distribution of risk is shared amongst elements within that unit of analysis is vital. This may be addressed in part, by using multiple units of analysis.

Acknowledging subjectivity

Natural scientists tend to think of science as a "value-free" endeavor through which one conducts objective measurement, and this perception pervades thinking concerning ecological risk (Douglas 2000, 2009). Natural scientists focus on risk assessment, with a perspective that experts conduct objective risk assessment and determine the 'true' risk from an action (Fischhoff et al. 1984, Kasperson et al. 1988, Hermansson 2012). This true risk level is then compared to how the public *perceives* the risk (Hermansson 2012). Subjectivity and human biases in this circumstance are only factored in with regards to decision-making and risk communication (Hermansson 2012). This is one perspective within risk research (Kasperson et al. 1988).

In contrast, fundamental to the social science approach to risk analysis is the understanding that it is not a value-free endeavor (Fischhoff 1995, Renn 2008a). That is, where the ecological sciences think of risk assessment as an objective process, the social sciences acknowledge subjectivity and the understanding that information is filtered through one's personal and cultural perspective (Freudenburg 1988, Hermansson 2012, Renn and Benighaus 2013). In this view, group- or individual-specific values must be reconciled with values that are meaningful in the broader social context of multiple groups to understand risk fully (Renn 1992). For some, this perspective holds that risk is purely a social construction (Zinn and Taylor-Gooby 2006, Hermansson 2012).

Hence, there is a dichotomy posed in risk research as the objective vs. subjective ways of approaching risk (Fischhoff et al. 1984, Hansson 2010, Hermansson 2012), that has resulted in a decades-long debate (Kasperson et al. 1988). We argue that natural scientists would benefit from recognizing where biases and personal perspectives come in. Risk analysis is not a purely scientific undertaking (NRC 1983) and technical risk assessment involves decisions that include subjectivity, such as the method chosen and the unit of analysis (Douglas 2000). For example, a natural scientist studying the risk from a management strategy may choose a set of biological metrics based on traditional indicators (e.g., mean trophic level) or a legal framework (e.g., 20%

B_{MSY}), however, identifying that those are important components of the system to consider naturally involves subjectivity. Recognizing this reality may contribute to a stronger understanding between disciplines and lead to better risk analysis.

Timelines

Understanding the timeline within which the risk assessment needs to be conducted will dictate the resource requirements and the depth to which any topic can be explored. Is the risk assessment occurring in the presence of an environmental or management crisis? Is it a one-time project or management decision for which an assessment is needed, or is it ongoing management for which risk assessment will need to occur on a semi-regular basis? Risk assessment can be conducted for any of the three scenarios noted above: crises, one-time (non-crisis) decisions and long-term ongoing management. We recognize the possible high resource requirements for conducting an integrated risk analysis when considering ecological, social and economic impacts and timeline identification is a critical component of the process.

Dynamic feedbacks and amplification

Social-ecological systems are highly complex and interconnected. Decisions do not occur in isolation and repercussions can last through time and lead to unexpected feedbacks or amplifications (Liu et al. 2007, Holsman et al. 2017). These feedbacks can occur in many forms within and between the social and ecological components of the system (Kates 1985, Holsman et al. 2017). Feedbacks can be characterized as direct, tangible changes in natural conditions such as an unexpected change in abundance of a particular species, or socially derived effects through processes such as social amplification (or attenuation) (Kasperson et al. 1988). Social amplification is a phenomenon that results from the filtering of risk assessment and communication through social structures (individuals, communities and institutions) whereby responses of those structures can actually contribute to consequences (Kasperson et al. 1988). For example, fear of a potential impact may lead to behavioral change that influences a part of the economic system, such as public perceptions of genetically modified foods (Frewer et al. 2002). In this way, the process of identifying risks can lead to further societal changes (Kasperson et al. 1988). Thus, a single decision can have consequences with unknown impacts on the system. As a result, a truly integrated risk assessment is an ongoing process whereby decisions are made, impacts are monitored and possible modifying factors are identified, in an ongoing feedback process. Kates and Kasperson (1983) discuss the process as a “linked causal chain” (see Figure 1 in (Kates and Kasperson 1983)).

Conclusions

Humans live in linked social-ecological systems; any management decision to act (or not act) has implications for multiple components within that system. With growing recognition of the importance of understanding the approaches used in different disciplines and collaborating across fields in the social and natural sciences (Levins and Lewontin 1980, Liu et al. 2007, Bennett et al. 2017, Spalding et al. 2017) we take a step here towards improving that understanding and collaboration. Working with a team of natural and social scientists, we outlined the approaches to risk analysis across three dimensions of social, ecological and economic spheres. We then introduced a number of key factors that would need to be considered in any application of an integrated approach, and outlined the steps in an integrative framework. Approaches to ecosystem management would benefit from moving towards approaching EBFM using risk-tradeoffs in an integrative risk analysis framework.

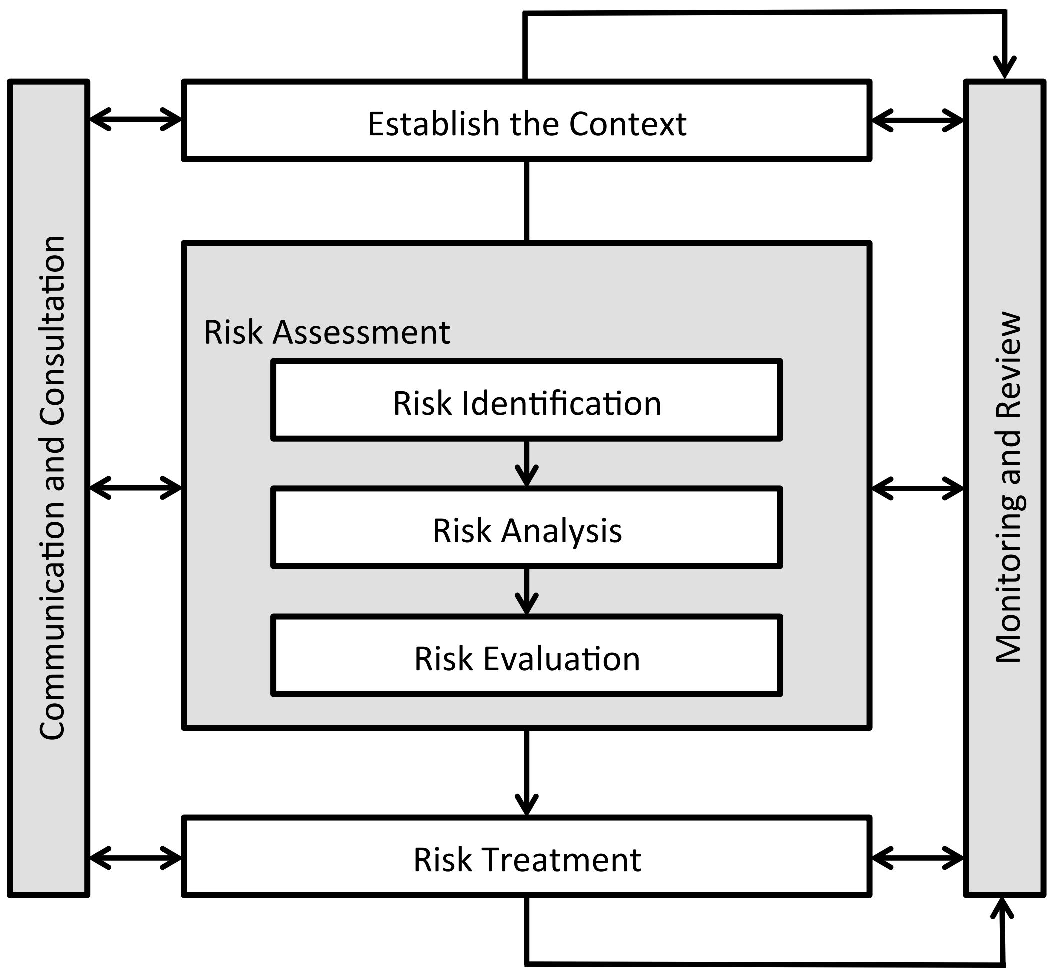

Figure 4.1 Traditional risk management framework.

Adapted from ISO Risk Assessment Standards (ISO 2009).

Synthesis

Anthropogenic modifications of marine environments result from a variety of activities and have effects across ecological scales, with feedbacks between social and ecological components of the system. Humans influence species both directly and indirectly through actions such as resource extraction (e.g., fishing), pollution and development. These actions have consequences and whether they impact an individual life stage of an organism (Dupont-Prinet et al. 2013), or a population of a species (Flockhart et al. 2015), they have the potential to scale up and have larger ecological implications (Griffith et al. 2012, Reum et al. 2015). These larger impacts may be felt by populations, entire ecosystems and the human communities that rely on living marine resources. Understanding the consequences of our actions requires a diverse set of tools able to tackle the various levels of complexity. This necessitates the improvement and modification of existing tools, development of novel approaches and unique combinations of approaches used across fields. This dissertation was focused on those elements: using and improving existing tools in marine ecology as well as incorporating insights from across disciplines. My research ranges across ecological scales, investigating population and ecosystem responses to stress, and the connections between social and ecological communities.

At the scale of a species, we may have some knowledge of the impact of a stressor on an individual life stage, but what does that mean for an entire population? Life stage impacts can be seen through changes in both physiological processes such as calcification or acid-base regulation (Fabry et al. 2008) and demographic rates, such as growth, survival or reproduction (Kroeker et al. 2010). In both circumstances the stressor may have a population impact, though translating the process into a quantifiable population change is not the same in all cases. Not all physiological impacts can be easily translated into population model parameters in which case we need tools that can use such information in a more qualitative manner, such as vulnerability analysis (Hare et al. 2016). In contrast, changes in demographic rates can be used to directly quantify population level impacts through the use of population models (Power 1997, Caswell 2001). Each of these offers a different type of output, but provides insights into the population implications of exposure to particular stressors.

In this dissertation, both semi-quantitative vulnerability analysis and population models were used to advance our understanding of the population impacts of single or multiple stressors. In both cases I considered circumstances where organisms may experience stressors at multiple points in their life cycle. Because direct changes in response to ocean acidification in demographic rates were unknown, I used vulnerability analysis, modifying existing methods (e.g., Samhouri and Levin 2012) to explicitly consider life stage exposure, consequence and relative population contribution (Chapter 1). In modifying this tool, I introduced a method to gain a better sense of population vulnerability to ocean acidification. In comparison, in Chapter 3 I introduced a framework for understanding when we would expect multiple stressors, acting across life history stages, to be mitigated or magnified at the population level. For this, I expanded on the rich history of population modeling (Cushing 1998, Caswell 2001) to better understand the theoretical basis for different population responses. With both of these chapters, I have expanded the uses of these tools to understand population impacts from stressors occurring across life history.

Moving beyond individual population assessments, ecologists and managers recognize the importance of considering ecosystem scale processes, their responses to novel stressors and how they influence human communities. While ecosystems are very complex, there are increasing numbers of tools available to address this complexity as computing capacity grows

(Plagányi 2007, Fulton 2010). At the ecosystem level there can be a variety of processes measured: the direct and indirect effects of stressors on individual species (Marshall et al. 2017), ecosystem indicators designed to represent different ecosystem attributes (Fulton et al. 2005), or specific economic measures such as changes in fisheries catch or revenue (Fernandes et al. 2016). In Chapter 2, I used a highly detailed ecosystem model, Atlantis (Fulton et al. 2004a, Kaplan et al. 2010), fed with an oceanographic and with outputs connected to an economic input-output model (Leonard and Watson 2011) to understand ecosystem change from ocean acidification. I used this as a type of scenario analysis (Amer et al. 2013) to get a sense of what a possible future may be in the California Current under projected acidification levels. That is, which species might show substantial changes in biomass and which ports along the coast may experience the largest changes in catch, revenue, income and employment. This integrated approach provided considerable insights into the high dependence of the west coast fishery revenues on Dungeness crab, and the potential vulnerability that communities will experience if crab populations decline.

Although it is important to improve our understanding of the impacts of human actions on marine species and subsequent economic repercussions for human communities, that is not the whole picture. Taking a step back, we recognize the many ways that repercussions may be experience by human communities. Traditionally within fisheries, decision making processes have used benefit-benefit tradeoffs, where outputs are framed as performance metrics and the strategy that optimizes amongst competing objectives is the best one (Hall and Mainprize 2004). However, as I identified in my fourth chapter, this may lead to ignoring potential losses to the system, particularly invisible losses in cultural benefits from resource access and participation (Turner et al. 2008). Thus, I proposed that we would benefit from thinking about management decisions in a risk-risk tradeoff framework, and specifically the ways in which natural scientists would gain from a broader understanding of risk analysis across disciplines.

The two themes that have come up time and again in this dissertation are the importance of considering scale (Levin 1992, Hunsicker et al. 2016) and the links within social-ecological systems (Holling 2001, Ostrom 2009). In order to understand impacts on populations, we need to think about the life stages contributing to them. In order to understand impacts on ecosystems, we need to think about the species that contribute to system processes and the many connections between organisms. And in order to understand how to manage the complexities of linked social-ecological-economic systems, we need to think about the different players involved. Critical to forward movement is stepping out of our specific focus and thinking about the larger context in which it sits, whether that means physiologists working with population modelers or natural scientists working with social scientists. Research is an iterative process. As a PhD student I have learned from the rich and diverse work across the fields of population modeling, ecosystem modeling, cumulative impacts assessment, vulnerability assessment and risk assessment. Only from learning what has been done before, and taking a step back to look at the whole picture, have I been able to provide my own contribution.

Literature Cited

Abrams, P. A. 2009. When does greater mortality increase population size? The long history and diverse mechanisms underlying the hydra effect. Ecology Letters **12**:462-474.

Adamack, A. T., K. A. Rose, D. L. Breitburg, A. J. Nice, and W. S. Lung. 2012. Simulating the effect of hypoxia on bay anchovy egg and larval mortality using coupled watershed, water quality, and individual-based predation models. Marine Ecology Progress Series **445**:141-160.

Adger, W. N. 2006. Vulnerability. Global Environmental Change **16**:268-281.

Ådlandsvik, B., and M. Bentsen. 2007. Downscaling a twentieth century global climate simulation to the North Sea. Ocean Dynamics **57**:453-466.

Ainsworth, C. H., J. F. Samhouri, D. S. Busch, W. W. L. Cheung, J. Dunne, and T. A. Okey. 2011. Potential impacts of climate change on Northeast Pacific marine foodwebs and fisheries. ICES Journal of Marine Science **68**:1217-1229.

Allison, E. H., A. L. Perry, M.-C. Badjeck, W. Neil Adger, K. Brown, D. Conway, A. S. Halls, G. M. Pilling, J. D. Reynolds, N. L. Andrew, and N. K. Dulvy. 2009. Vulnerability of national economies to the impacts of climate change on fisheries. Fish and Fisheries **10**:173-196.

Amer, M., T. U. Daim, and A. Jetter. 2013. A review of scenario planning. Futures **46**:23-40.

Anderson, J. J. 2000. A vitality-based model relating stressors and environmental properties to organism survival. Ecological Monographs **70**:445-470.

Armsworth, P. R., and J. E. Roughgarden. 2001. An invitation to ecological economics. Trends in Ecology & Evolution **16**:229-234.

Arnberg, M., P. Calosi, J. Spicer, A. Tandberg, M. Nilsen, S. Westerlund, and R. Bechmann. 2012. Elevated temperature elicits greater effects than decreased pH on the development, feeding and metabolism of northern shrimp (Pandalus borealis) larvae. Marine Biology:1-12.

Arquette, M., M. Cole, K. Cook, B. LaFrance, M. Peters, J. Ransom, E. Sargent, V. Smoke, and A. Stairs. 2002. Holistic risk-based environmental decision making: a Native perspective. Environmental Health Perspectives **110**:259-264.

Astles, K. L., P. J. Gibbs, A. S. Steffe, and M. Green. 2009. A qualitative risk-based assessment of impacts on marine habitats and harvested species for a data deficient wild capture fishery. Biological Conservation **142**:2759-2773.

Astles, K. L., M. G. Holloway, A. Steffe, M. Green, C. Ganassin, and P. J. Gibbs. 2006. An ecological method for qualitative risk assessment and its use in the management of fisheries in New South Wales, Australia. Fisheries Research **82**:290-303.

Aven, T., and O. Renn. 2009. On risk defined as an event where the outcome is uncertain. Journal of Risk Research **12**:1-11.

Baker, R., A. Buckland, and M. Sheaves. 2014. Fish gut content analysis: robust measures of diet composition. Fish and Fisheries **15**:170-177.

Ban, N. C., M. Mills, J. Tam, C. C. Hicks, S. Klain, N. Stoeckl, M. C. Bottrill, J. Levine, R. L. Pressey, T. Satterfield, and K. M. A. Chan. 2013. A social–ecological approach to conservation planning: embedding social considerations. Frontiers in Ecology and the Environment **11**:194-202.

Baram, M. S. 1979. Cost-benefit analysis: an inadequate basis for health, safety, and environmental regulatory decisionmaking. Ecology LQ **8**:473.

Barange, M., G. Merino, J. L. Blanchard, J. Scholtens, J. Harle, E. H. Allison, J. I. Allen, J. Holt, and S. Jennings. 2014. Impacts of climate change on marine ecosystem production in societies dependent on fisheries. Nature Clim. Change **4**:211-216.

Barnthouse, L. W. 1992. The role of models in ecological risk assessment: a 1990's perspective. Environmental Toxicology and Chemistry **11**.

Baumann, H., S. C. Talmage, and C. J. Gobler. 2011. Reduced early life growth and survival in a fish in direct response to increased carbon dioxide. Nature Climate Change. **2**: 38-41.

Bechmann, R. K., I. C. Taban, S. Westerlund, B. F. Godal, M. Arnberg, S. Vingen, A. Ingvarsdottir, and T. Baussant. 2011. Effects of ocean acidification on early life stages of shrimp (Pandalus borealis) and mussel (Mytilus edulis). J Toxicol Environ Health A **74**:424-438.

Beckerman, A., T. G. Benton, E. Ranta, V. Kaitala, and P. Lundberg. 2002. Population dynamic consequences of delayed life-history effects. Trends in Ecology & Evolution **17**:263-269.

Bednaršek, N., R. A. Feely, J. C. P. Reum, B. Peterson, J. Menkel, S. R. Alin, and B. Hales. 2014. Limacina helicina shell dissolution as an indicator of declining habitat suitability owing to ocean acidification in the California Current Ecosystem. Proceedings of the Royal Society B: Biological Sciences **281**.

Bednarsek, N., G. A. Tarling, D. C. E. Bakker, S. Fielding, E. M. Jones, H. J. Venables, P. Ward, A. Kuzirian, B. Leze, R. A. Feely, and E. J. Murphy. 2012. Extensive dissolution of live pteropods in the Southern Ocean. Nature Geosci **5**:881-885.

Beierle, T. C. 2002. The Quality of Stakeholder-Based Decisions. Risk Analysis **22**:739-749.

Bellows, T. S. 1981. The Descriptive Properties of Some Models for Density Dependence. Journal of Animal Ecology **50**:139-156.

Bennett, N. J., R. Roth, S. C. Klain, K. Chan, P. Christie, D. A. Clark, G. Cullman, D. Curran, T. J. Durbin, G. Epstein, A. Greenberg, M. P. Nelson, J. Sandlos, R. Stedman, T. L. Teel, R. Thomas, D. Veríssimo, and C. Wyborn. 2017. Conservation social science: Understanding and integrating human dimensions to improve conservation. Biological Conservation **205**:93-108.

Berryman, A. A. 1992. The origins and evolution of predator prey theory. Ecology **73**:1530-1535.

Beverton, R. J., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Springer.

Bi, H., L. Feinberg, C. T. Shaw, and W. T. Peterson. 2011. Estimated development times for stage-structured marine organisms are biased if based only on survivors. Journal of Plankton Research **33**:751-762.

Biedenweg, K., K. Stiles, and K. Wellman. 2016. A holistic framework for identifying human wellbeing indicators for marine policy. Marine Policy **64**:31-37.

Boer, J. T., M. Pastor, J. L. Sadd, and L. D. Snyder. 1997. Is There Environmental Racism? The Demographics of Hazardous Waste in Los Angeles County. Social Science Quarterly **78**:793-810.

Bolten, A. B., K. A. Bjorndal, H. R. Martins, T. Dellinger, M. J. Biscoito, S. E. Encalada, and B. W. Bowen. 1998. Transatlantic developmental migrations of loggerhead sea turtles demonstrated by mtDNA sequence analysis. Ecological Applications **8**:1-7.

Bostrom, A. 2014. Ethics, science, technology and engineering: a global resource. MacMillan Reference USA.

Bradshaw, M., L. Wood, and S. Williamson. 2001. Applying qualitative and quantitative research: a social impact assessment of a fishery. Applied Geography **21**:69-85.
Branch, T. A., B. M. Dejoseph, L. J. Ray, and C. A. Wagner. 2012. Impacts of ocean acidification on marine seafood. Trends Ecol Evol. **28**: 178-186.
Breitburg, D. L., A. Adamack, K. A. Rose, S. E. Kolesar, M. B. Decker, J. E. Purcell, J. E. Keister, and J. H. Cowan. 2003. The pattern and influence of low dissolved oxygen in the Patuxent River, a seasonally hypoxic estuary. Estuaries **26**:280-297.
Burgman, M. 2005. Risks and decisions for conservation and environmental management. Cambridge University Press.
Busch, D. S., and P. McElhany. 2016. Estimates of the Direct Effect of Seawater pH on the Survival Rate of Species Groups in the California Current Ecosystem. PLoS ONE **11**:e0160669.
CalCOFI. 2012. Pacific hake egg and larval survey 1984-2012.*in* CCOF Investigation, editor. http://www.calcofi.org/new.data/.
Caldeira, K., and M. E. Wickett. 2005. Ocean model predictions of chemistry changes from carbon dioxide emissions to the atmosphere and ocean. J. Geophys. Res **110**:C09S04.
Caldeira, K. W., M.E. 2003. Anthropogenic carbon and ocean pH. Nature **425**.
Carpenter, R. A. 1995. Risk assessment. Impact Assessment **13**:153-187.
Caswell, H. 1996. Demography meets ecotoxicology: untangling the population level effects of toxic substances. Pages 255-292 Ecotoxicology: A hierarchical treatment. CRC Press, United States of America.
Caswell, H. 2001. Matrix population models: construction, analysis and interpretation. 2nd ed edition. Sinauer Associates, Sunderland, MA, USA.
Caswell, H. 2008. Perturbation analysis of nonlinear matrix population models. Demographic Research **18**:59-116.
Chambers, R. C., A. C. Candelmo, E. A. Habeck, M. E. Poach, D. Wieczorek, K. R. Cooper, C. E. Greenfield, and B. A. Phelan. 2014. Effects of elevated CO2 in the early life stages of summer flounder, Paralichthys dentatus, and potential consequences of ocean acidification. Biogeosciences **11**:1613-1626.
Chan, K. M. A., A. D. Guerry, P. Balvanera, S. Klain, T. Satterfield, X. Basurto, A. Bostrom, R. Chuenpagdee, R. Gould, B. S. Halpern, N. Hannahs, J. Levine, B. Norton, M. Ruckelshaus, R. Russell, J. Tam, and U. Woodside. 2012. Where are Cultural and Social in Ecosystem Services? A Framework for Constructive Engagement. BioScience **62**:744-756.
Chapin, F. S., B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. Science **277**:500-504.
Chaumot, A., S. Charles, P. Flammarion, J. Garric, and P. Auger. 2002. Using aggregation methods to assess toxicant effects on population dynamics in spatial systems. Ecological Applications **12**:1771-1784.
Chen, N., B. Ribeiro, and A. Chen. 2016. Financial credit risk assessment: a recent review. Artificial Intelligence Review **45**:1-23.
Chen, S., B. Chen, and B. D. Fath. 2013. Ecological risk assessment on the system scale: A review of state-of-the-art models and future perspectives. Ecological Modelling **250**:25-33.

Cheung, W. W. L., J. Dunne, J. L. Sarmiento, and D. Pauly. 2011. Integrating ecophysiology and plankton dynamics into projected maximum fisheries catch potential under climate change in the Northeast Atlantic. ICES Journal of Marine Science **68**:1008-1018.
Cheung, W. W. L., T. L. Frölicher, R. G. Asch, M. C. Jones, M. L. Pinsky, G. Reygondeau, K. B. Rodgers, R. R. Rykaczewski, J. L. Sarmiento, C. Stock, and J. R. Watson. 2016. Building confidence in projections of the responses of living marine resources to climate change. ICES Journal of Marine Science: Journal du Conseil.
Cheung, W. W. L., V. W. Y. Lam, J. L. Sarmiento, K. Kearney, R. E. G. Watson, D. Zeller, and D. Pauly. 2010. Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. Global Change Biology **16**:24-35.
Clark, D., M. Lamare, and M. Barker. 2009. Response of sea urchin pluteus larvae (Echinodermata: Echinoidea) to reduced seawater pH: a comparison among a tropical, temperate, and a polar species. Marine Biology **156**:1125-1137.
Clark, J. S., S. R. Carpenter, M. Barber, S. Collins, A. Dobson, J. A. Foley, D. M. Lodge, M. Pascual, R. Pielke, Jr., W. Pizer, C. Pringle, W. V. Reid, K. A. Rose, O. Sala, W. H. Schlesinger, D. H. Wall, and D. Wear. 2001. Ecological forecasts: an emerging imperative. Science **293**:657-660.
Collie, J. S., L. W. Botsford, A. Hastings, I. C. Kaplan, J. L. Largier, P. A. Livingston, É. Plagányi, K. A. Rose, B. K. Wells, and F. E. Werner. 2016. Ecosystem models for fisheries management: finding the sweet spot. Fish and Fisheries **17**:101-125.
Cooley, S. R., and S. C. Doney. 2009. Anticipating ocean acidification's economic consequences for commercial fisheries. Environmental Research Letters **4**:024007.
Cooley, S. R., J. E. Rheuban, D. R. Hart, V. Luu, D. M. Glover, J. A. Hare, and S. C. Doney. 2015. An Integrated Assessment Model for Helping the United States Sea Scallop (Placopecten magellanicus) Fishery Plan Ahead for Ocean Acidification and Warming. PLoS ONE **10**:e0124145.
NRC, National Research Council. 1983. Risk assessment in the federal government: managing the process. National Academies Press.
Crain, C. M., K. Kroeker, and B. S. Halpern. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecol Lett **11**:1304-1315.
Cripps, G., P. Lindeque, and K. J. Flynn. 2014. Have we been underestimating the effects of ocean acidification in zooplankton? Global Change Biology **20**:3377-3385.
Crone, E. E. 1997. Delayed Density Dependence and the Stability of Interacting Populations and Subpopulations. Theoretical Population Biology **51**:67-76.
Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology **68**:1412-1423.
Cushing, J. M. 1998. An introduction to structured population dynamics. Society for Industrial and Applied Mathematics, USA.
Dambacher, J. M., P. C. Rothlisberg, and N. R. Loneragan. 2015. Qualitative mathematical models to support ecosystem-based management of Australia's Northern Prawn Fishery. Ecological Applications **25**:278-298.
Darling, E. S., and I. M. Côté. 2008. Quantifying the evidence for ecological synergies. Ecology Letters **11**:1278-1286.
Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. Beyond predictions: biodiversity conservation in a changing climate. Science **332**:53-58.

de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: The relative contribution of demographic parameters to population growth rate. Ecology **67**:1427-1431.
De Lange, H., S. Sala, M. Vighi, and J. Faber. 2010. Ecological vulnerability in risk assessment—a review and perspectives. Science of The Total Environment **408**:3871-3879.
De Lange, H. J., J. Lahr, J. J. C. Van der Pol, Y. Wessels, and J. H. Faber. 2009. Ecological vulnerability in wildlife: An expert judgment and multicriteria analysis tool using ecological traits to assess relative impact of pollutants. Environmental Toxicology and Chemistry **28**:2233-2240.
DePasquale, E., H. Baumann, and C. J. Gobler. 2015. Vulnerability of early life stage Northwest Atlantic forage fish to ocean acidification and low oxygen. Marine Ecology Progress Series **523**:145-156.
Diaz, R. J., and R. Rosenberg. 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanography and Marine Biology: an Annual Review **33**.
Dichmont, C. M., N. Ellis, R. H. Bustamante, R. Deng, S. Tickell, R. Pascual, H. Lozano-Montes, and S. Griffiths. 2013. EDITOR'S CHOICE: Evaluating marine spatial closures with conflicting fisheries and conservation objectives. Journal of Applied Ecology **50**:1060-1070.
Dixson, D. L., P. L. Munday, and G. P. Jones. 2009. Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. Ecology Letters **13**:68-75.
Dobson, A. D. M., and S. E. Randolph. 2011. Modelling the effects of recent changes in climate, host density and acaricide treatments on population dynamics of Ixodes ricinus in the UK. Journal of Applied Ecology **48**:1029-1037.
Douglas, H. 2000. Inductive Risk and Values in Science. Philosophy of Science **67**:559-579.
Douglas, H. 2009. Science, policy, and the value-free ideal. University of Pittsburgh Pre.
Dulvy, N. K., Y. Sadovy, and J. D. Reynolds. 2003. Extinction vulnerability in marine populations. Fish and Fisheries **4**:25-64.
Dunne, J. P., J. G. John, A. J. Adcroft, S. M. Griffies, R. W. Hallberg, E. Shevliakova, R. J. Stouffer, W. Cooke, K. A. Dunne, M. J. Harrison, J. P. Krasting, S. L. Malyshev, P. C. D. Milly, P. J. Phillipps, L. T. Sentman, B. L. Samuels, M. J. Spelman, M. Winton, A. T. Wittenberg, and N. Zadeh. 2012. GFDL's ESM2 Global Coupled Climate–Carbon Earth System Models. Part I: Physical Formulation and Baseline Simulation Characteristics. Journal of Climate **25**:6646-6665.
Dunne, J. P., J. G. John, E. Shevliakova, R. J. Stouffer, J. P. Krasting, S. L. Malyshev, P. C. D. Milly, L. T. Sentman, A. J. Adcroft, W. Cooke, K. A. Dunne, S. M. Griffies, R. W. Hallberg, M. J. Harrison, H. Levy, A. T. Wittenberg, P. J. Phillips, and N. Zadeh. 2013. GFDL's ESM2 Global Coupled Climate–Carbon Earth System Models. Part II: Carbon System Formulation and Baseline Simulation Characteristics. Journal of Climate **26**:2247-2267.
Dupont-Prinet, A., M. Vagner, D. Chabot, and C. Audet. 2013. Impact of hypoxia on the metabolism of Greenland halibut (Reinhardtius hippoglossoides). Canadian Journal of Fisheries and Aquatic Sciences **70**:461-469.

