Exxon Valdez Oil Spill
Long-Term Monitoring Program (Gulf Watch Alaska) Final Report

Long-Term Monitoring: Synthesis and Conceptual Modeling - Conceptual Ecological Modeling

Exxon Valdez Oil Spill Trustee Council Project 16120114-I
Final Report

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Study History: Conceptual models were developed to support the synthesis of data and serve as a framework and guide for development of monitoring priorities, to meet the overall goals of the long-term monitoring program. The models were also developed to serve as communication tools among program investigators and outreach tools to external audiences, such as the scientific community and other stakeholders.

In November 2012, we held a modeling session during the Gulf Watch Alaska program principal investigator meeting to elicit input for a conceptual ecological model for the Gulf of Alaska. Based on the input received from principal investigators, we developed a parsimonious general conceptual model for the northern Gulf of Alaska which visually linked components based on the existing knowledge and expert opinion of Gulf Watch principal investigators. Visualizations categorized model elements into forcing factors, biophysical processes, and biophysical components. The spatial arrangement of elements indicated the spatial scale at which the model components operated, and linkages represented interactions in the conceptual model. At this meeting, principal investigators also provided expert ratings about plankton – herring – baleen whale dynamics using the tool we developed. Experts provided a rating score assessing the state of knowledge, the strength of ecological impact, and the state of management or research attention devoted to each component in the model. The results from this exercise were published in 2015 and attached as an Appendix (Sethi and Hollmen 2015).

The conceptual model for the Gulf of Alaska was completed in 2014. Re-evaluation and updating of the general model was conducted in 2016 to assess and communicate learning objectives achieved during the first five years of the Gulf Watch Alaska program; this manuscript is still a work in progress. Over 2014-2016, we also constructed four additional subsystem models to synthesize understanding and generate research hypotheses about the trophic dynamics of a subset of key processes in the Gulf of Alaska ecosystem. These four models ranged in complexity from conceptual system visualization to quantitative network models.

In 2016, our project funds were reduced following realignment of Gulf Watch Alaska funding allocations. The conceptual modeling development, application, and visualization objectives from our original proposal were successfully achieved. However, to accommodate decreased project funding, activities related to the development of web-based interactive model graphics were postponed.

Abstract: Conceptual models assist in consolidating knowledge of the ecosystem, identifying data gaps, and providing a tool to facilitate communication among scientists, resource managers, policy-makers, and the general public. We developed conceptual ecological models to support the synthesis and planning relating to the Gulf Watch Alaska program. To develop these models, we summarized system elements, processes, and influences into a synthesized general conceptual ecosystem model for the Gulf of Alaska. Subsequently, we used conceptual modeling to investigate a subset of key trophic processes in the Gulf of Alaska. We used Bayesian Belief Networks to examine predator-prey interactions in nearshore ecosystems. We developed and utilized a novel linkage rating tool that assessed the state of knowledge, the strength of ecological impact, and the state of management or research attention devoted to zooplankton-herring-baleen whale interactions. Additionally, we visualized conceptual frameworks for two other subsystem models: (1) to examine the ecological linchpin hypothesis with forage fish abundance, and (2) biological effect pathways of temperature increase in the Gulf of Alaska ecosystem, including impacts on plankton abundance, plankton community composition, and microbial biomass. In each case, conceptual models provided a framework to describe Gulf of Alaska ecosystem understanding by Gulf Watch Alaska program scientists, provided information to prioritize research needs, provided scenario tools to simulate effects of changing nearshore conditions, and provided model visualization tools to support outreach and education efforts, including highlighting knowledge contributions made by the Gulf Watch Alaska program.

Key words: Bayesian Belief Networks, conceptual ecosystem modeling, Gulf of Alaska, predator-prey interactions

Project Data: This project relied on primary data from Gulf Watch Alaska principal investigators and external cooperators. Additional primary information was obtained from published literature. Hence primary data and associated metadata are curated by other investigators. Model visualizations and output generated from this project are contained within this report, and supporting model structures for Bayesian Belief Networks are available on the Gulf Watch Alaska data portal.

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EXECUTIVE SUMMARY

Conceptual ecological models have been used to support research and facilitate communication between researchers and managers by synthesizing information, providing working hypotheses, and identifying data gaps. We developed conceptual ecological models to support the synthesis and planning relating to the Gulf Watch Alaska long-term monitoring program in Prince William Sound, outer Kenai coast, and lower Cook Inlet/Kachemak Bay. The objectives of the Conceptual Modeling Program were to (1) develop conceptual ecological models, summarizing key elements, processes, and functions of the study system; and (2) develop interactive data exploration and visualization tools. In general we followed a basic set of steps: (1) identify the goals and objectives of the model; (2) conduct a literature review and assess the available data for the model elements and linkages; (3) assemble a core modeling team; (4) create a preliminary model for review by the principal investigators; (5) perform iterative updates until a final model is approved by principal investigators; (6) visualize results and communicate outcomes. Some models also incorporated quantitative data and expert rating tools to further enhance our understanding of the ecosystem and research needs.

Over the course of this work, we accomplished the modeling objectives set out in the original proposal. However, due to reduced funding, project activities related to the interactive data exploration and visualization tools have been postponed. In the first few years of the program we created a general conceptual ecosystem model for the Gulf of Alaska and developed a novel quantitative rating tool to systematically incorporate expert opinion into a process of assessing model component and model linkage properties . As several hypotheses were laid out to describe the underlying mechanisms shaping the structure and function of the Gulf of Alaska, we then used multiple approaches to investigate four mesoscale submodels: 1) Key Trophic Linkages in Nearshore Northern Gulf of Alaska Ecosystem; 2) Ecological Linchpin Hypothesis with Forage Fish Abundance; 3) Top-down Control with Humpback Whale Predation; 4) Bottom-up Control with Environmental Forcing on Plankton Populations. We used Bayesian Belief Networks to examine predator-prey interactions in the nearshore northern Gulf of Alaska ecosystem. We used a custom-developed linkage rating tool that assessed the state of knowledge, the strength of ecological impact, and the state of management or research attention devoted to zooplankton-herring-baleen whale interactions. We also developed a framework to examine the ecological linchpin hypothesis with forage fish abundance and how bottom-up forcing such as temperature changes result in cascading effects, ultimately altering plankton abundance and community composition and microbial biomass.

In order to facilitate communication of Gulf Watch Alaska progress, we re-evaluated the northern Gulf of Alaska conceptual model to assess how perceptions of the ecosystem changed with the knowledge gained over the first five years of the Gulf Watch Alaska Program. Several ecosystem elements were added (dust-storms, glacial input, jellyfish, and temperature) whereas others were removed (recreational traffic, sea ice, and sea level rise) or replaced. Thus our results highlight the need to periodically re-assess conceptual ecosystem model as knowledge is gained. We also noted that current events alter what elements are in the forefront of experts' minds. For example, the Tohoku earthquake and associated tsunami resulted in large amounts of marine debris; thus marine debris was

retained in the 2012 model but was later replaced by microplastics - a current topic in marine ecosystem research.

For the first submodel, we used Bayesian Belief Networks to combine quantitative and expert opinion to examine responses of two key nearshore consumer species in the Gulf of Alaska, the northern sea otter (*Enhydra lutris*) and the Barrow's goldeneye (*Bucephala islandica*), to changes in benthic invertebrate prey fields potentially associated with changing marine climate at high latitudes. Bayesian Belief Networks are structured frameworks that use probabilities to represent relationships among variables (Cain 2001, Neapolitan and others 2004, Marcot et al. 2006, McCann et al. 2006). We explored demographic consequences of changes to prey availability in both a generic (site-independent) model representing sea otter trophic dynamics for the "average" site and models for specific locations (site-specific models). Model results indicated that reproductive success and adult survival in sea otters were relatively stable and high regardless of the prey scenario modeled, which accurately reflects empirical observations of sea otter life history. For the generic, site-independent models, sea otter populations which had been established in an area for less than 15 years had higher reproductive success than populations in areas occupied for longer time spans with lower prey resources associated with sustained otter foraging pressure. Model results indicated that Katmai National Park and Preserve showed the greatest sensitivity in sea otter reproductive success to prey reductions among sites. Reducing all prey items at Katmai National Park led to the widest distribution of survival estimates and lowest reproductive success in sea otters, representing a worst-case and unsustainable scenario. Reproductive rates in Barrow's goldeneye (number of ducklings produced per female) were found to be the most responsive demographic parameters to changes in nearshore marine prey availability. When mussel availability was lowest, expected adult survival declined by 2% to 3% and variability in adult survival increased. The quantitative aspect of the Bayesian Belief Network conceptual model also helped to identify a mismatch between field collection methods for prey availability data and consumer foraging behavior which resulted in lower energy recovery rates than expected. Thus the current sampling protocols may need to be re-visited and updated foraging models may be needed to account for these differences.

Submodels 2-4 investigated a suite of top-down driven, bottom-up driven, and ecological linchpin (i.e., trophic dynamics mediated by middle trophic taxa) trophic processes in the Gulf of Alaska. Using expert elicitation, we constructed a conceptual model detailing the structure of a forage-fish mediated pelagic system to generate hypotheses related to the impact of middle-trophic level stock dynamics in driving upper trophic level dynamics (Submodel 2). In contrast to middle-trophic level mediation of key trophic processes, we developed a model to explore potential for top-down mediation of forage stocks from whale predation, using conceptual modeling and expert-based quantitative scoring of model attributes. Synthesizing beliefs about whale-herring-zooplankton dynamics in the Gulf of Alaska, this model indicated top-down control of forage stocks may not be common as well as highlighted hypotheses related to the importance of ocean acidification in impact zooplankton and subsequently forage fish stocks.

Finally, submodel 4 targeted the link between environmental drivers and primary productivity. Since the winter of 2013, several large masses of warm water have formed off the Western coast of the United States and Canada, including in the Gulf of Alaska (Bond et al. 2015, Whitney 2015, Cavole et al. 2016, Di Lorenzo and Mantua 2016, Zaba and Rudnick 2016). Nicknamed "the Blob", this warm water has coincided with changes in environmental forcing and plankton communities and abundance which are critical to the survival of many larger predators (Whitney 2015, Zaba and Rudnick 2016). Understanding the mechanisms of these bottom-up processes is key to predicting ecosystem changes. Thus we have combined the original intent of submodel 4 with the most current issues in the Gulf of Alaska. The bottom-up conceptual model focused on plankton production and the various environmental conditions that are thought to act as drivers of primary and secondary production in the northern Gulf of Alaska. We developed a visual framework to examine how temperature changes alter plankton abundance and community composition and microbial biomass. Our current model indicates that stratification plays a central role in the ecosystem. The depth of stratification will likely change with changes in fresh water input and temperature, and future modeling efforts will benefit by capturing variable stratification dynamics in more detail.

To date, we have published one paper and have one manuscript in preparation. We have shared findings in posters, oral presentations and community outreach at meetings. Overall, the original goals of the project were met and exceeded in some elements, but funding reductions altered the work plan under the original proposal to enhance some visual frameworks into more quantitative models with utility to test additional system change scenarios.

INTRODUCTION

The Gulf of Alaska is a highly productive ecosystem with spatial and temporal variability in physical and biological components (Stabeno et al. 2004, Mundy 2005). High temporal and spatial variability are known to occur throughout the marine ecosystem- for example, data from Gulf Watch Alaska indicate that Pacific blue mussel (*Mytilus trossulus*) abundance and biomass vary dramatically from place to place and year to year (Bodkin et al. 2018) and variation in prey availability impacts predator demographic responses (Sztukowski et al. in prep).

Large-scale ecological variation and change reinforce the need to understand ecosystem processes and function, and create new challenges for conservation, management and policy-makers. Knowledge of these large-scale ecosystems is often incomplete and scattered. Conceptual ecosystem models coalesce information about complex ecosystems, helping researchers to identify information gaps and develop hypotheses (Radomski and Goeman 1996, Ogden et al. 2005, Sethi and Hollmen 2015). Models define scope and provide a scientific framework for monitoring programs by describing current understanding of system structure, processes, and function, including key system elements and their interactions. By providing a method to integrate current knowledge of the system originating from a variety of data sources, conceptual ecological models provide critical tools to address uncertainties or incomplete understanding of ecosystem function, and provide the basis for development of causal hypotheses among environmental or anthropogenic stressors, ecological effects, and management actions. Conceptual models provide a schematic framework to organize and illustrate complex system structure and linkages, thus serving as a tool to facilitate understanding and communication among scientists, managers, and the public. Thus conceptual ecological models are considered a key element of environmental and biological monitoring programs, and provide a qualitative representation of the structure and dynamic properties of the ecosystem.

Conceptual ecological models can provide a basis for long-term monitoring of ecosystems and restoration planning, and have been applied in a range of ecosystem monitoring and management settings. For example, more than 11 models are used to describe environmentally sensitive areas in the South Florida Everglades region, describing subsystems, key features, drivers, and stressors for local and regional planning and management (Ogden et al. 2005). Because conceptual models are goal specific, submodels or multiple models for the same system are common.

Depending on the objective of the project, conceptual ecological modeling typically involves qualitative analyses to synthesize understanding about ecosystem elements into a visual model of the system. However, qualitative models facilitate further development of quantitative data models (such as predictive scenario models). Thus we expanded some of our conceptual ecological models to include quantitative analyses, such as an expert-informed scoring tool we developed to understand the relationships between the state of knowledge and importance of each component in the system, or the use of Bayesian Belief Networks. We used both visualizations and semi-quantitative conceptual ecological models to support the Gulf Watch Alaska program, based on the needs and objectives of program investigators. Analytical and visualization tools and methods included structural and influence diagrams, tabulated data, narratives, and mathematical modeling (presented within this report and available on the Gulf Watch Alaska data portal).

We first synthesized a general conceptual ecosystem model for the Gulf of Alaska, identifying key elements and linkages in the ecosystem. The goal of this conceptual model was to produce a parsimonious framework, which was minimally sufficient complexity to describe the northern Gulf of Alaska ecosystem.

In addition to the general model for the Gulf of Alaska, we developed of a series of submodels to explore hypotheses regarding trophic dynamics within the key program components: nearshore (Submodel 1), pelagic (Submodels 2, 3), and environmental drivers (Submodel 4). These models differed in complexity and the underlying methods used.

Submodel 1: Key Trophic Linkages in Nearshore Northern Gulf Ecosystems

The benthic nearshore model examined the impact of changes in invertebrate prey fields on consumers of interest (northern sea otter (*Enhydra lutris*) and Barrow's goldeneye (*Bucephala islandica*)) as measured by a suite of behavioral and demographic performance metrics. The overall goals of the modeling effort were to organize understanding about trophic linkages in the nearshore system, provide quantitative simulation models to forecast demographic outcomes resulting from changes in invertebrate prey fields potentially associated with changing climate at high latitudes, identify data gaps, and prioritize research to fill data gaps. This model framework also demonstrates the broad applicability of Bayesian Belief Networks to combine quantitative and qualitative data. Considerable empirical, quantitative information exists on diet compositions for sea otters, however we found that the modeling framework was useful for less data rich species (Barrow's goldeneye) as well.