Eakin, H., and A. L. Luers. 2006. Assessing the vulnerability of social-environmental systems. Pages 365-394 Annual Review of Environment and Resources. Annual Reviews, Palo Alto.

Eeva, T., and E. Lehikoinen. 1996. Growth and mortality of nestling great tits (Parus major) and pied flycatchers (Ficedula hypoleuca) in a heavy metal pollution gradient. Oecologia **108**:631-639.

Ekstrom, J. A., L. Suatoni, S. R. Cooley, L. H. Pendleton, G. G. Waldbusser, J. E. Cinner, J. Ritter, C. Langdon, R. van Hooidonk, D. Gledhill, K. Wellman, M. W. Beck, L. M. Brander, D. Rittschof, C. Doherty, P. E. T. Edwards, and R. Portela. 2015. Vulnerability and adaptation of US shellfisheries to ocean acidification. Nature Clim. Change **5**:207-214.

Ekström, M., M. R. Grose, and P. H. Whetton. 2015. An appraisal of downscaling methods used in climate change research. Wiley Interdisciplinary Reviews: Climate Change **6**:301-319.

EPA, U. S. 1998. Guidelines for ecological risk assessment. . U.S. Environmental Protection Agency, Washington DC. .

Fabry, V. J., B. A. Seibel, R. A. Feely, and J. C. Orr. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. ICES Journal of Marine Science: Journal du Conseil **65**:414-432.

Falkenberg, L. J., and A. Tubb. 2017. Economic effects of ocean acidification: Publication patterns and directions for future research. Ambio:1-11.

Feely, R. A., S. R. Alin, B. Carter, N. Bednaršek, B. Hales, F. Chan, T. M. Hill, B. Gaylord, E. Sanford, R. H. Byrne, C. L. Sabine, D. Greeley, and L. Juranek. 2016. Chemical and biological impacts of ocean acidification along the west coast of North America. Estuarine, Coastal and Shelf Science **183, Part A**:260-270.

Feely, R. A., C. L. Sabine, J. M. Hernandez-Ayon, D. Ianson, and B. Hales. 2008. Evidence for upwelling of corrosive "acidified" water onto the continental shelf. Science **320**:1490-1492.

Feely, R. A., C. L. Sabine, K. Lee, W. Berelson, J. Kleypas, V. J. Fabry, and F. J. Millero. 2004. Impact of anthropogenic CO2 on the CaCO3 system in the oceans. Science **305**:362-366.

Fernandes, J. A., E. Papathanasopoulou, C. Hattam, A. M. Queirós, W. W. W. L. Cheung, A. Yool, Y. Artioli, E. C. Pope, K. J. Flynn, G. Merino, P. Calosi, N. Beaumont, M. C. Austen, S. Widdicombe, and M. Barange. 2016. Estimating the ecological, economic and social impacts of ocean acidification and warming on UK fisheries. Fish and Fisheries:n/a-n/a.

Fernández, M. 1999. Cannibalism in Dungeness crab Cancer magister: effects of predator-prey size ratio, density, and habitat type. Marine Ecology Progress Series **182**:221-230.

Festa-Bianchet, M., J.-M. Gaillard, and S. D. Côté. 2003. Variable age structure and apparent density dependence in survival of adult ungulates. Journal of Animal Ecology **72**:640-649.

Finnoff, D., and J. Tschirhart. 2003. Harvesting in an eight-species ecosystem. Journal of Environmental Economics and Management **45**:589-611.

Fischer, J., and N. E. Phillips. 2014. Carry-over effects of multiple stressors on benthic embryos are mediated by larval exposure to elevated UVB and temperature. Global Change Biology **20**:2108-2116.

Fischhoff, B. 1995. Risk Perception and Communication Unplugged: Twenty Years of Process1. Risk Analysis **15**:137-145.

Fischhoff, B., S. R. Watson, and C. Hope. 1984. Defining risk. Policy Sciences **17**:123-139.
Fletcher, W. 2005. The application of qualitative risk assessment methodology to prioritize issues for fisheries management. ICES Journal of Marine Science: Journal du Conseil **62**:1576-1587.
Fletcher, W. J. 2014. Review and refinement of an existing qualitative risk assessment method for application within an ecosystem-based management framework. ICES Journal of Marine Science: Journal du Conseil. **72**: 1043-1056.
Flockhart, D. T. T., J.-B. Pichancourt, D. R. Norris, and T. G. Martin. 2015. Unravelling the annual cycle in a migratory animal: breeding-season habitat loss drives population declines of monarch butterflies. Journal of Animal Ecology **84**:155-165.
Forrester, G. E. 1995. Strong density-dependent survival and recruitment regulate the abundance of a coral reef fish. Oecologia **103**:275-282.
Freckleton, R. P., A. R. Watkinson, R. E. Green, and W. J. Sutherland. 2006. Census error and the detection of density dependence. Journal of Animal Ecology **75**:837-851.
Freudenburg, W. R. 1988. Perceived risk, real risk: social science and the art of probabilistic risk assessment. Science **242**:44.
Frewer, L. J., S. Miles, and R. Marsh. 2002. The Media and Genetically Modified Foods: Evidence in Support of Social Amplification of Risk. Risk Analysis **22**:701-711.
Friedrich, T., A. Timmermann, A. Abe-Ouchi, N. R. Bates, M. O. Chikamoto, M. J. Church, J. E. Dore, D. K. Gledhill, M. Gonzalez-Davila, M. Heinemann, T. Ilyina, J. H. Jungclaus, E. McLeod, A. Mouchet, and J. M. Santana-Casiano. 2012. Detecting regional anthropogenic trends in ocean acidification against natural variability. Nature Clim. Change **2**:167-171.
Froehlich, H., T. Essington, A. Beaudreau, and P. Levin. 2014. Movement patterns and distributional shifts of Dungeness crab (Metacarcinus magister) and English sole (Parophrys vetulus) during seasonal hypoxia. Estuaries and Coasts **37**:449-460.
Frommel, A. Y., R. Maneja, D. Lowe, A. M. Malzahn, A. J. Geffen, A. Folkvord, U. Piatkowski, T. B. H. Reusch, and C. Clemmesen. 2011. Severe tissue damage in Atlantic cod larvae under increasing ocean acidification. Nature Climate Change. **2**: 42-46.
Frommel, A. Y., R. Maneja, D. Lowe, C. K. Pascoe, A. J. Geffen, A. Folkvord, U. Piatkowski, and C. Clemmesen. 2014. Organ damage in Atlantic herring larvae as a result of ocean acidification. Ecological Applications **24**:1131-1143.
Fulton, E., and R. Gorton. 2014. Adaptive futures for SE australian fisheries and aquaculture: climate adaptation simulations. CSIRO. Climate Adaptation Flagship (issuing body.) and Fisheries Research and Development Corporation (Australia) (sponsoring body.), Hobart, Tasmania.
Fulton, E., A. Smith, and A. Punt. 2005. Which ecological indicators can robustly detect effects of fishing? ICES Journal of Marine Science **62**:540-551.
Fulton, E. A. 2010. Approaches to end-to-end ecosystem models. Journal of Marine Systems **81**:171-183.
Fulton, E. A. 2011. Interesting times: winners, losers, and system shifts under climate change around Australia. ICES Journal of Marine Science **68**:1329-1342.
Fulton, E. A., J. S. Link, I. C. Kaplan, M. Savina-Rolland, P. Johnson, C. Ainsworth, P. Horne, R. Gorton, R. J. Gamble, A. D. M. Smith, and D. C. Smith. 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. Fish and Fisheries **12**:171-188.

Fulton, E. A., J. S. Parslow, A. D. M. Smith, and C. R. Johnson. 2004a. Biogeochemical marine ecosystem models II: the effect of physiological detail on model performance. Ecological Modelling **173**:371-406.
Fulton, E. A., A. D. Smith, and C. R. Johnson. 2004b. Biogeochemical marine ecosystem models I: IGBEM—a model of marine bay ecosystems. Ecological Modelling **174**:267-307.
Fulton, E. A., A. D. M. Smith, and C. R. Johnson. 2004c. Effects of spatial resolution on the performance and interpretation of marine ecosystem models. Ecological Modelling **176**:27-42.
Fulton, E. A., A. D. M. Smith, D. C. Smith, and P. Johnson. 2014a. An Integrated Approach Is Needed for Ecosystem Based Fisheries Management: Insights from Ecosystem-Level Management Strategy Evaluation. Plos One **9**.
Fulton, E. A., A. D. M. Smith, D. C. Smith, and P. Johnson. 2014b. An Integrated Approach Is Needed for Ecosystem Based Fisheries Management: Insights from Ecosystem-Level Management Strategy Evaluation. PLoS ONE **9**:e84242.
Gaichas, S. K., G. Odell, K. Y. Aydin, and R. C. Francis. 2012. Beyond the defaults: functional response parameter space and ecosystem-level fishing thresholds in dynamic food web model simulations. Canadian Journal of Fisheries and Aquatic Sciences **69**:2077-2094.
Gardali, T., N. E. Seavy, R. T. DiGaudio, and L. A. Comrack. 2012. A climate change vulnerability assessment of California's at-risk birds. PLoS ONE **7**:e29507.
Gelman, A., and D. B. Rubin. 1992. Inference from Iterative Simulation Using Multiple Sequences. Statistical Science **7**:457-472.
Grantham, B. A., G. L. Eckert, and A. L. Shanks. 2003. Dispersal potential of marine invertebrates in diverse habitats. Ecological Applications **13**:108-116.
Gregory, R., L. Failing, M. Harstone, G. Long, T. McDaniels, and D. Ohlson. 2012. Structured decision making: a practical guide to environmental management choices. John Wiley & Sons.
Griffith, G. P., E. A. Fulton, R. Gorton, and A. J. Richardson. 2012. Predicting Interactions among Fishing, Ocean Warming, and Ocean Acidification in a Marine System with Whole-Ecosystem Models. Conservation Biology **26**:1145-1152.
Griffith, G. P., E. A. Fulton, and A. J. Richardson. 2011. Effects of fishing and acidification-related benthic mortality on the southeast Australian marine ecosystem. Global Change Biology **17**:3058-3074.
Grimble, R., and K. Wellard. 1997. Stakeholder methodologies in natural resource management: a review of principles, contexts, experiences and opportunities. Agricultural Systems **55**:173-193.
Gruber, N., C. Hauri, Z. Lachkar, D. Loher, T. L. Frölicher, and G.-K. Plattner. 2012. Rapid progression of ocean acidification in the California Current System. Science **337**:220-223.
Guthery, F. S., M. J. Peterson, and R. R. George. 2000. Viability of Northern Bobwhite Populations. The Journal of Wildlife Management **64**:646-662.
Haidvogel, D. B., H. Arango, W. P. Budgell, B. D. Cornuelle, E. Curchitser, E. Di Lorenzo, K. Fennel, W. R. Geyer, A. J. Hermann, L. Lanerolle, J. Levin, J. C. McWilliams, A. J. Miller, A. M. Moore, T. M. Powell, A. F. Shchepetkin, C. R. Sherwood, R. P. Signell, J. C. Warner, and J. Wilkin. 2008. Ocean forecasting in terrain-following coordinates: Formulation and skill assessment of the Regional Ocean Modeling System. Journal of Computational Physics **227**:3595-3624.

Hall, S. J., and B. Mainprize. 2004. Towards ecosystem-based fisheries management. Fish and Fisheries **5**:1-20.

Halpern, B. S., C. V. Kappel, K. A. Selkoe, F. Micheli, C. M. Ebert, C. Kontgis, C. M. Crain, R. G. Martone, C. Shearer, and S. J. Teck. 2009. Mapping cumulative human impacts to California Current marine ecosystems. Conservation Letters **2**:138-148.

Halpern, B. S., K. A. Selkoe, F. Micheli, and C. V. Kappel. 2007. Evaluating and Ranking the Vulnerability of Global Marine Ecosystems to Anthropogenic Threats. Conservation Biology **21**:1301-1315.

Halpern, B. S., S. Walbridge, K. A. Selkoe, C. V. Kappel, F. Micheli, C. D'Agrosa, J. F. Bruno, K. S. Casey, C. Ebert, and H. E. Fox. 2008. A global map of human impact on marine ecosystems. Science **319**:948-952.

Hampel, J. 2006. Different concepts of risk – A challenge for risk communication. International Journal of Medical Microbiology **296,** Supplement 1:5-10.

Hansson, S. O. 2010. Risk: objective or subjective, facts or values. Journal of Risk Research **13**:231-238.

Harding, R. 1998. Environmental Decision-Making: The roles of scientists, engineers, and the public. Federation Press, New South Wales.

Hare, J. A., W. E. Morrison, M. W. Nelson, M. M. Stachura, E. J. Teeters, R. B. Griffis, M. A. Alexander, J. D. Scott, L. Alade, R. J. Bell, A. S. Chute, K. L. Curti, T. H. Curtis, D. Kircheis, J. F. Kocik, S. M. Lucey, C. T. McCandless, L. M. Milke, D. E. Richardson, E. Robillard, H. J. Walsh, M. C. McManus, K. E. Marancik, and C. A. Griswold. 2016. A Vulnerability Assessment of Fish and Invertebrates to Climate Change on the Northeast U.S. Continental Shelf. PLoS ONE **11**:e0146756.

Harley, C. D. G., A. Randall Hughes, K. M. Hultgren, B. G. Miner, C. J. B. Sorte, C. S. Thornber, L. F. Rodriguez, L. Tomanek, and S. L. Williams. 2006. The impacts of climate change in coastal marine systems. Ecology Letters **9**:228-241.

Harvey, H. R., S.-J. Ju, S. K. Son, L. R. Feinberg, C. T. Shaw, and W. T. Peterson. 2010. The biochemical estimation of age in Euphausiids: Laboratory calibration and field comparisons. Deep Sea Research Part II: Topical Studies in Oceanography **57**:663-671.

Hassell, M. P., J. H. Lawton, and R. M. May. 1976. Patterns of Dynamical Behaviour in Single-Species Populations. Journal of Animal Ecology **45**:471-486.

Hatton, I. A., K. S. McCann, J. Umbanhowar, and J. B. Rasmussen. 2006. A dynamical approach To evaluate risk In resource management. Ecological Applications **16**:1238-1248.

Hauri, C., N. Gruber, M. Vogt, S. C. Doney, R. A. Feely, Z. Lachkar, A. Leinweber, A. M. P. McDonnell, M. Munnich, and G. K. Plattner. 2013. Spatiotemporal variability and long-term trends of ocean acidification in the California Current System. Biogeosciences **10**:193-216.

Hawkins, E., and R. Sutton. 2009. The Potential to Narrow Uncertainty in Regional Climate Predictions. Bulletin of the American Meteorological Society **90**:1095-1107.

Healey, M. 2011. The cumulative impacts of climate change on Fraser River sockeye salmon (Oncorhynchus nerka) and implications for management. Canadian Journal of Fisheries and Aquatic Sciences **68**:718-737.

Hegmann, G., C. Cocklin, R. Creasey, S. Dupuis, A. Kennedy, L. Kingsley, W. Ross, H. Spaling, and D. Stalker. 1999. Cumulative effects assessment practitioners guide. Prepared by AXYS Environmental Consulting Ltd. and the CEA Working Group for the Canadian Environmental Assessment Agency, Hull, Quebec.

Hendriks, I. E., C. M. Duarte, and M. Álvarez. 2010. Vulnerability of marine biodiversity to ocean acidification: A meta-analysis. Estuarine, Coastal and Shelf Science **86**:157-164.
Heppell, S., C. Pfister, and H. de Kroon. 2000. Elasticity analysis in population biology: Methods and applications 1. Ecology **81**:605-606.
Heppell, S. S. 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia:367-375.
Hermansson, H. 2005. Consistent risk management: Three models outlined. Journal of Risk Research **8**:557-568.
Hermansson, H. 2010. Towards a fair procedure for risk management. Journal of Risk Research **13**:501-515.
Hermansson, H. 2012. Defending the Conception of "Objective Risk". Risk Analysis **32**:16-24.
Hobday, A., A. Smith, I. Stobutzki, C. Bulman, R. Daley, J. Dambacher, R. Deng, J. Dowdney, M. Fuller, and D. Furlani. 2011. Ecological risk assessment for the effects of fishing. Fisheries Research **108**:372-384.
Hodgson, E. E., T. E. Essington, and I. C. Kaplan. 2016. Extending Vulnerability Assessment to Include Life Stages Considerations. PLoS ONE **11**:e0158917.
Hoffmann, S. 2011. Overcoming Barriers to Integrating Economic Analysis into Risk Assessment†. Risk Analysis **31**:1345-1355.
Hofmann, G. E., T. G. Evans, M. W. Kelly, J. L. Padilla-Gamiño, C. A. Blanchette, L. Washburn, F. Chan, M. A. McManus, B. A. Menge, B. Gaylord, T. M. Hill, E. Sanford, M. LaVigne, J. M. Rose, L. Kapsenberg, and J. M. Dutton. 2014a. Exploring local adaptation and the ocean acidification seascape – studies in the California Current Large Marine Ecosystem. Biogeosciences **11**:1053-1064.
Hofmann, G. E., T. G. Evans, M. W. Kelly, J. L. Padilla-Gamiño, C. A. Blanchette, L. Washburn, F. Chan, M. A. McManus, B. A. Menge, B. Gaylord, T. M. Hill, E. Sanford, M. LaVigne, J. M. Rose, L. Kapsenberg, and J. M. Dutton. 2014b. Exploring local adaptation and the ocean acidification seascape; studies in the California Current Large Marine Ecosystem. Biogeosciences **11**:1053-1064.
Hofmann, G. E., J. E. Smith, K. S. Johnson, U. Send, L. A. Levin, F. Micheli, A. Paytan, N. N. Price, B. Peterson, and Y. Takeshita. 2011. High-frequency dynamics of ocean pH: a multi-ecosystem comparison. PLoS ONE **6**:e28983.
Holling, C. S. 2001. Understanding the Complexity of Economic, Ecological, and Social Systems. Ecosystems **4**:390-405.
Hollowed, A. B., N. A. Bond, T. K. Wilderbuer, W. T. Stockhausen, Z. T. A'mar, R. J. Beamish, J. E. Overland, and M. J. Schirripa. 2009. A framework for modelling fish and shellfish responses to future climate change. ICES Journal of Marine Science: Journal du Conseil **66**:1584-1594.
Holsman, K., J. Samhouri, G. Cook, E. Hazen, E. Olsen, M. Dillard, S. Kasperski, S. Gaichas, C. R. Kelble, M. Fogarty, and K. Andrews. 2017. An ecosystem-based approach to marine risk assessment. Ecosystem Health and Sustainability **3**:e01256-n/a.
Horne, P. J., I. C. Kaplan, K. N. Marshall, P. S. Levin, C. J. Harvey, A. J. Hermann, and E. A. Fulton. 2010. Design and parameterization of a spatially explicit ecosystem model of the central California Current.
Hunsicker, M. E., C. V. Kappel, K. A. Selkoe, B. S. Halpern, C. Scarborough, L. Mease, and A. Amrhein. 2016. Characterizing driver–response relationships in marine pelagic ecosystems for improved ocean management. Ecological Applications **26**:651-663.

Hurst, T. P., E. R. Fernandez, and J. T. Mathis. 2013. Effects of ocean acidification on hatch size and larval growth of walleye pollock (Theragra chalcogramma). ICES Journal of Marine Science: Journal du Conseil **70**:812-822.
IPCC. 2014. Climate Change 2014: impacts, adaptation, and vulnerability. Part A: global and sectoral aspects. contribution of working group II to the fifth assessment report of the Intergovernmental Panel on Climate Change Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
ISO, I. O. o. S. 2009. Risk management; principles and guidelines. International Organisation of Standards, Geneva, Switzerland.
Jobling, S., D. Sheahan, J. A. Osborne, P. Matthiessen, and J. P. Sumpter. 1996. Inhibition of testicular growth in rainbow trout (Oncorhynchus mykiss) exposed to estrogenic alkylphenolic chemicals. Environmental Toxicology and Chemistry **15**:194-202.
Jonzen, N., and P. Lundberg. 1999. Temporally structured density-dependence and population management. Annales Zoologici Fennici **36**:39-44.
Kahneman, D., and A. Tversky. 1979. Prospect Theory: An Analysis of Decision under Risk. Econometrica **47**:263-291.
Kaplan, I. C., I. A. Gray, and P. S. Levin. 2013a. Cumulative impacts of fisheries in the California Current. Fish and Fisheries **14**:515-527.
Kaplan, I. C., D. S. Holland, and E. A. Fulton. 2013b. Finding the accelerator and brake in an individual quota fishery: linking ecology, economics, and fleet dynamics of US West Coast trawl fisheries. ICES Journal of Marine Science: Journal du Conseil. **71**:308-319.
Kaplan, I. C., and J. Leonard. 2012. From krill to convenience stores: Forecasting the economic and ecological effects of fisheries management on the US West Coast. Marine Policy **36**:947-954.
Kaplan, I. C., P. S. Levin, M. Burden, and E. A. Fulton. 2010. Fishing catch shares in the face of global change: a framework for integrating cumulative impacts and single species management. Canadian Journal of Fisheries and Aquatic Sciences **67**:1968-1982.
Kasperski, S., and D. S. Holland. 2013. Income diversification and risk for fishermen. Proceedings of the National Academy of Sciences **110**:2076-2081.
Kasperson, R. E., O. Renn, P. Slovic, H. S. Brown, J. Emel, R. Goble, J. X. Kasperson, and S. Ratick. 1988. The Social Amplification of Risk: A Conceptual Framework. Risk Analysis **8**:177-187.
Kates, R. W. 1985. The interaction of climate and society. Pages 3-36. SCOPE.
Kates, R. W., and J. X. Kasperson. 1983. Comparative risk analysis of technological hazards (a review). Proceedings of the National Academy of Sciences **80**:7027-7038.
King, J. R., V. N. Agostini, C. J. Harvey, G. A. McFarlane, M. G. G. Foreman, J. E. Overland, E. Di Lorenzo, N. A. Bond, and K. Y. Aydin. 2011. Climate forcing and the California Current ecosystem. ICES Journal of Marine Science **68**:1199-1216.
Kingsolver, J. G., H. Arthur Woods, L. B. Buckley, K. A. Potter, H. J. MacLean, and J. K. Higgins. 2011. Complex Life Cycles and the Responses of Insects to Climate Change. Integrative and Comparative Biology.
Kittinger, J. N., J. Z. Koehn, E. Le Cornu, N. C. Ban, M. Gopnik, M. Armsby, C. Brooks, M. H. Carr, J. E. Cinner, A. Cravens, M. D'Iorio, A. Erickson, E. M. Finkbeiner, M. M. Foley, R. Fujita, S. Gelcich, K. S. Martin, E. Prahler, D. R. Reineman, J. Shackeroff, C. White, M. R. Caldwell, and L. B. Crowder. 2014. A practical approach for putting people in ecosystem-based ocean planning. Frontiers in Ecology and the Environment **12**:448-456.

Kjaer, C., N. Elmegaard, J. A. Axelsen, P. N. Andersen, and N. Seidelin. 1998. The impact of phenology, exposure and instar susceptibility on insecticide effects on a chrysomelid beetle population. Pesticide Science **52**:361-371.
Koehn, J. Z., D. R. Reineman, and J. N. Kittinger. 2013. Progress and promise in spatial human dimensions research for ecosystem-based ocean planning. Marine Policy **42**:31-38.
Kroeker, K. J., M. C. Gambi, and F. Micheli. 2013. Community dynamics and ecosystem simplification in a high-CO2 ocean. Proceedings of the National Academy of Sciences.
Kroeker, K. J., R. L. Kordas, R. N. Crim, and G. G. Singh. 2010. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. Ecology Letters **13**:1419-1434.
Kruitwagen, G., T. Hecht, H. B. Pratap, and S. E. W. Bonga. 2006. Changes in morphology and growth of the mudskipper (Periophthalmus argentilineatus) associated with coastal pollution. Marine Biology **149**:201-211.
Kurihara, H. 2008. Effects of CO2-driven ocean acidification on the early developmental stages of invertebrates. Marine Ecology Progress Series **373**:275-284.
Landry, C. A., S. L. Steele, S. Manning, and A. O. Cheek. 2007. Long term hypoxia suppresses reproductive capacity in the estuarine fish, Fundulus grandis. Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology **148**:317-323.
Lane, D. E., and R. L. Stephenson. 1998. A framework for risk analysis in fisheries decision-making. ICES Journal of Marine Science **55**:1-13.
Le Quesne, W. J. F., and J. K. Pinnegar. 2012. The potential impacts of ocean acidification: scaling from physiology to fisheries*. Fish and Fisheries **13**:333-344.
Leonard, J., and P. Watson. 2011. Description of the input-output model for Pacific Coast Fisheries (IOPAC). NOAA Technical Memorandum NMFS-NWFSC **111**:1-64.
Levin, S. A. 1992. The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. Ecology **73**:1943-1967.
Levins, R., and R. Lewontin. 1980. Dialectics and reductionism in ecology. Synthese **43**:47-78.
Linkov, I., F. K. Satterstrom, J. Steevens, E. Ferguson, and R. C. Pleus. 2007. Multi-criteria decision analysis and environmental risk assessment for nanomaterials. Journal of Nanoparticle Research **9**:543-554.
Liu, J., T. Dietz, S. R. Carpenter, M. Alberti, C. Folke, E. Moran, A. N. Pell, P. Deadman, T. Kratz, J. Lubchenco, E. Ostrom, Z. Ouyang, W. Provencher, C. L. Redman, S. H. Schneider, and W. W. Taylor. 2007. Complexity of Coupled Human and Natural Systems. Science **317**:1513.
Liz, E., and A. Ruiz-Herrera. 2016. Potential Impact of Carry-Over Effects in the Dynamics and Management of Seasonal Populations. PLoS ONE **11**:e0155579.
LNG, P. N. 2016. Environmental Assessment Report. Canadian Environmental Assessment Agency.
Lohbeck, K. T. R., U.; Reusch, T.B.H. 2012. Adaptive evolution of a key phytoplankton species to ocean acidification. Nature Geosciences **5**:346-351.
Mahmoudi, H., O. Renn, F. Vanclay, V. Hoffmann, and E. Karami. 2013. A framework for combining social impact assessment and risk assessment. Environmental Impact Assessment Review **43**:1-8.
Marshall, K. N., I. C. Kaplan, E. E. Hodgson, A. Hermann, D. S. Busch, P. McElhany, T. E. Essington, C. J. Harvey, and E. A. Fulton. 2017. Risks of ocean acidification in the

California Current food web and fisheries: ecosystem model projections. Global Change Biology **23**: 1525–1539.
Marvelde, L. t., P. L. Meininger, R. Flamant, and N. J. Dingemanse. 2009. Age-Specific Density-Dependent Survival in Mediterranean Gulls Larus melanocephalus. Ardea **97**:305-312.
Mastrandrea, M. D., C. B. Field, T. F. Stocker, O. Edenhofer, K. L. Ebi, D. J. Frame, H. Held, E. Kriegler, K. J. Mach, P. R. Matschoss, G.-K. Plattner, G. W. Yohe, and F. W. Zwier. 2010. Guidance note for lead authors of the IPCC fifth assessment report on consistent treatment of uncertainties. Intergovernmental Panel on Climate Change (IPCC).
Maxwell, S. M., E. L. Hazen, S. J. Bograd, B. S. Halpern, G. A. Breed, B. Nickel, N. M. Teutschel, L. B. Crowder, S. Benson, P. H. Dutton, H. Bailey, M. A. Kappes, C. E. Kuhn, M. J. Weise, B. Mate, S. A. Shaffer, J. L. Hassrick, R. W. Henry, L. Irvine, B. I. McDonald, P. W. Robinson, B. A. Block, and D. P. Costa. 2013. Cumulative human impacts on marine predators. Nat Commun. **4**.
May, R. M. 1976. Simple mathematical models with very complicated dynamics. Nature **261**:459-467.
McCarthy, J. J., Canziani, O.F., Leary, N.A., Dokken, D.J., White, K.S., and (Eds.). 2001. Climate change 2001: impacts, adaptation and vulnerability. Cambridge University Press, Cambridge.
Melbourne-Thomas, J., S. Wotherspoon, B. Raymond, and A. Constable. 2012. Comprehensive evaluation of model uncertainty in qualitative network analyses. Ecological Monographs **82**:505-519.
Melzner, F., M. Gutowska, M. Langenbuch, S. Dupont, M. Lucassen, M. C. Thorndyke, M. Bleich, and H.-O. Pörtner. 2009. Physiological basis for high CO2 tolerance in marine ectothermic animals: pre-adaptation through lifestyle and ontogeny? Biogeosciences Discussions **6**:4693-4738.
Metcalf, S. J. 2010. Qualitative Models to Complement Quantitative Ecosystem Models for the Analysis of Data-Limited Marine Ecosystems and Fisheries. Reviews in Fisheries Science **18**:248-265.
Metzger, M. J., R. Leemans, and D. Schröter. 2005. A multidisciplinary multi-scale framework for assessing vulnerabilities to global change. International Journal of Applied Earth Observation and Geoinformation **7**:253-267.
Miller, J. J., M. Maher, E. Bohaboy, C. S. Friedman, and P. McElhany. 2016. Exposure to low pH reduces survival and delays development in early life stages of Dungeness crab (Cancer magister). Marine Biology **163**:1-11.
Miller, T. W., R. D. Brodeur, G. Rau, and K. Omori. 2010. Prey dominance shapes trophic structure of the northern California Current pelagic food web: evidence from stable isotopes and diet analysis. Marine Ecology Progress Series **420**:15-26.
Moe, S. J., S. Nils Chr, and R. H. Smith. 2002. Density-Dependent Compensation in Blowfly Populations Give Indirectly Positive Effects of a Toxicant. Ecology **83**:1597-1603.
Moore, A. M., H. G. Arango, G. Broquet, B. S. Powell, A. T. Weaver, and J. Zavala-Garay. 2011. The Regional Ocean Modeling System (ROMS) 4-dimensional variational data assimilation systems: Part I – System overview and formulation. Progress in Oceanography **91**:34-49.
Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates Sunderland, Massachusetts, USA.

Moyle, P. B., J. D. Kiernan, P. K. Crain, and R. M. QuiÒones. 2013. Climate change vulnerability of native and alien freshwater fishes of california: a systematic assessment approach. PLoS ONE **8**:e63883.
Munday, P. L., D. L. Dixson, J. M. Donelson, G. P. Jones, M. S. Pratchett, G. V. Devitsina, and K. B. Døving. 2009. Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. Proceedings of the National Academy of Sciences **106**:1848-1852.
Nelson, E., G. Mendoza, J. Regetz, S. Polasky, H. Tallis, D. Cameron, K. M. A. Chan, G. C. Daily, J. Goldstein, P. M. Kareiva, E. Lonsdorf, R. Naidoo, T. H. Ricketts, and M. Shaw. 2009. Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Frontiers in Ecology and the Environment **7**:4-11.
Oken, K. L., and T. E. Essington. 2015. How detectable is predation in stage-structured populations? Insights from a simulation-testing analysis. Journal of Animal Ecology **84**:60-70.
Orr, J. C., V. J. Fabry, O. Aumont, L. Bopp, S. C. Doney, R. A. Feely, A. Gnanadesikan, N. Gruber, A. Ishida, F. Joos, R. M. Key, K. Lindsay, E. Maier-Reimer, R. Matear, P. Monfray, A. Mouchet, R. G. Najjar, G. K. Plattner, K. B. Rodgers, C. L. Sabine, J. L. Sarmiento, R. Schlitzer, R. D. Slater, I. J. Totterdell, M. F. Weirig, Y. Yamanaka, and A. Yool. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature **437**:681-686.
Ostrom, E. 2009. A General Framework for Analyzing Sustainability of Social-Ecological Systems. Science **325**:419-422.
Owen-Smith, N. 2006. Demographic determination of the shape of density dependence for three African ungulate populations. . Ecological Monographs **76**:93-109.
Pacific Fisheries Information Network (PacFIN) 2013 catch and revenue data. Retrieval dated February 2, 2016, Pacific States Marine Fisheries Commission, Portland, Oregon (www.psmfc.org).
Pauly, D., V. Christensen, and C. Walters. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. Ices Journal of Marine Science **57**:697-706.
Pespeni, M. H., F. Chan, B. A. Menge, and S. R. Palumbi. 2013. Signs of Adaptation to Local pH Conditions across an Environmental Mosaic in the California Current Ecosystem. Integrative and Comparative Biology **53**:857-870.
Peterman, R. M. 1978. Testing for Density-Dependent Marine Survival in Pacific Salmonids. Journal of the Fisheries Research Board of Canada **35**:1434-1450.
Peterson, G. D., G. S. Cumming, and S. R. Carpenter. 2003. Scenario Planning: a Tool for Conservation in an Uncertain World. Conservation Biology **17**:358-366.
PFMC (Pacific Fishery Management Council). 2004. Acceptable biological catch and optimum yield specification and management measures for the 2005–2006 Pacific Coast groundfish fishery. Final environmental impact statement and regulatory analysis. PFMC, Portland, OR.
Pichavant, K., J. Person-Le-Ruyet, N. Le Bayon, A. Severe, A. Le Roux, and G. Boeuf. 2001. Comparative effects of long-term hypoxia on growth, feeding and oxygen consumption in juvenile turbot and European sea bass. Journal of Fish Biology **59**:875-883.
Pihl, L., S. Baden, and R. Diaz. 1991. Effects of periodic hypoxia on distribution of demersal fish and crustaceans. Marine Biology **108**:349-360.

Pikitch, E. K., C. Santora, E. A. Babcock, A. Bakun, R. Bonfil, D. O. Conover, P. Dayton, P. Doukakis, D. Fluharty, B. Heneman, E. D. Houde, J. Link, P. A. Livingston, M. Mangel, M. K. McAllister, J. Pope, and K. J. Sainsbury. 2004. Ecosystem-Based Fishery Management. Science **305**:346-347.

Pinsky, M. L., and N. J. Mantua. 2014. Emerging adaptation approaches for climate-ready fisheries management. Oceanography **27**:146.

Pinsky, M. L., B. Worm, M. J. Fogarty, J. L. Sarmiento, and S. A. Levin. 2013. Marine taxa track local climate velocities. Science **341**:1239-1242.

Plagányi, É. E. 2007. Models for an ecosystem approach to fisheries. FAO Fisheries Technical Paper, Rome, FAO.

Plagányi, É. E., I. van Putten, T. Hutton, R. A. Deng, D. Dennis, S. Pascoe, T. Skewes, and R. A. Campbell. 2013. Integrating indigenous livelihood and lifestyle objectives in managing a natural resource. Proceedings of the National Academy of Sciences **110**:3639-3644.

Plummer, M. 2016. rjags: Bayesian Graphical Models using MCMC. R package version 4-6.

Poloczanska, E. S., C. J. Brown, W. J. Sydeman, W. Kiessling, D. S. Schoeman, P. J. Moore, K. Brander, J. F. Bruno, L. B. Buckley, M. T. Burrows, C. M. Duarte, B. S. Halpern, J. Holding, C. V. Kappel, M. I. O'Connor, J. M. Pandolfi, C. Parmesan, F. Schwing, S. A. Thompson, and A. J. Richardson. 2013. Global imprint of climate change on marine life. Nature Clim. Change **3**: 919-925.

Postma, T. J. B. M., and F. Liebl. 2005. How to improve scenario analysis as a strategic management tool? Technological Forecasting and Social Change **72**:161-173.

Power, M. 1997. Assessing the effects of environmental stressors on fish populations. Aquatic Toxicology **39**:151-169.

Przeslawski, R., M. Byrne, and C. Mellin. 2014. A review and meta-analysis of the effects of multiple abiotic stressors on marine embryos and larvae. Global Change Biology:n/a-n/a.

Punt, A. E., R. J. Foy, M. G. Dalton, W. C. Long, and K. M. Swiney. 2015. Effects of long-term exposure to ocean acidification conditions on future southern Tanner crab (Chionoecetes bairdi) fisheries management. ICES Journal of Marine Science: Journal du Conseil.

Punt, A. E., D. Poljak, M. G. Dalton, and R. J. Foy. 2014. Evaluating the impact of ocean acidification on fishery yields and profits: The example of red king crab in Bristol Bay. Ecological Modelling **285**:39-53.

Punt, A. E., and T. I. Walker. 1999. Stock assessment and risk analysis for the school shark *Galeorhinus galeus* off southern Australia. Marine and Freshwater Research **49**:719-731.

Purcell, S. W., A. Mercier, C. Conand, J.-F. Hamel, M. V. Toral-Granda, A. Lovatelli, and S. Uthicke. 2013. Sea cucumber fisheries: global analysis of stocks, management measures and drivers of overfishing. Fish and Fisheries **14**:34-59.

Radchuk, V., C. Turlure, and N. Schtickzelle. 2013. Each life stage matters: the importance of assessing the response to climate change over the complete life cycle in butterflies. Journal of Animal Ecology **82**:275-285.

Ratikainen, I. I., J. A. Gill, T. G. Gunnarsson, W. J. Sutherland, and H. Kokko. 2008. When density dependence is not instantaneous: theoretical developments and management implications. Ecology Letters **11**:184-198.

Renn, O. 1992. Risk communication: Towards a rational discourse with the public. Journal of Hazardous Materials **29**:465-519.

Renn, O. 1998. Three decades of risk research: accomplishments and new challenges. Journal of Risk Research **1**:49-71.

Renn, O. 2008a. Concepts of Risk: An Interdisciplinary Review Part 1: Disciplinary Risk Concepts. GAIA - Ecological Perspectives for Science and Society **17**:50-66.
Renn, O. 2008b. Risk governance: coping with uncertainty in a complex world. Earthscan, London UK.
Renn, O., and C. Benighaus. 2013. Perception of technological risk: insights from research and lessons for risk communication and management. Journal of Risk Research **16**:293-313.
Reum, J. C. P., S. R. Alin, R. A. Feely, J. Newton, M. Warner, and P. McElhany. 2014. Seasonal carbonate chemistry covariation with temperature, oxygen, and salinity in a fjord estuary: Implications for the design of ocean acidification experiments. PLoS ONE **9**:e89619.
Reum, J. C. P., B. E. Ferriss, P. S. McDonald, D. M. Farrell, C. J. Harvey, T. Klinger, and P. S. Levin. 2015. Evaluating community impacts of ocean acidification using qualitative network models. Marine Ecology Progress Series **536**:11-24.
Richter, B. D., D. P. Braun, M. A. Mendelson, and L. L. Master. 1997. Threats to Imperiled Freshwater Fauna. Conservation Biology **11**:1081-1093.
Ricker, W. E. 1954. Stock and Recruitment. Journal of the Fisheries Research Board of Canada **11**:559-623.
Rumrill, S. S. 1990. Natural mortality of marine invertebrate larvae. Ophelia **32**:163-198.
Salice, C. J., C. L. Rowe, J. H. K. Pechmann, and W. A. Hopkins. 2011. Multiple stressors and complex life cycles: Insights from a population-level assessment of breeding site contamination and terrestrial habitat loss in an amphibian. Environmental Toxicology and Chemistry **30**:2874-2882.
Samhouri, J. F., and P. S. Levin. 2012. Linking land-and sea-based activities to risk in coastal ecosystems. Biological Conservation **145**:118-129.
Satterfield, T., L. Robertson, N. Turner, and A. Pitts. 2011. Being Gitka'a'ata: A Baseline Report on Gitka'a'ata Way of Life, a Statement of Cultural Impacts Posed by the Northern Gateway Pipeline, and a Critique of the ENGP Assessment Regarding Cultural Impacts. Submission to the Joint Review Panel for Review of the Enbridge Northern Gateway Project, starting December.
Schindler, D. E., and R. Hilborn. 2015. Prediction, precaution, and policy under global change. Science **347**:953-954.
Schipper, A. M., H. W. M. Hendriks, M. J. Kauffman, A. J. Hendriks, and M. A. J. Huijbregts. 2013. Modelling interactions of toxicants and density dependence in wildlife populations. Journal of Applied Ecology **50**:1469-1478.
Seung, C. K., and E. C. Waters. 2006. A Review of Regional Economic Models for Fisheries Management in the U.S. Marine Resource Economics **21**:101-124.
Shaffer, G., S. M. Olsen, and J. O. P. Pedersen. 2009. Long-term ocean oxygen depletion in response to carbon dioxide emissions from fossil fuels. Nature Geosci **2**:105-109.
Shapiro, M. D. 2005. Equity and Information: Information Regulation, Environmental Justice, and Risks from Toxic Chemicals. Journal of Policy Analysis and Management **24**:373-398.
Sharma, R., A. B. Cooper, and R. Hilborn. 2005. A quantitative framework for the analysis of habitat and hatchery practices on Pacific salmon. Ecological Modelling **183**:231-250.
Shelton, A. O., J. F. Samhouri, A. C. Stier, and P. S. Levin. 2014. Assessing trade-offs to inform ecosystem-based fisheries management of forage fish. Sci. Rep. **4**.

Shelton, A. O., W. H. Satterthwaite, M. P. Beakes, S. B. Munch, S. M. Sogard, and M. Mangel. 2013. Separating Intrinsic and Environmental Contributions to Growth and Their Population Consequences. The American Naturalist **181**:799-814.
Shuter, B. J. 1990. Population-level indicators of stress. Pages 145-166 *in* American Fisheries Society Symposium.
Small-Lorenz, S. L., L. A. Culp, T. B. Ryder, T. C. Will, and P. P. Marra. 2013. A blind spot in climate change vulnerability assessments. Nature Climate Change **3**:91-93.
Smith, A. D. M., E. J. Fulton, A. J. Hobday, D. C. Smith, and P. Shoulder. 2007. Scientific tools to support the practical implementation of ecosystem-based fisheries management. Ices Journal of Marine Science **64**:633-639.
Smith, P. E. 1995. Development of the population biology of the Pacific hake, Merluccius productus. California Cooperative Oceanic Fisheries Investigations Reports **36**:144-152.
Sorte, C. J. B., S. L. Williams, and J. T. Carlton. 2010. Marine range shifts and species introductions: comparative spread rates and community impacts. Global Ecology and Biogeography **19**:303-316.
Spalding, A. K., K. Biedenweg, A. Hettinger, and M. P. Nelson. 2017. Demystifying the human dimension of ecological research. Frontiers in Ecology and the Environment **15**:119-119.
Starfield, A. M. 1997. A Pragmatic Approach to Modeling for Wildlife Management. The Journal of Wildlife Management **61**:261-270.
Starmer, C. 2000. Developments in Non-Expected Utility Theory: The Hunt for a Descriptive Theory of Choice under Risk. Journal of Economic Literature **38**:332-382.
Stobutzki, I., M. Miller, and D. Brewer. 2001. Sustainability of fishery bycatch: a process for assessing highly diverse and numerous bycatch. Environmental Conservation **28**:167-181.
Su, Y.-S., and M. Yajima. 2015. R2jags: Using R to Run 'JAGS'. R package version 0.5-7.
Sunday, J. M., R. N. Crim, C. D. Harley, and M. W. Hart. 2011. Quantifying rates of evolutionary adaptation in response to ocean acidification. PLoS ONE **6**:e22881.
Swift, T. L., and S. J. Hannon. 2010. Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. Biological Reviews **85**:35-53.
Teck, S. J., B. S. Halpern, C. V. Kappel, F. Micheli, K. A. Selkoe, C. M. Crain, R. Martone, C. Shearer, J. Arvai, B. Fischhoff, G. Murray, R. Neslo, and R. Cooke. 2010. Using expert judgment to estimate marine ecosystem vulnerability in the California Current. Ecological Applications **20**:1402-1416.
Thomsen, J., M. A. Gutowska, J. Saphörster, A. Heinemann, K. Trübenbach, J. Fietzke, C. Hiebenthal, A. Eisenhauer, A. Körtzinger, M. Wahl, and F. Melzner. 2010. Calcifying invertebrates succeed in a naturally CO2-rich coastal habitat but are threatened by high levels of future acidification. Biogeosciences **7**:3879-3891.
Thorpe, R. B., W. J. F. Le Quesne, F. Luxford, J. S. Collie, and S. Jennings. 2015. Evaluation and management implications of uncertainty in a multispecies size-structured model of population and community responses to fishing. Methods in Ecology and Evolution **6**:49-58.
Turner, B. L., R. E. Kasperson, P. A. Matson, J. J. McCarthy, R. W. Corell, L. Christensen, N. Eckley, J. X. Kasperson, A. Luers, and M. L. Martello. 2003. A framework for vulnerability analysis in sustainability science. Proceedings of the National Academy of Sciences **100**:8074-8079.

Turner, N., R. Gregory, C. Brooks, L. Failing, and T. Satterfield. 2008. From Invisibility to Transparency: Identifying the Implications. Ecology and Society **13**.

van Putten, I. E., R. J. Gorton, E. A. Fulton, and O. Thebaud. 2012. The role of behavioural flexibility in a whole of ecosystem model. ICES Journal of Marine Science **70**:150-163.

Vanclay, F. 2003. International Principles For Social Impact Assessment. Impact Assessment and Project Appraisal **21**:5-12.

Vanclay, F. 2004. The triple bottom line and impact assessment: how do TBL, EIA, SIA, SEA and EMS relate to each other? Journal of Environmental Assessment Policy and Management **6**:265-288.

Vanhoudt, N., H. Vandenhove, A. Real, C. Bradshaw, and K. Stark. 2012. A review of multiple stressor studies that include ionising radiation. Environmental Pollution **168**:177-192.

Venter, O., N. N. Brodeur, L. Nemiroff, B. Belland, I. J. Dolinsek, and J. W. A. Grant. 2006. Threats to Endangered Species in Canada. BioScience **56**:903-910.

Vorosmarty, C. J., P. B. McIntyre, M. O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S. E. Bunn, C. A. Sullivan, C. R. Liermann, and P. M. Davies. 2010. Global threats to human water security and river biodiversity. Nature **467**:555-561.

Washington State Blue Ribbon Panel on Ocean Acidification (2012): Ocean Acidification: From Knowledge to Action, Washington State's Strategic Response. H. Adelsman and L. Whitely Binder (eds). Washington Department of Ecology, Olympia, Washington. Publication no. 12-01-015.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. Trends in Ecology & Evolution **17**:76-83.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying Threats to Imperiled Species in the United States. BioScience **48**:607-615.

Wilen, J. E., M. D. Smith, D. Lockwood, and L. W. Botsford. 2002. Avoiding Surprises: Incorporating Fisherman Behavior into Management Models. Bulletin of Marine Science **70**:553-575.

Williams, A., J. Dowdney, A. D. M. Smith, A. J. Hobday, and M. Fuller. 2011. Evaluating impacts of fishing on benthic habitats: A risk assessment framework applied to Australian fisheries. Fisheries Research **112**:154-167.

Williams, R. A., and K. M. Thompson. 2004. Integrated Analysis: Combining Risk and Economic Assessments While Preserving the Separation of Powers. Risk Analysis **24**:1613-1623.

Williams, S. E., L. P. Shoo, J. L. Isaac, A. A. Hoffmann, and G. Langham. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. PLoS Biol **6**:e325.

Yasui, S. 2005. A Critical Review of the Traditional Methodology of Cost-Benefit Analysis and a Proposed Alternative. Human and Ecological Risk Assessment: An International Journal **11**:411-432.

Zhou, S., and S. P. Griffiths. 2008. Sustainability Assessment for Fishing Effects (SAFE): A new quantitative ecological risk assessment method and its application to elasmobranch bycatch in an Australian trawl fishery. Fisheries Research **91**:56-68.

Zimmerman, R. 1993. Social Equity and Environmental Risk. Risk Analysis **13**:649-666.

Zinn, J. O., and P. Taylor-Gooby. 2006. Risk as an interdisciplinary research area. Oxford University Press, New York.

Appendix A—Chapter 1

Appendix A.1: Details on mapping species distributions

Table A.1.1. Description of distributions for species life stages and associated maps.

Species	Life Stage	Assumptions	Citations
Metacarcinus magister	Eggs	The eggs of Dungeness crab are retained on female crabs and are found off the coasts of Washington and Oregon between October-March and off California between September-February. They are along the bottom.	(Reilly 1983, Pauley et al. 1986, Rasmuson 2013)
	Zoea	Dungeness crab larvae have exhibited movement far offshore, starting over the continental shelf and progressively moving out past the continental shelf before metamorphosing into megalops. As a result, larvae were mapped as close to shore for the first month in the water column and progressively moving farther out. Down to a depth of 70 m.	(Reilly 1983, Hobbs and Botsford 1992, Hobbs et al. 1992, Rasmuson 2013)
	Megalops	Megalopae have also been found off the continental shelf, but move into the nearshore environment to settle. Megalopal distributions were only mapped for the planktonic portion of their life since once they move inshore to settle, they tend to go into estuaries – regions for which we do not have any oceanographic estimates. Their distributions match that of Zoea in the last month of where zoea are found before metamorphosing also at 70 m.	(Reilly 1983, Rasmuson 2013)
	Juveniles i and ii	Research has shown that newly settled juvenile crabs tend to settle in estuaries, however given the relatively few estuaries along the outer coast of the California Current Rasmuson (2013) note that they settle where adults are found.	Rasmuson (2013)
	Adults	Dungeness crab adults are predominantly found between 30-90 m depth; they are only occasionally found in the surfzone. Thus the distribution of adult Dungeness crab has been assumed to be between 30-90 m depth, from the outer coast of Washington to Santa Barbra California. Along the bottom.	Rasmuson (2013)
Pandalus jordani	Eggs	Females retain their eggs and ovigerous females are found off Oregon and Washington in October-March, off Northern California in October-April	(Dahlstrom 1970, 1973)

		and Southern California November-June. Eggs are assumed to be where adults are found along the bottom of the ocean. Found along the bottom.	
	Larvae	The distribution of pink shrimp larvae has been minimally investigated, with most of the research conducted in the 1970s. The estimated distribution of pink shrimp larvae therefore depend on a number of assumptions. Larvae are found within 55 km of shore for the first month present in the water column, and then out to 110 km as they disperse via advection and diffusion. Therefore larval shrimp distribution covers a large area from 2 km offshore out to 110 km from during most months of the year when they are present. Pink shrimp larvae have been found between the neuston and 150 m depth, with the majority above 100 m, thus the depth of 100 m was used in this analysis.	(Rothlisberg and Pearcy 1976, Rothlisberg and Miller 1983)
	Adults and Juveniles	The highest concentration of shrimp adults and juveniles are found between 80-230 m bathymetries, along the bottom of the ocean.	(Hannah 2011)
Merluccius productus	Eggs	The distribution of pacific hake eggs comes from CalCOFI surveys (1984-2012). CalCOFI data were only used for years when greater than 500 samples were collected, and we disregarded tows with fewer than 5 individual hake egg or larvae. Survey data is available for all months except December and thus the distribution of eggs during December was assumed to be the same as January (sensitivity to using January vs. November was tested and had no impact). A convex hull was created in ArcGIS around the presence points. Eggs were assumed to be found down to 150 m	(Moser et al. 1997, CalCOFI 2012)
	Larvae	Maps of hake larvae were developed using the same methods as for hake eggs. Larvae were assumed to be found down to 100 m	(Cass‐Calay 2003, CalCOFI 2012)
Euphausia pacifica	Eggs	Spawning for *E. pacifica* occurs March-October, but most heavily in July and August. Due to the more rapid development time of eggs spawned earlier in the season, there are two sets of durations – March-May eggs for the early spawners, and June-October eggs for late spawners. Eggs are also thought to be found onshore, where adults are offshore – thus were mapped from the coast to the 300 bathymetry line.	(Brinton 1976, Feinberg and Peterson 2003, Feinberg et al. 2010, Harvey et al. 2010, Feinberg et al. 2013) Keister pers. comm.

	Larvae	Larvae have the same spatial distribution as eggs, and a duration of 2 months, thus are found March-June for early spawners and June-November for the late spawners	(Lu et al. 2003c, Bi et al. 2011) Peterson pers. comm.
	Juveniles	Juveniles are assumed to have the same distribution as adults which is off the shelf. They are assumed to occur from the 200 m isobaths outwards off the shelf, and down to a depth of 300 m. Early spawned juveniles are present May through August and late spawned juveniles are present August through the following April.	(Lu et al. 2003c, Vance et al. 2003) Peterson and Keister pers. comm.
	Sub-adults	Sub-adults have the same distribution as adults, as they are essentially adults, just slightly smaller and less fecund. The early spawned sub-adults are found July through November and late spawned sub-adults are January through the following July.	(Lu et al. 2003a, Vance et al. 2003) Peterson and Keister pers. comm.
	Adults	Adults are found offshore of the shelf-break during all months of the year at a depth of 300 m.	(Lu et al. 2003a, Vance et al. 2003) Peterson and Keister pers. comm.
Thysanoessa spinifera	Eggs	Thysanoessa is thought to be an on-shelf species. Thus all stages of this species are inwards of the 200 m isobath. Spawning occurs February to September.	(Feinberg and Peterson 2003, Lu et al. 2003c, Feinberg et al. 2010)
	Larvae	Larvae are then present February through October developing from eggs (also on shelf)	
	Juveniles	Juveniles and adults are both found all months of the year	
	Adults	Juveniles and adults are both found all months of the year	
Limacina helicina	Eggs/Larv	There is evidence for continuous spawning through the year (Wang 2014) however, Wang found there to be much stronger spawning in the spring through fall with little to none in the winter. From this we assume eggs and larvae are present March-September which is the dominant period of spawning. Depth of 100 m used for all stages from Bednarsek et al. (2014)	(Bednaršek et al. 2014, Wang 2014) Pers. comm. Bednarsek
	Juveniles	Juvenile duration is thought to be approximately three months, thus they are present in the water column after larvae have developed (estimated as 2 months) and are found May-November.	Pers. comm. Bednarsek
	Sub-adults	Sub-adults are also estimated to have a three month duration and are	Pers. comm. Bednarsek

		assumed to be found in the water column July-February	
	Adults	Adults are found year round and with the same spatial distributions of the other life stages	(Wang 2014) Pers. comm. Bednarsek

Appendix A.1 Figures

Dungeness crab, *Metacarcinus magister*, maps

Fig A.1.1. Adult Dungeness crab distributions, January-December

Fig A.1.2. Dungeness crab egg distribution, September.

Fig A.1.3. Dungeness crab egg distribution, October to February.

Fig A.1.4. Dungeness crab egg distribution, March.

Fig A.1.5. Dungeness crab larval distribution, December.

Fig A.1.6. Dungeness crab larval distribution, January.

Fig A.1.7. Dungeness crab larval distribution, February.

Fig A.1.8. Dungeness crab larval distribution, March.

Fig A.1.9. Dungeness crab larval distribution, April through June.

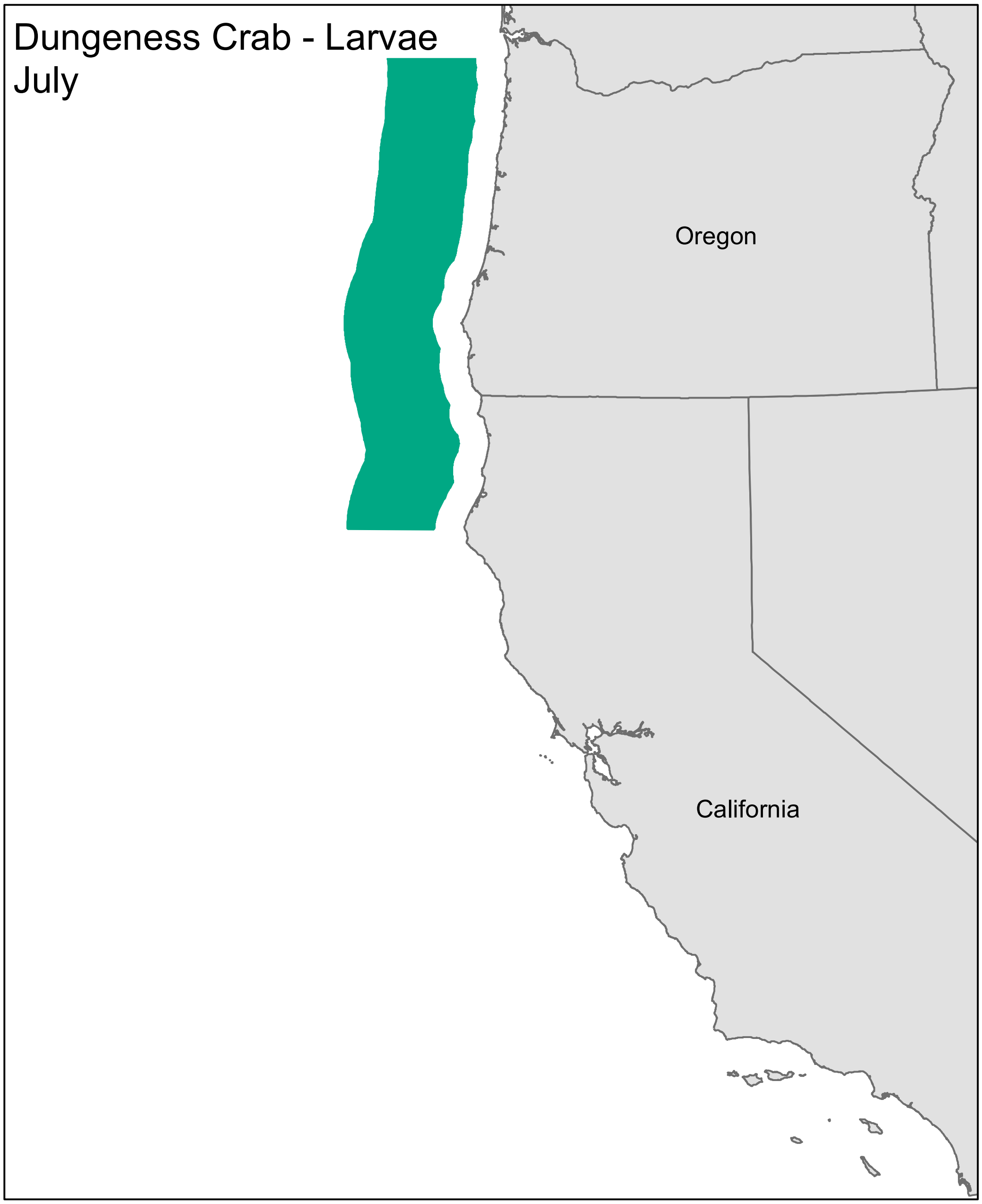

Fig A.1.10. Dungeness crab larval distribution, July.

Fig A.1.11. Dungeness crab megalopae, March.

Fig A.1.12. Dungeness crab megalopae, April through June.

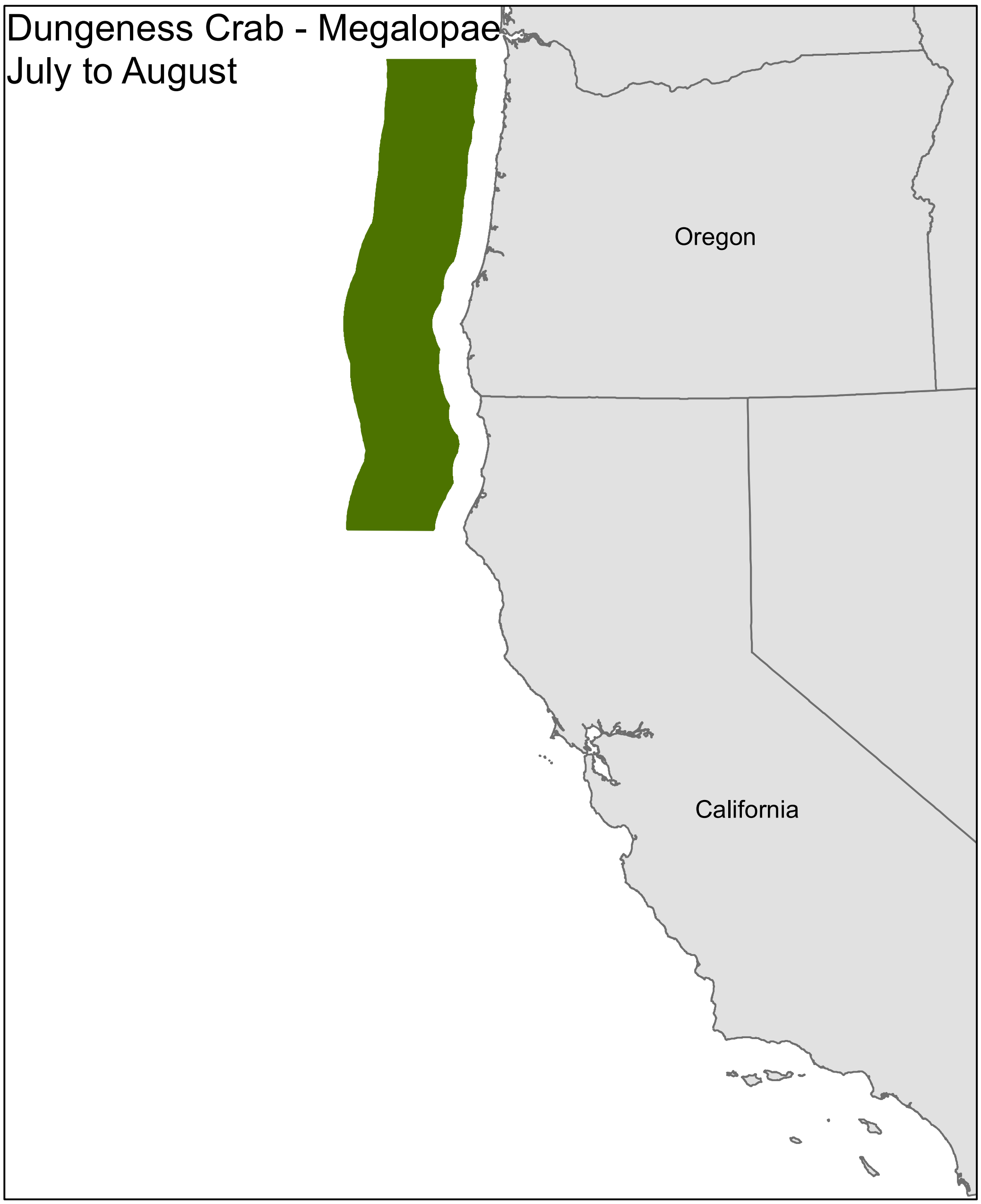

Fig A.1.13. Dungeness crab larvae, July and August.