Submodel 2: Ecological Linchpin Hypothesis with Forage Fish Abundance

This conceptual submodel focuses on the dynamics of a suite of forage fish found in the northern Gulf of Alaska. Utilizing expert input to develop a detailed schematic for the structure of a pelagic Gulf of Alaska forage fish system, this submodel was used to explore hypotheses about linkages among forage fish prey, a suite of selected forage fish species, and higher trophic species populations. Salmon and other pelagic, marine forage fishes such as capelin, sand lance, and herring play important roles in the marine food web as predators, competitors, and prey. These connections, when examined through functional groups or shared similarities (i.e. examining loss of shared prey items across multiple species) can provide unique insights into food web dependencies and future management considerations of key forage fish species, such as herring, and their predators.

Submodel 3: Top-down Forage Fish Control with Humpback Whale Predation

Much speculation regarding controlling factors for schooling and highly fecund fishes, such as Pacific herring, has focused on bottom up factors including availability of prey and suitable habitat. An alternative hypothesis with supporting evidence suggests that increasing predator populations may be acting as a top down controlling agent for these fish. This conceptual submodel explored the relationships between humpback whale prey types and seasonal patterns that can lead to a better understanding of the influence that predation may have on suppressed, economically important fisheries, such as herring. Current understanding about the processes affecting herring-whale dynamics in the northern Gulf of Alaska was explored in a submodel exercise, which rated properties of linkages, such as state of knowledge, in a zooplankton-herring-whale food web.

Submodel 4: Bottom-up Control with Environmental Forcing on Plankton Populations

Since winter of 2013, several large masses of warm, nutrient poor water have formed off the western coast of the United States and Canada, including in the Gulf of Alaska. Nicknamed "the Blob", this warm water has coincided with changes in environmental forcing and plankton communities and abundance which are critical to the survival of many larger predators. Understanding mechanisms of these bottom-up processes are key to predicting ecosystem changes. This conceptual submodel focuses on plankton production and the various environmental conditions that are thought to act as drivers of primary and secondary production in the northern Gulf of Alaska as it relates to potential effects of warmer ocean temperatures and associated environmental changes on primary production. Primary productivity is related to nutrient availability and solar input. Other environmental factors that influence plankton and microbial communities include stratification and mixing, freshwater input, topography, and upwelling of nutrients. This submodel explored ecosystem responses to changing climate whereby plankton production is a primary source of energy conversion for higher trophic levels.

OBJECTIVES

The objectives of the conceptual modeling program were to (1) develop conceptual ecological models, summarizing key elements, processes, and functions of the study system; and (2) develop interactive data exploration and visualization tools for the Gulf Watch Alaska program. These objectives were structured into developing a parsimonious conceptual model which minimally sufficient complexity to describe the northern Gulf of Alaska ecosystem, developing submodel visualizations based on Gulf Watch Alaska project specific needs, and developing and using semi-quantitative analytical tools. In addition to developing and re-evaluating the general conceptual ecosystem model for the Gulf of Alaska, we identified four submodels for exploration:

Submodel 1: Key Trophic Linkages in Nearshore Northern Gulf of Alaska Ecosystem

Submodel 2: Ecological Linchpin Hypothesis with Forage Fish Abundance

Submodel 3: Top-down Forage Fish Control with Humpback Whale Predation

Submodel 4: Bottom-up Control with Environmental Forcing on Plankton Populations

As this project was collaborative across a number of the Gulf Watch Alaska research groups, specific aims of each submodel were tailored to the needs of the Gulf Watch Alaska group involved.

METHODS

Development of conceptual ecological models to support synthesis and planning of the long-term monitoring program is a multi-phase process. In all conceptual ecological models we follow a basic set of steps: (1) identify the goals and objectives of the model; (2) conduct a literature review and assess the available data for the model elements and linkages; (3) assemble a core modeling team; (4) create a preliminary model for review by the principal investigators; (5) perform iterative updates until a final model is approved; (6) visualize results and communicate outcomes.

Model goals and the spatiotemporal scope of modeled systems were defined at the start of each respective analysis effort. The scope of our models ranged from ecosystem level (ie. General North Gulf of Alaska Conceptual Ecosystem Model) to site-specific models in the nearshore predator-prey models.

Identification of key elements, processes, and functions of the system involved literature review and information gained from the principal investigators from some or all of the benthic, pelagic, and environmental components of the project, and coordination with other scientists and groups with expertise relating to the study system. While the conceptual modeling efforts here varied in scope and complexity, they all shared commonalities: i) models all had a goal of representing the structure, processes, and key interactions of an investigated system, ii) models synthesized available primary information as well as Gulf Watch Alaska investigator expert knowledge, and iii) models generated hypotheses about key linkages between system components (e.g. environmental stressors associated with changing climate and ecological responses from key functional groups).

General North Gulf of Alaska Conceptual Ecosystem Model

Initially, information about previous conceptual modeling efforts relating to our study area and objectives was compiled and reviewed, and evaluation of best suited modeling tools for our program purposes was conducted. The approach taken involved drafting of a parsimonious general conceptual model describing the current understanding of the structure and dynamics of our entire study area, with goals to further develop a suite of submodels that addressed specific scientific questions and management linkages of our program.

A one-day modeling session was included in the agenda of the annual Gulf Watch Alaska principal investigator meeting held in November 2012. The modeling session began with a series of introductory presentations focusing on ecosystem modeling tools, conceptual ecological models, and decision support tools for resource management. The introductory presentations were followed by a half-day breakout session. In this session, the principal investigators worked on two exercises to gather expert input into the development of conceptual ecological models. The first exercise focused on the development of a general northern Gulf of Alaska ecosystem model. The primary objective of this exercise was to develop a minimally but sufficiently detailed conceptual model which identified: a) natural and anthropogenic forcing factors, b) key biophysical processes and biophysical components to monitor which play a central role in the functioning of the system, and c) linkages between model elements in our study system. The principal investigators, working in smaller break out groups, provided their expert input by expanding or reducing a starting set of conceptual model elements, provided by the modeling team, and translating the outcome list to a conceptual model diagram. These investigator responses were analyzed to produce the first version of our consensus conceptual model. Steps of the data analysis included: consolidation of a comprehensive list of model elements, refinement of the list of model components, generation of a conceptual model response matrix that was used to translate visual arrangement of model elements into a numeric matrix, generation of a matrix for the spatial domain of elements on the master list, and using R script, determining expert consensus on a) which elements from the master list should be retained in a final conceptual model, b) the spatial domain of elements retained in the final model, and c) the linkages between elements retained in the final model. The final step of the process involved reconstructing a visual representation of the conceptual model. The results were used to create two visualizations: 1) a comprehensive model incorporating the full set of elements and linkages indicated by investigators; and 2) a parsimonious model with minimally sufficient detail to adequately describe the North Gulf of Alaska ecosystem which contained only those linkages and model elements which ≥ 3 investigators included.

The North Gulf of Alaska ecosystem model was then re-evaluated in 2016 with Gulf Watch Alaska investigator input. We presented the general conceptual ecological model at the annual principal investigator meeting held in October 2016 and asked those present to update the consensus model structure to reflect knowledge gained over the five years. This request and associated documents were also sent to all Gulf Watch Alaska participants. We used their responses to update the Gulf of Alaska conceptual ecological model. Elements and linkages were added or removed from the consensus model when three or more principal investigators indicated changes to the elements that play a central role in the functioning of the system.

After developing the ecosystem level model, we examined several submodels related to trophic dynamics in nearshore (Submodel 1) and pelagic (Submodels 2, 3) ecosystems, and the influence of environmental drivers on primary production (Submodel 4).

Submodel 1: Key Trophic Linkages in Nearshore Northern Gulf of Alaska Ecosystem

The overall goals of the modeling effort are to 1) examine the impact of changes in invertebrate prey fields on two key nearshore consumers in the Gulf of Alaska (northern sea otter and Barrow's goldeneye) as measured by a suite of behavioral and demographic performance metrics, 2) provide simulation models to forecast demographic outputs, 3) identify data gaps and the present state of knowledge of these two key nearshore consumers through the process of model development, and 4) provide insight into research priorities moving forward.

After reviewing the available methods used to create conceptual models (including Bayesian Belief Networks, EcoPath models, and the expert-elicitation methods used by Sethi and Hollmen 2015) we decided to employ goal-specific Bayesian Belief Network for the nearshore submodel as it provides a suitable modeling framework that allows for the use of a combination of quantitative information and expert opinion. Bayesian Belief Networks are structured networks that use probabilities to represent relationships among variables (Cain 2001, Neapolitan and others 2004, Marcot et al. 2006, McCann et al. 2006). These "causal webs" model ecological and management predictions explicitly displaying assumptions. Because they combine quantitative and qualitative input, Bayesian Belief Networks can operate in both data rich and data poor environments.

We used Netica software (version 5.23, Norsys Systems Corp., Vancouver, British Columbia) to model predator-prey interactions and assess demographic outcome likelihoods following the guidelines set out in Marcot et al. (2006). We collaborated with the Gulf Watch Alaska nearshore group to define clear objectives, decide site-specific and population-level spatio-temporal boundaries, and determine the model structure. Using data collected by the near-shore group and expert opinion, we completed the network structure linking nodes with equations and set frequency distributions based on the best available knowledge. The network structure was too complex for conditional probability tables, thus we used a sampling approach which estimated outcome probabilities based on $4*10^6$ samples. Further sampling did not change model results. The overall model framework was similar for both sea otters and Barrow's goldeneye (Fig. 1). Input variables were the proportions of prey species in a consumer's diet, and the prey availabilities of each species in the diet. These inputs are subsequently linked to an energy recovery rate (energy gained per minute of forage effort) for each prey species. We calculated the total energy recovery rate by summing the weighted recovery rates ($\sum_i proportion\_prey_i \times recovery\_rate\_prey_i$). After calculating the total energy recovery rate, the total time spent foraging was calculated by dividing the consumer-specific total daily energy by total recovery rate. Time spent foraging was then related to the demographic outputs. Please see Sztukowski et al. in prep for further details.

For sea otters, a suite of simulations was constructed to identify population- and site-specific patterns and sensitivities to changes in prey availability and diets. Site-specific sea otter diets and site-specific prey availability were constructed for Katmai National Park and Preserve, Kenai Fjords National Park, and western Prince William Sound. We ran scenarios in which diet composition and prey availability were adjusted by (1) reducing clam availability only; (2) reducing mussel availability only; and (3) reducing all prey availability, which included clams, mussels, urchins, crabs, fish, epibenthic prey and other infaunal species. Reductions for clams and all non-mussel prey types occurred by reducing the prey species uniformly to the lowest prey availability category, which translates to reduced sea otter prey recovery rates.

In contrast to the relatively data-rich sea otter modeling effort, little primary information is available on Barrow's goldeneye foraging ecology and thus goldeneye modeling was restricted to three non-site-specific scenarios. Because Barrow's goldeneyes are dietary specialists in winter, feeding primarily on Pacific blue mussels; we created Bayesian Belief Network models reflecting high, medium, and low mussel availability scenarios, without varying any other prey types.

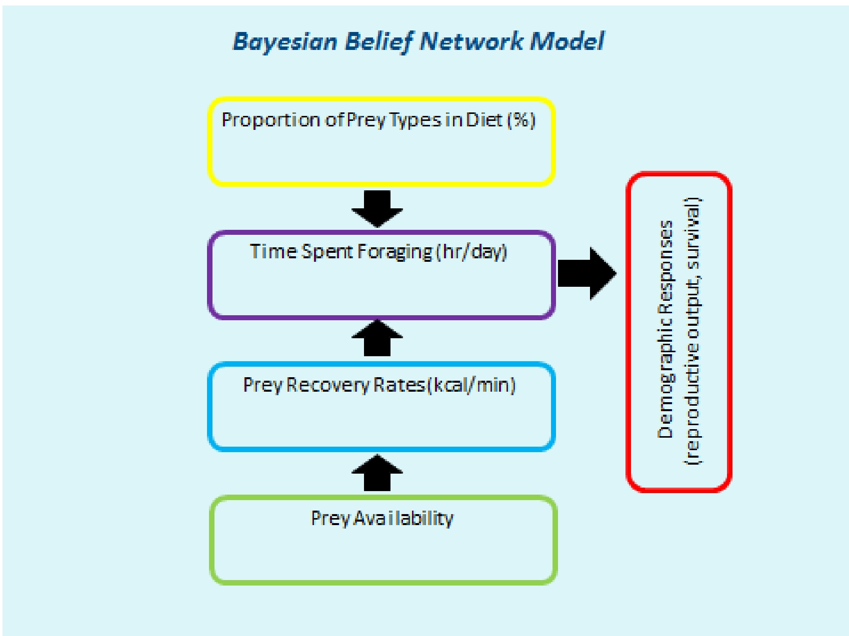


Figure 1. Overall model framework for both sea otters and Barrow's goldeneye.

Submodel 2: Ecological Linchpin Hypothesis with Forage Fish Abundance

This conceptual submodel examined linkages among environmental indices, forage fish prey, a suite of selected forage fish species, and higher trophic species populations. We constructed a visualization for the forage fish framework associated with the ecological linchpin theory based on literature review. We then solicited opinions within the Gulf Watch pelagic working group to refine the conceptual ecological model to produce the framework in Fig. 6.

Submodel 3: Top-down Forage Fish Control with Humpback Whale Predation

A modeling workshop was conducted in November 2012, to elicit input from Gulf Watch Alaska principal investigators. In addition to contributing to the creation of a parsimonious general conceptual ecological model for the Gulf of Alaska, participants contributed expert opinion about strength of linkages among ecosystem components. Specifically, participants explored zooplankton-Pacific herring- baleen whales interactions in a submodel exercise rating properties of linkages. This novel linkage-rating tool included assessments of the state of knowledge, the strength of ecological impact, and the state of management or research attention devoted to a given component. See Sethi and Hollmen 2015 for further details on this model framework.

Submodel 4: Bottom-up Control with Environmental Forcing on Plankton Populations

The bottom-up forcing conceptual model focused on plankton production and the various environmental conditions that are thought to act as drivers of primary and secondary production in the northern Gulf of Alaska. Draft models were design based on literature review and then modified in an iterative process with input from several experts. We then created Bayesian Belief Network structures to formalize links between model elements.

RESULTS

General North Gulf of Alaska Conceptual Ecosystem Model

We received 19 responses to questionnaires which included lists of model elements and visual representations of a general North Gulf of Alaska conceptual model from program principal investigators in 2012. We created two visualizations: one general model which included all elements and linkages listed in the responses, and a parsimonious consensus model which included elements and linkages that had three or more investigator responses (Fig. 2).

The visual representation of a general North Gulf of Alaska conceptual ecological model was re-evaluated by 18 program principal investigators in 2016. The resulting model and visualization (Fig. 3) added the following ecosystem elements: dust-storms, glacial input, jellyfish, and temperature. Marine debris was replaced by microplastics. Recreational traffic, sea ice, and sea level rise were removed from the model as three or more participants indicated the elements did not play a central role in the functioning of the system. Flow, contaminants, larval transport, microbial processes, pelagic macroinvertebrates, noise, ship strike, and stratification were mentioned as important elements in the ecosystem by one or two participants, but were not included in the consensus model.