Pink shrimp, *Pandalus jordani*, maps

Fig A.1.14. Pink shrimp adult distribution, all months.

Fig A.1.15. Pink shrimp egg distribution, October.

Fig A.1.16. Pink shrimp egg distribution, November through March.

Fig A.1.17. Pink shrimp egg distribution, April.

Fig A.1.18. Pink shrimp egg distribution, May and June.

Fig A.1.19. Pink shrimp larval distribution, March

Fig A.1.20. Pink shrimp larval distribution April through July.

Pacific hake, *Merluccius productus,* maps

Fig A.1.21. Pacific hake egg distribution, October.

Fig A.1.22. Pacific hake egg distribution, November

Fig A.1.23. Pacific hake egg distribution, January. This map was used to represent December as well as there was not enough to map their distribution then. No difference in overall exposure found when November or January were used for December.

Fig A.1.24. Pacific hake egg distribution, February.

Fig A.1.25. Pacific hake egg distribution, March.

Fig A.1.26. Pacific hake egg distribution, April.

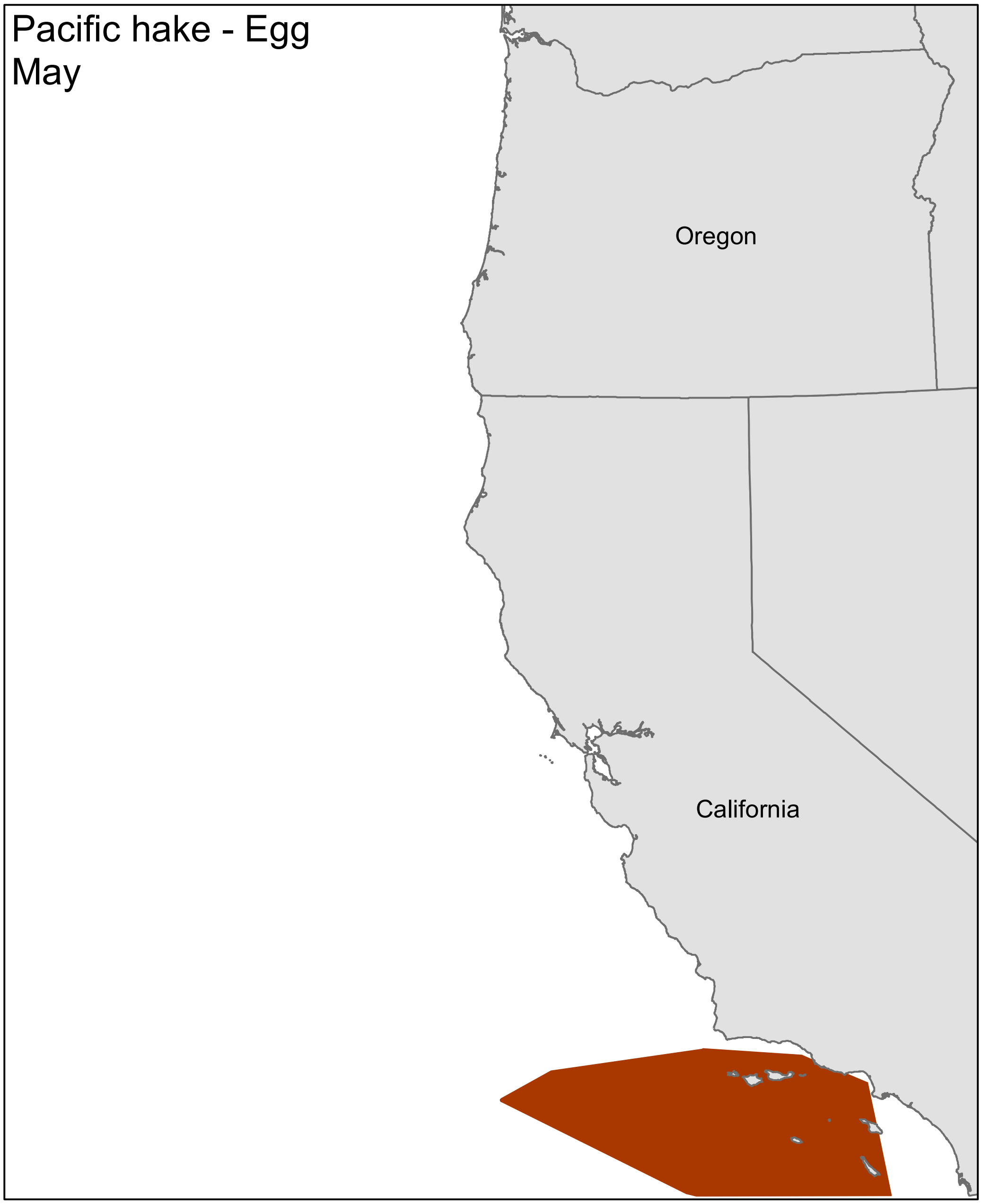

Fig A.1.27. Pacific hake egg distribution, May.

Fig A.1.28. Pacific hake larval distribution, October.

Fig A.1.29. Pacific hake larval distribution, November.

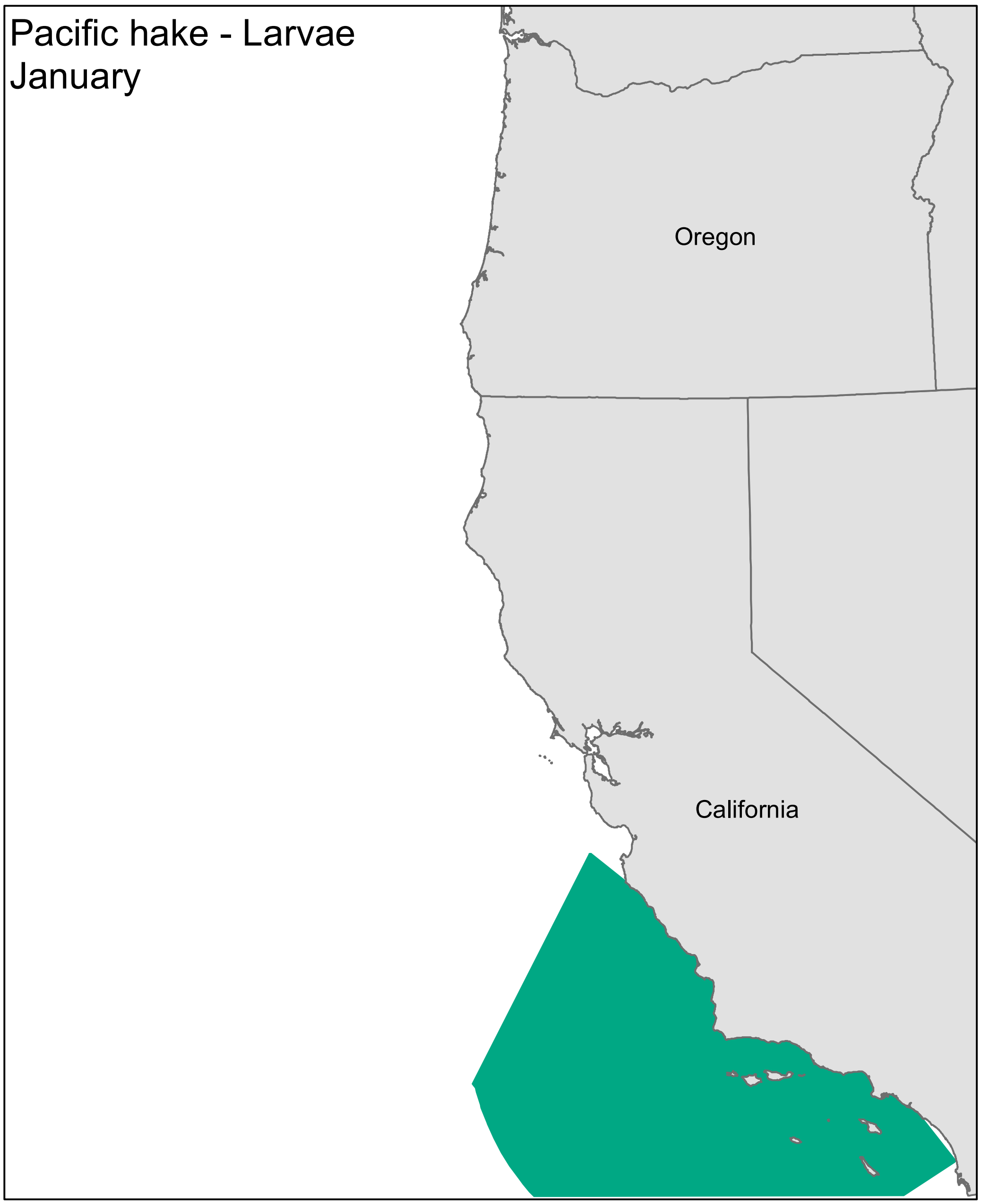

Fig A.1.30. Pacific hake larval distribution, January. This map was used to represent their distribution in December as well.

Fig A.1.31. Pacific hake larval distribution, February.

Fig A.1.32. Pacific hake larval distribution, March.

Fig A.1.33. Pacific hake larval distribution, April. This distribution goes very far north – which may only occur during some years, however truncating the distribution had no effect on exposure calculated.

Fig A.1.34. Pacific hake larval distribution, May.

Krill, *Euphausia pacifica*, maps

Fig A.1.35. Krill *E. pacifica* adult, sub-adult and juvenile distribution – all months of the year.

Fig A.1.36. Krill *E. pacifica* egg and larval distribution (on shelf) months they are present.

Krill, *Thysanoessa spinifera*, maps

Fig A.1.37. Krill *T. spinifera* distribution of all stages during months they are present (on shelf).

Pteropod, *Limacina helicina*, maps

Fig A.1.38. Pteropod *L. helicina* distribution of all stages, during months they are present.

Appendix A.2: Sensitivity of exposure estimates to form of pH exposure function

We tested the sensitivity of our conclusions to the shape of the pH exposure function in the process of translating exposure to particular pH values into a single exposure estimate. We considered two main approaches that bracket the range of possible effects. The first example assumed a sigmoidal relationship between consequence and pH. The second example assumed that adverse effects are minimal until pH drops below a threshold value, below which effects increase to some maximum level. This latter method was ultimately reported in the paper, but here we document the results for the sigmoidal relationship as well. In addition to these functional forms, we also considered alternative placement of these curves along the pH axis. For sigmoidal relationships, we adjusted the pH at which the exposure curve was one-half its maximum value; while for threshold relationships we simply adjusted the pH of the threshold (called the *critical* pH henceforth in the Appendix).

We explored three relationships between pH and relative consequence, and three critical pH values. The three functional forms (Fig B1 A and B) include: (1) *threshold*, (2) *sigmoid50%* for which the pH level that has no effect exceeds the critical pH by 50% (3) *sigmoid100%*; pH level that has no effect exceeds the critical pH by 100%. Note that since pH is in log space, to increasing pH by 50% simply involves adding 0.176 to the critical pH and to increasing by 100% involves adding 0.301.The three critical pH values used were 7.6, 7.65 and 7.7 (Fig B1).

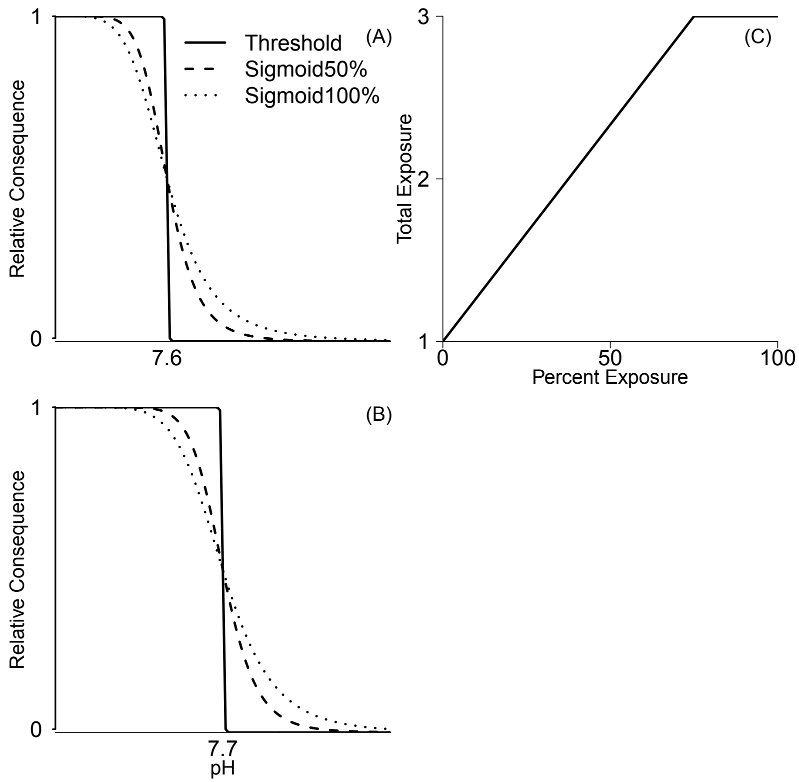

Fig A.2.1. Determining exposure from pH values experienced. Showing the relationship between pH and relative consequence for three functional forms (A) and (B), at a critical pH of 7.6 (A) and 7.7 (B), and conversion between percent exposure and final total exposure estimate (C).

<u>Results from this sensitivity test:</u>

Exposure estimates were sensitive to the exposure function, producing a wide range of exposure estimates for each species' life history stage (Table B1). The critical pH had a larger effect on exposure estimates than the form of the exposure function (Fig B2 A and B). For example, changing critical pH from 7.6 to 7.65 increased the median exposure from 1.74 to 2.70 while changing the critical pH to 7.7 led to a median exposure of 3.00 across all species and life stages (Fig B2 A). In other words, if the critical pH was high, then there was widespread exposure, regardless of the shape of the exposure function. In contrast, the median estimated exposure was nearly identical across functional forms (*sigmoid100* 2.29, *sigmoid50* 2.29, *threshold* 2.39) (Fig B2 B). We did however find some sensitivity to the shape of the exposure function at the lowest critical pH (Fig B2 C). This sensitivity arose because the threshold model predicts little to no exposure for many species at critical pH 7.6. However, at that pH the sigmoid curves allow for partial exposure from pH values that are slightly above the critical. For example, very little of the distribution of eggs and larvae for *L. helicina* will experience pH at or below the critical 7.6 (Fig B3) so the threshold model predicts low exposure (1.04). Conversely, substantial portions of the distribution are predicted to experience pH slightly above the critical (Fig B3) and under the sigmoid models these get partial exposure scores (1.48 and 1.68 for sig50 and sig100 respectively, Table B1).

This provided a forum to test the sensitivity of our conclusions to the form of the relationship. We found that the shape of the curve (sigmoidal versus threshold) had much less of an influence on estimates of exposure than did the value of the critical pH and thus only presented results for the threshold relationship. Other stressors might not exhibit the same lack of sensitivity to functional form, and including variation in the shape of the curve in addition to the critical would only add a source of uncertainty.

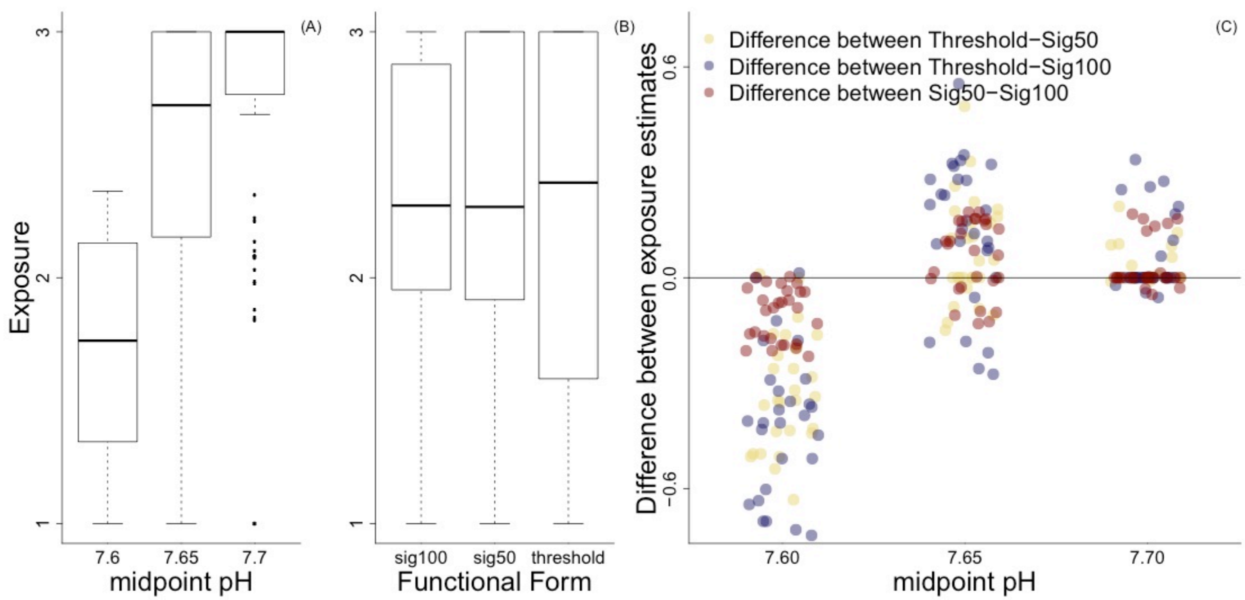

Fig A.2.2. Comparison of exposure estimates when using different mid-point pH values. Comparison is across all species and life stages (A), different forms of the functional relationship (B) and a plot of the differences in exposure estimates when comparing pairs of the three methods used (C).

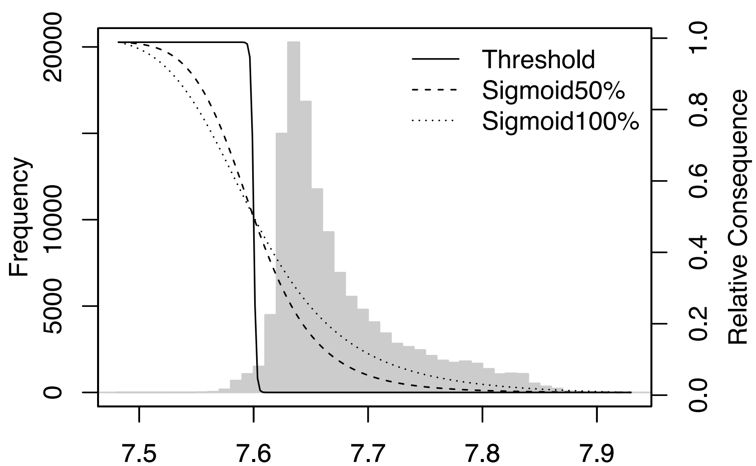

Fig A.2.3. Histogram of pH values experienced by *L. helicina* larvae/eggs. Different functional forms of the relationship between pH and relative consequence are plotted on top assuming critical pH 7.6.

Table A.2.1. Exposure estimates using all model functional forms and midpoints.

Species	Life Stage	Thresh mid 7.6	Thresh mid 7.65	Thresh mid 7.7	Sig50 mid 7.6	Sig50 mid 7.65	Sig50 mid 7.7	Sig100 mid 7.6	Sig100 mid 7.65	Sig100 mid 7.7
Metacarcinus magister	Eggs	1.67	3.00	3.00	2.11	2.95	3.00	2.18	2.76	3.00
	Larvae	1.03	1.43	2.09	1.23	1.58	2.08	1.39	1.70	2.11
	Megalops	1.00	1.39	1.98	1.19	1.51	1.98	1.35	1.65	2.03
	Juvenile i	1.49	3.00	3.00	2.00	2.81	3.00	2.09	2.65	3.00
	Juvenile ii	1.49	3.00	3.00	2.00	2.81	3.00	2.09	2.65	3.00

	Adult	1.49	3.00	3.00	2.00	2.81	3.00	2.09	2.65	3.00
Pendalus jordani	Eggs	1.90	3.00	3.00	2.22	3.00	3.00	2.26	2.84	3.00
	Larvae	1.04	2.61	3.00	1.55	2.28	3.00	1.76	2.28	2.82
	Juveniles	1.89	3.00	3.00	2.17	2.95	3.00	2.21	2.77	3.00
	Adult	1.89	3.00	3.00	2.17	2.95	3.00	2.21	2.77	3.00
Limacina helicina	Eggs & larvae	1.04	2.24	3.00	1.48	2.12	2.80	1.68	2.15	2.66
	Juvenile	1.03	2.42	3.00	1.53	2.21	2.87	1.72	2.21	2.73
	Subadult	1.04	2.56	3.00	1.58	2.30	2.97	1.77	2.28	2.80
	Adult	1.04	2.42	3.00	1.54	2.23	2.90	1.74	2.23	2.75
Merluccius productus	Eggs	1.01	3.00	3.00	1.64	2.51	3.00	1.86	2.45	3.00
	Larvae	1.06	2.15	3.00	1.50	2.18	2.91	1.71	2.21	2.74
	Adult	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Euphausia pacifica Early spawners	Eggs	1.67	3.00	3.00	2.03	2.85	3.00	2.11	2.68	3.00
	Larvae	1.02	1.37	1.83	1.18	1.46	1.84	1.31	1.55	1.87
	Juveniles	1.99	3.00	3.00	2.25	3.00	3.00	2.28	2.87	3.00
	Sub-adults	2.35	3.00	3.00	2.34	3.00	3.00	2.34	2.92	3.00
	Adult	2.13	3.00	3.00	2.29	3.00	3.00	2.30	2.90	3.00
Euphausia pacifica Late spawners	Eggs	1.59	3.00	3.00	2.02	2.85	3.00	2.11	2.68	3.00
	Larvae	1.02	1.59	2.34	1.28	1.69	2.24	1.45	1.80	2.23
	Juveniles	2.19	3.00	3.00	2.30	3.00	3.00	2.31	2.90	3.00
	Sub-Adults	1.87	3.00	3.00	2.23	3.00	3.00	2.26	2.86	3.00
	Adults	2.13	3.00	3.00	2.29	3.00	3.00	2.30	2.90	3.00
Thysanoessa spinifera	Larvae	1.71	3.00	3.00	2.05	2.83	3.00	2.12	2.67	3.00
	Juveniles	1.02	1.52	2.15	1.25	1.61	2.09	1.40	1.70	2.09
	Adult	1.74	3.00	3.00	2.09	2.89	3.00	2.16	2.72	3.00

Appendix A.3: Life stage consequences

Table A.3.1. Consequence rankings and citations. Provided for each species' life history stage used in the assessment.

Species	Life Stage	Consequence	Citations	Justification	Consequence Uncertainty
Metacarcinus magister	Eggs	*1*	(Miller 2015)	There are no papers directly on the eggs of this species, Miller did some preliminary experiments and found no impact on survival, however experiments were not standardized. Experiments on other crab species have found no impact on growth but longer time to hatching (Long et al. 2013)	3
	Larvae	*3*	(Christmas 2013, Descoteaux 2014, Miller 2015)	Descoteaux found a small impact on survival in their low pH 7.4-7.6 experiment and possibly at intermediate pH ~7.75 Christmas also found in a five day experiment – no impact on feeding rate or survival but changes in movement patterns – low pH at 7.5. Miller 2015 found a 2.5-3 fold decline in survival of larvae in waters with pH 7.5 and 7.1	2
	Megalops	*3*	Miller unpublished results, conclusions from larvae	Miller also did some preliminary experiments on megalops and found an impact on survival, but with no published literature, we gave them the same response to OA as larvae, but with higher uncertainty.	3
	Juvenile i	*3*	Miller unpublished results	In Miller's preliminary experiment, juveniles from the first instar onwards appeared to show some coping capacity, but this is highly uncertain.	3
	Juvenile ii	*1*	NA	Juveniles have a second phase after survival through the first year and since this stage is	3

				getting more similar to adults, we assumed their sensitivity to OA to be more similar to adults – but again high uncertainty	
	Adult	*1*	(Pane and Barry 2007, Hans et al. 2014)	Adult crabs show clear ability to buffer in hypercapnia situations, as do other crab species	1
Pendalus jordani	Eggs	*1*	(Arnberg et al. 2012)	No impact on hatching success after two weeks in pH 7.6 for *P. borealis*	2
	Larvae	*2*	(Bechmann et al. 2011, Arnberg et al. 2012)	Both the cited papers on *P. borealis* found no impact on mortality but an increase in development and pers. comm. with both primary authors suggest a rating of 2 for consequence, a pH=7.6 was used.	2
	Juvenile	*1*	NA	The sensitivity of shrimp juveniles was assumed to be equivalent to that of adults, but ranked as highly uncertain	3
	Adult	*1*	(Hammer 2012)	Hammer found *P. borealis* to be able to buffer low pH waters, pH=6.86 was used, and an ability to tolerate such low levels demonstrates clear tolerance	2
Limacina helicina	Eggs & larvae	*3*	(Bednaršek et al. 2012)	There are no papers on the eggs and larvae of *L. helicina* so we assumed their sensitivity level to be the same as later life stages of the same species – recognizing that we do not have as high confidence in this conclusion. Pers. comm. Nina Bednarsek	2
	Juvenile	*3*	(Bednaršek et al. 2012, Bednaršek et al. 2014)	Juveniles are the most studied with clear dissolution of shells when in undersaturated waters. Undersaturation in the system occurd at pH=7.7 in Bednarsek 2012	1
	Subadult	*3*	(Bednaršek et al. 2012, Bednaršek et al. 2014)	Subadults were also collected in the California Current analysis and found to have strong shell dissolution in undersaturated	1

				waters.	
	Adult	*2*	(Bednaršek et al. 2012, Bednaršek et al. 2014, Busch et al. 2014)	Busch et al. (2014) found shell dissolution in adult pteropods in undersaturated conditions, but only a severe impact on mortality in waters highly unsaturated, demonstrating some tolerance in a 5-week period to undersaturation. As well, from conversations with Nina Bednarsek, adults may be sensitive like earlier stages, but have a thicker external organic layer with slight resistance to OA.	2
Merluccius productus	Eggs	*1*	(Munday et al. 2009, Bignami et al. 2013, Frommel et al. 2013, Frommel et al. 2014)	Numerous papers have been published on different teleost fish species, none of which are on the same genus as hake. Some are cited here, and conclusions were made through literature review and recommendations from experts (pers. comm. Phil Munday and Sean Bigmani) Most have found no impact on fish eggs.	3
	Larvae	*2*	(Munday et al. 2009, Bignami et al. 2013, Frommel et al. 2013, Frommel et al. 2014)	Fish larvae tend to show more variable responses, with some having no effect, some showing increase in otolith size and some with clear impacts on larval growth and organ development.	3
	Adult	*1*	(Bromhead et al. , Melzner et al. 2009, Kroeker et al. 2010)	Although adult coral reef fish have shown some behavioral responses to OA, we assume no real impact on Pacific hake adults. Example paper nothing this: Bromhead et al. (2014)	1
Euphausia pacifica Early and late spawners	Eggs	*1*	[Cite McLasky paper once it is out – shortly], (Kawaguchi et al. 2011, Kawaguchi et al. 2013)	Kawaguchi did not find any impact on hatching success for *E. superba*. McLaskey preliminary results also found no change in hatching success of eggs	2
	Larvae	*2*	[Cite McLasky paper once	McLaskey found a delay in development	2

			it is out – shortly]	time, but no clear impact on survival, thus a value of 2.	
	Juveniles	*2*	(Saba et al. 2012)	Assumed to be same as adults	3
	Sub-adults	*2*	(Saba et al. 2012)	Assumed to be same as adults	3
	Adult	*2*	(Saba et al. 2012)	This paper was on *E. superba* and the authors found that there was an increase of both ingestion and metabolism suggesting that there could be a negative consequence because of increasing energy requirements	3
Thysanoessa spinifera	Eggs	*1*	[Cite McLasky paper once it is out – shortly], (Kawaguchi et al. 2011, Kawaguchi et al. 2013)	All *T. spinifera* consequences were assumed to match *E. pacifica*	3
	Larvae	*2*	[Cite McLasky paper once it is out – shortly]	All *T. spinifera* consequences were assumed to match *E. pacifica*	3
	Sub-adults	*2*	NA	All *T. spinifera* consequences were assumed to match *E. pacifica*	3
	Adult	*2*	(Saba et al. 2012)	All *T. spinifera* consequences were assumed to match *E. pacifica*	3

Appendix A.4: Life history model parameters and details

***Dungeness crab,* Metacarcinus magister**

The model developed for Dungeness crab includes four life history stages: eggs, larvae, juveniles and adults. Other models of Dungeness crab model the population of males and females separately (McKelvey et al. 1980), however, to maintain a simple approach, this model includes both males and females grouped together. Life stage parameters were obtained from the literature and are listed with their sources in Table 1.

Table A.4.1. Parameter values for four Dungeness crab life history stages, and their sources. Note that survival values are rounded to 4 decimal places although more were used in the code.

Parameter	Values (daily)	Source	Notes (this column may be cut for publication)
e_{sc} = egg survival	0.9999 day^{-1}	(Shirley et al. 1987)	The authors found 98% survival over their 160-day experiment. Egg survival is likely high due to female retention of eggs.
e_{dc} = egg duration	122 days	(Shirley et al. 1987, Rasmuson 2013)	Eggs are found on females for ~4 months per of the year (Rasmuson 2013, Table 3.1). Eggs survived hatched after 42-160 days (Shirley et al. 1987).
l_{sc} = larval survival	0.9361 day^{-1}	(Hobbs et al. 1992)	Hobbs et al. (1992) found ~13% survival over one month through field estimates. Lab based estimates have also be found (Reed 1969). Others have used a combination of the two (Moloney et al. 1994), however, the field estimate was used here as lab estimates do not account for predation (Rumrill 1990), and many species predate on crab larvae.
l_{dc} = larval duration	122 days	(Rasmuson 2013)	Crab larvae are present in the water column for a range of 105-215 days off California and 89-143 off OR and WA (Rasmuson 2013). An assumed value of ~120 days was used for this analysis.

$j1_{sc}$ = juvenile 1 survival	0.9931 day^{-1}	(Stevens and Armstrong 1984, Wainwright et al. 1992)	There are two papers with estimates of juvenile survival which are highly different – Wainwright et al. (1992) estimates 8.1% survival per year, by regressing the logarithm of population abundance on age. From this method they found 5 estimates of annual survival were found with an average of 8.1%. Alternatively Stevens and Armstrong (1984) write that since mortality rates are unknown, they use an assumed range of 0.5-0.8. Since the latter uses an assumed survival rate, the estimate from Wainwright et al. (1992) was used. There is support fort this survival rate, and now this stage represents early settled megalopae and early juveniles, until they reach the next summer and are 1+ age
$j1_{dc}$	365 days	(P. Sean MacDonald pers. comm.)	This stage is present for the first year – from recommendations by P Sean McDonald.
$j2_{sc}$ = juvenile survival	0.9955 day^{-1}	(Wainwright et al. 1992, Armstrong et al. 2003)	Armstrong et al. (2003) write that the Wainwright paper reported survival from 1+ to 2+ as 19.5%
$j2_{dc}$ = juvenile duration	365 days	(Rasmuson 2013)	Fig 3.2 – they have lived for 1 year in the J1 stage and so now they are second year juveniles and last for another year before recruiting QUESTION: does this last 12 months or 24???
a_{sc} = adult survival	0.9991 day^{-1}	(Higgins 1997, Higgins et al. 1997)	Higgens et al. (1997) report estimates of adult survival Table 1 that average to a value of 0.725. Some authors have suggested that males and females may have different

			survival rates (McKelvey et al. 1980) however the specific values are not known.
f_{ac} = adult fecundity	2739.73 day^{-1}	(McKelvey et al. 1980, Rasmuson 2013)	Females produce between 1.5-2.5 million eggs, thus the value of ~2 million was used, and divided by 12 to get a per month estimate, then by 2 to determine the number per female in the population (since it is a male and female model). Fecundity is not correlated to egg carapace width (Rasmuson 2013, citing: (Wickham 1979a, Wickham 1979c, Hankin et al. 1989))

Transition and Elasticity Matrices

Using values in Table A.4.1. The final transition matrix is:

	Eggs	Larvae	Juvenile1	Juvenile2	Adults
Eggs	0.99	0	0	0	2739.73
Larvae	0.01	0.94	0	0	0
Juvenile1	0	0	0.99	0.00	0
Juvenile2	0	0	0	0.99	0
Adults	0	0	0	0	1.00

In order to ensure a null growth rate, $\lambda = 1$, all values in the transition matrix were multiplied by the multiplier 0.996786.

The output was the following elasticity matrix:

	Eggs	Larvae	Juvenile1	Juvenile2	Adults
Eggs	0.1556	0	0	0	0.0018
Larvae	0.0018	0.0251	0	0	0
Juvenile1	0	0.0018	0.1673	0	0

Juvenile2	0	0	0.0018	0.2042	0
Adults	0	0	0	0.0018	0.4387
Sums	**0.1574**	**0.0269**	**0.1691**	**0.2060**	**0.4405**

***Pink shrimp,* Pandalus jordani**

The life stage model for *Pandalus jordani*, pink shrimp, consists of four life history stages: eggs, larvae, juveniles, and adults. Males and females are both modeled in the same pool of individuals. The final life stage of adults currently lumps all reproductively mature individuals into one stage. This stage however, could be subdivided into two – of adult 1 and adult 2 – which would represent the fact that adult shrimp differ in size, and the larger shrimp are more fecund. Life stage parameters were obtained from the literature and are listed in Table 1.

Table A.4.2. Life history parameters and sources for *Pandalus jordani*. Stages include eggs, larvae, juveniles and adults. Parameters include survival rates and duration times.

Parameter	Value	Source	Notes
e_{sp} = egg survival	0.9949043 day^{-1}	(Brillon et al. 2005)	This paper reports that eggs can be lost from females due to cannibalism by neighbouring shrimp, of being knocked off during scavenging (in Icelandic waters). As a result, egg mortality might be 'high' for this species.
e_{dp} = egg duration	152 days	(Modin and Cox 1967)	These authors just write that the species takes ~5 months for eggs to develop
l_{sp} = larval survival	0.9629563 day^{-1}	(Rothlisberg 1975)	Field based estimate was from sampling at different times and observing that ~1% or less made it to stage VII in each of the two years sampled (p.104 and Fig 28). This would give daily mortality of 0.01^(1/duration of larvae) = 0.9629563
l_{dp} = larval duration	122 days	(Rothlisberg 1975)	Fig 22 in this paper shows trends of larval stage over time, based on different temperatures. Larvae seem to reach their final stage after between 90-120 days, which I think is why they seem to write ~100 days later on. (Table XI has actual values for time and it is 96 or 111 days for temp 14 and 11 C respectively)
j_{sp} = juvenile survival	0.9958988 day^{-1}	(Rothlisberg 1975)	Rothlisberg (1975) uses the value 1.5, and so do Rothlisberg and Miller (1983). This translates to 0.223 total – and seems to represent 1.5 years, giving 0.223^(1/537) for daily survival. And so monthly survival = $(1.5^{(1/537)})^{30}$ = 0.92102

j_{dp} = juvenile duration	457 days	(Rothlisberg 1975)	Rothlisberg (1975) writes that there are ~18 months between hatching and commercial recruitment (hence 18-larvalduration). However, Hannah writes that the juveniles recruit to the fishery after a few months of the season starting, so juveniles would be around ~12 months
a_{sp} = adult survival	Winter mortality =0.9970535 day^{-1} Summer mortality = 0.9980347 day^{-1} Weighted survival = 0.9975717 day^{-1} (assuming summer is 5 months and winter 7)	(Hannah 1995, Gallagher et al. 2004)	Gallagher et al. (2004) believe there is a difference in summer and winter mortalities due to differing levels of predation. Winter mortality is for Nov-March and summer is April-October, when Pacific whiting are migrating north and consume pink shrimp. Hannah (1995) found range in monthly natural mortalities of 0.03-0.17. RANGES in mortality rates used by Gallagher were Mw 0.03-0.10 and Ms = 0.04-0.12 (using the SD from Hannah's results)
f_{ap} = adult fecundity	3.425 eggs day^{-1}	(Hannah 1995)	The number of eggs seems to depend on the size of the shrimp (Hannah 1995). Smaller individuals produce ~2000 eggs and larger ones produce ~3000 eggs. This is why I am trying to decide between a model with one adult stage, that produces ~2500 eggs or two that produce 2000 and 3000 eggs respectively. The number of eggs is divided by 12 to get monthly rates and then by 2 to get female-only egg production. With one adult stage – lambda will be larger, because the first year they will produce 2500 and the number that survive to the next year will make the same amount, but in that first year they will have contributed 2500 and not 2000

Transition and Elasticity Matrices:

Using values in Table A.4.2 the final transition matrix is:

	Eggs	Larvae	Juvenile	Adults

Eggs	0.9906	0	0	3.4247
Larvae	0.0043	0.9626	0	0
Juvenile	0	0.0004	0.9952	0
Adults	0	0	0.0007	0.9976

In order to ensure a null growth rate, $\lambda = 1$, all values in the transition matrix were multiplied by the multiplier 1.000011.

The output was the following elasticity matrix:

	Eggs	Larvae	Juvenile	Adults
Eggs	0.1395	0	0	0.0013
Larvae	0.0013	0.0342	0	0
Juvenile	0	0.0013	0.2734	0
Adults	0	0	0.0013	0.5477
Sums	**0.1408**	**0.0355**	**0.2747**	**0.5490**

***Pacific Hake,* Merluccius productus**

This model is female only, as the model is taken from Smith (1995) and provides numbers of surviving female embryos produced per individual per day. The Lefkovitch matrix that is provided by Smith (1995) includes two larval stages and four juvenile stages. In order to finish our model with only one elasticity for each life stage (eggs, larvae, juveniles, pre-recruits and adults) we combined the estimates for larval and juvenile stages into 1, through waiting survivals by duration of each sub-stage. This model is also on a daily time step since that is what Smith (1995) used and as a result all survival rates are shown in daily rates.

Table A.4.3. Pacific hake model parameter values. Note that for all of this is Smith (1995) Table 4, there is also some information in Hollowed (1992) but Smith was the main source used.

Parameter	Value	Citation
e_{sh} = egg survival	0.865 day^{-1}	(Hollowed 1992)
e_{dh} = egg duration	16 days	(Smith 1995)
l_{sh} = larval survival	0.9325446 day^{-1}	(Smith 1995)
l_{dh} = larval duration	112 days	(Smith 1995)
j_{sh} = juvenile survival	0.9955708 day^{-1}	(Smith 1995)
j_{dh} = juvenile duration	602 days	(Smith 1995)
pr_{sh} = pre-recruit survival	0.999452 day^{-1}	(Smith 1995)
pr_{dh} = pre-recruit duration	730 days	(Smith 1995)
a_{sh} = adult survival	0.999452 day^{-1}	(Smith 1995)
f_{prh} = pre-recruit fecundity	10.5 surviving female embryos/female/d (Smith gives it as sfe/f/d)	(Smith 1995)
f_{ah} = adult fecundity	199.2 sfe/female/d	(Smith 1995)

Transition and Elasticity Matrices:

The transition matrix using parameter values from Table A.4.3 is:

	Eggs	Larvae	Juvenile	Pre-recruit	Adults
Eggs	0.8503	0	0	10.5000	199.2000
Larvae	0.0147	0.9325	0	0	0
Juvenile	0	0	0.9952	0	0
Pre-recruit	0	0	0.0003	0.9983	0
Adults	0	0	0	0.0011	0.9995

In order to ensure a null growth rate, $\lambda = 1$, all values in the transition matrix were multiplied by the multiplier 1.000133.

Elasticity matrix:

	Eggs	Larvae	Juvenile	Pre-recruit	Adults
Eggs	0.0017	0	0	0	0.0003
Larvae	0.0003	0.0043	0	0	0
Juvenile	0	0.0003	0.0661	0	0
Pre-recruit	0	0	0.0003	0.2007	0
Adults	0	0	0	0.0003	0.7256
SUMS	0.0021	0.0046	0.0665	0.2010	0.7259

Krill,* Euphausia pacifica*—Model Methods and Parameters

The model for *Euphausia pacifica* is a stage structured model that includes eggs, larvae, juveniles, pre-recruits and adults. Detailed durations and survivals are available for the larval stages of nauplius, calyptopes and furcilia (Rumsey and Franks 1999, Bi et al. 2011) but for our purposes these were lumped into one larval stage. The model groups males and females together assuming the same parameter values for both.

E. pacifica has biological characteristics requiring a slightly different approach from the other models. Depending on when eggs are spawned, there seems to be some evidence that the juveniles mature after a different number of months (pers comm. Julie Keister, (Harvey et al. 2010)). Brinton (1976) notes that full size was reached after 7 months for early year recruits and about 1 year for summer recruits. If spawned in early spring, then they may mature into pre-recruits and thus start spawning after only a few (2) months. However if they are spawned towards the end of the season, then they will likely overwinter as juveniles and mature in the following spring (5 month juvenile stage). As a result we developed two separate models to investigate the different conclusions that would be reached depending duration of the juvenile stage. The two models therefore only differed in their juvenile durations. Brinton (1976) did note that survival is lower for those spawned earlier in the year, however here we assume them to be constant. Different exposures were calculated for each krill 'type' based on the timing of when each spawning population is present in the water column.

Table A.4.4. Life history stages included in the model for *E. pacifica*. Including survival rates and duration times with sources provided. Note: there are two alternative sources for early life stage parameter values – models have been tested for both and show little difference in population growth rate.

Parameter	**Value** (daily values)	**Source**	**Notes**
e_{se} = egg survival	0.91	(Heath 1977, Bi et al. 2011)*	Bi et al. (2011) estimates an egg mortality rate of 9% per day. Heath estimated a lower value at 6% per day, but the more recent estimate was used.
e_{de} = egg duration	2 days	(Bi et al. 2011)	Eggs are present for 2 days before hatching
l_{se} = larval survival	0.9756061 day^{-1}	(Bi et al. 2011)	From Bi et al. (2011) there are estimates of the durations of larval stages nauplii, furcilia and calyptopes – these were combined into one larval survival using weighted sum based on the durations of each of the stages
l_{de} = larval duration	66 days	(Bi et al. 2011)	Total number of days nauplii, fucilia and calyptopes are present in the water column
j_{se} =	0.9867395	(Brinton 1976)	

juvenile survival			
je_{de} = juvenile duration for early spawners	61	(Brinton 1976, Harvey et al. 2010)	Brinton (1976) suggests that juveniles are only present for 2 months, and Harvey et al. (2010) writes that *pacifica* can recruit to spawning size after 4-7 months in the water column. With ~2 months in the egg and larval stages this means that on the lower end juveniles are present for 2 months and the higher end 5 months.
jl_{de} = juvenile duration for late spawners	152	(Brinton 1976, Harvey et al. 2010)	For this model with the longer juvenile stage, the higher end of 5 months was used.
pr_{se} = pre-recruit survival	0.9852339	(Brinton 1976)	
pr_{de} = pre-recruit duration	91 days	Based on information in (Harvey et al. 2010)	Harvey et al. (2010) shows that brood size can increase almost three-fold for smaller vs. larger krill. To account for the fact that brood sizes increase with body size, we included a pre-recruit stage. This stage was determined to be approximately 3 months as in Harvey et al. (2010) there is a ~100 day period when smaller brood sizes have been observed.
a_{se} = adult survival	0.9831166	(Brinton 1976)	
f_{pre} = pre-recruit fecundity	$f_{ap}/3$	(Feinberg et al. 2007)	Feinberg et al. (2007) report differing fecundity values based on body size, however from personal communication with Julie Keister, she suggested that pre-recruits have spawning output that is almost the same as adults and is only slightly lower during this life stage. Therefore the fecundity is assumed to be 90% of adult fecundity.
f_{ae} = adult fecundity	7.15	(Feinberg et al. 2013)	These authors report three different daily fecundity estimates for *E. pacifica* in the California Current, from these we calculated

			total fecundity based on length of spawning season, averaged the three and obtained a daily estimate of fecundity for the entire year.

* Note: there are two alternative sources for early life stage parameter values – models have been tested for both and show little difference in population growth rate.

Transition and Elasticity Matrices:

Early spawners (shorter juvenile life stage) transition matrix from parameters in Table A.4.4:

	Eggs	Larvae	Juvenile	Pre-recruit	Adults
Eggs	0.4764	0	0	2.3845	7.1534
Larvae	0.4336	0.9697	0	0	0
Juvenile	0	0.0059	0.9762	0	0
Pre-recruit	0	0	0.0105	0.9801	0
Adults	0	0	0	0.0051	0.9831

Later spawners (longer juvenile life stage) transition matrix:

	Eggs	Larvae	Juvenile	Pre-recruit	Adults
Eggs	0.4764	0	0	2.3845	7.1534
Larvae	0.4336	0.9697	0	0	0
Juvenile	0	0.0059	0.9847	0	0
Pre-recruit	0	0	0.0020	0.9801	0
Adults	0	0	0	0.0051	0.9831

Multipliers for the two models, to ensure $\lambda = 1$, h_e= 0.9714854, h_l= 0.9885264.

The elasticity matrix for the early spawners:

	Eggs	Larvae	Juvenile	Pre-recruit	Adults
Eggs	0.0133	0	0	0.0115	0.0039
Larvae	0.0154	0.2502	0	0	0

Juvenile	0	0.0154	0.2828	0	0
Pre-recruit	0	0	0.0154	0.3064	0
Adults	0	0	0	0.0039	0.0819
SUMS	0.0287	0.2656	0.2982	0.3218	0.0858

The elasticity matrix for the late spawners:

	Eggs	Larvae	Juvenile	Pre-recruit	Adults
Eggs	0.0082	0	0	0.0060	0.0032
Larvae	0.0092	0.2136	0	0	0
Juvenile	0	0.0092	0.3386	0	0
Pre-recruit	0	0	0.0092	0.2874	0
Adults	0	0	0	0.0032	0.1120
SUMS	0.0175	0.2229	0.3478	0.2966	0.1152

Krill,* Thysanoessa spinifera—*Model Methods and Parameters

The model for *Thysanoessa spinifera* is a stage structured model that includes eggs, larvae, juveniles, and adults. Most model parameters for *E. pacifica* were used to fill in the many unknowns about this species, however since *E. pacifica* exhibits different larval duration than has been found for *T. spinifera* we decided to make a separate model for this species. Note that it does not include the sub-adult stage, as there was no mention of sub-adults in the Summers (1993) thesis which seems to be the most detailed outline of life history.

Table A.4.5. Life history stages included in the model for *T. spinifera*. Survival rates and duration times are all the same as the *E. pacifica model* except where written in red. Sources provided.

Parameter	**Value** (daily values)	**Source**	**Notes**
e_{st} = egg survival	0.91	(Heath 1977, Bi et al. 2011)	Bi et al. (2011) estimates an egg mortality rate of 9% per day. Heath estimated a lower value at 6% per day, but the more recent estimate was used.
e_{dt} = egg duration	2 days	(Summers 1993, Bi et al. 2011)	Eggs are present for 2 days before hatching. Summers (1993) found this for *T. spinifera* as well.
l_{st} = larval survival	0.9756061 day^{-1}	(Bi et al. 2011)(Bi et al. 2011)(Bi et al. 2011)(Bi et al. 2011)	From Bi et al. (2011) there are estimates of the durations of larval stages nauplii, furcilia and calyptopes – these were combined into one larval survival using weighted sum based on the durations of each of the stages
l_{dt} = larval duration	66 days	(Summers 1993, Bi et al. 2011)	Total number of days nauplii, fucilia and calyptopes are present in the water column. Note that while Summers (1993) did not outline the durations of all larval stages, they approximated a total of 67 days from egg to juvenile, therefore the same value as *E. pacifica* was used.
j_{st} = juvenile survival	0.9867395	(Brinton 1976)	
j_{dt} = juvenile duration for	183	(Summers 1993)	Summers (1993) found that juveniles took approximately 6 months to develop into adults.
a_{st} = adult	0.9831166	(Brinton 1976)	

survival			
f_{at} = adult fecundity	7.15	(Feinberg et al. 2013)	These authors report three different daily fecundity estimates for *E. pacifica* in the California Current, from these we calculated total fecundity based on length of spawning season, averaged the three and obtained a daily estimate of fecundity for the entire year.

Transition and Elasticity Matrices:

T. spinifera transition matrix:

	Eggs	Larvae	Juvenile	Adults
Eggs	0.4764	0	0	7.1534
Larvae	0.4336	0.9697	0	0
Juvenile	0	0.0059	0.9835	0
Adults	0	0	0.0032	0.9831

Multiplier to ensure $\lambda = 1$, h_t= 0.9738514.

The elasticity matrix:

	Eggs	Larvae	Juvenile	Adults
Eggs	0.0129	0	0	0.0149
Larvae	0.0149	0.2531	0	0
Juvenile	0	0.0149	0.3387	0.0000
Adults	0	0	0.0149	0.3356
SUMS	0.0278	0.2680	0.3536	0.3505

Appendix A.5: Justification for uncertainty conclusions

Table A.5.1. Justifications for uncertainty conclusions. Including uncertainty regarding consequence, exposure and population model, for each species' life stage.

Species	Life Stage	U_c	Justification *For Consequence Uncertainty*	U_e	Justification *For Exposure Uncertainty*
Metacarcinus magister	Eggs	3	No direct studies that were controlled	1	We know where adults are from fishing and eggs are on adults
	Larvae	2	Three recent studies from theses, however inconsistent results on survival impact indicate some uncertainty	3	Has been minimally studied
	Megalops	3	No direct studies, some observations from Miller, but conclusions from larvae	3	Has been minimally studied
	Juvenile i	3	No published studies, and only pilot experiments noted	1	We know where adults are and juveniles are found there
	Juvenile ii	3	No published studies, assumed same as other life stage as same species	1	Same as above
	Adult	1	Two studies have both shown strong capabilities of tolerating low pH	1	We know where adults are from fishing
Pendalus jordani	Eggs	2	Studies on species in the same genus with agreement	1	We know where adults are from fishing and eggs are on adults
	Larvae	2	Studies on species in the same genus with agreement	3	Has been minimally studied
	Juvenile	3	Studies on other life stages of species in same genus	1	We know where they settle
	Adult	2	Studies on species in the same genus with agreement	1	We know where adults are from fishing
Limacina helicina	Eggs & larvae	2	Based on consequence conclusions from juveniles and subadults, with expert opinion.	3	With a highly patchy distribution, thus is very hard to be conclusive where it is found and the timing of when they are in the water column is unclear
	Juvenile	1	Multiple papers show pteropod dissolution and negative consequences	3	Same as above

	Subadult	1	Multiple papers show pteropod dissolution and negative consequences	3	Same as above
	Adult	2	Based on consequence conclusions from juveniles and subadults, with expert opinion.	3	Same as above
Merluccius productus	Eggs	3	On other species not in same genus	1	Many years of CalCOFI surveys
	Larvae	3	On other species not in same genus	1	Many years of CalCOFI surveys
	Adult	1	Adult fish are robust	1	Adult distributions not mapped as consequence assume to be 1
Euphausia pacifica Early and late spawners	Eggs	2	Only one study on this species, and one from another – although results are in agreement	2	Somewhat well studied, we have a fairly good idea of their distribution
	Larvae	2	Only one study on this species life stage	2	Same as above
	Juveniles	3	Based on adults	2	Same as above
	Sub-adults	3	Based on adults	2	Same as above
	Adult	3	Only one paper on a different species in same genus and not very strong conclusions	2	Same as above
Thysanoessa spinifera	Eggs	3	Based on *E. pacifica*	2	Somewhat well studied, we have a fairly good idea of their distribution
	Larvae	3	Based on *E. pacifica*	2	Same as above
	Adult	3	Based on *E. pacifica*	2	Same as above

Appendix A Literature Cited

Armstrong, D., C. Rooper, and D. Gunderson. 2003. Estuarine production of juvenile dungeness crab (cancer magister) and contribution to the Oregon-Washington coastal fishery. Estuaries **26**:1174-1188.

Arnberg, M., P. Calosi, J. Spicer, A. Tandberg, M. Nilsen, S. Westerlund, and R. Bechmann. 2012. Elevated temperature elicits greater effects than decreased pH on the development, feeding and metabolism of northern shrimp (Pandalus borealis) larvae. Marine Biology:1-12.

Bechmann, R. K., I. C. Taban, S. Westerlund, B. F. Godal, M. Arnberg, S. Vingen, A. Ingvarsdottir, and T. Baussant. 2011. Effects of ocean acidification on early life stages of shrimp (Pandalus borealis) and mussel (Mytilus edulis). J Toxicol Environ Health A **74**:424-438.

Bednaršek, N., R. A. Feely, J. C. P. Reum, B. Peterson, J. Menkel, S. R. Alin, and B. Hales. 2014. Limacina helicina shell dissolution as an indicator of declining habitat suitability owing to ocean acidification in the California Current Ecosystem. Proceedings of the Royal Society B: Biological Sciences **281**.

Bednaršek, N., G. A. Tarling, D. C. E. Bakker, S. Fielding, A. Cohen, A. Kuzirian, D. McCorkle, B. Lézé, and R. Montagna. 2012. Description and quantification of pteropod shell dissolution: a sensitive bioindicator of ocean acidification. Global Change Biology **18**:2378-2388.

Bi, H., L. Feinberg, C. T. Shaw, and W. T. Peterson. 2011. Estimated development times for stage-structured marine organisms are biased if based only on survivors. Journal of Plankton Research **33**:751-762.

Bignami, S., I. C. Enochs, D. P. Manzello, S. Sponaugle, and R. K. Cowen. 2013. Ocean acidification alters the otoliths of a pantropical fish species with implications for sensory function. Proceedings of the National Academy of Sciences **110**:7366-7370.

Brillon, S., Y. Lambert, and J. Dodson. 2005. Egg survival, embryonic development, and larval characteristics of northern shrimp (Pandalus borealis) females subject to different temperature and feeding conditions. Marine Biology **147**:895-911.

Brinton, E. 1976. Population biology of *Euphausia pacifica* off Southern California. Fishery Bulletin **74**:733-762.

Bromhead, D., V. Scholey, S. Nicol, D. Margulies, J. Wexler, M. Stein, S. Hoyle, C. Lennert-Cody, J. Williamson, J. Havenhand, T. Ilyina, and P. Lehodey. The Potential Impact of Ocean Acidification Upon Eggs and Larvae of Yellowfin Tuna (Thunnus albacares). Deep Sea Research Part II: Topical Studies in Oceanography.

Busch, D. S., M. Maher, P. Thibodeau, and P. McElhany. 2014. Shell Condition and Survival of Puget Sound Pteropods Are Impaired by Ocean Acidification Conditions. Plos One **9**.

CalCOFI. 2012. Pacific hake egg and larval survey 1984-2012.*in* C. C. O. F. Investigation, editor., http://www.calcofi.org/new.data/.

Cass-Calay, S. L. 2003. The feeding ecology of larval Pacific hake (Merluccius productus) in the California Current region: an updated approach using a combined OPC/MOCNESS to estimate prey biovolume. Fisheries Oceanography **12**:34-48.

Christmas, A.-M. F. 2013. Effects of ocean acidification on dispersal behavior in the larval stage of the Dungeness crab and the Pacific Green Shore crab. Western Washington University.

Dahlstrom, W. A. 1970. Synopsis of biological data on the ocean shrimp Pandalus jordani Rathbun. FAO Fisheries Report **57**:377-1416.
Dahlstrom, W. A. 1973. Status of the California ocean shrimp resource and its management. Marine Fisheries Review **35**:55-59.
Descoteaux, R. 2014. Effects of ocean acidification on development of Alaskan crab larvae. University of Alaska Fairbanks.
Feinberg, L., and W. Peterson. 2003. Variability in duration and intensity of euphausiid spawning off central Oregon, 1996–2001. Progress in Oceanography **57**:363-379.
Feinberg, L. R., W. T. Peterson, and C. Tracy Shaw. 2010. The timing and location of spawning for the Euphausiid Thysanoessa spinifera off the Oregon coast, USA. Deep Sea Research Part II: Topical Studies in Oceanography **57**:572-583.
Feinberg, L. R., C. Shaw, and W. T. Peterson. 2007. Long-term laboratory observations of Euphausia pacifica fecundity: comparison of two geographic regions. Marine Ecology Progress Series **341**:141-152.
Feinberg, L. R., C. T. Shaw, W. T. Peterson, M. Décima, Y. Okazaki, and S.-J. Ju. 2013. Euphausia pacifica brood sizes: a North Pacific synthesis. Journal of Plankton Research.
Frommel, A., A. Schubert, U. Piatkowski, and C. Clemmesen. 2013. Egg and early larval stages of Baltic cod, Gadus morhua, are robust to high levels of ocean acidification. Marine Biology **160**:1825-1834.
Frommel, A. Y., R. Maneja, D. Lowe, C. K. Pascoe, A. J. Geffen, A. Folkvord, U. Piatkowski, and C. Clemmesen. 2014. Organ damage in Atlantic herring larvae as a result of ocean acidification. Ecological Applications **24**:1131-1143.
Gallagher, C. M., R. W. Hannah, and G. Sylvia. 2004. A comparison of yield per recruit and revenue per recruit models for the Oregon ocean shrimp, Pandalus jordani, fishery. Fisheries Research **66**:71-84.
Hammer, K. M. 2012. Acid-base regulation and metabolite responses in shallow-and deep-living marine invertebrates during environmental hypercapnia. Norwegian University of Science and Technology.
Hankin, D. G., N. Diamond, M. S. Mohr, and J. Ianelli. 1989. Growth and reproductive dynamics of adult female Dungeness crabs (Cancer magister) in northern California. Journal du Conseil: ICES Journal of Marine Science **46**:94-108.
Hannah, R. W. 1995. Variation in geographic stock area, catchability, and natural mortality of ocean shrimp (Pandalus jordani): some new evidence for a trophic interaction with Pacific hake (Merluccius productus). Canadian Journal of Fisheries and Aquatic Sciences **52**:1018-1029.
Hannah, R. W. 2011. Variation in the distribution of ocean shrimp (Pandalus jordani) recruits: links with coastal upwelling and climate change. Fisheries Oceanography **20**:305-313.
Hans, S., S. Fehsenfeld, J. Treberg, and D. Weihrauch. 2014. Acid–base regulation in the Dungeness crab (Metacarcinus magister). Marine Biology:1-15.
Harvey, H. R., S.-J. Ju, S. K. Son, L. R. Feinberg, C. T. Shaw, and W. T. Peterson. 2010. The biochemical estimation of age in Euphausiids: Laboratory calibration and field comparisons. Deep Sea Research Part II: Topical Studies in Oceanography **57**:663-671.
Heath, W. A. 1977. The ecology and harvesting of euphausiids in the strait of georgia. University of British Columbia.
Higgins, K. 1997. Stochastic Dynamics and Deterministic Skeletons: Population Behavior of Dungeness Crab. Science **276**:1431-1435.

Higgins, K., A. Hastings, J. N. Sarvela, and L. W. Botsford. 1997. Stochastic Dynamics and Deterministic Skeletons: Population Behavior of Dungeness Crab. Science **276**:1431-1435.

Hobbs, R., and L. Botsford. 1992. Diel vertical migration and timing of metamorphosis of larvae of the Dungeness crab Cancer magister. Marine Biology **112**:417-428.

Hobbs, R. C., L. W. Botsford, and A. Thomas. 1992. Influence of hydrographic conditions and wind forcing on the distribution and abundance of Dungeness crab, Cancer magister, larvae. Canadian Journal of Fisheries and Aquatic Sciences **49**:1379-1388.

Hollowed, A. B. 1992. Spatial and temporal distributions of Pacific hake, Merluccius productus, larvase and estimates of survival during early life stages California Cooperative Oceanic Fisheries Investigations Reports **33**:100-123.

Kawaguchi, S., A. Ishida, R. King, B. Raymond, N. Waller, A. Constable, S. Nicol, M. Wakita, and A. Ishimatsu. 2013. Risk maps for Antarctic krill under projected Southern Ocean acidification. Nature Clim. Change **advance online publication**.