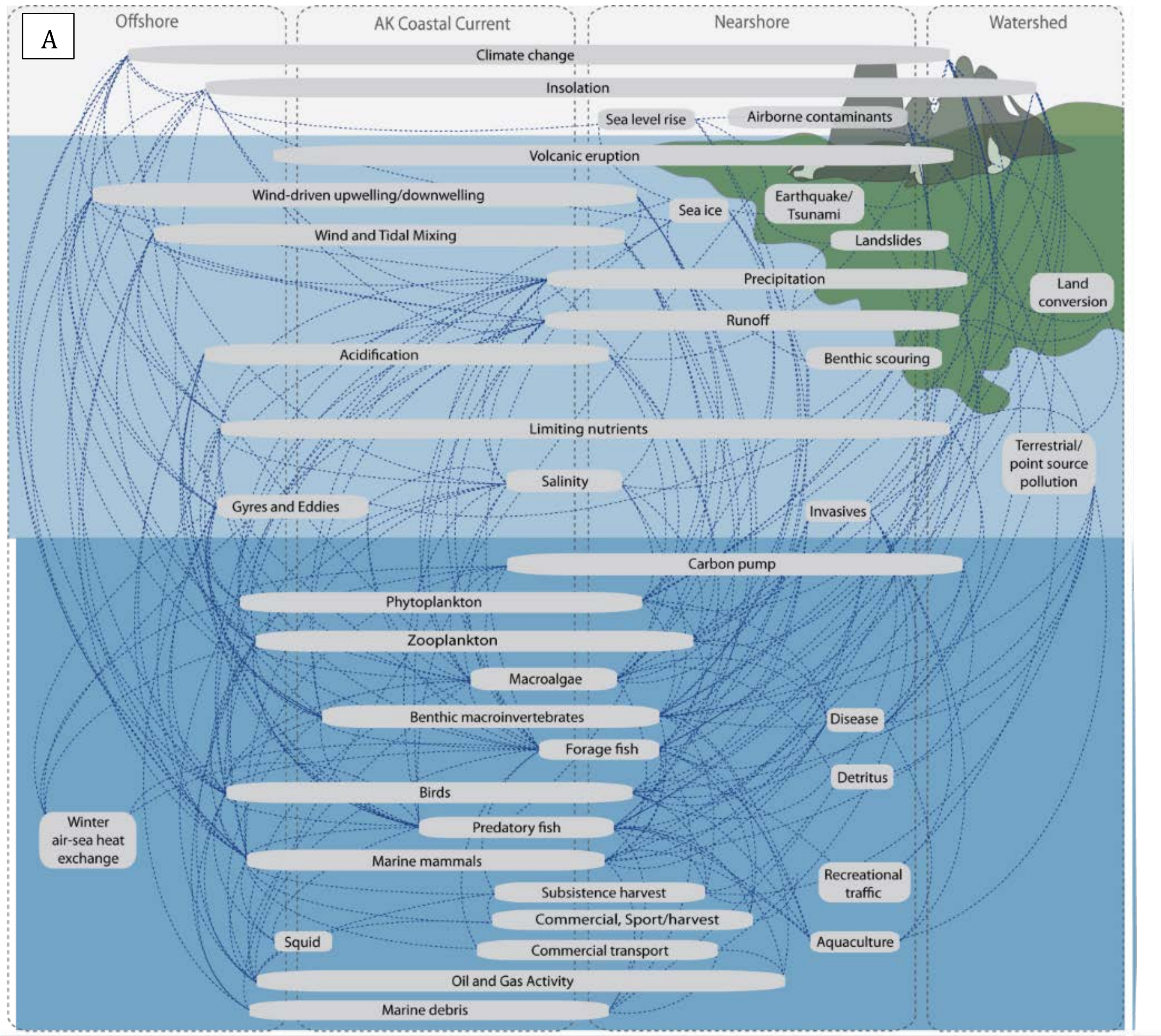


Figure 2. General North Gulf of Alaska conceptual model from 2012. A) comprehensive model incorporating the full set of elements and linkages indicated by investigators; B) parsimonious model containing only those linkages and model elements which ≥ 3 investigators included during model development.

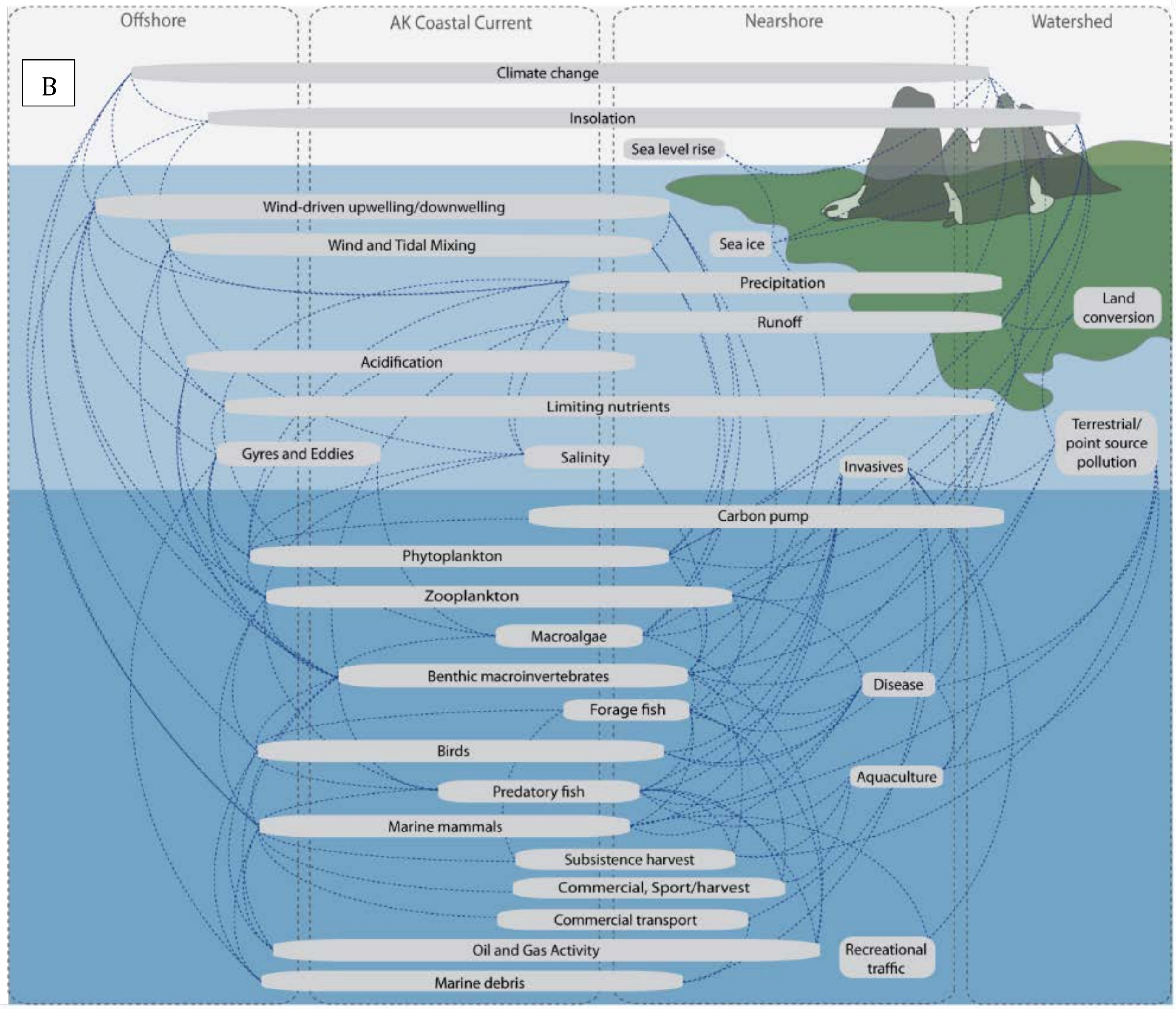


Figure 2 continued.

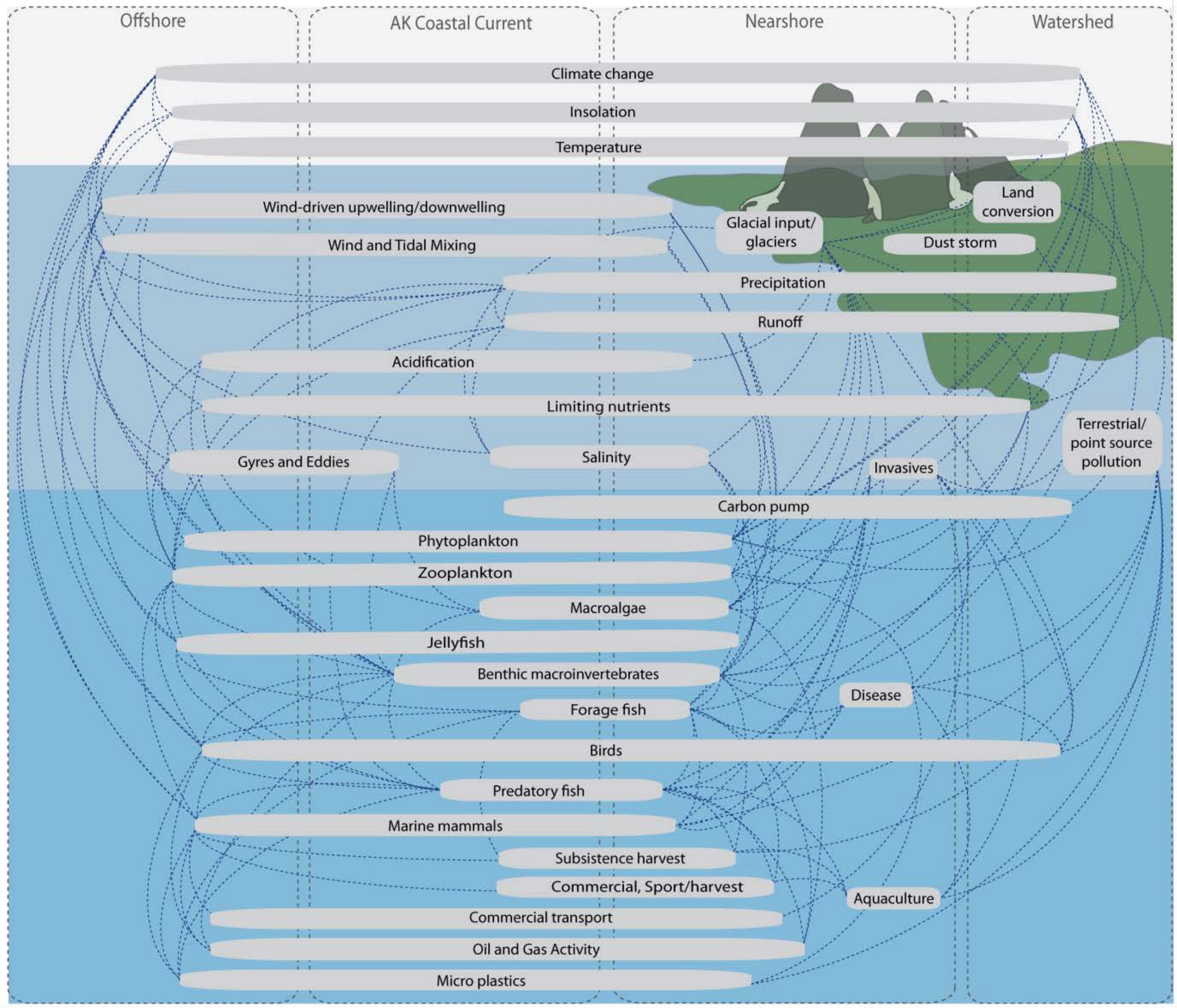


Figure 3. Visual representation of a census conceptual ecological model for North Gulf of Alaska as re-evaluated in 2016.

The results from the 2012 conceptual ecological model for the Gulf of Alaska have been presented at the 2013 PISCES meeting (http://meetings.pices.int/), Alaska Marine Science Symposium 2015 and numerous principal investigators meetings. Both the 2012 and 2016 results are part of a manuscript in preparation.

Submodel 1: Key Trophic Linkages in Nearshore Northern Gulf of Alaska Ecosystem

Sea Otter

Reproductive rate and adult survival were relatively stable and high regardless of the prey scenario modeled, which accurately reflects empirical observations of sea otter life history (Fig. 4; Monson et al. 2000). Reproductive success (pup survival through weaning) demonstrated more variability than other demographic responses, with changes in means and distributions between scenarios and in relation to length of occupancy (Fig. 4). For the generalized, non-site-specific models, scenarios reflecting newly occupied sites, where prey resources are high, had higher reproductive success than scenarios reflecting long-occupied sites with reduced prey availability associated with a history of foraging pressure.

Among the site-specific models (Fig. 4), Katmai National Park showed the largest changes in reproductive success; pup survival was lowered more by reduced clam availability than by reduced mussel availability. However, at Kenai Fjords, where mussels were more dominant in the diet, demographic responses were robust to reductions in clams. Reducing all prey items at Katmai National Park led to the widest distribution of survival probabilities and lowest reproductive success in sea otters, representing a worst-case and likely unsustainable scenario. Reproductive success in western Prince William Sound was consistent across all scenarios, due to the relatively small adjustments between prey availability in the western Prince William Sound baseline model and the reduced prey simulations.

Barrow's Goldeneye

Adult survival was high and relatively stable across different prey scenarios, with a small decline (2 to 3%) and increased variability in adult survival corresponding to the lowest mussel availability scenario (Fig. 5). Juvenile survival, while lower than adult survival, showed similar responses of declining survival and increasing variability with declining mussel availability (Fig. 5). When confronted with low mussel availability, juvenile survival declined by approximately 4%, with substantially increased variability in survival outcomes.

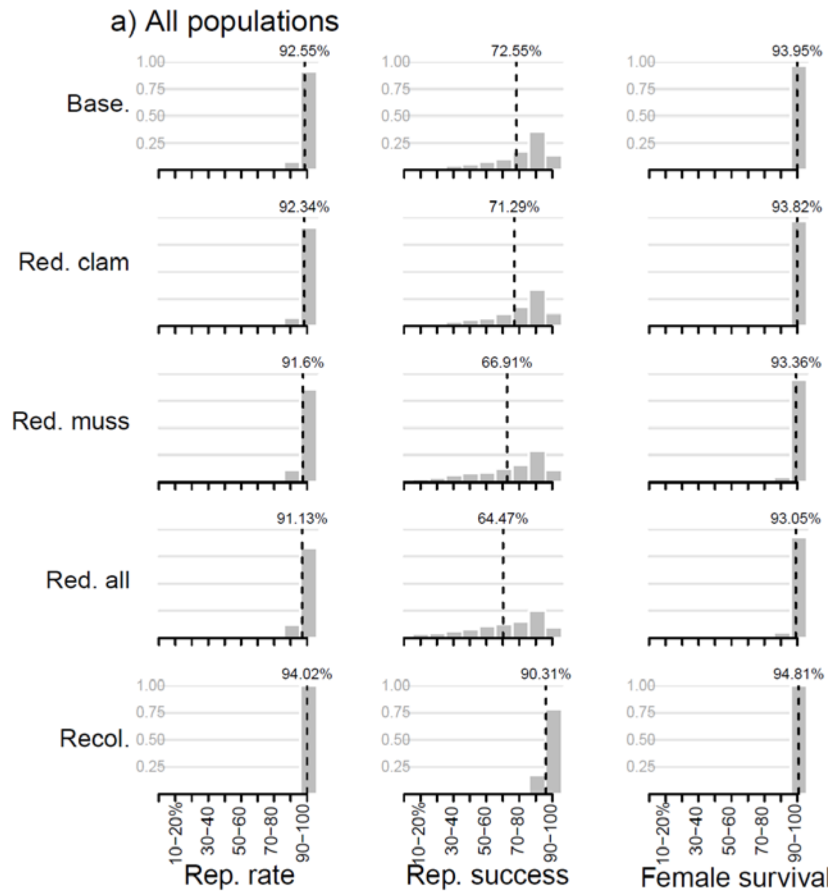
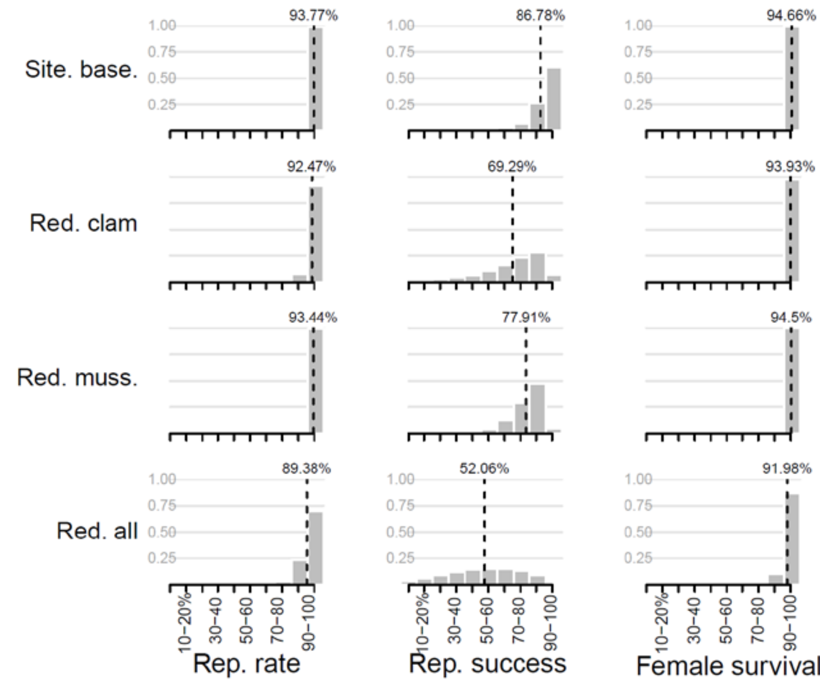


Figure 4. Frequency histograms for Bayesian Belief Network model output for sea otter (*Enhydra lutris*) simulations. Prey availability and diet composition inputs were modeled as the average across all subpopulations combined (a) or as site-specific (b-d). Reproductive rate (Rep. rate) is the percentage of mature females that give birth in a season. Reproductive success (Rep. success) is the percentage of pups that survive their first year. Female survival is the annual survival rate (in percentage points) for adult females. Vertical dashed lines are the mean value of output distributions. Simulation scenarios for the all-populations model (rows in panel a): Base. = baseline, prey availability and diet compositions associated with long occupied sea otter sites; Red. clam = clam availability reduced to the lowest availability bin; Red. muss. = mussel availability reduced to the lowest availability bin and reduced mussel in the diet; Red. all = all prey items reduced to their lowest availability bins, respectively; Recol.= prey availability specified to match prey availability conditions upon sea otters occupying a new site, when prey conditions should be ideal. Simulation scenarios for the site-specific models (rows in panels b-d): Site. base. = site-specific baseline prey availability and diet composition (Katmai, Kenai Fjords, or W Prince William Sound); Red. clam, Red. muss., and Red. all scenarios are specified as above.

b) Katmai



c) Kenai Fjords

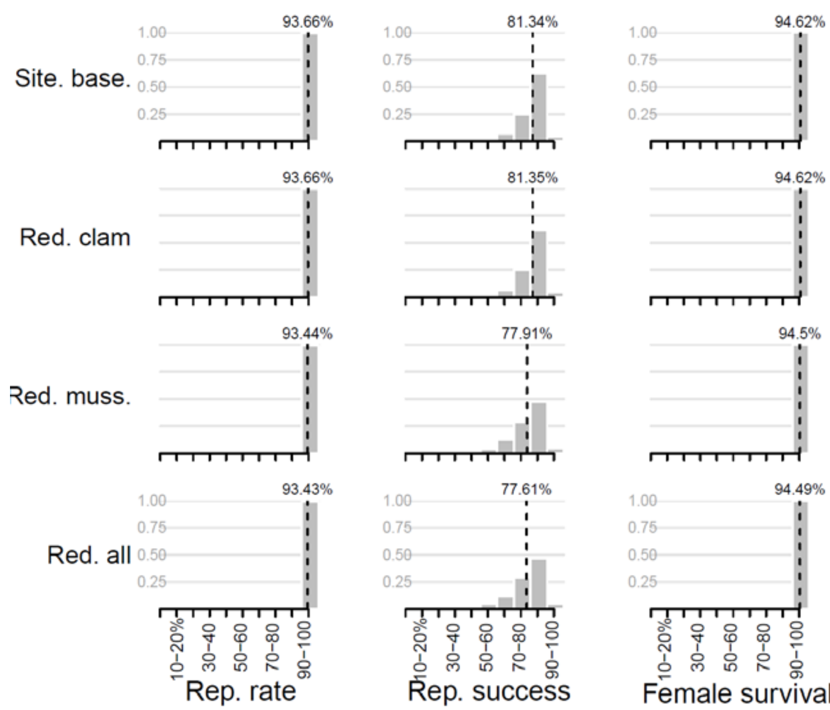


Figure 4, continued.

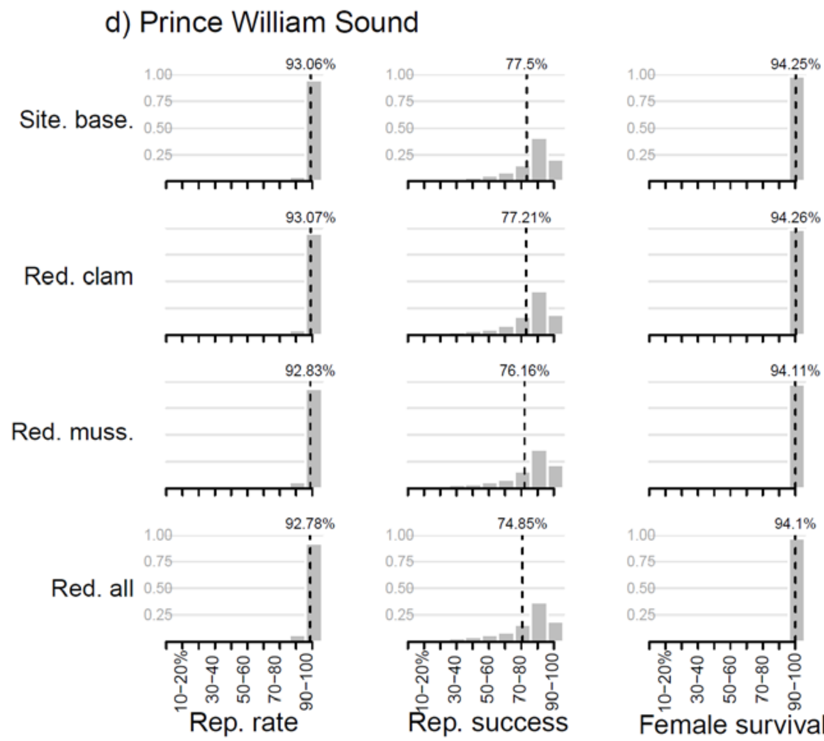


Figure 4, continued.

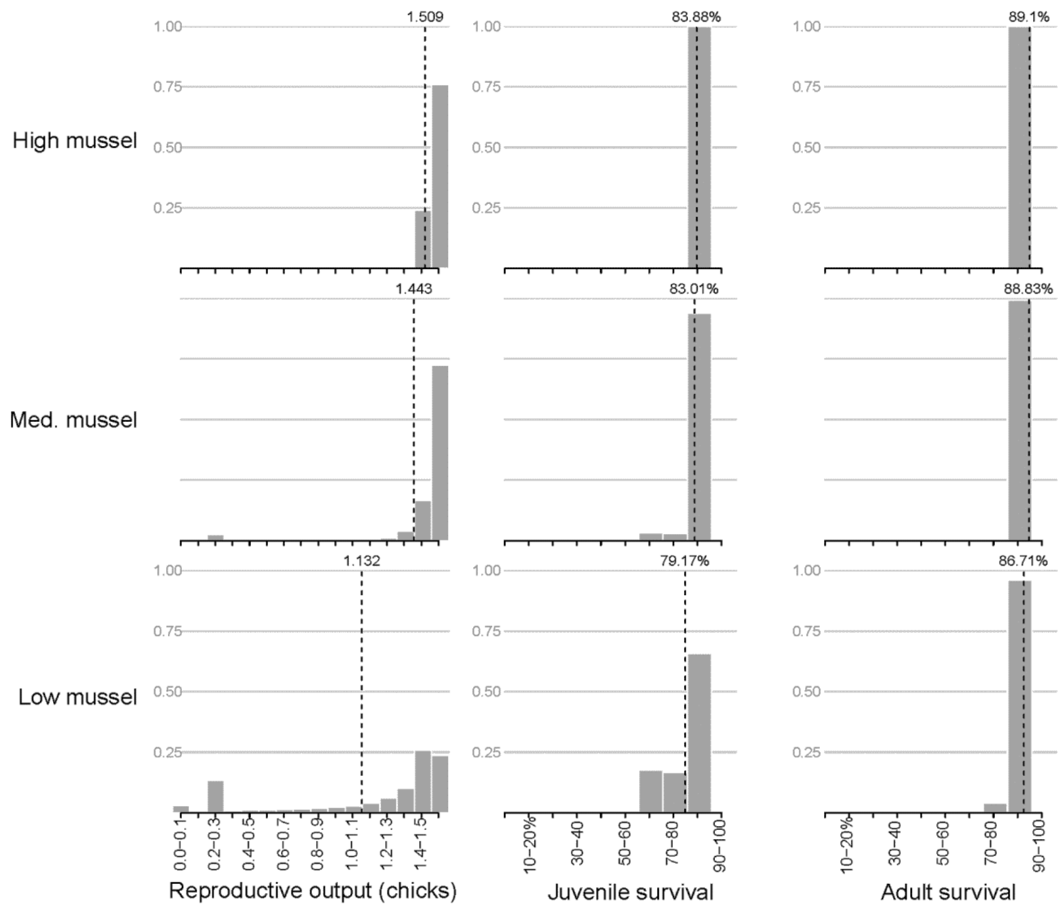


Figure 5. Frequency histograms for Bayesian Belief Network model output for Barrow's goldeneye (*Bucephala islandica*) simulations. Reproductive output is the expected number of ducklings fledged by a reproductive female. Juvenile and adult survival are annual survival rates (in percentage points). Vertical dashed lines are mean values for a given model structure and performance metric plotted on a continuous 0-100% scale for survival, and on a continuous scale between 0.0 and 1.6 ducklings fledged for reproductive output. Simulations scenarios along rows represent high, medium, or low mussel availability, respectively.

Submodel 2: Ecological Linchpin Hypothesis with Forage Fish Abundance

Working with Gulf Watch Alaska pelagic component principal investigators, we constructed two visualizations for the forage fish framework associated with the ecological linchpin hypothesis that upper trophic level dynamics are driven by the dynamics of mid-trophic forage stocks (Fig. 6). These visual conceptual ecological models were presented in a poster at Alaska Marine Science Symposium 2015 and then again at the principal investigators meeting and public outreach open house in Cordova, AK in 2016.

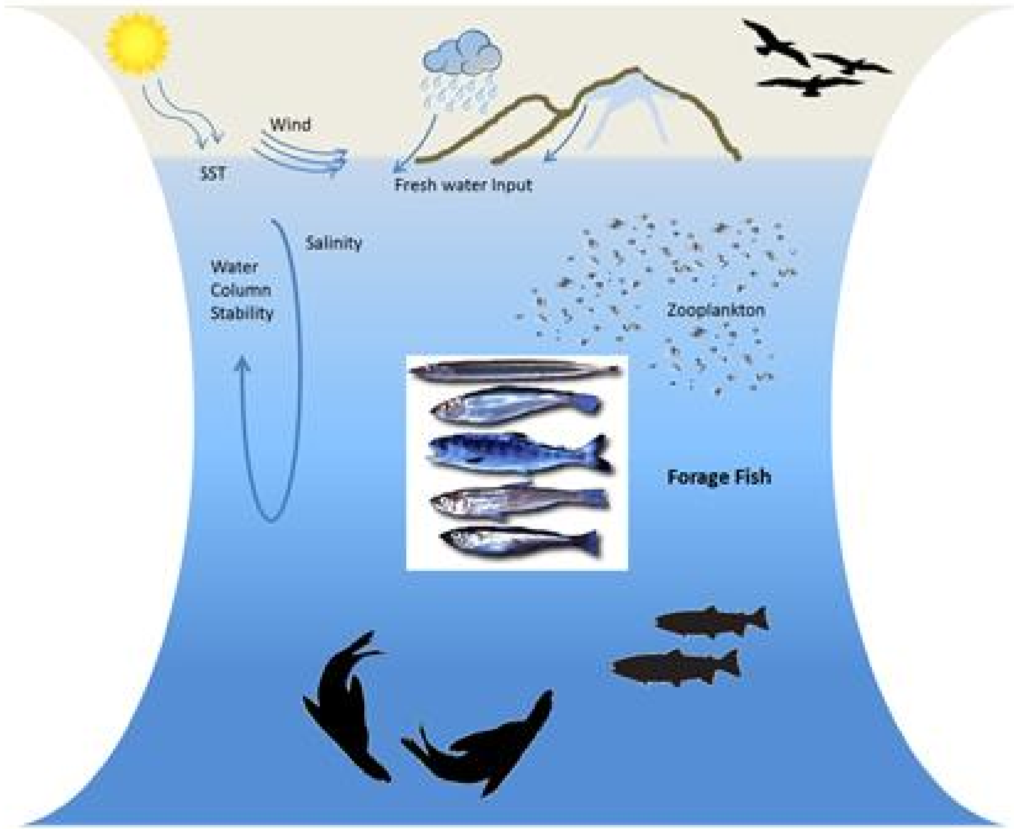


Figure 6. Visualizations for the forage fish framework associated with the ecological linchpin hypothesis.