Kawaguchi, S., H. Kurihara, R. King, L. Hale, T. Berli, J. P. Robinson, A. Ishida, M. Wakita, P. Virtue, S. Nicol, and A. Ishimatsu. 2011. Will krill fare well under Southern Ocean acidification? Biol Lett **7**:288-291.

Kroeker, K. J., R. L. Kordas, R. N. Crim, and G. G. Singh. 2010. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. Ecology Letters **13**:1419-1434.

Long, W. C., K. M. Swiney, C. Harris, H. N. Page, and R. J. Foy. 2013. Effects of Ocean Acidification on Juvenile Red King Crab (Paralithodes camtschaticus) and Tanner Crab (Chionoecetes bairdi) Growth, Condition, Calcification, and Survival. PLoS ONE **8**:e60959.

Lu, B., D. L. Mackas, and D. F. Moore. 2003a. Cross-shore separation of adult and juvenile euphausiids in a shelf-break alongshore current. Progress in Oceanography **57**:381-404.

Lu, B., D. L. Mackas, and D. F. Moore. 2003c. Cross-shore separation of adult and juvenile euphausiids in a shelf-break alongshore current. Progress in Oceanography **57**:381-404.

McKelvey, R., D. Hankin, K. Yanosko, and C. Snygg. 1980. Stable cycles in multistage recruitment models: an application to the northern California Dungeness crab (Cancer magister) fishery. Canadian Journal of Fisheries and Aquatic Sciences **37**:2323-2345.

Melzner, F., M. Gutowska, M. Langenbuch, S. Dupont, M. Lucassen, M. C. Thorndyke, M. Bleich, and H.-O. Pörtner. 2009. Physiological basis for high CO 2 tolerance in marine ectothermic animals: pre-adaptation through lifestyle and ontogeny? Biogeosciences Discussions **6**:4693-4738.

Miller, J. 2015. Effect of low pH on early life stages of the decapod crustacean, Dungeness crab (Cancer magister). University of Washington.

Modin, J. C., and K. W. Cox. 1967. Post-Embryonic Development of Laboratory-Reared Ocean Shrimp, Pandalus jordani Rathbun. Crustaceana **13**:197-219.

Moloney, C., L. Botsford, and J. Largier. 1994. Development, survival and timing of metamorphosis of planktonic larvae in a variable environment: the Dungeness crab as an example. Marine ecology progress series. Oldendorf **113**:61-79.

Moser, H. G., N. C. H. Lo, and P. E. Smith. 1997. Vertical distribution of Pacific hake eggs in relation to stage of development and temperature. California Cooperative Oceanic Fisheries Investigations Report:120-126.

Munday, P. L., J. M. Donelson, D. L. Dixson, and G. G. K. Endo. 2009. Effects of Ocean Acidification on the early Life History of a Tropical Marine Fish. Proceedings: Biological Sciences **276**:3275-3283.
Pane, E. F., and J. P. Barry. 2007. Extracellular acid-base regulation during short-term hypercapnia is effective in a shallow-water crab, but ineffective in a deep-sea crab. Marine Ecology Progress Series **334**:1-9.
Pauley, G. B., D. A. Armstrong, T. W. Heun, U. S. A. E. W. E. S. C. E. Group, C. National Wetlands Research, U. S. Fish, Wildlife, U. S. Fish, R. Wildlife, Development, and S. United States. Army. Corps of Engineers. Waterways Experiment. 1986. Species profiles : life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest) : dungeness crab. Fish and Wildlife Service ; Coastal Ecology Group, Waterways Experiment Station, Washington, DC; Vicksburg, MS.
Rasmuson, L. K. 2013. The Biology, Ecology and Fishery of the Dungeness crab, Cancer magister. Adv Mar Biol **65**:95-148.
Reed, P. H. 1969. Culture methods and effects of temperature and salinity on survival and growth of Dungeness crab (Cancer magister) larvae in the laboratory. Journal of the Fisheries Board of Canada **26**:389-397.
Reilly, P. N. 1983. Dynamics of Dungeness crab, Cancer magister, larvae off central and northern California. Life history, environment, and mariculture studies of Dungeness crab, Cancer magister, with emphasis on the central California® fishery resource. Calif. Dept Fish Game, Fish. Bull **172**:57-84.
Rothlisberg, P., and W. G. Pearcy. 1976. An epibenthic sampler used to study the ontogeny of vertical migration of pandalus dordani (Decapoda caridea).
Rothlisberg, P. C. 1975. Larval ecology of Pandalus jordani Rathbun. Oregon State University.
Rothlisberg, P. C., and C. B. Miller. 1983. *Factors affectin*g the distribution, abundance and survival of Pandalus jordani (Decapoda, Pandalidae) larvae off the Oregon coast. Fisheries Bulletin **81**:455-472.
Rumrill, S. S. 1990. Natural mortality of marine invertebrate larvae. Ophelia **32**:163-198.
Rumsey, S. M., and P. J. S. Franks. 1999. Influence of variability in larval development on recruitment success in the euphausiid Euphausia pacifica: elasticity and sensitivity analyses. Marine Biology **133**:283-291.
Saba, G. K., O. Schofield, J. J. Torres, E. H. Ombres, and D. K. Steinberg. 2012. Increased Feeding and Nutrient Excretion of Adult Antarctic Krill, Euphausia superba, Exposed to Enhanced Carbon Dioxide (CO2). PLoS ONE **7**:1-12.
Shirley, S. M., T. C. Shirley, and S. D. Rice. 1987. Latitudinal variation in the Dungeness crab, Cancer magister: zoeal morphology explained by incubation temperature. Marine Biology **95**:371-376.
Smith, P. E. 1995. Development of the population biology of the Pacific hake, Merluccius productus. California Cooperative Oceanic Fisheries Investigations Reports **36**:144-152.
Stevens, B. G., and D. A. Armstrong. 1984. Distribution, abundance, and growth of juvenile Dungeness crabs, Cancer magister, in Grays Harbor estuary, Washington. Fishery Bulletin **82**.
Summers, P. L. 1993. Life history, growth and aging in Thysanoessa spinifera. University of Victoria.

Vance, P., J. Keister, and W. Peterson. 2003. Seasonal and annual variation in the population composition and depth distributions of the euphausiid, Euphausia pacifica. Eos Transactions, AGU **84**:52.

Wainwright, T., D. Armstrong, P. Dinnel, J. Orensanz, and K. McGraw. 1992. Predicting effects of dredging on a crab population: An equivalent adult loss approach. Fishery Bulletin **90**:171-182.

Wang, K. 2014. The life cycle of the pteropod Limacina helicina in Rivers Inlet University of British Columbia.

Wickham, D. 1979a. The relationship between megalopae of the Dungeness Crab, Cancer magister, and the hydroid, Velella velella, and its influence on abundance estimates of C. magister megalopae. California Fish and Game **65**:184-186.

Wickham, D. E. 1979c. Predation by the nemertean Carcinonemertes errans on eggs of the Dungeness crab Cancer magister. Marine Biology **55**:45-53.

Appendix B—Chapter 2

Appendix B.1: Details on spatial allocation of fishing

Here we provide further detail regarding the method used for setting constant fishing mortalities for each functional group at each port.

Fishing mortality rates were set so that the biomass of catch after one year of the model run, with no species directly responding to pH and using 2013 oceanographic conditions (*Baseline2013*) matched the biomass of known catch for each functional group from PacFIN for 2013. Each port fished in the Atlantis polygons which were within the 200 km radius of the main city associated with each port group. The 200 km radius was used to determine the fraction of overlap in the north-south direction with each polygon representing the 0-50m bathymetry range. The port was then assumed to be able to access the same proportion of each polygon in offshore polygons, out to 1200m.

As noted in the main text, biomass used to set port-specific fishing mortality rates came from 10 of the 17 fleet types reported by PacFIN (Table B.1). The 10 vessel types with landings accounted for at the port level are called *Spatial-vessels* here in. The catch from the 7 vessel types not included was accounted for in a *Generic* fishery that fished all polygons within U.S. waters from 0-1200m. The catch accounted for in the *Spatial-vessels* was between 62.7-99.8% (median 85.0%) of the revenue landed at each port for 2013 (Table B.1.1). Groups making up the top fraction of catch in the *Generic* catch were primarily Chinook salmon, Deep demersal fish (a mixture of CA slickhead, eelpouts, grenadiers and hagfish), Large pelagic predators (tuna), and Dungeness crab. The first three groups in that list all fell to very low biomass levels in our model (<2% of starting biomass).

The fishing mortality rate was determined using an iterative procedure to ensure catch after one year in the model run to expected biomass of catch from PacFIN (values in Table B.1.2). This was iterated until an acceptable ratio between expected/realized ratio was found (Table B.1.3). That is, when the realized sum across all ports for a single functional group was within 1% of the expected across ports.

This iterative procedure was also used to set the *Generic* fishing mortalities as well as the fishing mortalities for Canada and Mexico

Discards were determined by comparing the ratio of total expected catch of each functional group we found using 2013 PacFIN data against the catch estimates from Marshall et al. (2017).

Table B.1.1. Percent of total revenue from commercial catches accounted for in our port-specfic fisheries. All biomass not accounted for was included in the *Generic* fishery.

Port	Percent of Catch accounted for in 10 vessel types included
N_WA	63.7%

S_WA	73.6%
Astoria	83.2%
Tillamook	62.7%
Newport	84.6%
Coos Bay	83.6%
Brookings	95.3%
Crescent City	99.8%
Eureka	94.2%
Fort Bragg	74.1%
Bodega Bay	81.4%
San Francisco	85.1%
Monterey	87.8%
Morro Bay	85.5%
Santa Barbara	96.5%
Los Angeles	97.8%
San Diego	90.1%

Table B.1.2. Total catch per fleet in mT for all fleet types: Generic coast-wide fleet, 17 port fleets, Mexico and Canada, according to Atlantis functional groups (see Marshall et al. (2017) Supporting information for detailed model information.

Location/Fleet designation	FDP	FPO	FVV	SHC	YEL	FBP	FDD	FDC	FDO	DAR	FDF	FDE
Generic	0.00	0.00	0.00	0.00	0.20	0.00	2514.87	0.00	0.00	0.00	0.00	83.16
N_WA	93.33	2.06	0.00	0.00	0.52	0.00	25.21	0.03	50.33	0.02	157.54	0.01
S_WA	343.90	3.74	1.58	0.00	0.07	0.00	3.09	56.28	61.98	8.26	31.00	0.00
Astoria	2925.08	4.29	0.07	0.00	0.07	0.00	18.97	110.93	278.82	34.02	468.36	0.03
Tillamook	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.31	0.00	0.00	0.01
Newport	767.92	1.06	0.61	0.00	0.27	0.00	34.98	46.73	133.18	27.91	44.51	0.00
Coos Bay	778.00	1.70	0.00	0.00	0.74	0.00	136.95	136.93	85.39	34.12	92.72	0.00
Brookings	806.40	0.05	0.00	0.00	0.10	0.00	47.43	113.27	81.80	9.17	52.67	0.07
Crescent City	34.34	0.00	0.00	0.00	0.00	0.00	0.00	7.55	8.00	0.00	4.72	0.00
Eureka	1266.65	0.71	0.00	0.01	0.00	0.00	68.05	244.88	138.66	2.23	75.55	0.00
Fort Bragg	487.95	0.96	0.02	0.03	0.02	0.00	6.83	230.55	143.86	1.49	24.29	0.00
Bodega Bay	0.00	0.00	0.00	0.00	0.00	0.00	61.35	0.00	3.78	0.00	0.00	0.03
San Francisco	279.56	0.10	0.01	0.12	0.02	0.00	0.00	64.74	18.02	0.02	72.44	2.61
Monterey	55.83	0.00	0.00	0.02	0.00	0.00	42.35	46.05	33.84	0.27	14.60	0.10
Morro Bay	111.91	0.01	0.00	0.03	0.00	0.00	23.20	51.37	120.59	0.09	1.68	0.55
Santa Barbara	0.20	0.00	0.00	0.00	0.00	0.00	5.35	2.12	38.89	0.00	1.28	24.06
Los Angeles	0.11	0.00	0.00	0.00	0.00	0.00	20.45	5.42	25.40	0.00	3.68	8.40
San Diego	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.06	39.07	0.00	1.80	6.87
Mexico	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	189.54	70.10
Canada	1174.46	558.96	0.00	0.00	1.51	0.00	13.67	314.94	421.34	59.17	278.77	0.21

Table B.1.2. Continued…

FDS	BOC	POP	FDB	SHR	FMM	FMN	FVD	ARR	PET	FVS
0.00	2.64	0.00	4.71	107.08	126086.95	158.93	108.68	0.00	0.00	58.57
351.89	0.10	0.01	0.38	0.00	0.00	305.69	74.52	0.00	136.53	63.31
147.04	0.17	10.98	1.12	0.00	27183.89	295.02	12.86	116.36	161.24	61.93
887.62	0.40	25.10	23.29	3.44	32636.65	590.04	5.92	1341.40	779.90	219.46
0.14	0.00	0.00	0.00	7.37	0.00	4.72	3.15	0.00	0.00	4.88
134.85	0.20	11.39	1.30	8.04	43499.20	598.16	51.37	205.88	219.84	12.16
1.42	0.00	3.11	1.65	9.34	0.21	383.77	13.42	160.75	338.62	11.05
3.27	0.00	0.33	0.24	119.85	0.08	283.55	2.83	40.92	50.69	45.53
0.95	0.00	0.00	0.01	45.43	0.00	41.28	0.00	3.39	0.01	4.27
1.52	0.03	0.08	0.74	0.00	0.11	272.13	0.00	79.85	226.76	14.17
281.82	8.14	0.01	1.62	3.18	1.58	317.41	0.00	41.75	100.43	12.76
0.61	0.03	0.00	0.14	0.29	0.00	52.34	0.06	0.00	0.00	0.26
66.66	3.22	0.00	2.21	9.25	0.00	91.37	83.19	0.46	84.74	6.40
3.00	0.48	0.00	1.94	1.90	2.29	111.29	4.69	0.21	22.87	6.45
11.80	0.86	0.00	26.13	38.80	2.05	353.99	2.75	0.00	37.05	27.22
2.25	0.46	0.00	0.65	6.25	0.00	178.96	29.61	0.00	0.27	8.90
0.99	0.89	0.00	0.01	0.56	0.00	55.96	4.33	0.00	0.00	0.33
1.66	0.17	0.00	0.16	0.61	0.00	49.49	5.38	0.00	0.00	0.37
0.00	0.00	0.00	0.00	1.71	0.00	1.71	0.00	0.00	0.00	0.00
3567.85	31.43	828.96	29.82	275.49	54096.00	275.49	732.16	7881.68	466.33	387.45

Table B.1.2. Continued…

FVT	FPL	JAC	FPS	SAR	ANC	HER	FVB	SHD	SHB	DOG
9768.63	0.00	0.00	141.13	0.00	0.00	0.00	6276.30	3471.05	0.00	0.00
16.91	0.00	0.00	0.00	0.00	0.00	85.73	0.00	97.50	0.00	38.37
2009.69	211.51	79.75	0.03	29932.18	29.73	0.01	0.00	37.32	0.02	87.05
187.68	480.21	115.65	0.77	26302.48	12.68	0.05	0.00	23.29	1.37	19.83
50.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.96	0.00	0.00
613.54	2.34	7.80	4.47	0.01	0.00	0.01	0.00	40.91	1.22	11.38
300.74	0.00	0.00	0.00	0.00	0.00	0.00	0.00	156.39	0.00	0.64
115.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00	54.78	0.00	1.58
59.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.77	0.00	0.00
29.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	66.63	0.00	0.00
15.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	354.72	0.01	0.32
5.33	0.00	0.00	0.00	0.00	0.00	0.03	0.00	188.58	0.00	0.00
26.13	0.00	0.00	0.07	1.37	0.00	2114.94	0.00	315.08	0.00	0.02
17.51	0.07	0.00	1.35	895.44	5557.79	0.03	0.00	37.14	0.28	0.58
0.00	0.00	0.00	12.19	0.00	0.00	0.00	0.00	8.76	0.00	0.01
0.13	0.38	0.03	0.03	222.00	195.75	0.00	0.00	0.41	0.00	0.07
0.00	8847.46	892.97	51.36	6039.00	10.72	0.00	0.00	0.00	0.00	0.00
1.87	0.03	0.23	0.00	2.40	171.91	0.00	0.00	0.00	0.00	0.01
3622.00	326.50	0.00	0.00	41760.00	2715.73	0.00	0.00	0.00	1.87	0.00
5119.00	0.00	0.08	0.54	7421.00	0.00	17.51	373.41	0.07	94.59	251.01

Table B.1.2. Continued…

SHP	SSK	BD	BFD	BFF	NUR	PSP	PWN	BMD	BMS	BML
98.01	0.00	52.03	0.00	212.74	465.63	0.00	35.27	0.00	0.00	0.00
0.00	70.32	0.00	0.00	0.00	0.00	0.00	38.22	0.00	0.80	0.05
0.02	44.76	0.00	0.00	0.00	0.00	6166.17	21.02	0.00	0.02	0.00
0.30	509.71	0.00	0.00	0.00	0.04	3313.69	0.76	0.00	1.29	0.02
0.00	0.28	0.00	0.00	0.00	0.00	14.92	0.35	0.00	0.02	0.00
0.02	112.25	0.00	0.00	0.00	0.00	7288.32	3.76	0.00	0.20	0.00
0.00	88.04	0.00	0.00	0.00	0.00	9019.66	5.81	0.00	0.63	0.00
0.00	46.50	0.00	0.00	0.00	0.00	2012.86	0.00	0.00	0.82	0.00
0.00	1.01	0.00	0.00	0.00	0.00	2951.71	36.93	0.00	0.00	0.00
0.00	89.91	0.00	0.00	0.00	0.00	997.33	0.00	0.00	0.00	0.00
0.08	51.37	1.79	0.00	0.00	1903.29	0.00	0.00	0.00	0.57	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.13	0.00	0.02	4.84
0.20	16.05	0.00	0.00	0.00	0.00	0.00	36.83	0.00	0.50	5.05
0.00	6.61	0.13	0.00	0.00	0.20	0.00	18.31	0.00	0.08	2.11
0.07	16.54	0.92	0.00	0.00	0.00	0.00	10.65	0.00	0.00	34.23
1.94	2.53	83.02	0.00	14.78	3153.15	0.00	80.12	0.00	0.03	780.03
1.22	1.59	35.62	0.00	19.89	500.62	0.00	50.30	0.00	0.12	228.74
2.90	2.28	4.54	0.00	4.77	246.83	0.00	58.21	0.00	1.08	166.91
3525.34	110.83	71.06	0.00	991.71	4074.35	31.21	31.21	0.00	1.04	721.07
0.00	155.16	0.13	0.57	239.99	0.00	0.22	0.22	0.47	0.53	1.29

Table B.1.2. Continued…

DUN	CEP	MSQ	HSQ
899.49	0.00	0.00	0.00
526.80	0.00	0.00	0.00
8315.49	2.12	0.00	0.00
2977.03	5.84	0.06	0.00
438.04	0.00	0.00	0.00
3544.27	10.62	0.00	0.00
2727.04	0.00	0.00	0.00
3347.14	0.00	0.00	0.00
5794.91	0.00	0.00	0.00
4405.33	0.00	0.00	0.00
426.56	0.16	0.02	0.00
1320.42	0.00	0.01	0.00
3181.56	0.00	7235.75	0.00
322.52	0.02	13768.34	0.00
267.47	0.05	1938.87	0.00
2.94	0.06	45336.37	0.00
0.00	0.00	36321.10	0.00
0.00	0.00	0.06	0.00
0.00	0.00	13911.01	2754.51
1.51	15.10	13.62	0.00

Table B.1.3. Ratio of catch data to realized catch after one year in the model run. "NA" indicates low biomass levels in the model leading to no realized catch, and "--" indicates that there was no estimated catch for that species.

Location/Fleet designation	FDP	FPO	FVV	SHC	YEL	FBP	FDD	FDC	FDO	DAR	FDF	FDE
midwcCEP	--	--	--	--	1.00	--	1.00	--	--	--	--	1.00
pseineFP	1.00	1.00	--	--	1.00	--	1.00	1.00	1.00	1.00	1.00	1.00
trapBMS	1.00	1.00	1.03	--	1.00	--	1.00	1.00	1.00	1.00	1.00	--
trapFD	1.00	1.00	1.03	--	1.00	--	1.00	1.00	1.00	1.00	1.00	1.00
dtrawlBMS	NA	--	--	--	--	--	--	--	1.00	--	--	1.01
dtrawlCEP	1.00	1.00	1.03	--	1.00	--	1.00	1.00	1.00	1.00	1.00	--
dtrawlFD	1.00	1.00	--	--	1.00	--	1.00	1.00	1.00	1.00	1.00	1.00
dtrawlFDB	1.00	1.00	--	--	1.00	--	1.00	1.00	1.00	1.00	0.99	1.00
dtrawlFDO	1.00	--	--	--	--	--	--	1.00	1.00	1.00	0.99	--
midwcFD	1.00	1.00	--	1.00	--	--	1.00	1.00	1.00	1.00	0.99	--
dseineFDB	1.00	1.00	1.05	1.00	1.00	--	1.00	1.00	1.00	1.00	0.99	--
dlineFD	--	--	--	--	--	--	1.00	--	1.00	--	1.00	NA
dlineFVS	1.00	1.00	0.97	1.00	1.00	--	--	1.00	1.00	1.00	1.00	1.00
dlineSH	1.00	0.99	--	1.00	--	--	1.00	1.00	1.00	1.00	1.00	1.00
diveBG	1.00	1.00	--	1.00	--	--	1.00	1.00	1.00	1.00	1.00	1.00
pseineFVS	1.00	--	--	--	--	--	1.00	1.00	1.00	--	1.00	1.00
cullPIN	1.04	--	--	--	--	--	1.00	1.00	1.00	--	1.00	1.00
ptrawlPWN	--	--	--	--	--	--	--	1.00	1.00	--	1.00	1.00
dtrawlFBP	--	--	--	--	--	--	--	--	--	--	1.00	1.00
midwcZL	1.00	1.00	--	--	1.00	--	1.00	1.00	1.00	1.00	1.00	1.00
Ratio of totals	**1.00**	**1.00**	**0.97**	**1.00**	**1.00**	**NA**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**

Table B.1.3. Continued…

FDS	BOC	POP	FDB	SHR	FMM	FMN	FVD	ARR	PET	FVS	FVT	FPL	JAC	FPS
--	1.00	--	1.00	1.00	1.00	1.00	1.00	--	--	1.00	1.00	--	--	1.00
1.00	1.00	1.00	1.00	--	--	1.00	1.00	--	1.00	1.00	1.00	--	--	--
1.00	1.00	1.00	1.00	--	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01	1.00	1.03
1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01	1.00	1.00
1.01	--	--	--	1.00	--	1.00	1.00	--	--	1.00	1.00	--	--	--
1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01	1.00	1.00
1.00	--	1.00	1.00	1.00	0.98	1.00	1.00	1.00	1.00	1.00	1.00	--	--	--
1.00	--	1.00	1.00	0.98	1.05	1.00	0.99	1.00	0.98	1.00	1.00	--	--	--
1.00	1.00	--	1.00	0.97	--	1.00	--	0.99	0.98	1.00	1.00	--	--	--
1.00	1.00	1.00	1.00	0.98	0.97	1.00	--	1.00	0.98	1.00	1.00	--	--	--
1.00	1.00	1.00	1.00	1.00	1.00	1.00	--	1.00	0.99	1.00	1.00	--	--	--
1.00	1.00	--	1.00	1.00	--	1.00	1.00	--	--	1.00	1.00	--	--	--
1.00	1.00	1.00	1.00	1.00	NA	1.00	1.00	1.00	1.01	1.00	1.00	--	--	1.01
1.00	1.00	--	1.00	1.00	1.00	1.00	1.00	1.00	1.01	1.00	1.00	0.19	--	1.00
1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	--	1.00	1.00	--	--	--	1.00
1.00	1.00	--	1.00	1.00	--	1.00	1.00	--	1.00	1.00	1.00	0.38	1.03	0.98
1.00	1.00	--	1.00	1.00	--	1.00	1.00	--	--	1.00	--	1.01	1.00	1.00
1.00	NA	--	1.00	1.00	--	1.00	1.00	--	--	1.00	1.00	0.04	1.00	--
--	--	--	--	1.00	--	NA	--	--	--	--	1.00	1.01	--	--
1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	--	0.96	0.99
1.00	**1.00**	**1.00**	**1.00**	**1.01**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**0.99**	**1.00**	**1.00**

Table B.1.3. Continued…

SAR	ANC	HER	FVB	SHD	SHB	DOG	SHP	SSK	BD	BFF	NUR	PSP	PWN
--	--	--	NA	NA	--	--	1.00	--	1.12	1.00	0.98	--	1.00
--	--	1.01	--	NA	--	1.00	--	1.00	--	--	--	--	1.00
1.00	1.04	0.96	--	NA	1.00	1.00	1.00	1.00	--	--	--	1.01	1.00
1.00	1.04	1.00	--	NA	1.00	1.00	1.00	1.00	NA	NA	1.97	1.01	1.00
--	--	--	--	NA	--	--	--	1.00	--	--	--	1.01	1.00
1.02	--	1.00	--	NA	1.00	1.00	1.00	1.00	--	--	--	1.01	1.00
--	--	--	--	NA	--	1.00	--	1.00	--	--	--	1.01	1.00
--	--	--	--	NA	--	1.00	--	0.99	--	--	--	1.01	--
--	--	--	--	NA	--	--	--	0.99	--	--	--	1.01	1.00
--	--	--	--	NA	--	--	--	0.99	--	--	--	1.01	--
--	--	--	--	NA	1.01	1.00	1.00	1.00	0.96	--	1.96	--	--
--	--	1.00	--	NA	--	--	--	--	--	--	--	--	1.00
1.00	--	1.01	--	NA	--	1.00	1.00	1.00	--	--	--	--	1.00
1.00	1.04	1.01	--	NA	1.00	1.00	--	1.00	1.53	--	1.81	--	1.00
--	--	--	--	NA	--	1.01	1.00	1.00	0.95	--	--	--	1.00
1.00	1.04	--	--	NA	--	1.00	1.00	1.00	1.00	1.00	0.99	--	1.00
1.00	1.04	--	--	--	--	--	1.00	1.00	1.03	1.00	0.99	--	1.00
1.00	1.04	--	--	--	--	NA	1.00	1.00	0.88	1.00	0.99	--	1.00
1.00	1.04	--	--	--	1.00	--	1.00	1.00	1.02	1.00	0.98	NA	1.00
1.00	--	1.01	0.81	0.00	1.00	1.00	--	1.00	NA	1.00	--	1.00	1.01
1.00	**0.96**	**0.99**	**0.07**	**0.01**	**1.00**	**1.00**	**1.00**	**1.00**	**0.97**	**1.00**	**0.93**	**0.99**	**1.00**

Table B.1.3. Continued…

BMD	BMS	BML	DUN	CEP	MSQ	HSQ
--	--	--	0.83	--	--	--
--	1.01	1.01	0.84	--	--	--
--	1.00	--	0.84	1.00	--	--
--	1.00	1.01	0.84	1.00	0.62	--
--	0.99	--	0.84	--	--	--
--	0.98	--	0.85	1.00	--	--
--	1.02	--	0.88	--	--	--
--	1.06	--	0.93	--	--	--
--	--	--	0.94	--	--	--
--	--	--	0.94	--	--	--
--	1.11	--	0.93	1.00	0.63	--
--	1.02	1.02	0.86	--	0.61	--
--	0.99	1.02	0.84	--	0.62	--
--	0.99	1.02	0.84	1.02	0.62	--
--	0.90	1.01	0.88	1.00	0.62	--
--	1.01	1.00	0.91	1.00	0.62	--
--	1.02	1.00	--	--	0.62	--
--	1.00	1.00	--	--	0.63	--
--	0.98	1.01	--	--	0.62	1.00
NA	0.96	1.01	0.86	1.00	0.62	--
--	**0.99**	**1.00**	**1.14**	**1.00**	**1.61**	**1.00**

Appendix B.2: Evidence for direct effect of OA

Table B.2.1. Direct effects of ocean acidification on five groups parameterized to respond directly to pH, with effect sizes $E > |0.2|$. Columns indicate the scenario, with all groups responding or only one group with a pH response turned on, with rows representing the five functional groups and their total effect size for each run. Entirely direct effects are identified with red.

	Scenario										
Functional Group	**All**	**Benthic herbivorous grazers**	**Meso-zooplankton**	**Bivalve**	**Pteropod**	**Shallow benthic filter feeders**	**Crangon shrimp**	**Dungeness crab**	**Crabs**	**Benthic carnivores**	**Deposit feeders**
Benthic herbivorous grazers	-0.61	-0.62	0.02	0.05	0.01	0.02	0.04	0.03	0.01	-0.01	-0.03
Meso-zooplankton	-0.07	-0.04	-0.02	-0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bivalves	-0.29	0.02	0.01	-0.37	0.00	0.01	0.07	0.00	0.00	0.01	0.00
Pteropods	-0.09	-0.04	-0.04	-0.01	-0.01	0.00	0.00	0.00	0.00	0.00	0.00
Shallow benthic filter feeders	0.11	-0.01	0.01	0.09	0.00	-0.04	0.04	0.00	0.00	0.01	0.00
Crangon shrimp	-0.19	0.00	0.01	0.06	0.00	0.00	-0.23	0.01	0.00	-0.06	0.00
Dungeness crab	-0.42	0.05	0.00	-0.45	0.00	0.01	0.09	-0.02	0.00	0.01	0.00
Crabs	-0.12	-0.48	0.00	-0.15	0.00	0.01	0.01	-0.02	-0.33	0.14	0.00
Benthic carnivores	-0.22	0.01	-0.02	-0.01	0.00	0.00	0.07	0.01	0.00	-0.25	-0.01
Deposit feeders	-0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	-0.40

Appendix B.3: Comparison of Atlantis revenue outputs to PacFIN

Across the 17 U.S. ports, 16 functional groups were found to comprise >90% of revenue from catch within the model in 2013, compared to 21 in PacFIN (Figure 3, Table B.3.1). At each port revenue was comprised of between 1-6 functional groups (median 3), and 2-7 (median 4) for Atlantis and PacFIN, respectively. Six functional groups from the PacFIN primary revenue groups were not included in our analyses (because their biomass was not well represented), of the 15 remaining species 12 overlapped with primary catch in Atlantis outputs Table B.3.1. These groups include: anchovies, Dungeness crab, pandalid shrimp, Petrale sole, Dover sole, mackerel, market squid, Pacific hake, Pacific herring, sablefish, sardines, shallow large rockfish. Groups in Atlantis and not PacFIN top 90%: Bocaccio, midwater rockfish, shallow miscellaneous fish, small flatfish. Finally, groups in PacFIN top 90% not in Atlantis included six groups with biomass not well represented: Chinook salmon, crabs, large demersal predators, large pelagic predators, nearshore sea urchins and crangon shrimp, with three other species: deep large rockfish, large piscivorous flatfish and shallow small rockfish (Table B.3.1).

Table B.3.1. Species making up at minimum 90% of the revenue of catch for each of the 17 port groups within our model, from PacFIN 2013 catch data, *2013Basline* and *2063pHmortality* (the last two are an average of the last 10 years from a 100 year model). Prices per pound use 2013 price values.

Port	**PacFIN Catch**		**Base2013 Catch**		**pHmortality2063**	
	Functional Group	**Percent**	**Functional Group**	**Percent**	**Functional Group**	**Percent**
North Coast, WA	Dungeness crab	35	Dungeness crab	54	Dungeness crab	47
	Sablefish	24	Petrale sole	16	Small flatfish	16
	Chinook salmon	11	Small flatfish	12	Midwater rockfish	12
	Large piscivorous flatfish	9	Midwater rockfish	9	Petrale sole	11
	Crangon shrimp	7			Sablefish	7
	Petrale sole	4				
South Coast, WA	Dungeness crab	61	Dungeness crab	65	Dungeness crab	45
	Pacific hake	10	Sardines	19	Sardines	29
	Sardines	9	Pandalid shrimp	10	Pandalid shrimp	18
	Pandalid shrimp	8				
	Large pelagic predators	7				
Astoria, OR	Dungeness crab	34	Dungeness crab	35	Sardines	37
	Pacific hake	19	Sardines	25	Pandalid shrimp	16

	Sardines	14	Petrale sole	13	Dungeness crab	14
	Pandalid shrimp	8	Pandalid shrimp	9	Petrale sole	9
	Dover sole	6	Small flatfish	5	Small flatfish	7
	Sablefish	6	Pacific hake	4	Pacific hake	6
	Petrale sole	5			Midwater rockfish	4
Tillamook, OR	Dungeness crab	86	Dungeness crab	97	Dungeness crab	83
	Large pelagic predators	5			Shallow large rockfish	9
Newport, OR	Dungeness crab	40	Dungeness crab	58	Pandalid shrimp	68
	Pacific hake	25	Pandalid shrimp	26	Pacific hake	16
	Pandalid shrimp	18	Pacific hake	7	Petrale sole	4
	Sablefish	6			Dungeness crab	4
	Large pelagic predators	4				
Coos Bay, OR	Dungeness crab	46	Dungeness crab	44	Pandalid shrimp	84
	Pandalid shrimp	32	Pandalid shrimp	43	Petrale sole	6
	Chinook salmon	6	Petrale sole	8		
	Sablefish	5				
	Large pelagic predators	3				
Brookings, OR	Dungeness crab	73	Dungeness crab	53	Pandalid shrimp	55
	Pandalid shrimp	9	Pandalid shrimp	24	Shallow large rockfish	18
	Sablefish	5	Shallow large rockfish	10	Dungeness crab	10
	Dover sole	3	Dover sole	5	Dover sole	6
					Small flatfish	4
Crescent City, CA	Dungeness crab	89	Dungeness crab	62	Pandalid shrimp	77
	Pandalid shrimp	8	Pandalid shrimp	35	Dungeness crab	18
Eureka, CA	Dungeness crab	81	Dungeness crab	66	Dungeness crab	61
	Dover sole	4	Petrale sole	13	Pandalid shrimp	17
	Sablefish	3	Pandalid shrimp	10	Petrale sole	9
	Pandalid shrimp	3	Dover sole	7	Dover sole	7
Fort Bragg, CA	Chinook salmon	32	Dungeness crab	40	Dungeness crab	44
	Nearshore sea urchins	26	Petrale sole	20	Midwater rockfish	17
	Dungeness crab	17	Midwater rockfish	14	Petrale sole	11
	Sablefish	11	Dover sole	8	Bocaccio	7

	Dover sole	3	Bocaccio	6	Dover sole	7
			Sablefish	5	Sablefish	6
Bodega Bay, CA	Dungeness crab	72	Dungeness crab	98	Dungeness crab	98
	Chinook salmon	23				
San Francisco, CA	Dungeness crab	57	Market squid	61	Market squid	63
	Market squid	16	Dungeness crab	18	Dungeness crab	18
	Chinook salmon	14	Shallow misc. fish	5	Shallow misc. fish	4
	Pacific herring	3	Petrale sole	4	Pacific herring	4
			Pacific herring	4	Small flatfish	3
Monterey, CA	Market squid	66	Market squid	68	Market squid	68
	Dungeness crab	14	Anchovies	28	Anchovies	28
	Anchovies	5				
	Chinook salmon	4				
	Crangon shrimp	3				
Morro Bay, CA	Dungeness crab	24	Market squid	46	Market squid	49
	Sablefish	24	Dungeness crab	16	Dungeness crab	17
	Market squid	18	Shallow large rockfish	15	Shallow large rockfish	15
	Deep large rockfish	9	Shallow misc. fish	6	Shallow misc. fish	5
	Shallow large rockfish	5	Petrale sole	6	Sablefish	4
	Crangon shrimp	4	Sablefish	4		
	Shallow small rockfish	3				
	Large demersal predators	3				
Santa Barbara, CA	Market squid	66	Market squid	85	Market squid	86
	Crabs	15	Shallow misc. fish	13	Shallow misc. fish	11
	Nearshore sea urchins	10				
Los Angeles, CA	Market squid	70	Market squid	87	Market squid	88
	Crabs	12	Mackerel	4	Mackerel	4
	Mackerel	4				
San Diego, CA	Crabs	64	Shallow misc. fish	70	Shallow misc. fish	70
	Crangon shrimp	14	Anchovies	25	Anchovies	25
	Nearshore sea urchins	7				

Table B.3.2. Total revenue by port, across 10 fleets modeled spatially, for both PacFIN and Atlantis outputs (using *2013Baseline*), and the corresponding proportion of coast wide revenue landed at each port.

Port_Name	PacFIN Revenue	PacFIN Revenue proportion	Atlantis Revenue	Atlantis Revenue Proportions
North_WA_coast	$9,291,420	2.0%	$8,500,256	1.5%
South_WA_coast	$73,060,305	15.7%	$97,438,844	16.8%
Astoria	$45,509,886	9.8%	$67,460,151	11.6%
Tillamook	$2,763,064	0.6%	$3,923,206	0.7%
Newport	$46,778,417	10.0%	$54,050,186	9.3%
Coos_Bay	$31,466,219	6.7%	$39,199,176	6.7%
Brookings	$23,551,225	5.1%	$15,097,609	2.6%
Crescent_City	$34,331,063	7.4%	$13,741,704	2.4%
Eureka	$28,936,870	6.2%	$16,635,508	2.9%
Fort_Bragg	$12,841,101	2.8%	$5,343,488	0.9%
Bodega_Bay	$10,378,995	2.2%	$3,790,846	0.7%
San_Francisco	$32,336,679	6.9%	$23,064,372	4.0%
Monterey	$14,942,591	3.2%	$38,968,649	6.7%
Morro_Bay	$7,676,309	1.6%	$8,129,502	1.4%
Santa_Barbara	$48,425,418	10.4%	$101,207,149	17.4%
Los_Angeles	$36,532,224	7.8%	$79,863,880	13.7%
San_Diego	$7,437,268	1.6%	$4,961,611	0.9%

Table B.3.3. Comparison of catch composition between PacFIN 2013 data and Atlantis model projections (averaged over the last 10 years of 100 year model run) for each fleet type and port combination (where that fleet is landed at the identified port).

Vessel Type	**Port**	**PacFIN group**	**Percent of PacFIN catch**	**Atlantis Group**	**Percent of Atlantis catch**
Hake_trawler	North_WA_coast	Dungeness crab	64.48%	Dungeness crab	100.00%
Hake_trawler	North_WA_coast	Chinook salmon	35.52%		

Hake_trawler	South_WA_coast	Pacific hake	90.60%	Pacific hake	62.97%
Hake_trawler	South_WA_coast			Dungeness crab	13.76%
Hake_trawler	South_WA_coast			Squid	10.09%
Hake_trawler	South_WA_coast			Midwater rockfish	4.07%
Hake_trawler	Astoria	Pacific hake	86.87%	Pacific hake	54.76%
Hake_trawler	Astoria	Dungeness crab	5.97%	Dungeness crab	16.85%
Hake_trawler	Astoria			Midwater rockfish	12.01%
Hake_trawler	Astoria			Petrale sole	7.53%
Hake_trawler	Newport	Pacific hake	88.26%	Pacific hake	59.43%
Hake_trawler	Newport	Dungeness crab	6.05%	Dungeness crab	20.03%
Hake_trawler	Newport			Petrale sole	13.27%
Hake_trawler	Brookings	Dungeness crab	89.89%	Dungeness crab	82.44%
Hake_trawler	Brookings	Dover sole	4.55%	Dover sole	8.62%
Large_groundfish_trawl	North_WA_coast	Petrale sole	30.49%	Petrale sole	40.88%
Large_groundfish_trawl	North_WA_coast	Midwater rockfish	27.73%	Small flatfish	30.30%
Large_groundfish_trawl	North_WA_coast	Small flatfish	9.49%	Midwater rockfish	22.15%
Large_groundfish_trawl	North_WA_coast	Large demersal predators	6.15%		
Large_groundfish_trawl	North_WA_coast	Dover sole	5.82%		
Large_groundfish_trawl	North_WA_coast	Deep demersal fish	4.22%		
Large_groundfish_trawl	North_WA_coast	Chinook salmon	3.96%		
Large_groundfish_trawl	North_WA_coast	Skates and rays	3.55%		
Large_groundfish_trawl	South_WA_coast	Dungeness crab	43.24%	Petrale sole	44.73%
Large_groundfish_trawl	South_WA_coast	Petrale sole	19.90%	Dungeness crab	38.67%
Large_groundfish_trawl	South_WA_coast	Sablefish	13.20%	Small flatfish	6.38%
Large_groundfish_trawl	South_WA_coast	Dover sole	7.84%	Dover sole	4.79%
Large_groundfish_trawl	South_WA_coast	Large demersal predators	4.73%		
Large_groundfish_trawl	South_WA_coast	Deep large rockfish	3.07%		
Large_groundfish_trawl	Astoria	Dover sole	28.42%	Petrale sole	48.97%
Large_groundfish_trawl	Astoria	Petrale sole	24.45%	Small flatfish	18.54%

Large_groundfish_trawl	Astoria	Sablefish	13.42%	Dover sole	14.44%
Large_groundfish_trawl	Astoria	Midwater rockfish	6.52%	Midwater rockfish	6.96%
Large_groundfish_trawl	Astoria	Skates and rays	4.54%	Pandalid shrimp	3.62%
Large_groundfish_trawl	Astoria	Pandalid shrimp	4.05%		
Large_groundfish_trawl	Astoria	Small flatfish	4.04%		
Large_groundfish_trawl	Astoria	Dungeness crab	3.54%		
Large_groundfish_trawl	Astoria	Large demersal predators	3.39%		
Large_groundfish_trawl	Newport	Pacific hake	31.29%	Dungeness crab	48.22%
Large_groundfish_trawl	Newport	Dungeness crab	31.17%	Petrale sole	16.91%
Large_groundfish_trawl	Newport	Dover sole	13.10%	Dover sole	11.73%
Large_groundfish_trawl	Newport	Sablefish	10.18%	Pacific hake	9.84%
Large_groundfish_trawl	Newport	Petrale sole	4.60%	Small flatfish	4.89%
Large_groundfish_trawl	Coos_Bay	Dungeness crab	26.73%	Petrale sole	29.54%
Large_groundfish_trawl	Coos_Bay	Pandalid shrimp	26.31%	Pandalid shrimp	28.15%
Large_groundfish_trawl	Coos_Bay	Dover sole	15.10%	Dungeness crab	19.97%
Large_groundfish_trawl	Coos_Bay	Petrale sole	11.97%	Small flatfish	10.05%
Large_groundfish_trawl	Coos_Bay	Sablefish	10.91%	Dover sole	9.28%
Large_groundfish_trawl	Brookings	Pandalid shrimp	33.19%	Pandalid shrimp	49.81%
Large_groundfish_trawl	Brookings	Dungeness crab	20.87%	Dover sole	17.68%
Large_groundfish_trawl	Brookings	Dover sole	20.50%	Petrale sole	11.63%
Large_groundfish_trawl	Brookings	Sablefish	13.83%	Small flatfish	8.71%
Large_groundfish_trawl	Brookings	Petrale sole	3.55%	Dungeness crab	8.71%
Large_groundfish_trawl	Crescent_City	Dungeness crab	68.07%	Pandalid shrimp	73.92%
Large_groundfish_trawl	Crescent_City	Pandalid shrimp	31.93%	Dungeness crab	26.08%
Large_groundfish_trawl	Eureka	Dungeness crab	34.31%	Petrale sole	44.08%
Large_groundfish_trawl	Eureka	Dover sole	22.57%	Dover sole	22.22%
Large_groundfish_trawl	Eureka	Sablefish	14.25%	Dungeness crab	16.20%
Large_groundfish_trawl	Eureka	Petrale sole	12.11%	Small flatfish	8.33%
Large_groundfish_trawl	Eureka	Deep small rockfish	5.36%		

Large_groundfish_trawl	Eureka	Deep large rockfish	5.30%		
Large_groundfish_trawl	Fort_Bragg	Sablefish	25.58%	Petrale sole	32.82%
Large_groundfish_trawl	Fort_Bragg	Dover sole	21.12%	Midwater rockfish	25.81%
Large_groundfish_trawl	Fort_Bragg	Midwater rockfish	15.57%	Dover sole	16.84%
Large_groundfish_trawl	Fort_Bragg	Deep small rockfish	11.56%	Bocaccio	10.87%
Large_groundfish_trawl	Fort_Bragg	Petrale sole	10.79%	Small flatfish	5.95%
Large_groundfish_trawl	Fort_Bragg	Deep large rockfish	10.79%		
Large_groundfish_trawl	San_Francisco	Dungeness crab	32.41%	Petrale sole	28.82%
Large_groundfish_trawl	San_Francisco	Large piscivorous flatfish	31.42%	Small flatfish	24.29%
Large_groundfish_trawl	San_Francisco	Dover sole	10.15%	Shallow miscellaneous fish	13.12%
Large_groundfish_trawl	San_Francisco	Petrale sole	9.57%	Dover sole	7.82%
Large_groundfish_trawl	San_Francisco	Small flatfish	3.67%	Dungeness crab	5.63%
Large_groundfish_trawl	San_Francisco	Deep small rockfish	3.57%	Midwater rockfish	5.49%
Large_groundfish_trawl	San_Francisco			Bocaccio	5.02%
Large_groundfish_trawl	Monterey	Deep large rockfish	33.53%	Petrale sole	64.51%
Large_groundfish_trawl	Monterey	Sablefish	27.54%	Small flatfish	20.86%
Large_groundfish_trawl	Monterey	Petrale sole	18.98%	Sablefish	4.16%
Large_groundfish_trawl	Monterey	Deep small rockfish	9.36%	Bocaccio	2.88%
Large_groundfish_trawl	Monterey	Deep demersal fish	4.06%		
Large_groundfish_trawl	Morro_Bay	Deep large rockfish	46.65%	Petrale sole	68.67%
Large_groundfish_trawl	Morro_Bay	Petrale sole	20.98%	Dover sole	14.15%
Large_groundfish_trawl	Morro_Bay	Dover sole	16.91%	Bocaccio	5.90%
Large_groundfish_trawl	Morro_Bay	Deep small rockfish	6.45%	Deep large rockfish	3.74%
Large_groundfish_trawl	Santa_Barbara	Large piscivorous flatfish	90.45%	Crangon shrimp	99.43%
Large_groundfish_trawl	Bodega_Bay	Dungeness crab	100.00%	Dungeness crab	100.00%
Small_groundfish_trawl	North_WA_coast	Sablefish	29.92%	Petrale sole	57.98%
Small_groundfish_trawl	North_WA_coast	Large piscivorous flatfish	26.85%	Midwater rockfish	20.51%
Small_groundfish_trawl	North_WA_coast	Chinook salmon	20.98%	Sablefish	10.63%

Small_groundfish_trawl	North_WA_coast	Petrale sole	12.67%	Large piscivorous flatfish	7.92%
Small_groundfish_trawl	South_WA_coast	Midwater rockfish	57.34%	Midwater rockfish	50.16%
Small_groundfish_trawl	South_WA_coast	Spiny dogfish	38.31%	Squid	34.77%
Small_groundfish_trawl	South_WA_coast			Spiny dogfish	14.67%
Small_groundfish_trawl	San_Francisco	Large piscivorous flatfish	98.12%	Large piscivorous flatfish	52.41%
Small_groundfish_trawl	San_Francisco			Small flatfish	47.59%
Small_groundfish_trawl	Monterey	Dover sole	56.36%	Dover sole	41.75%
Small_groundfish_trawl	Monterey	Deep large rockfish	10.72%	Small flatfish	32.11%
Small_groundfish_trawl	Monterey	Sablefish	10.22%	Petrale sole	12.15%
Small_groundfish_trawl	Monterey	Deep small rockfish	10.00%	Bocaccio	10.00%
Small_groundfish_trawl	Monterey	Small flatfish	5.13%		
Small_groundfish_trawl	Morro_Bay	Large piscivorous flatfish	100.00%	Large piscivorous flatfish	100.00%
Small_groundfish_trawl	Santa_Barbara	Large piscivorous flatfish	57.56%	Crangon shrimp	77.67%
Small_groundfish_trawl	Santa_Barbara	Shallow miscellaneous fish	13.67%	Shallow miscellaneous fish	21.64%
Small_groundfish_trawl	Santa_Barbara	Deposit feeders	10.56%		
Small_groundfish_trawl	Santa_Barbara	Crangon shrimp	8.32%		
Small_groundfish_trawl	Los_Angeles	Large piscivorous flatfish	92.55%	Crangon shrimp	90.93%
Small_groundfish_trawl	San_Diego	Large piscivorous flatfish	76.60%	Shallow miscellaneous fish	92.08%
Small_groundfish_trawl	San_Diego	Large pelagic predators	17.55%		
Sablefish_fixed	North_WA_coast	Sablefish	53.73%	Sablefish	62.23%
Sablefish_fixed	North_WA_coast	Chinook salmon	27.43%	Dungeness crab	19.93%
Sablefish_fixed	North_WA_coast	Large piscivorous flatfish	11.37%	Large piscivorous flatfish	10.93%
Sablefish_fixed	South_WA_coast	Dungeness crab	61.77%	Dungeness crab	91.64%
Sablefish_fixed	South_WA_coast	Sablefish	36.65%		
Sablefish_fixed	Astoria	Sablefish	54.55%	Dungeness crab	87.09%
Sablefish_fixed	Astoria	Dungeness crab	44.99%	Sablefish	12.70%
Sablefish_fixed	Newport	Sablefish	65.55%	Dungeness crab	82.24%

Sablefish_fixed	Newport	Dungeness crab	33.86%	Sablefish	16.15%
Sablefish_fixed	Coos_Bay	Sablefish	77.16%	Sablefish	83.88%
Sablefish_fixed	Coos_Bay	Chinook salmon	15.23%	Small flatfish	11.61%
Sablefish_fixed	Brookings	Sablefish	85.21%	Sablefish	66.31%
Sablefish_fixed	Brookings	Large demersal predators	7.19%	Darkblotched rockfish	17.28%
Sablefish_fixed	Brookings			Shallow large rockfish	9.93%
Sablefish_fixed	Crescent_City	Dungeness crab	100.00%	Dungeness crab	100.00%
Sablefish_fixed	Eureka	Sablefish	96.78%	Sablefish	97.67%
Sablefish_fixed	Fort_Bragg	Sablefish	52.11%	Sablefish	39.08%
Sablefish_fixed	Fort_Bragg	Chinook salmon	29.37%	Shallow large rockfish	36.89%
Sablefish_fixed	Fort_Bragg	Dungeness crab	5.79%	Dungeness crab	19.06%
Sablefish_fixed	Fort_Bragg	Deep large rockfish	4.84%		
Sablefish_fixed	San_Francisco	Dungeness crab	91.73%	Dungeness crab	93.01%
Sablefish_fixed	Monterey	Sablefish	73.20%	Sablefish	74.10%
Sablefish_fixed	Monterey	Deep large rockfish	17.72%	Shallow large rockfish	10.73%
Sablefish_fixed	Monterey			Deep large rockfish	9.98%
Sablefish_fixed	Morro_Bay	Sablefish	76.86%	Sablefish	67.91%
Sablefish_fixed	Morro_Bay	Deep large rockfish	19.62%	Squid	12.76%
Sablefish_fixed	Morro_Bay			Deep large rockfish	9.11%
Sablefish_fixed	Morro_Bay			Shallow large rockfish	4.11%
Sablefish_fixed	Santa_Barbara	Sablefish	63.03%	Sablefish	71.29%
Sablefish_fixed	Santa_Barbara	Deep large rockfish	24.82%	Deep large rockfish	15.49%
Sablefish_fixed	Santa_Barbara	Nearshore sea urchins	7.30%	Shallow large rockfish	10.33%
Sablefish_fixed	Los_Angeles	Sablefish	73.96%	Bocaccio	39.76%
Sablefish_fixed	Los_Angeles	Deep large rockfish	20.22%	Sablefish	37.29%
Sablefish_fixed	Los_Angeles			Shallow miscellaneous fish	6.14%
Sablefish_fixed	Los_Angeles			Midwater rockfish	6.11%
Sablefish_fixed	Los_Angeles			Deep large rockfish	5.62%

Sablefish_fixed	Bodega_Bay	Sablefish	72.38%	Sablefish	60.39%
Sablefish_fixed	Bodega_Bay	Chinook salmon	10.14%	Dungeness crab	24.49%
Sablefish_fixed	Bodega_Bay	Dungeness crab	10.13%	Midwater rockfish	9.17%
Sablefish_fixed	San_Diego	Sablefish	58.01%	Sablefish	79.87%
Sablefish_fixed	San_Diego	Deep large rockfish	25.11%	Deep large rockfish	18.95%
Sablefish_fixed	San_Diego	Crabs	15.47%		
Other_groundfish_fixed	North_WA_coast	Large piscivorous flatfish	54.45%	Crangon shrimp	95.57%
Other_groundfish_fixed	North_WA_coast	Chinook salmon	30.59%		
Other_groundfish_fixed	North_WA_coast	Sablefish	10.07%		
Other_groundfish_fixed	South_WA_coast	Large piscivorous flatfish	57.22%	Large piscivorous flatfish	68.35%
Other_groundfish_fixed	South_WA_coast	Sablefish	24.60%	Sablefish	31.65%
Other_groundfish_fixed	South_WA_coast	Large pelagic predators	17.94%		
Other_groundfish_fixed	Astoria	Large piscivorous flatfish	98.43%	Large piscivorous flatfish	79.40%
Other_groundfish_fixed	Astoria			Shallow large rockfish	20.54%
Other_groundfish_fixed	Newport	Shallow large rockfish	48.30%	Shallow large rockfish	96.37%
Other_groundfish_fixed	Newport	Large demersal predators	27.97%		
Other_groundfish_fixed	Newport	Large piscivorous flatfish	16.69%		
Other_groundfish_fixed	Coos_Bay	Shallow large rockfish	42.44%	Shallow large rockfish	90.25%
Other_groundfish_fixed	Coos_Bay	Large piscivorous flatfish	27.60%		
Other_groundfish_fixed	Coos_Bay	Large demersal predators	22.63%		
Other_groundfish_fixed	Brookings	Shallow large rockfish	60.98%	Shallow large rockfish	97.41%
Other_groundfish_fixed	Brookings	Large demersal predators	24.54%		
Other_groundfish_fixed	Brookings	Chinook salmon	5.30%		
Other_groundfish_fixed	Crescent_City	Shallow large rockfish	87.48%	Shallow large rockfish	96.08%
Other_groundfish_fixed	Crescent_City	Large demersal predators	7.36%		
Other_groundfish_fixed	Fort_Bragg	Large demersal predators	58.43%	Shallow large rockfish	80.09%
Other_groundfish_fixed	Fort_Bragg	Shallow large rockfish	18.71%	Shallow small rockfish	10.22%
Other_groundfish_fixed	Fort_Bragg	Shallow small rockfish	14.47%		
Other_groundfish_fixed	San_Francisco	Large piscivorous flatfish	42.11%	Shallow large rockfish	66.85%

Other_groundfish_fixed	San_Francisco	Shallow large rockfish	29.14%	Shallow miscellaneous fish	20.71%
Other_groundfish_fixed	San_Francisco	Shallow small rockfish	9.11%	Large piscivorous flatfish	4.81%
Other_groundfish_fixed	San_Francisco	Large demersal predators	8.97%		
Other_groundfish_fixed	San_Francisco	Chinook salmon	6.44%		
Other_groundfish_fixed	Monterey	Large piscivorous flatfish	32.29%	Shallow miscellaneous fish	54.14%
Other_groundfish_fixed	Monterey	Chinook salmon	24.75%	Shallow large rockfish	21.84%
Other_groundfish_fixed	Monterey	Large demersal predators	21.69%	Large piscivorous flatfish	8.29%
Other_groundfish_fixed	Monterey	Sablefish	5.60%	Midwater rockfish	7.49%
Other_groundfish_fixed	Monterey	Shallow large rockfish	4.34%		
Other_groundfish_fixed	Monterey	Crabs	3.71%		
Other_groundfish_fixed	Morro_Bay	Shallow large rockfish	36.27%	Shallow large rockfish	63.58%
Other_groundfish_fixed	Morro_Bay	Shallow small rockfish	26.01%	Shallow miscellaneous fish	24.97%
Other_groundfish_fixed	Morro_Bay	Large demersal predators	21.50%	Shallow small rockfish	6.96%
Other_groundfish_fixed	Morro_Bay	Chinook salmon	7.30%		
Other_groundfish_fixed	Santa_Barbara	Deep large rockfish	20.37%	Shallow miscellaneous fish	84.29%
Other_groundfish_fixed	Santa_Barbara	Large piscivorous flatfish	17.40%	Shallow large rockfish	8.61%
Other_groundfish_fixed	Santa_Barbara	Shallow large rockfish	16.38%		
Other_groundfish_fixed	Santa_Barbara	Large demersal predators	15.06%		
Other_groundfish_fixed	Santa_Barbara	Shallow miscellaneous fish	8.73%		
Other_groundfish_fixed	Santa_Barbara	Crabs	8.42%		
Other_groundfish_fixed	Santa_Barbara	Sablefish	6.75%		
Other_groundfish_fixed	Los_Angeles	Deep large rockfish	71.27%	Small flatfish	84.83%
Other_groundfish_fixed	Los_Angeles	Sablefish	12.92%	Bocaccio	6.44%
Other_groundfish_fixed	Los_Angeles	Small flatfish	11.15%		
Other_groundfish_fixed	Tillamook	Large demersal predators	72.53%	Shallow large rockfish	81.26%

Other_groundfish_fixed	Tillamook	Shallow large rockfish	19.97%	Shallow miscellaneous fish	10.96%
Other_groundfish_fixed	Bodega_Bay	Chinook salmon	67.24%	Shallow large rockfish	94.57%
Other_groundfish_fixed	Bodega_Bay	Shallow large rockfish	15.83%		
Other_groundfish_fixed	Bodega_Bay	Large demersal predators	9.20%		
Other_groundfish_fixed	San_Diego	Deep large rockfish	89.14%	Deep large rockfish	74.78%
Other_groundfish_fixed	San_Diego	Deep small rockfish	5.71%	Mackerel	17.41%
Pelagic_netter	North_WA_coast	Pacific herring	100.00%	Pacific herring	100.00%
Pelagic_netter	South_WA_coast	Sardines	80.80%	Sardines	86.98%
Pelagic_netter	South_WA_coast	Dungeness crab	17.02%	Dungeness crab	9.71%
Pelagic_netter	Astoria	Sardines	98.53%	Sardines	98.54%
Pelagic_netter	Newport	Dungeness crab	100.00%	Dungeness crab	100.00%
Pelagic_netter	San_Francisco	Market squid	79.17%	Market squid	93.84%
Pelagic_netter	San_Francisco	Pacific herring	16.38%		
Pelagic_netter	Monterey	Market squid	90.61%	Market squid	70.18%
Pelagic_netter	Monterey			Anchovies	28.86%
Pelagic_netter	Morro_Bay	Market squid	99.95%	Market squid	99.71%
Pelagic_netter	Santa_Barbara	Market squid	99.44%	Market squid	97.91%
Pelagic_netter	Los_Angeles	Market squid	89.50%	Market squid	88.92%
Pelagic_netter	Los_Angeles	Mackerel	5.23%	Mackerel	4.52%
Pelagic_netter	Bodega_Bay	Chinook salmon	88.62%	Market squid	74.64%
Pelagic_netter	Bodega_Bay	Shallow miscellaneous fish	10.62%	Pacific herring	25.36%
Pelagic_netter	San_Diego	Anchovies	98.61%	Anchovies	99.78%
Shrimper	North_WA_coast	Crangon shrimp	58.43%	Crangon shrimp	99.79%
Shrimper	North_WA_coast	Dungeness crab	33.49%		
Shrimper	South_WA_coast	Pandalid shrimp	82.33%	Pandalid shrimp	84.66%
Shrimper	South_WA_coast	Dungeness crab	17.67%	Dungeness crab	15.34%
Shrimper	Astoria	Pandalid shrimp	59.81%	Crangon shrimp	50.24%