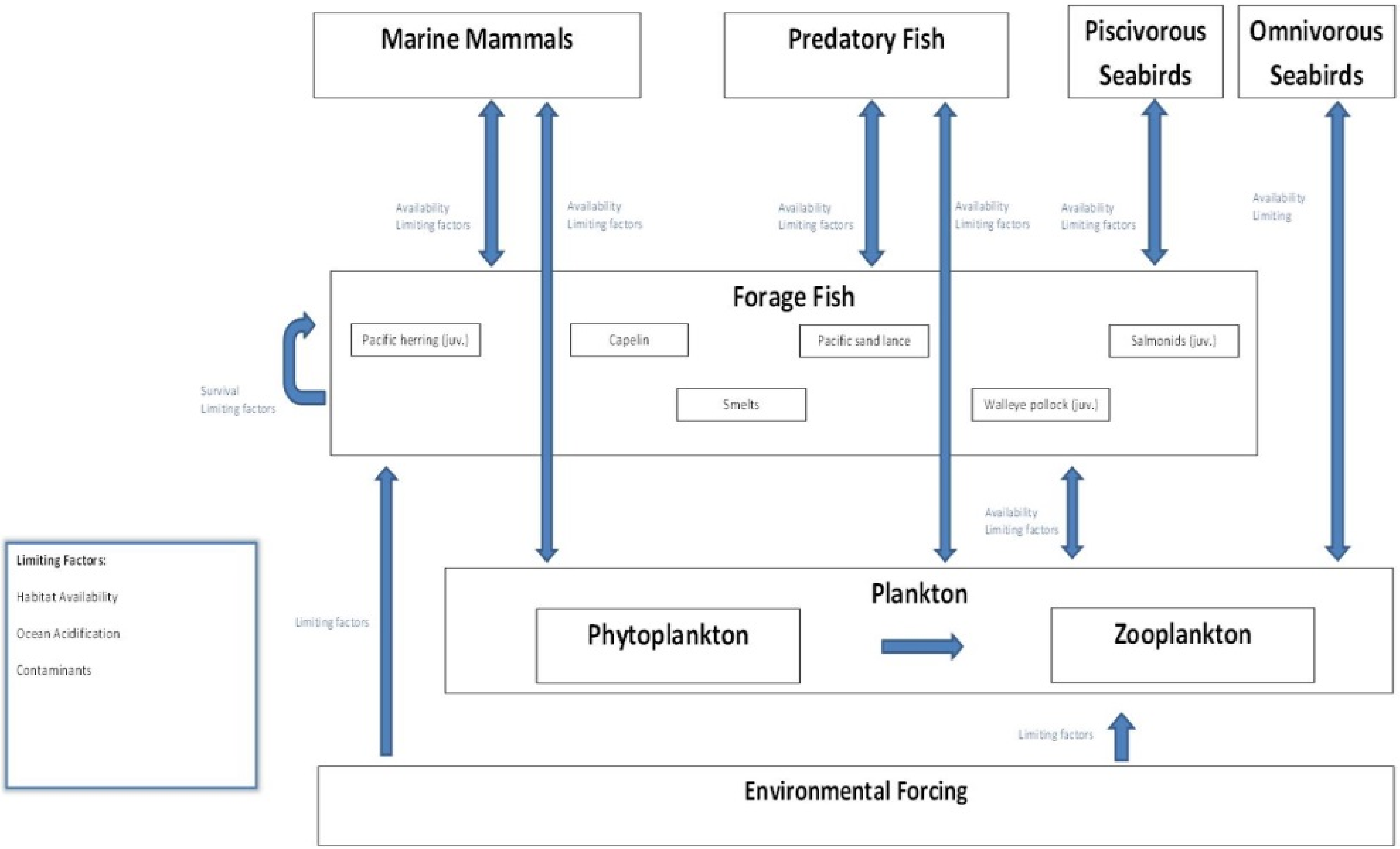


Figure 6, continued.

Submodel 3: Top-down Forage Fish Control with Humpback Whale Predation

The Gulf Watch Alaska pelagic component principal investigators explored movements and distribution of humpback whales in Prince William Sound, represented in a conceptual model. Current understanding about the processes affecting herring-whale dynamics in the northern Gulf of Alaska was explored in a submodel exercise rating properties of linkages in a zooplankton-herring-whale submodel system, including assessment of the state of knowledge, the strength of ecological impact of changes in the food web, and the state of management or research attention devoted to a given component. We received 19 responses from program principal investigators on the submodel linkage rating survey. The strongest linkages were the positive effect of zooplankton on herring, followed by the positive effect of upwelling on zooplankton and the positive effect of herring on whales. The weakest linkage was the effect of whales on zooplankton. The ratio of the consensus strength of interaction over the state of knowledge rating for linkages suggested research evaluating the effects of ocean acidification is high priority, followed by the effect of zooplankton on herring. This model framework has been published in Sethi and Hollmen (2015).

Submodel 4: Bottom-up Control with Environmental Forcing on Plankton Populations

We expect temperature changes to result in cascading effects ultimately altering plankton abundance and community composition and microbial biomass. We used published (e.g., Mundy 2005) Gulf Watch Alaska program data as well as expert opinion to define linkages between nodes. The initial framework focused on the upper 300 m of the water column and included temperature, glacial input and precipitation (later combined into fresh water input), salinity, stratification, iron, nitrate, and plankton. Temperature and salinity influenced the degree of stratification and the species and abundance of phytoplankton and zooplankton. Fresh water input is the addition of precipitation and glacier melt. Fresh water input will affect iron influx into the system and stratification through salinity differences. Stratification influences nutrient (iron and nitrate) availability through the degree of mixing and when that mixing occurs. However the latest version of the model structure incorporating expert opinion of Gulf Watch Alaska investigators reflects a stratified water column with both an upper layer of the water column (Upper) and the lower layer (Lower). We realize that the depth of this stratification will change with different ocean conditions (Fig. 7). The current model demonstrates that stratification plays a central role in the ecosystem. Pending future funding opportunities, we seek to continue populating the Bayesian Belief Network with node states and their associated conditional probabilities to test a range of scenarios with different temperatures, fresh water inputs and stratification depths.

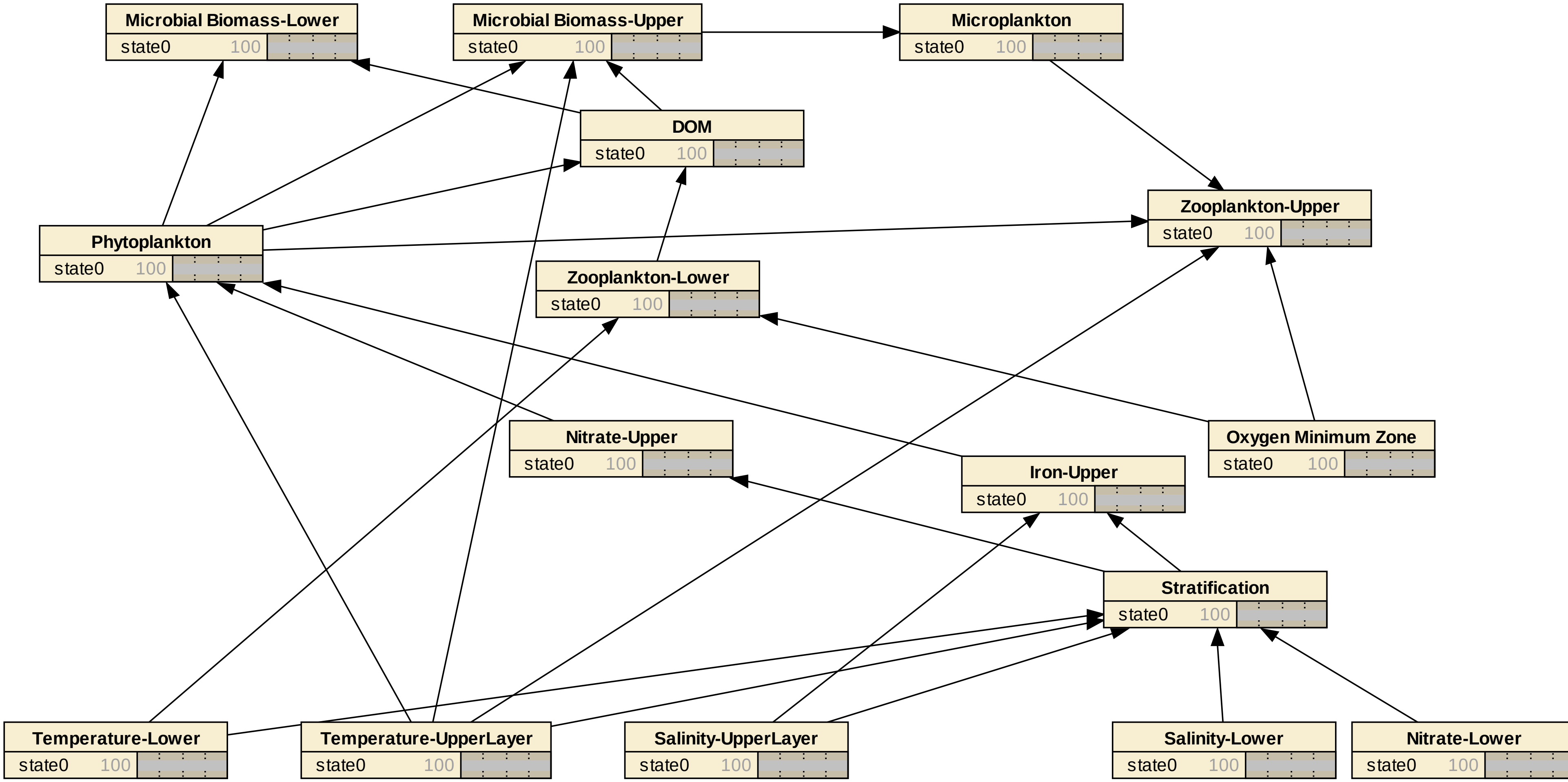


Figure 7. Bayesian Belief Network framework examine how temperature changes to result in cascading effects ultimately altering plankton abundance and community composition and microbial biomass.

DISCUSSION

Conceptual ecological models are now considered essential supporting elements of large scale ecosystem monitoring and restoration plans (Twilley et al. 2008). Capitalizing on the expertise of the Gulf Watch Alaska principal investigators, we created a visualization of a parsimonious conceptual model to synthesize understanding about the key ecosystem elements of the Gulf of Alaska, and to provide a program communication tool to discuss the scope of Gulf Watch Alaska projects and knowledge contributions.

By re-evaluating this model after an additional five years of research, we documented changes in the perception of critical elements in the ecosystem gained by Gulf Watch Alaska related work. For instance, dust-storms, glacial input, jellyfish, and temperature were added as critical elements to the conceptual ecological models whereas recreational traffic, sea ice, and sea level rise were removed from the model as participants indicated the elements did not play a central role in the functioning of the system. These changes demonstrate that current events alter what elements are in the forefront of experts' minds as well as the effect of new information. For example, the Tohoku earthquake and tsunami resulted in large amounts of marine debris; thus marine debris was retained in the 2012 model but was later replaced by microplastics-a current topic in research- during the later phase of the five year program. Also jellyfish were prominent in sampling thus were added to the later model noting that jellyfish blooms may affect forage fish and other zooplankton. Our results highlight the value and need to periodically re-assess conceptual ecosystem models to reflect knowledge gained and shifting perceptions.

Revisiting conceptual ecological models may be critical in long-term programs as it may alter the hypotheses of interest or change adaptive management strategies. However, re-evaluating conceptual models is not prominent in the literature. One program that explicitly includes reassessing models is Ecosystem Restoration Program's Delta Regional Ecosystem Restoration Implementation Plan (DiGennaro et al. 2012). This adaptive management framework allowed for the incorporation of new knowledge once restoration projects were implemented and evaluated. By following a similar adaptive approach, the Gulf Watch Alaska program can keep current with knowledge gained on the ecosystem, include recent discoveries, and update hypotheses and research goals. For example, the "blob" and warming of Gulf waters occurred after the start of the five-year program and initial conceptual modeling effort.

Conceptual modeling proved to be an effective and efficient tool for synthesizing information about ecological systems, and provided a transparent framework for prioritizing elements for future attention. By eliciting ratings of system component attributes from modeling participants, we were able to develop prioritization metrics tailored to different research or management objectives (Sethi and Hollmen 2015). To prioritize system elements for research activities, we used conceptual models to identify linkages that had high strength of interactions but for which the state of knowledge was poor (e.g., ocean acidification impacts on zooplankton). Alternatively, to assist in strategic planning to maximize complementarity with ongoing research or management efforts, we used conceptual models to identify high priority attention gaps for salmon systems.

We also gained insight through the process of creating conceptual ecological models as investigators focused on close examination of linkages in the environment. For instance, in our sea otter predator-prey models, examining the linkage between prey availability and recovery rates was informative as the relationships depended on prey type (e.g. "hidden" infaunal and epifaunal prey, density dependence); it highlighted a decoupled relationship between mussel availability and foraging behavior suggesting sea otters appear to utilize mussels when they find them in dense enough patches to forage at near maximum rates and ignore patches with densities below that required for efficient feeding. The linkage between prey availability and recovery rates for "hidden" infaunal and epifaunal prey were likely related to search effort and handling time, respectively (Sztukowski et al. in prep). When evaluating the sea otter predator-prey models, the link between prey availability and energy recovery rates produced demographic output values lower than expected. This suggests that field sampling may not be accurately characterizing sea otter behavior; knowledge that would have been difficult to detect without a holistic conceptual modeling approach.

Conceptual ecological models allowed us to identify important patterns throughout the visual frameworks and models we produced. Some of our visual conceptual ecological models prompted further questions. For example, we took a closer look at the mechanisms causing change in the "Bottom-up Control with Environmental Forcing on Plankton Populations" submodel by examining the framework in light of recent ocean warming in the Gulf of Alaska. We developed a visual framework to examine how temperature changes alter plankton abundance and community composition and microbial biomass. Our model structure illustrates and suggests that stratification plays a key role in the plankton and microbial communities which ultimately influence higher tropic levels. Data from the Gulf Watch Alaska program is well suited to develop a more analytical model, such as a Bayesian Belief Network, which could simulate changes in the ecosystem providing funding can be acquired.

We demonstrated the value and ability to expand visual conceptual ecological models into quantitative models, such as the rating tool we developed for the humpback whale-herring-zooplankton submodel, and the use of Bayesian Belief Networks. Our quantitative rating tool used expert input to evaluate the state of knowledge, the strength of ecological impact, and the state of management or research attention devoted to a given component. Using this modeling framework, we highlighted uncertainties about the mechanisms of energy movement in zooplankton-herring-whale system, and the potential importance of long-term effects of ocean acidification (see Sethi and Hollmen 2015). Similarly, by quantifying linkages between system components Bayesian Belief Network models also allowed for scenario simulations. For example, our sea otter simulations identified that adult survival may be insensitive to relatively dramatic mussel density changes; rather reduced reproductive success may be a more sensitive demographic response leading to declines in populations over time.

Common to all the conceptual modeling efforts conducted in this project, we found that systematic construction of system structure utilizing a mix of expert opinion, primary data, and published literature revealed key system information needs. For example, nearshore ecosystem Bayesian Belief Network modeling efforts showed that despite the fact that sea otters are relatively well studied, we lack information linking time spent foraging to demographic responses. Alternatively, the Barrow's goldeneye model was constructed with the best available information, but as a data poor species much of the relationships are based on information on related waterfowl. We have identified important relationships to quantify: foraging effort as a function of mussel density, survival in relation to foraging effort/mussel density, productivity in relation to foraging effort/mussel density. These data are necessary if more accurate predictions are desired.

Through the use of Bayesian Belief Networks, we were able to combine quantitative and qualitative information to create structured frameworks to examine relationships between nearshore marine prey abundance and demographic responses of two nearshore predators. These models matched our expectations and accurately reflected empirical observations; the models also served as a basis for testing scenarios and predicting demographic outcomes for these species of management concern. For example, the site-specific Kenai Fjords model for reduced prey simulations, we were not able to reduce mussels below the 20-40% diet contribution category as the resulting demographic performance outputs were consistently outside the probabilistic framework of the model (e.g. the outcomes are very unlikely to occur within the described model), reflecting insufficient energy available via alternative prey fields to support the population in the absence of mussels at Kenai Fjords. Empirical observations sea otter foraging data indicated that the proportion of mussels in the diet at Kenai Fjords never fell below 43%.

Overall, our sea otter predator-prey models suggest both ecosystem-wide and site-specific changes in the Gulf of Alaska nearshore ecosystem. At the broader scale, areas that have been occupied for over 15 years appear to be closer to their carrying capacity then re-colonized sites. At one re-colonized site (Katmai), we modeled site-specific responses at two time points, one in 2006 and one in 2015. Generally, prey recovery rates declined between 2006 and 2015 at Katmai as did demographic responses (Sztukowski et al. in prep). Site-specific models suggest sea otter reproductive success and survival are influenced by local factors, including available habitat types (Sztukowski et al. in prep). Western Prince William Sound showed the least response to the reduction in prey availability. Katmai demonstrated the strongest response in reproductive rate and reproductive success; reducing all prey items at Katmai led to the widest distribution and lowest reproductive success in sea otters, representing a worst-case and unsustainable scenario. The different impacts associated with length of occupancy and site-specific diets suggest site-specific research and management might be needed. These local effects may be mirrored in other species of interest, such as mussels and clams.

Our nearshore predator-prey models suggest the presence of 'tipping point' within the Gulf of Alaska ecosystem. For the Barrow's goldeneye models, we found a relatively large change in reproductive output and an increase in variability between medium and low mussel density simulations. These results suggest a tipping point associated with mussel density; however more data are needed to determine at what point mussel density drastically affect demographic outputs. For sea otters, our model results highlighted relatively high sensitivity of reproductive success to changes in prey availability, along with a general lack of response in reproductive rates and prime-age survival in populations existing at or near carrying capacity (Fig. 4). However, under sustained changes in foraging efforts associated with progressive reductions in prey abundance, a point will be reached where reproductive success (survival of pups to weaning) drops significantly (first tipping point), followed by reductions in female breeding propensity and adult survival (second and third tipping points). While our Bayesian Belief Networks highlighted population impact thresholds, the modeling construction and interpretation process also emphasized that high uncertainty still exists as to what level of foraging effort represents the tipping points for declines in demographic rates, prioritizing further research to better inform these demographic curves to forecast population impacts to changing environmental conditions.

CONCLUSIONS

Conceptual models assist in consolidating knowledge of the ecosystem, identifying data gaps, and provide a communication tool among scientists, resource managers, policy-makers, and the general public. Conceptual model development—which included synthesizing information, gathering data and expert opinion, populating quantitative system models, and examining the linkages and results in the Gulf of Alaska—was useful for identifying limitations to our understanding of the Gulf of Alaska ecosystem. Modeling efforts also provided insight into the degree of uncertainty in data or key ecosystem relationships. In turn, this allowed us to identify system elements where additional data or research on interactions would be particularly useful for improving our understanding of the ecosystem. Through model building, we revealed both findings that were expected as well as unexpected and non-intuitive results that would otherwise have been hard to detect. For instance, the quantitative aspect of Bayesian Belief Network conceptual model also helped to identify a mismatch between field collection methods for prey availability data and consumer foraging behavior; thus the current sampling protocols may need to be re-visited and new or adjusted foraging models may be needed to account for these differences. Overall, scenario models such as Bayesian Belief Network models developed for the Gulf Watch program, offer promising scenario tools to support management considerations in coastal ecosystems.

Conceptual ecological models form the backbone of successful programs and our re-evaluation of the general model for the Gulf of Alaska supports the need for an adaptive framework. By re-visiting conceptual ecological models periodically, new knowledge can be incorporated, unexpected events (such as the 'blob') examined, hypotheses updated, and monitoring efforts and techniques adjusted.

Conceptual ecological models facilitate communication between funding agencies, scientists, and system stakeholders, providing a tool to communicate complex information (Heemskerk et al. 2003). Our models provide as a communication tool within the Gulf Watch Alaska community as well as an outreach tool useful for communicating Gulf Watch Alaska program progress at conferences, in published literature, and at public events. Finally, as has been demonstrated by Gulf Watch Alaska work over the past 5 years, the Gulf of Alaska ecosystem is dynamic. Revisiting our Gulf of Alaska system-wide conceptual ecological model enabled us to incorporate new knowledge and account for unexpected events (such as the 'blob'). By initiating a process of periodically re-evaluating conceptual models hypotheses can be updated, providing a strategic planning tool to adapt research efforts to reflect evolving understanding about the Gulf of Alaska ecosystem.

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Appendix A
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Conceptual Models for Marine and Freshwater Systems in Alaska: Flexible Tools for Research Planning, Prioritization and Communication

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(*Received 2 December 2014; accepted in revised form 1 May 2015*)

ABSTRACT. Conceptual ecological models synthesize information about complex systems into simplified visual maps and can be used to prioritize system components for research or management attention. In this article, we introduce conceptual modeling methods that incorporate expert ratings about a suite of properties of system components, including assessment of the state of knowledge, the strength of ecological impact, and the state of management or research attention devoted to a given component. Quantitative ratings of the properties of system components are subsequently used to prioritize model components objectively for research or management attention. Two case studies, one on plankton-herring-baleen whale dynamics and one on Chinook salmon strategic research planning, are presented to illustrate techniques. For example, in the Chinook salmon case study, participants constructed a prioritization score that identified system components rated as high ecological impact, but low state of knowledge and low state of management or research attention. By addressing gaps in both knowledge and attention, participants implemented a strategy for research planning that complemented existing Chinook salmon research and management in the study region. The case studies demonstrated that conceptual ecological models could be completed successfully with an economy of time. Conceptual modeling has been implemented across a range of disciplines and provides a useful tool that natural resource management and research groups can use to organize collaborative efforts and communicate research or management progress to stakeholders or funders.

Key words: baleen whales; Chinook salmon; ecological modeling; herring; strategic planning; systems models

RÉSUMÉ. La modélisation conceptuelle écologique fait la synthèse de l'information de systèmes complexes pour produire des cartes visuelles simplifiées et permet de prioriser les éléments du système à des fins de recherche et de gestion. Dans cet article, nous présentons des méthodes de modélisation conceptuelle écologique qui englobent les données des experts au sujet d'une suite de propriétés d'éléments du système, y compris l'évaluation de l'état des connaissances, la force des incidences écologiques et la valeur de l'attention de gestion ou de recherche consacrée à un élément donné. Les notations quantitatives des propriétés des éléments du système servent, par la suite, à prioriser les éléments du modèle de manière objective aux fins de recherche et de gestion. Deux études de cas, une sur la dynamique du plancton, du hareng et du cétacé à fanons et l'autre sur la planification stratégique de la recherche sur le saumon quinnat, sont présentées pour illustrer les techniques. Par exemple, dans l'étude de cas sur le saumon quinnat, les participants ont établi une note de priorisation selon laquelle les éléments du système sont considérés comme ayant une incidence écologique élevée, mais un faible état des connaissances et de l'attention de gestion ou de recherche. En comblant les écarts en matière de connaissances et d'attention, les participants ont mis en œuvre une stratégie pour la planification de la recherche qui s'est greffée à la gestion et la recherche en cours sur le saumon quinnat dans la région à l'étude. Les études de cas ont démontré que la modélisation écologique pourrait être réalisée avec succès en moins de temps. La modélisation conceptuelle a été mise en place dans un large éventail de disciplines et offre un outil pratique que les groupes de gestion et de recherche des ressources naturelles peuvent utiliser pour organiser des interventions communes et communiquer les progrès de la recherche ou de la gestion aux intervenants ou fournisseurs de fonds.

Mots clés : cétacés à fanons; saumon quinnat; modélisation écologique; hareng; planification stratégique; modèles de systèmes

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INTRODUCTION

Recognizing the importance of interdependencies in socio-ecological systems, policy makers and scientists continue to move toward ecosystem approaches to natural resource management (Christensen et al., 1996; Botsford et al., 1997; MEA, 2005). Yet, even relatively simple systems like sea otters-urchins-kelp (Estes and Duggins, 1995) or single-species commercial fishing fleets (Branch et al., 2006; Fulton et al., 2011a) have proved challenging to understand. Furthermore, ecosystem-level management requires coordination across disciplines (e.g., between economists and

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biologists) and across stakeholder groups such as resource users and regulatory agencies. In this article, we demonstrate the use of conceptual models as a pragmatic tool to synthesize extant information about complex systems, communicate ideas to stakeholders and experts, and prioritize system components for strategic research or management planning. We introduce a conceptual modeling process that includes ways to generate quantitative ratings for a suite of properties of model components (such as the strength of ecological interactions and the state of knowledge about model components) using expert opinion. We demonstrate this process with two case studies related to aquatic and marine natural resource systems in which we discuss how the modeling process informs strategic research planning. Coupled with their relative simplicity to develop and implement, conceptual models provide a flexible tool for making informed decisions about how best to use limited time and financial resources to study or manage a socioecological system by focusing efforts on high-priority system components.

Systems models have played a critical role in understanding the dynamics of ecosystems. They span a gradient from purely qualitative conceptual models to fully quantitative end-to-end models (e.g., Ecopath: Pauly et al., 2000; Atlantis: Fulton et al., 2011b; also see Rose et al., 2010). Fully quantitative system models are challenging to implement and can suffer from high data requirements to parameterize simulation models (Marcot et al., 2006; Uusitalo, 2007; Fulton et al., 2011b). But conclusions about such implementations stress the benefit of the development process: existing knowledge about complex systems is synthesized, communication is facilitated across disciplines and between stakeholders involved in model interpretation, and information or management gaps are identified (Marcot et al., 2001; Zorrilla et al., 2010). Many of these benefits are also achievable with qualitative conceptual models, and depending on modeling objectives, a simplified approach may be an adequate and time-efficient way to move forward. Conceptual models extract diffuse information from experts or the literature and synthesize understanding of complex systems into tractable conceptual maps (Howard, 1989). They can be used to identify knowledge or management gaps (see below) and can also serve as a framework for conducting structured thought exercises or simple management simulations (Radomski and Goeman, 1996). Indeed, conceptual model development is often an initial step in designing quantitative systems models, providing a schematic for subsequent simulation model construction and highlighting key components to capture when simulating or designing management actions. While quantitative system models are important tools for designing specific management actions for ecosystems, such as harvest schedules or the placement and design of area closure networks, conceptual models allow for complex system representation without the explicit need for mathematical models or even quantitative data, if expert opinion is available to inform models. In other words, what conceptual models lack in mathematical rigor, they compensate for in their simplicity to develop and their practical usefulness for strategic research planning and synthesis of systems understanding.

Conceptual modeling exercises to synthesize information and visualize the structure of complex systems can be found across a wide range of disciplines—from operations research (Robinson et al., 2010) to education (Novak and Cañas, 2006) to ecosystem-based management (Harwell et al., 1996; Ogden et al., 2005 and related articles in the special issue of *Wetlands*, Vol. 25; King and Hobbs, 2006). In addition, conceptual models provide valuable support tools for structured decision analysis and have been widely used in that context (e.g., Conroy and Peterson, 2013). The conceptual modeling techniques we focus on in this paper are those that we have found to be both flexible and useful for strategic research planning. They are most closely related to conceptual modeling as employed in operations research (Robinson, 2008a, b) and similar to the cognitive mapping approach (Axelrod, 1976; Kosko, 1986) originally developed in political science. However, we do not implement a formal fuzzy logic approach (e.g., Özesmi and Özesmi, 2004) to synthesize model input, finding this to be unnecessary to achieve the objectives of many conceptual modeling exercises. Likewise, mental model applications in environmental science implement a similar process to elicit stakeholder beliefs about system attributes and highlight key model components, information gaps, and management priorities (e.g., Bostrom et al., 1992; Zaksek and Arvai, 2004).

Conceptual models take on a range of forms, depending on the application; however, they share commonalities. First, conceptual modeling exercises begin with formulation of the objectives to be achieved. Examples include:

- Research groups: identify high priority research areas for subsequent study; or, provide a working hypothesis of a complex socioecological system with which to communicate research efforts to the public and to funders, and track learning about the system as a result of research efforts.
- Natural resource management agencies: maximize conservation benefit from limited restoration funds by focusing efforts on critical system linkages; or, improve complementarity with other management agencies sharing jurisdiction over a socioecological system by identifying management gaps.

Second, existing information—be it from empirical data, published literature, or expert opinion—is synthesized into a set of system components. Third, interdependencies, or linkages, in the system are identified. Fourth (optional step), expert- or literature-derived assessments of attributes of system component or linkages are input into the model. Fifth, a visual representation of the structure of the system is constructed. Finally, results of the modeling exercise are disseminated among stakeholders and conclusions are discussed. The process is typically collaborative and iterative.

Below we outline a flexible process for implementing conceptual ecological models that incorporate expert input.

Instead of aiming to forecast system outcomes, we suggest that such modeling can synthesize understanding of a system, identify gaps in knowledge or management for strategic planning, and, if repeated over time, track the state of learning as research results inform system understanding. Techniques are demonstrated with two examples from Alaska, one on Pacific herring (*Clupea pallasii*)–baleen whale dynamics and one on strategic research planning for Chinook salmon (*Oncorhynchus tshawytscha*). Using ratings from experts to inform models, groups were able to prioritize areas of high ecological importance about which relatively little is known or which receive little management attention, providing a transparent and objective method for strategic planning.