Shrimper	Astoria	Dungeness crab	32.59%	Pandalid shrimp	31.31%
Shrimper	Astoria			Dungeness crab	15.37%
Shrimper	Newport	Pandalid shrimp	57.04%	Pandalid shrimp	42.31%
Shrimper	Newport	Dungeness crab	36.41%	Dungeness crab	26.75%
Shrimper	Newport			Crangon shrimp	26.65%
Shrimper	Coos_Bay	Pandalid shrimp	67.44%	Pandalid shrimp	72.88%
Shrimper	Coos_Bay	Dungeness crab	23.28%	Dungeness crab	17.57%
Shrimper	Brookings	Dungeness crab	60.84%	Pandalid shrimp	69.84%
Shrimper	Brookings	Pandalid shrimp	39.16%	Dungeness crab	30.16%
Shrimper	Crescent_City	Dungeness crab	53.31%	Pandalid shrimp	82.13%
Shrimper	Crescent_City	Pandalid shrimp	44.86%	Dungeness crab	16.15%
Shrimper	Eureka	Dungeness crab	39.24%	Pandalid shrimp	52.27%
Shrimper	Eureka	Pandalid shrimp	32.90%	Dungeness crab	17.18%
Shrimper	Eureka	Dover sole	14.41%	Dover sole	13.16%
Shrimper	Eureka	Sablefish	5.77%	Petrale sole	10.96%
Shrimper	San_Francisco	Dungeness crab	55.67%	Crangon shrimp	99.62%
Shrimper	San_Francisco	Crangon shrimp	43.15%		
Shrimper	Monterey	Crangon shrimp	93.86%	Crangon shrimp	100.00%
Shrimper	Morro_Bay	Crangon shrimp	92.57%	Crangon shrimp	99.99%
Shrimper	Santa_Barbara	Crangon shrimp	85.15%	Crangon shrimp	99.56%
Shrimper	Santa_Barbara	Deposit feeders	5.81%		
Shrimper	Los_Angeles	Crangon shrimp	86.21%	Crangon shrimp	100.00%
Shrimper	Los_Angeles	Crabs	13.65%		
Shrimper	Tillamook	Dungeness crab	95.46%	Crangon shrimp	74.86%
Shrimper	Tillamook			Dungeness crab	24.33%
Shrimper	Bodega_Bay	Dungeness crab	100.00%	Dungeness crab	100.00%
Shrimper	San_Diego	Crangon shrimp	71.37%	Crangon shrimp	99.99%
Shrimper	San_Diego	Crabs	28.00%		
Crabber	North_WA_coast	Dungeness crab	79.12%	Crangon shrimp	96.79%

Crabber	North_WA_coast	Crangon shrimp	8.55%		
Crabber	North_WA_coast	Large piscivorous flatfish	4.68%		
Crabber	South_WA_coast	Dungeness crab	86.59%	Dungeness crab	56.68%
Crabber	South_WA_coast	Large pelagic predators	10.92%	Crangon shrimp	42.70%
Crabber	Astoria	Dungeness crab	91.08%	Dungeness crab	98.37%
Crabber	Newport	Dungeness crab	74.30%	Dungeness crab	96.65%
Crabber	Newport	Large pelagic predators	12.67%		
Crabber	Newport	Sablefish	4.19%		
Crabber	Coos_Bay	Dungeness crab	70.83%	Crangon shrimp	77.98%
Crabber	Coos_Bay	Chinook salmon	11.01%	Dungeness crab	19.41%
Crabber	Coos_Bay	Large pelagic predators	5.99%		
Crabber	Coos_Bay	Pandalid shrimp	4.49%		
Crabber	Brookings	Dungeness crab	88.92%	Dungeness crab	93.22%
Crabber	Brookings	Chinook salmon	3.40%		
Crabber	Crescent_City	Dungeness crab	95.40%	Crangon shrimp	93.55%
Crabber	Eureka	Dungeness crab	89.88%	Dungeness crab	82.47%
Crabber	Eureka	Chinook salmon	3.06%	Pandalid shrimp	9.16%
Crabber	Fort_Bragg	Chinook salmon	53.77%	Dungeness crab	73.10%
Crabber	Fort_Bragg	Dungeness crab	32.44%	Petrale sole	10.14%
Crabber	Fort_Bragg	Sablefish	9.30%	Midwater rockfish	4.87%
Crabber	Fort_Bragg			Sablefish	4.77%
Crabber	San_Francisco	Dungeness crab	78.54%	Crangon shrimp	90.38%
Crabber	San_Francisco	Chinook salmon	18.82%		
Crabber	Monterey	Dungeness crab	79.61%	Dungeness crab	65.89%
Crabber	Monterey	Chinook salmon	14.26%	Crangon shrimp	25.18%
Crabber	Morro_Bay	Dungeness crab	85.02%	Dungeness crab	96.08%
Crabber	Morro_Bay	Sablefish	7.52%		
Crabber	Santa_Barbara	Crabs	97.10%	Bivalves	40.04%
Crabber	Santa_Barbara			Shallow miscellaneous	34.62%

				fish	
Crabber	Santa_Barbara			Shallow large rockfish	7.65%
Crabber	Santa_Barbara			Dungeness crab	7.60%
Crabber	Santa_Barbara			Bocaccio	7.21%
Crabber	Los_Angeles	Crabs	91.76%	Bivalves	92.98%
Crabber	Tillamook	Dungeness crab	85.73%	Dungeness crab	98.36%
Crabber	Tillamook	Large pelagic predators	6.95%		
Crabber	Bodega_Bay	Dungeness crab	75.78%	Crangon shrimp	70.50%
Crabber	Bodega_Bay	Chinook salmon	21.53%	Dungeness crab	29.35%
Crabber	San_Diego	Crabs	92.81%	Shallow miscellaneous fish	82.50%
Crabber	San_Diego			Bivalves	14.09%
Lobster_vessel	San_Francisco	Chinook salmon	99.94%	Bocaccio	69.31%
Lobster_vessel	San_Francisco			Shallow large rockfish	30.69%
Lobster_vessel	Monterey	Chinook salmon	100.00%		
Lobster_vessel	Morro_Bay	Chinook salmon	97.00%		
Lobster_vessel	Santa_Barbara	Crabs	96.54%	Shallow miscellaneous fish	99.45%
Lobster_vessel	Los_Angeles	Crabs	97.12%	Crangon shrimp	87.18%
Lobster_vessel	Los_Angeles			Shallow miscellaneous fish	12.34%
Lobster_vessel	Bodega_Bay	Chinook salmon	100.00%		
Lobster_vessel	San_Diego	Crabs	96.75%	Crangon shrimp	53.48%
Lobster_vessel	San_Diego			Shallow miscellaneous fish	45.85%
Diver_vessel	Fort_Bragg	Nearshore sea urchins	98.51%	Dungeness crab	89.11%
Diver_vessel	Fort_Bragg			Midwater rockfish	8.99%
Diver_vessel	Monterey	Deposit feeders	52.83%	Deposit feeders	100.00%
Diver_vessel	Monterey	Nearshore sea urchins	47.17%		
Diver_vessel	Morro_Bay	Deposit feeders	100.00%	Deposit feeders	100.00%

Diver_vessel	Santa_Barbara	Nearshore sea urchins	88.62%	Crangon shrimp	75.26%
Diver_vessel	Santa_Barbara	Deposit feeders	10.16%	Shallow miscellaneous fish	19.30%
Diver_vessel	Los_Angeles	Nearshore sea urchins	74.49%	Deposit feeders	66.94%
Diver_vessel	Los_Angeles	Deposit feeders	24.18%	Bivalves	33.05%
Diver_vessel	Bodega_Bay	Dungeness crab	100.00%	Dungeness crab	100.00%
Diver_vessel	San_Diego	Nearshore sea urchins	94.64%	Deposit feeders	69.75%
Diver_vessel	San_Diego			Bivalves	30.25%

<u>Appendix B.4:</u> Economic impacts for all ports

Table B.4.1. Proportional changes in biomass of catch, revenue, income and employment by port.

Port_Name	Port_ID	Change in Catch	Change in Revenue	Change in Income	Change in Employment
North_WA_coast	PGID_102	-0.18	-0.29	-0.29	-0.31
South_WA_coast	PGID_103	-0.05	-0.38	-0.36	-0.40
Astoria	PGID_105	-0.06	-0.34	-0.31	-0.35
Tillamook	PGID_106	-0.96	-1.01	-1.00	-1.00
Newport	PGID_107	-0.10	-0.64	-0.64	-0.72
Coos_Bay	PGID_108	0.02	-0.42	-0.40	-0.47
Brookings	PGID_109	-0.15	-0.57	-0.59	-0.62
Crescent_City	PGID_110	-0.02	-0.58	-0.59	-0.71
Eureka	PGID_111	-0.19	-0.37	-0.36	-0.37
Fort_Bragg	PGID_112	-0.17	-0.15	-0.15	-0.15
Bodega_Bay	PGID_113	-0.05	-0.05	-0.05	-0.05
San_Francisco	PGID_114	-0.05	-0.06	-0.07	-0.07
Monterey	PGID_115	-0.03	-0.04	-0.04	-0.04
Morro_Bay	PGID_116	-0.05	-0.07	-0.06	-0.07
Santa_Barbara	PGID_117	-0.04	-0.06	-0.06	-0.08
Los_Angeles	PGID_118	-0.04	-0.05	-0.05	-0.05
San_Diego	PGID_119	-0.05	-0.13	-0.11	-0.14

Appendix C—Chapter 3

Appendix C.1: Full Taylor Expansion and Stability Analysis

We provide more detail for the Taylor expansions for both population models.

Population Model 1

We start with the generic forms, since they provide the key foundation.

Response to a single stressor:

$$\Delta\tilde{N}_{2\Delta s_i} \approx \frac{\partial g}{\partial s_i}(s_1, s_2)\Delta s_i + \frac{1}{2}\frac{\partial^2 g}{\partial s_i^2}(s_1, s_2)\Delta s_i^2$$

Additive response to two stressors:

$$(\Delta\tilde{N}_{2\Delta s_1} + \Delta\tilde{N}_{2\Delta s_2}) \approx \sum_{i=1}^{2}\left[\frac{\partial g}{\partial s_i}(s_1, s_2)\Delta s_i + \frac{1}{2}\frac{\partial^2 g}{\partial s_i^2}(s_1, s_2)\Delta s_i^2\right]$$

Realized response to two stressors (full multi-variate Taylor expansion):

$$\Delta\tilde{N}_{2\Delta s_1\Delta s_2} \approx \sum_{i=1}^{2}\left[\frac{\partial g}{\partial s_i}(s_1, s_2)\Delta s_i + \frac{1}{2}\frac{\partial^2 g}{\partial s_i^2}(s_1, s_2)\Delta s_i^2\right] + \frac{\partial}{\partial s_1}\left[\frac{\partial g}{\partial s_2}\right](s_1, s_2)\Delta s_1\Delta s_2$$

The key pieces in all three of the equations above are the five derivatives of $g(s_1,s_2)$: $\frac{\partial g}{\partial s_1}$, $\frac{\partial g}{\partial s_2}$, $\frac{\partial^2 g}{\partial s_1^2}$, $\frac{\partial^2 g}{\partial s_2^2}$, and $\frac{\partial}{\partial s_1}\left[\frac{\partial g}{\partial s_2}\right]$. Since we define the function g in terms of x where $x = (1- s_2)/s_1$, we can use the chain rule to find the five derivatives:

$$\frac{\partial g}{\partial s_1} = \frac{dg}{dx}\frac{\partial x}{\partial s_1}$$

$$\frac{\partial g}{\partial s_2} = \frac{dg}{dx}\frac{\partial x}{\partial s_2}$$

$$\frac{\partial^2 g}{\partial s_1^2} = \frac{d^2 g}{dx^2}\left(\frac{\partial x}{\partial s_1}\right)^2 + \frac{dg}{dx}\frac{\partial^2 x}{\partial s_1^2}$$

$$\frac{\partial^2 g}{\partial s_2^2} = \frac{d^2 g}{dx^2}\left(\frac{\partial x}{\partial s_2}\right)^2 + \frac{dg}{dx}\frac{\partial^2 x}{\partial s_2^2}$$

$$\frac{\partial}{\partial s_1}\left[\frac{\partial g}{\partial s_2}\right] = \frac{d^2 g}{dx^2}\frac{\partial x}{\partial s_1}\frac{\partial x}{\partial s_2} + \frac{dg}{dx}\frac{\partial}{\partial s_1}\left[\frac{\partial x}{\partial s_2}\right]$$

In all of these equations, both $\frac{dg}{dx}$ and $\frac{d^2 g}{dx^2}$ depend on the functional form for density dependence and cannot be solved further, however, we know the derivatives for $x=(1-s_2)/s_1$

$$\frac{\partial x}{\partial s_1} = -\frac{1-s_2}{s_1^2}$$

$$\frac{\partial x}{\partial s_2} = -\frac{1}{s_1}$$

$$\frac{\partial^2 x}{\partial s_1^2} = \frac{2(1-s_2)}{s_1^3}$$

$$\frac{\partial^2 x}{\partial s_2^2} = 0$$

$$\frac{\partial}{\partial s_1}\left[\frac{\partial x}{\partial s_2}\right] = \frac{1}{s_1^2}$$

Ultimately what matters most is the second derivative, $\frac{\partial}{\partial s_1}\left[\frac{\partial g}{\partial s_2}\right]$, from the multi-variable Taylor expansion. This is the term that makes the realized impacts from two stressors different from the expected effect with additive interactions. We can substitute the solutions for the first and second derivatives of x into $\frac{\partial}{\partial s_1}\left[\frac{\partial g}{\partial s_2}\right]$ to get our final equation:

$$\frac{\partial}{\partial s_1}\left[\frac{\partial g}{\partial s_2}\right] = \frac{1}{s_1^2}[\frac{dg}{dx} + \frac{1-s_2}{s_1}\frac{d^2 g}{dx^2}].$$

Population Model 2

The second population model turns out to be slightly more complicated because of the additional term s_0^{-1} (where $\tilde{N}_2 = \frac{f^{-1}(\frac{1-s_2}{s_0})}{s_0}$). Thus, for simplicity in this framework we define $\tilde{N}_2=h=g(y)/s_0$, where $y=(1-s_2)/s_0$.

We now care about the five derivatives of h. For this model we focus on the key derivative from the multi-variable Taylor expansion, $\frac{\partial}{\partial s_0}\left[\frac{\partial h}{\partial s_2}\right]$. Again, this is the term that defines the difference between the realized and additive effects. Because of the additional term in $\tilde{N}_2$ for this second population model, s_0^{-1}, the derivative is more involved than the similar derivative for the first population model. Since we have to take the derivative of both the numerator and the denominator of $h= g(y)/s_0$ we call the denominator, $j= s_0$. We know that $\frac{dj}{ds_2} = 0$ and that $\frac{d^2 j}{ds_0^2} = 0$, so that we can use these two equations within the process of finding the second derivative $\frac{\partial}{\partial s_0}\left[\frac{\partial h}{\partial s_2}\right]$ in order to to simplify it. This gives us the final equation for this second derivative:

$$\frac{\partial}{\partial s_0}\left[\frac{\partial h}{\partial s_2}\right] = \frac{j^2\left[j\frac{d^2 g}{dy^2}\frac{\partial y}{\partial s_0}\frac{\partial y}{\partial s_2} + j\frac{dg}{dy}\frac{\partial}{\partial s_0}\left[\frac{\partial y}{\partial s_2}\right] - \frac{dj}{ds_0}\frac{dg}{dy}\frac{\partial y}{\partial s_2}\right]}{j^4}$$

Again we know the derivatives for y and can substitute them in to find the solution for $\frac{\partial}{\partial s_0}\left[\frac{\partial h}{\partial s_2}\right]$. The three derivatives needed include:

$$\frac{\partial y}{\partial s_0} = -\frac{1-s_2}{s_0^2}$$

$$\frac{\partial y}{\partial s_2} = -\frac{1}{s_0}$$

$$\frac{\partial}{\partial s_0}\left[\frac{\partial y}{\partial s_2}\right] = \frac{1}{s_0^2}$$

Substituting these three into the equation for $\frac{\partial}{\partial s_0}\left[\frac{\partial h}{\partial s_2}\right]$ gives the solution documented in the main text:

$$\frac{\partial}{\partial s_0}\left[\frac{\partial h}{\partial s_2}\right] = \frac{1}{s_0^3}\left[2\frac{dg}{dy} + \frac{1-s_2}{s_0}\frac{d^2g}{dy^2}\right].$$

<u>*Stability Analysis*</u>

This approach relies on measurement of equilibrium population size, yet it is possible that the equilibrium population size is unstable. We performed a stability analysis to determine the minimum value the slope of the density dependence curve could take at equilibrium population size before the model becomes unstable. Following methods in Cushing (1998) we use the Jacobian matrix to find the eigenvalues,

$$\lambda_{1,2} = \frac{s_2}{2} \pm \frac{\sqrt{s_2^2 + 4s_1(p\hat{N}_2 + f(\hat{N}_2))}}{2} \tag{11}$$

where $p = \frac{df(\hat{N}_2)}{d\hat{N}_2}$ is the slope at equilibrium population size. We are interested in the minimum value of p where the population is stable. We focused our calculation on the circumstance where the eigenvalue is complex, $s_2^2 + 4s_1(p\hat{N}_2 + f(\hat{N}_2)) < 0$, such that the magnitude could be large enough to create unstable dynamics. The magnitude is then

$$M = \sqrt{\left(\frac{s_2}{2}\right)^2 + \left(\frac{\sqrt{|s_2^2 + 4s_1(p\hat{N}_2 + f(\hat{N}_2))|}}{2}\right)^2} \tag{12}$$

and we are interested in when the equilibrium is stable, such that M<1. This gives

$$\frac{s_2 - 2}{s_1 \hat{N}_2} \leq p \leq \frac{-s_2^2 + 2s_2}{2s_1 \hat{N}_2} \qquad (13).$$

We see from eqn 13 that the right side of the inequality will always be positive, thus will always be true since $p = \frac{df(\hat{N}_2)}{d\hat{N}_2}$ and $\frac{df}{dN_2} < 0$. Thus stability depends on the two survival rates and the equilibrium population size. We modify this to the final inequality $\left.\frac{df(N_2^*)}{dN_2^*}\right|_{\tilde{N}_2^*} \geq \frac{s_2 - 2}{s_1}$ where N_2^* is adult density standardized to units so that $\tilde{N}_2$=1.

For population model 2 we can repeat this method of calculating numerical stability. Using the Jacobian matrix we find the minimum value of the slope of the density dependence function at equilibrium where the population exhibits stable dynamics. For this model we find

$$\frac{s_2 - 2}{s_0 \hat{N}_1} \leq p \leq \frac{-s_2^2 + 2s_2}{2s_0 \hat{N}_1} \qquad (18).$$

In this circumstance, the model is more likely to be unstable, with the reproductive value in the denominator *p* only has to become a small negative number before instability will result. Again we simplify this in the main text to the final inequality $\left.\frac{df(N_1^*)}{dN_1^*}\right|_{\tilde{N}_1^*} \geq \frac{s_2 - 2}{s_0}$, where N_1^* is the density of the non-reproductive stage standardized to units so that $\tilde{N}_1$=1.

Appendix C.2: Explanation for stronger magnification in Model 2

As noted in the main text, Population Model 2 was found to have a stronger tendency for magnified interactions on N_2 when two stressors are acting. We see this from the two equations dictating the difference from an additive effect:

Population Model 1: $\frac{\partial}{\partial s_1}\left[\frac{\partial g}{\partial s_2}\right] = \frac{1}{s_1^2}\left[\frac{dg}{dx} + \frac{1-s_2}{s_1}\frac{d^2 g}{dx^2}\right]$

Population Model 2: $\frac{\partial}{\partial s_0}\left[\frac{\partial h}{\partial s_2}\right] = \frac{1}{s_0^3}\left[2\frac{dg}{dy} + \frac{1-s_2}{s_0}\frac{d^2 g}{dy^2}\right]$.

What is clear from the equation for Population Model 2, is that the first derivative of *g(y)* is multiplied by 2 and so the second derivative of a concave functional form has to have a larger change in slope (stronger curvature and second derivative) for mitigated impacts to occur.

The reason for this difference comes down to the timing of density dependence within population processes. In the first population model, density dependence controls recruitment into the first stage, thus stressors act on stages after density dependence has occurred. In the second model, density dependence controls survival from stage one to stage two, so that a decrease in the rate s_0 influences both recruitment into stage one, but also influences the density dependence process because it acts prior to density dependence. Density dependence is generally able to counter act the impact from a decline in s_0 by increasing the survival rate of each individual (compensation), but in this model, a reduction in s_0 is harder to counter act because it acts on the population through two mechanisms.

We demonstrate this graphically in Figure S1. In Population Model 1, the reductions in both s_1 and s_2 only act to move the points along the lines demonstrating the relationship between $f(N_2)$~N_2 and N_1~N_2. In this model we see the mitigated impacts on N_2. In Population Model 2, a reduction in s_2 only moves the points along the lines demonstrating $f(N_1)$~N_1 and N_2~N_1, where a reduction in s_0 actually shifts the line itself (Fig. S1, panel D blue line). Here, we see that a reduction in s_0 decreases the number of N_1 individuals, but the reduction in N_1 causes a smaller change in N_2 than would have been observed because of the change in the slope of the line $N_2=(1/s_0)N_1$. As the points get closer to the origin, the two lines become closer together (with the original and new s_0), so that at smaller values of N_1 there is less of a compensatory effect. When both stressors then act in tandem, we move to much smaller values of N_1 and we see the decreased ability of the density dependence function to counteract these impacts (the shift between the two lines is smaller). The result with this example is an additive effect because we have used our example function from the polynomial fraction family.

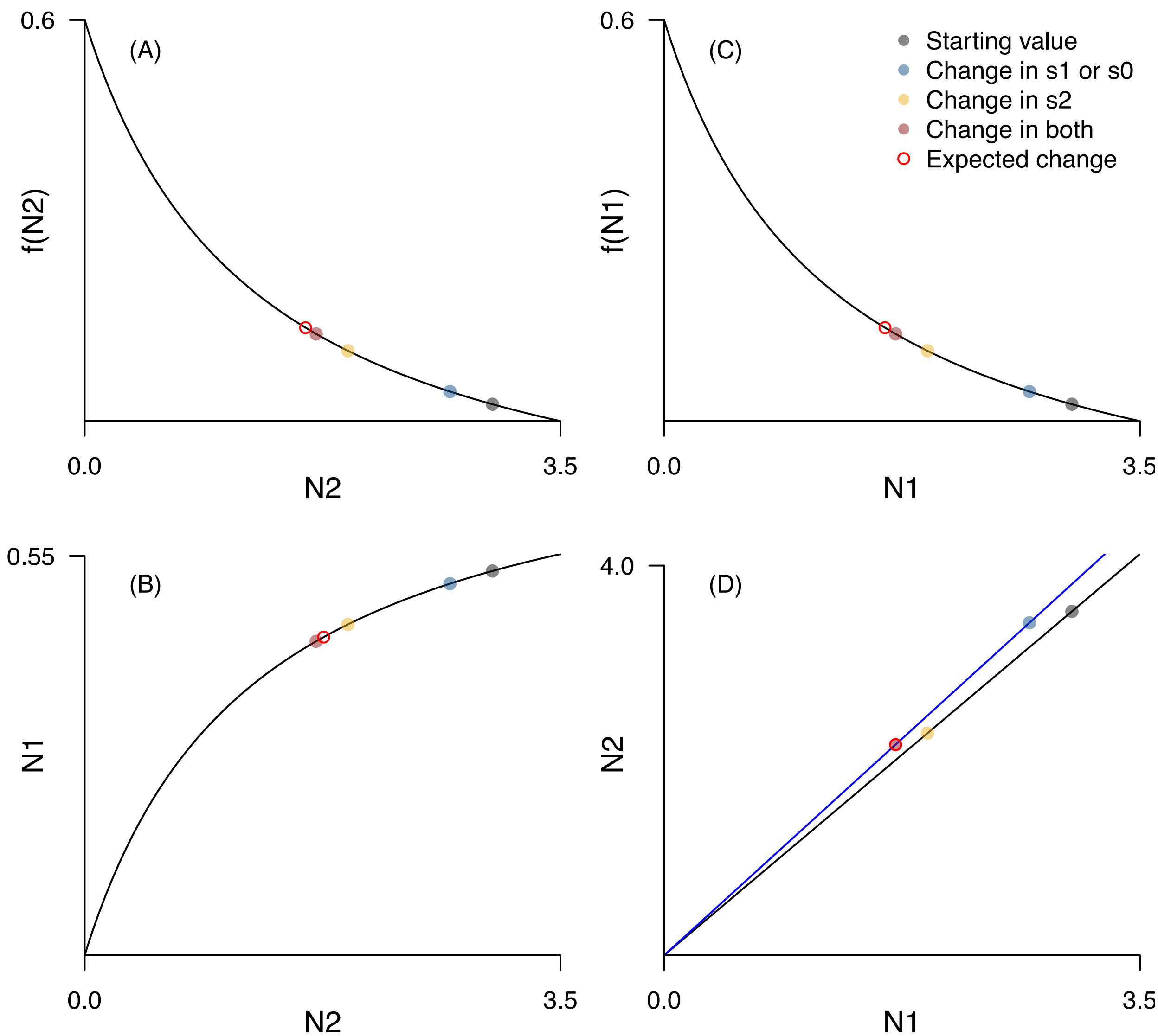

Figure C.1. Responses of stages N_1 and N_2 to two stressors under both population models. Panels (A) and (B) are plots representing the first population model, where panels (C) and (D) are plots for the second population model. In both (A) and (C), where the density dependent relationship is represented, the mitigation of multiple stressors can be clearly observed by comparing the expected change under an additive null hypothesis (open red circle) to the realized change when both stressors act (closed red circle). Thus in population model one we see a mitigation of impacts on stage N_2 and in population model two we see a mitigation of impacts on stage N_1. The bottom two panels show how the stage in which density dependence acts, responds to two stressors and how this in turn affects the other stage in the population model. Panel (B) we see that a magnification of effects on N_1. Panel (D) we see the dual role that s_0 plays, both causing a change in N_2 from a reduction in the number of N_1 individuals, but also shifting the line demonstrating the relationship between N_2 and N_1 from the starting line (black) to a line with a lower s_0 value (blue line) (where the slope of the line is $1/s_0$).

Appendix C.3: JAGS code from Bayesian analysis

Here we provide the code that was used in a text file to run our JAGS model, using the example dataset we extracted from Peterman (1978).

```
model {
# Priors on parameters
yzero~dunif(.001,.999)
logbeta~dunif(-1,50)
beta<-exp(logbeta)
k~dunif(-0.000000092,0)
x0~dunif(-114997000,136907000)
ymax<-yzero*(1+exp(k*x0))

###############################
## Calculate Likelilhood
for(i in 1:ndata){
phat[i]<-ymax/(1+exp(-k*(x[i]-x0)))
alpha[i]<-phat[i]*beta/(1-phat[i])
Y[i]~dbeta(alpha[i],beta)
}
# Calculate predictions based on xindex
for(i in 1:nindex){
phatindex[i]<-ymax/(1+exp(-k*(xindex[i]-x0)))
```

```
secondder[i]<-(2*k^2*ymax*exp(-2*k*(xindex[i] - x0)))/

(exp(-k*(xindex[i] - x0)) + 1)^3 -

(k^2*ymax*exp(-k*(xindex[i] - x0)))/

(exp(-k*(xindex[i] - x0)) + 1)^2


}

}
```

Data for this iteration of our Bayesian analysis are available from:

Peterman, R. M. 1978. Testing for Density-Dependent Marine Survival in Pacific Salmonids. Journal of the Fisheries Research Board of Canada **35**:1434-1450.

Appendix C.4: Three functional forms of density dependence

In our graphical representation we used equations representing the three functional forms and focused on comparing the realized change in $\tilde{N}_2$ from the same expected effect under an additive hypothesis. Thus we compared the realized $\Delta\tilde{N}_{2,\Delta s_1,\Delta s_2}$ to the expected change $\Delta\tilde{N}_{2,\Delta s_1} + \Delta\tilde{N}_{2,\Delta s_2}$. In order to make the results comparable across the three functional forms, we first parameterized three functional forms so that they would meet at two points, *f(0)* and $f(\tilde{N}_2)$. Using these equations, we then found different Ds_1 and Ds_2 values for each of the three curves that would produce the same change in $\tilde{N}_2$ ($\Delta\tilde{N}_{2,\Delta s_1}$ and $\Delta\tilde{N}_{2,\Delta s_2}$ respectively). Thus, all three have different changes in $f(\tilde{N}_2)$ because changes in survival rates differ. However, the expected additive effect on $\tilde{N}_2$ was the same across all three curves, and we can compare the realized change ($\Delta\tilde{N}_{2,\Delta s_1,\Delta s_2}$) to the same expected change.

The three functional forms were as follows:

(a) Linear: $f(N_2) = a_{max} - bN_2$ (B1)

(b) Concave: $f(N_2) = 1/(\frac{1}{a_{max}} + \beta_{bh}N_2)$ (B2)

(c) Convex: $f(N_2) = a_{max} + \alpha(1 - e^{\beta N_2})$ (B3)

where a_{max} is the maximum value of the function $f(N_2)$ when N_2=0, and β_{bh}, b, α and β are all parameters that define the shapes of the three compensatory functions. The first point, *f(0)*, was simple and set as (0, 0.6) since we arbitrarily chose a_{max}=0.6. The second point, $f(\tilde{N}_2)$, was also chosen, we set $\tilde{N}_2$=3 and found $f(\tilde{N}_2)$ from the survival rates: s_1, s_2 = 0.85 ($f(\tilde{N}_2)$=0.176). We then had to find the values of the parameters for each of the three functions that ensured all three went through the two points: (0, 0.6) and (3, 0.1765).

Linear density dependence— The linear case was the straightforward; we found the value for the slope, *b*, that ensures the line goes through the two points (0, 0.6) and (3, 0.1765). This gave b=0.1412.

Concave density dependence— For the concave example, we also only had to find the value for one parameter: β_{bh}. Using Solver in Microsoft Excel, we found the value for β_{bh} that set eqn B1 equal to eqn B2 (using our value found for b) at $\tilde{N}_2$, which gave β_{bh}=1.3333)

Convex density dependence—Finally, for the convex functional form, our method was slightly more involved because we had two unknowns α and β. We found two equations that individually equal zero, we squared them and again used Solver in Microsoft Excel to find the values of α and β that would ensure that the sum of the two squared equations was zero. The first was to set eqn B3 equal to (1-s_2)/s_1. The second equation assumed that the slope of the concave down function at $\tilde{N}_2$, the first derivative at $\tilde{N}_2$, should be equal to twice the slope of the linear function at $\tilde{N}_2$. This assumed value for the slope was arbitrary, and was just chosen to ensure a convex shape that was visibly different from the linear functional form. Using these two equations to solve our two unknown gave us: α=0.1081 and β=0.5311.

Using these three functional forms, we found Ds_1 and Ds_2 values for each of the three curves that would produce the same change in $\tilde{N}_2$ ($\Delta\tilde{N}_{2,\Delta s_1}$ and $\Delta\tilde{N}_{2,\Delta s_2}$). For the linear, these were Ds_1=-0.17 and Ds_2=-0.1275. For the convex, they were Ds_1=-0.2680 and Ds_2=-0.1949. And for the concave, they were Ds_1=-0.06250 and Ds_2=-0.05000. Evident from these different values for Ds_1 and Ds_2 is the fact that in order to produce the same change in $\tilde{N}_2$ we need much smaller changes in s_1 and s_2 for the concave functional form.