METHODS

Our approach to the conceptual modeling process to synthesize knowledge and prioritize system components for research or management attention has followed a regular sequence of steps (also see Suter, 1996; Gross, 2003): i) define objectives of the modeling exercise and organize relevant modeling participants, ii) determine the set of components to include in the model, iii) define linkages among model components, iv) score attributes of model components that are relevant to the modeling objectives and, if desired, generate prioritization ratings, and v) visualize results and communicate outcomes. Conceptual ecological models can be informed by scientific literature (e.g., Simenstad et al., 2006), expert opinion (e.g., Radomski and Goeman, 1996), or some combination thereof (e.g., Harwell et al., 2010; see below). Whether organizing a literature review or garnering expert input to inform a conceptual model, the project will require one or more core facilitators to move the process along. Here we focus on efforts to inform conceptual ecological models through a combination of literature and expert opinion: model facilitators use their existing knowledge base and relevant literature to propose an initial conceptual model structure, which is then refined with expert opinion. The model development material discussed below, such as protocols to reach consensus about final models, also applies to models informed purely by literature.

Define Objectives and Organize Participants

We begin conceptual model development by identifying the objectives for conducting a modeling exercise, typically with the goal of writing down a concise statement that summarizes the desired outcome(s) of the model development process. For example, the objectives of the zooplankton-herring-whale modeling exercise were to synthesize understanding about the key processes affecting Pacific herring–baleen whale foraging dynamics and to refine a rating system for quantifying expert opinion about the properties of linkages in northern Gulf of Alaska ecosystems in a group of principal investigators involved in a large-scale monitoring project (Gulf Watch Alaska project; www.gulfwatch.org). In the Chinook salmon modeling case study, the objective was to synthesize current understanding of the Chinook salmon life cycle and the associated stressors affecting survival through life stages in order to identify knowledge and management gaps in the south-central and western regions of Alaska. Once identified, knowledge and management gaps would then be used to prioritize future research efforts.

After identifying the objectives of the exercise, we organize a set of expert participants from whom to seek input into a conceptual model. In many cases, the universe of participants derives directly from the objectives of the modeling exercise. For example, in the Chinook salmon case study, the objective involved strategic planning for a management agency (U.S. Fish and Wildlife Service), and thus the universe of participants was constrained to agency staff. In the zooplankton-herring-whale case study, the express purpose of the exercise was to synthesize the system dynamics knowledge of the Gulf Watch Alaska program principal investigators. Depending on the objectives of the exercise, participants may have similar expertise (e.g., salmon ecology), or the process may be designed to have a balance of expertise when working with ecosystem-level models (e.g., models of intertidal ecology or physical oceanography). More formally, experts could be asked to rate their ability to contribute to parts of a conceptual model, and consensus models could summarize this information throughout different components of the final model (e.g., McDaniels et al., 2010), for example, by presenting linkage rating values weighted by experts' self-rating scores (or ratings based upon a set of calibration questions; cf., Wittmann et al., 2015).

Some conceptual ecological modeling efforts, particularly those involving resource allocation, encompass diverse stakeholders with potentially conflicting interests. Modeling participants may bring perspectives about the modeled system specific to their experience, knowledge base, or special interest agenda. In such cases, obtaining a diverse set of participants with representation from the set of stakeholder groups encompassed by the objectives of the modeling exercise may help balance individual-specific biases to produce a group consensus model that adequately represents the system as a whole (e.g., Hastie and Kameda, 2005; but see Kerr et al., 1996). In other situations, it may be possible to census all stakeholders encompassed by a modeling process—a scenario similar to the Chinook salmon research planning modeling effort for a single management agency, as detailed below. Finally, participants with experience in conceptual modeling can improve the efficiency of the process. Similarly, avoiding people whose personalities can disrupt the process or who actively seek to prevent progress in a modeling effort is of practical importance, particularly when a modeling effort is centered around contentious resource systems with opposing stakeholder interests.

Appendix A
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Define Model Structure and Score Attributes

After the participant pool has been organized, we propose a starting conceptual model informed by the appropriate scientific literature, presenting the group with a "prior" model to be updated by participants' input. The structure of the starting model matches the modeling exercise objectives. For example, in the Chinook salmon case study, the objective of the modeling exercise was to identify and prioritize research efforts for key stressors on juvenile Chinook salmon; thus, the conceptual model contained life stages and stressors. In other modeling exercises, such as the herring-whale modeling case study presented below, the focus may be on understanding the structure of the system. In these applications, models focus on ecosystem components as opposed to anthropogenic stressors. While providing participants with a prior model is not a necessary step, we have found that presenting respondents a framework from which to build facilitates group input, as opposed to starting from scratch and dealing with group unwillingness to participate or paralysis faced with the complexity of writing down a model in a short time. Furthermore, by preparing a prior model, facilitators can draw from the extant literature at the time of the exercise (e.g., Cormier et al., 2009).

Next, we incorporate participants' input to update the model structure. In this step, respondents are asked to decide which components of a conceptual ecological model should be retained, discarded, or added. Then, to represent interactions in the conceptual model, the respondents are asked to define linkages between model components, and optionally, to rate properties of the linkages using a series of questions related to the objectives of the exercise. For example, in the Chinook salmon case study, we asked respondents to rate linkages between stressors and Chinook salmon life stages in terms of severity of impact, state of knowledge about the impact, and state of research or management attention currently being devoted to the stressor and its impact on a given life stage. For the herring-whale model, we asked respondents to rate a suite of properties of linkages among ecosystem components, including strength of interaction, variability of interaction, and spatiotemporal scales. We also asked respondents to rate the current state of knowledge about linkages to facilitate further analysis of research priorities for the program.

Participants could conduct modeling exercises as a group and collaboratively discuss decisions to include or discard model components or linkages, or alternatively, these exercises could be conducted individually. Both approaches have benefits and weaknesses. Modeling exercises conducted as a group facilitate flow of information and spur creativity, benefiting brainstorming and problem solving (e.g., Hill, 1982); however, they can result in "group think," whereby group responses gravitate toward the more vocal participants or majority points of view, potentially reducing the diversity of information input into conceptual models (Maier, 1967; Schmoldt and Peterson, 2000). Individually completed modeling exercises reduce the time necessary to keep a group of participants together and, if assigned as a task to be completed at a later date, allow participants ample time to reflect on their responses or consult literature. We caution, however, that facilitators will have limited ability to provide clarification on the conceptual modeling or ratings process if modeling exercises are assigned as a task to be completed at a later date. Furthermore, significant follow-up communication may be required to ensure that all participants successfully complete the responses.

Regardless of the method of conducting and recording input, the next step is to generate a consensus model based upon participants' responses. Consensus on model components and linkages can be achieved using a majority rule (e.g., retain a component if 50% or more of the respondents included it) or a threshold rule (e.g., include a component if at least three respondents included it). Linkage ratings can be summarized using descriptive statistics such as means or medians. Furthermore, the degree of consensus on a linkage rating can be summarized by examining the variability in rating responses; low variability suggests agreement (and high variability, disagreement) within the group. For transparency, when presenting results from a conceptual modeling exercise, we recommend including information about the expertise of modeling participants, as well as information on the degree of consensus among participants for final consensus models.

Prioritize Scores

In addition to synthesizing existing information about a modeled ecosystem, an important practical use of conceptual ecological models is to prioritize system components for follow-up study to fill knowledge gaps or to identify high-priority components in need of management attention. Expert ratings of model components or linkages can be used to generate numerical prioritization scores that address modeling objectives related to strategic research and management planning. A ratio score that takes the strength of interaction over the state of knowledge is useful for highlighting system linkages that are ecologically important and which are poorly understood. An alternative approach is to construct an additive score that incorporates multiple factors in a prioritization effort, such as consideration for the strength of a given interaction, the state of knowledge about the interaction, and the state of attention devoted to managing or understanding the interaction. With composite scores, modelers can either implement equal weighting of the prioritization factors or assert different weights for different factors. An advantage of generating numerical scores is that the process of prioritizing model components or linkages for research or management attention can be made transparent, clearly communicating the rationale for planning decisions. Furthermore, numerical scores enable comparison of differences in prioritization emphasis across groups of scorers. For example, prioritization scoring for a given conceptual model could be carried out separately with focus groups—such as regulators, user groups, or scientists in a natural resource management system—so that a comparison of scores could be used to highlight commonalities and differences among stakeholder groups in the perceived importance of system components (e.g., Zaksek and Arvai, 2004).

Visualize and Communicate Results

The final consensus model represents the prior model updated by expert opinion. The last step in the process is then to communicate the results to the group of respondents and other interested parties to achieve the objectives outlined in the first step. A visual representation of the final consensus model presents a succinct working hypothesis of the modeled system and serves as a tool to communicate beliefs about the structure of a system across stakeholders. If model components were scored as part of the effort, the conceptual model visualization can be augmented with tables or figures that summarize model ratings scores. The conceptual modeling development process and the communication of results can be repeated iteratively, for example, to examine whether system understanding has changed as a result of research and management efforts over time. They could also be conducted with multiple groups independently, for example, if logistical constraints prevented gathering modeling participants together at the same place and time, and then results could be merged into an updated consensus model.

Case Study 1: A Zooplankton-Herring-Whale Model

This modeling exercise was conducted over one day at a November 2012 meeting of principal investigators for the Gulf Watch Alaska project, a multidisciplinary project funded by the Exxon Valdez Oil Spill Trustee Council to address long-term changes in the northern Gulf of Alaska. The objectives of the zooplankton-herring-whale modeling exercise were to synthesize current understanding about the key processes affecting Pacific herring–baleen whale dynamics in Prince William Sound, Alaska, identify linkages in the system, and refine a linkage rating system to quantify expert opinion, in order to facilitate strategic planning among the investigators involved in the long-term monitoring program. The group of modeling participants consisted of 19 investigators familiar with Gulf of Alaska ecosystems and with expertise balanced among marine ecology (n = 7), physical and biological oceanography (n = 6), and wildlife biology (n = 6). The exercise was facilitated by the authors, who also provided model responses. This conceptual modeling exercise focused on one subsystem within the Gulf of Alaska ecosystem, herring and baleen whales, and was undertaken to train experts for a later broader conceptual modeling exercise with the goal of developing a parsimonious conceptual model to describe the key ecosystem processes for the northern Gulf of Alaska (see www.gulfwatchalaska.org for additional details).

Respondents were provided with a "prior" zooplankton-herring-whale system model and asked first to draw in relevant linkages and then to rate properties of linkages. Linkage rating questions examined whether a given linkage had a positive or negative impact from the upstream to the downstream component, the strength of the linkage, the degree of stability of the linkage, the temporal and spatial scales at which a linkage operates, and the state of knowledge about the linkage (online Appendix 1; the prior model handout provided to the group is available from the authors upon request). Respondents indicated ratings on a scale of 1 to 5 and completed individual questionnaire worksheets. The scale of 1 to 5 was selected on the basis of pilot rating exercises with a three point, "high-medium-low" rating scale, in which a subset of modeling participants indicated a desire for additional categories.

After completion of the modeling session, linkage-rating data were processed in the R statistical programming environment (R Development Core Team, 2013), accounting for both the directions of linkages and values for linkage ratings questions (example data matrices available from the authors upon request). We used a simple majority rule to determine whether a linkage should be retained in a final consensus model, retaining any linkage included by 50% or more of the respondents. A consensus threshold of 75% was also tested; however, the group of experts had a high degree of agreement on the existence of linkages, and the set of linkages remained unchanged. We used the mean linkage rating value among those respondents who included a retained linkage to reflect a consensus rating, and we assessed group agreement by calculating the standard deviation of the numerical expert ratings for a retained linkage. To prioritize areas for future research attention, we calculated the ratio of mean strength of interaction response to mean state of knowledge response for each linkage. Linkages with high scores indicate high strength of interaction but low current state of knowledge, which makes them high-priority research targets. Finally, at the end of the modeling exercise, we asked the respondents to critique the linkage rating questions and suggest improvements.

Case Study 2: Stressor-Impact Modeling of Chinook Salmon

This modeling exercise, conducted in one day at the U.S. Fish and Wildlife Service field office in Kenai, Alaska in September 2013, was an assessment of risks to Chinook salmon undertaken to help the group prioritize research and management efforts for Chinook salmon in south-central and western Alaska (cf. U.S. EPA, 1992). The objectives were to identify the key Chinook salmon life history stages, identify key stressors affecting survival through each life stage, and finally rate the stressor impacts at each life stage in terms of the strength of the impact, the state of knowledge about the stressor and its impact, and the state of management and research attention being provided to the stressor and its impact by the U.S. Fish and Wildlife Service or other organizations (e.g., State of Alaska management agencies, academic institutions, and nonprofit research groups). The group of modeling participants consisted of 10 investigators from the U.S. Fish and Wildlife Service with expertise in fisheries and aquatic ecology. The exercise was facilitated by one of the authors (S.A. Sethi), who also provided model responses. The consensus model including life stages and relevant stressors represented a working hypothesis for Chinook salmon in south-central and western Alaska, and stressor impact ratings were used to identify gaps in knowledge or management/research attention, providing a tool to help administration staff prioritize future research efforts.

Respondents were provided an initial set of Chinook salmon life stages drawn from the salmon ecology literature (cf. Groot et al., 1995; Spence et al., 1996), and the group collaboratively reasoned through the prior model to aggregate, disaggregate, retain, or discard life stages. Consensus was reached in a group discussion session, using a simple majority rule and verbal voting to set the list of agreed-upon life stages. Next, respondents were provided an initial set of stressors, grouped into "environmental," "biological," and "anthropogenic" categories. Working from the prior list of stressors, a group discussion was undertaken to modify, add, or remove stressors, again using verbal voting and a majority rule to set the final list of stressors.

In the final step of the modeling exercise, respondents were given a worksheet with all possible stressor–life stage combinations and asked to rank the stressor impact according to three ratings attributes outlined above (for detailed results, see online Appendix 2). Stressors were rated on a 1 to 5 scale; respondents could indicate that a stressor was irrelevant at a given life stage by giving it a "1" for its impact rating. Ratings were processed in R using mean values to reflect consensus ratings and standard deviations to assess agreement within the group. To summarize consensus ratings for stressor–life stage ratings and separate out unimportant stressors, we used a threshold rule, retaining a given stressor–life stage combination if at least 50% of the group provided an impact rating greater than 1. To prioritize future research efforts for Chinook salmon, we constructed a composite score that equally weighted the strength of impact, state of knowledge, and attention ratings for each retained stressor–life stage combination; stressors rated as high impact, poor state of knowledge, and garnering little research or management attention were ranked as high-priority areas for future work.

RESULTS

Case Study 1: Zooplankton-Herring-Whale Model

The consensus model contained eight linkages throughout the zooplankton-herring-whale model (Fig. 1). Overall, participants had the highest degree of consensus when rating the temporal and spatial scale at which linkages operate (Table 1) and the lowest when rating the strength of linkages.

The strongest linkages were the positive effect of zooplankton on herring (mean rating = 3.9 out of 5.0), the positive effect of upwelling on zooplankton (mean rating = 3.6), and the positive effect of herring on whales (mean rating = 3.5; Fig. 1). Appendix 1 provides additional detail on the rating scales employed in this exercise; however, a strength of interaction rating of 3.0 indicates that a change in one component in a system results in a moderate change in the state of another component, but is not considered a main driver of that change, whereas a rating of 5.0 indicates that one component is a main driver of change in another component. Experts rated the effect of whales on zooplankton as the weakest linkage retained in the consensus model.

The most localized interactions in the consensus model were related to predation (Fig. 1), with these processes occurring at the scale of tens of kilometers (mean ratings from 2.4 to 3.2; online Appendix 1). The largest-scale processes involved the effect of ocean acidification on zooplankton (mean rating = 4.9) and the effect of upwelling on ocean acidification (mean rating = 4.6), which occurred at the scale of thousands of kilometers, i.e., basin-wide in the Gulf of Alaska (online Appendix 1). The range of experts' ratings of temporal scales was more compressed, with mean ratings across linkages of 1.8 to 3.4. The fastest interactions involved predation, occurring on a monthly or seasonal time scale, and the slowest interaction involved the effect of ocean acidification on zooplankton, occurring on a scale of years.

Respondents determined that linkages in the zooplankton-herring-whale model were similar in terms of the variability of the interaction between components, with mean ratings ranging from 2.6 to 3.5 (Fig. 1). A rating of 3.0 for this question indicates that an interaction has some predictability, but is inherently stochastic; a rating of 5.0 indicates that an interaction is direct and persistent, and a change in one element produces a predictable response from another element (rating of 5.0; online Appendix 1). The most stable interactions involved the upwelling-zooplankton-herring chain, whereas the most variable interactions involved the effect of whale predation on herring and zooplankton and the effect of upwelling on ocean acidification.

Finally, respondents rated the state of knowledge about the effect of ocean acidification on zooplankton to be the poorest, while the effect of zooplankton on herring was rated as the best understood linkage. However, the highest mean rating for any linkage was 3.5, which indicates that although some empirical evidence exists to support a linkage, the evidence is not conclusive (online Appendix 1).

On the basis of the prioritization score, defined as the ratio of the consensus strength of interaction to the state-of-knowledge rating for linkages, interactions involving ocean acidification were rated as highest priority, followed by the effect of zooplankton on herring (Table 2). Although the latter linkage was rated as the best understood, it was also rated as a high-impact effect. Top-down effects of whale on zooplankton were rated as having a relatively lower priority in this system.

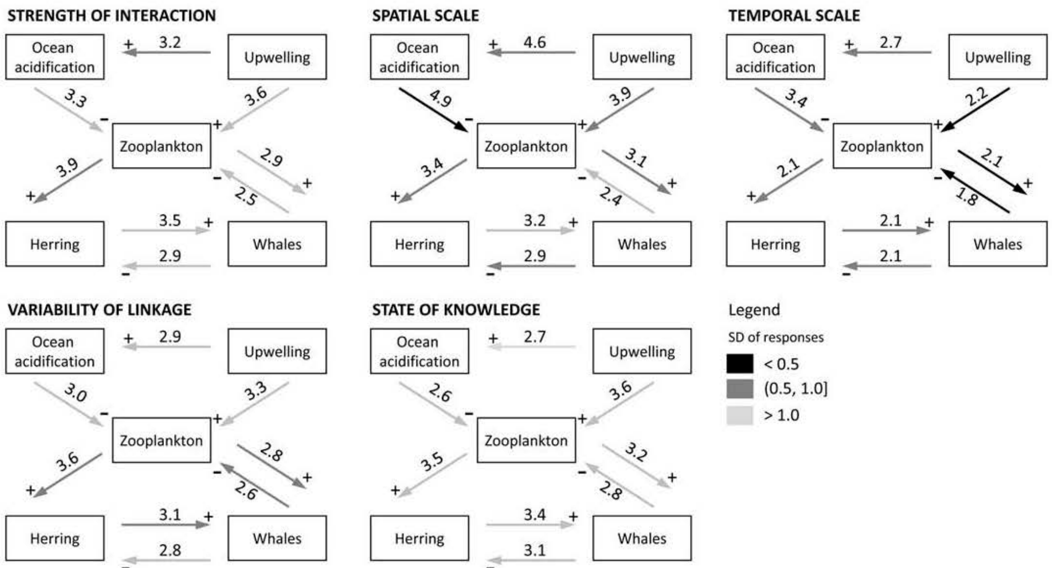

FIG. 1. Consensus model results for the zooplankton-herring-whale model. A linkage of $X \rightarrow Y$ indicates that X affects Y, and the direction of effect (+ for positive or – for negative) is indicated on linkage arrows. A given linkage was retained in the consensus model if 50% or more respondents included it. Numerical values from 1 to 5 represent mean ratings among participants who rated a given linkage (see online Appendix 1). Linkage arrow shading corresponds to the level of agreement by respondents about a given linkage rating as measured by the standard deviation of ratings, with darker shades indicating higher agreement.

TABLE 1. Assessment of the degree of consensus about linkage ratings for the zooplankton-herring-whale model.

Linkage property	SD[1]
Strength of interaction	1.11
State of knowledge	1.09
Variability of linkage	1.01
Spatial scale	0.87
Temporal scale	0.62

[1] Values are the mean standard deviation (SD) of responses for a given rating question across all linkages.

TABLE 2. Ratio of strength of interaction to state of knowledge for linkages in the zooplankton-herring-whale model.[1]

Linkage	Ratio
acidification-zooplankton	1.26
upwelling-acidification	1.19
zooplankton-herring	1.13
herring-whale	1.04
upwelling-zooplankton	1.02
whale-herring	0.96
zooplankton-whale	0.91
whale-zooplankton	0.90

[1] *X-Y* represents the effect of *X* on *Y*.

Case Study 2: Stressor-Impact Modeling of Chinook Salmon

The group produced a consensus Chinook salmon life history model containing eight discrete life history stages (Fig. 2). The initial prior model (not shown) involved only six life stages, condensing freshwater rearing and spawning into single stages; however, the group decided that these critical life stages should be disaggregated into finer steps.

Fourteen key stressors were identified as being important in affecting survival through life stages in the conceptual model for Alaskan Chinook salmon (Table 3). Experts had consistent agreement for stressor–life stage ratings (grand mean of standard deviation of responses = 1.03). Standard deviations of ratings also remained consistent for both high- and low-rated stressor–life stage combinations (online Appendix 3).

The stressors rated with the highest strength of impact on the egg to alevin stages were related to siltation and water condition (Fig. 2; online Appendix 3). For the juvenile stages in freshwater, the highest impact stressors were related to predation, food availability, and habitat access, although cold water temperatures were a top stressor for overwinter juvenile rearing. Similarly, food availability, predation, and water temperature were perceived as important stressors on the juvenile ocean rearing stage. Finally, fishing harvest, fishery selectivity, and habitat access were rated as top stressors on the spawning life stages.

Appendix A
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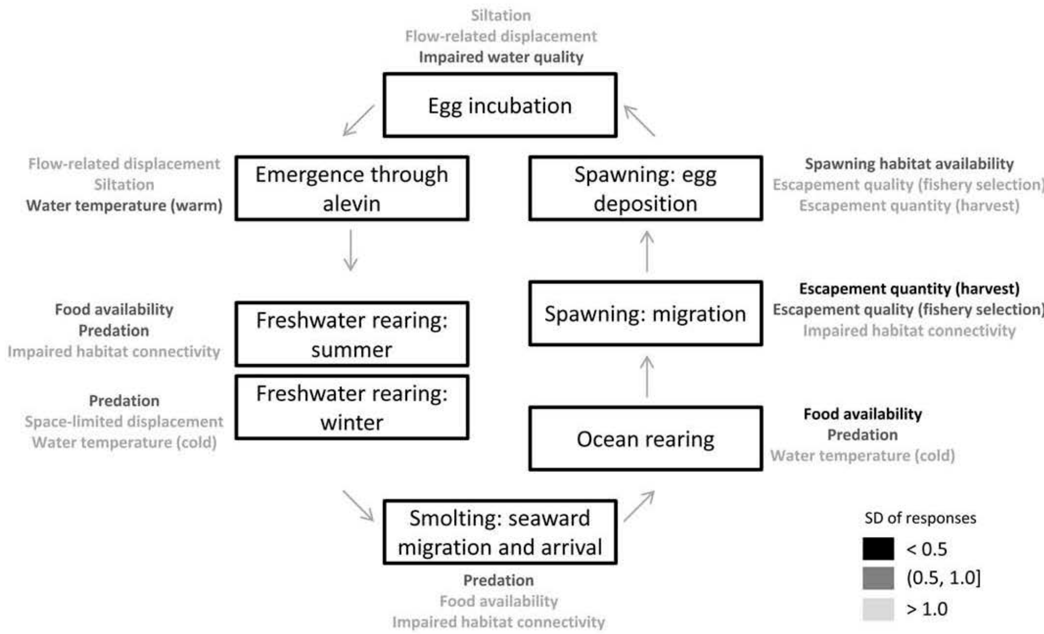

FIG. 2. The consensus Chinook salmon life history model. The three top-rated stressors in terms of "strength of impact on a life stage" are indicated next to each life stage, in descending order from greatest to least impact. Font shading corresponds to the level of agreement on stressor impact ratings as measured by the standard deviation of responses, with darker shading indicating higher agreement (see online Appendix 2).

TABLE 3. Stressors on Chinook salmon life history stages.

Category	Stressor
Environmental	Water temperature (cold)
	Water temperature (warm)
	Flow-related displacement
	Impaired habitat connectivity
	Siltation
	Impaired water quality
Biological	Food availability
	Disease
	Predation
	Spawning habitat availability
	Space-limited displacement (competition)
Anthropogenic	Escapement quantity (harvest)
	Escapement quality and fishery selection
	Hatchery-related genetic introgression

In general, experts rated few stressors as receiving much research or management attention, with the exception of harvest levels and escapement quantity, which have received considerable research and management effort in the region (Fig. 2; online Appendix 3). Habitat connectivity during freshwater rearing, water temperature during ocean rearing, and disease during spawning migration were rated as receiving intermediate amounts of research and management attention.

From the composite prioritization scores, population genetic effects related to harvest and hatchery introgression were rated as top priority on the egg to alevin stages, as was the role of disease (Table 4; online Appendix 3). Predation and habitat access were consistently high priority for the freshwater life stages. During ocean rearing, food availability was a top priority stressor, as were the effects of hatchery introgression. Finally, during spawning, hatchery introgression, water quality, and stressors related to habitat access were top priorities based upon the composite scoring metric.

DISCUSSION

Case studies demonstrated that conceptual modeling was an effective tool for synthesizing and presenting information about ecological systems and subsequently prioritizing system components for research or management attention. The zooplankton-herring-whale model identified several important insights among the group of modeling participants. While considerable debate persists about the relative roles of top-down versus bottom-up mediation of forage fish stocks in temperate oceans, the zooplankton-herring-whale modeling effort indicated potential for bottom-up control of Pacific herring stocks in Prince William Sound. Interactions between zooplankton and herring, and between herring and whales, indicated higher strength of

TABLE 4. Top-ranked stressors based upon prioritization scores for the consensus Chinook salmon model.[1]

Life stage	Rank	Stressor[2]
Egg incubation (11)	1	Hatchery introgression
	2	Escapement quality
	2	Impaired water quality
	3	Escapement quantity
Emergence-alevin (9)	1	Hatchery introgression
	2	Flow-related displacement
	3	Disease
Freshwater rearing: summer (12)	1	Flow-related displacement
	2	Water temperature (warm)
	3	Predation
Freshwater rearing: winter (13)	1	Predation
	2	Food availability
	3	Space-limited displacement
Smolting migration/ocean arrival (11)	1	Food availability
	2	Water temperature (cold)
	3	Space-limited displacement
Ocean rearing (9)	1	Food availability
	2	Hatchery introgression
	3	Predation
Spawning: migration (12)	1	Hatchery introgression
	2	Flow-related displacement
	3	Impaired water quality
Spawning: egg deposition (13)	1	Spawning habitat availability
	2	Hatchery introgression
	3	Predation
	3	Space-limited displacement
	3	Impaired habitat connectivity

[1] Results are from 10 respondents, and stressors within each life stage are ranked by impact rating. (See online Appendix 2 for rating questions.) The number of retained stressors affecting life stages is indicated parenthetically.

[2] Stressor prioritization score = 0.33 × (impact rating) + 0.33 × (absolute value (knowledge rating − 5.0)) + 0.33 × (absolute value (attention rating − 5.0)). The knowledge and attention ratings were translated in such a way that a high score indicates a low state of knowledge or little research or management attention devoted to a stressor and its impact. High scores therefore indicated high-priority items for future management and research efforts.

relationship moving up the food web (i.e., interactions representing energy flow from lower to higher trophic levels). Similarly, ocean acidification was highlighted as a significant long-term process that may indirectly affect Pacific herring stocks in Prince William Sound by harming their zooplankton prey base; this process was rated as having a relatively strong impact and occurring over basin-wide scales, but with relatively poor state of understanding about the dynamics of ocean acidification and the subsequent impacts on planktonic organisms. While several studies have shown the potential for substantial ecosystem-wide reorganization and trophic transfer impacts associated with ocean acidification (Fabry et al., 2008, 2009; Rossol et al., 2012), much of the research on biological impacts of ocean acidification to date has been focused on laboratory trials (Branch et al., 2013). The zooplankton-herring-whale modeling group's prioritization of potential impacts from ocean acidification on an important forage fish resource in Prince William Sound emphasizes the need for field studies to examine impacts on specific fish taxa to complement laboratory trials.

Implementation of composite prioritization scores as part of the Chinook salmon conceptual modeling effort at the U.S. Fish and Wildlife Service allowed for management and research strategic planning that simultaneously considered a suite of factors important for the organization's operations planning. This conceptual modeling effort provided information that enables the group to tailor research projects to fill existing gaps in management of Chinook salmon resources in the study region; indeed, top priority stressor–life stage combinations were different from those rated purely on strength of impact (Table 4; Appendix 3). The exercise highlighted the dearth of information about Chinook salmon life history in Alaska, where most of the available management and field budgets are focused on fishery-related monitoring projects necessary to implement subsistence, commercial, and sport fisheries. The process of constructing the Chinook salmon stressor conceptual model and generating prioritization scores was well received at the U.S. Fish and Wildlife Service in Alaska and has since been incorporated into strategic operations planning efforts for other stocks of Pacific salmon under the agency's jurisdiction.

Feedback from conceptual modeling participants involved in the zooplankton-herring-whale and Chinook salmon case studies was generally positive, emphasizing that the process helped assemble groups' understanding of systems by formalizing lists of system components and ultimately producing a visual representation of how system components interact. Many participants were surprised by the amount of organization and synthesis achievable during the one-day conceptual modeling workshops. Furthermore, the conceptual modeling exercises provided a transparent and objective method for prioritizing system components for research or management attention. The steps taken to create a conceptual model, information about modeling participants, system component rating methods, and the raw expert rating data can be made available to stakeholders for critique. Sensitivity analyses can be carried out by testing different rules for reaching consensus about including a system component (e.g., majority- versus threshold-based rules), different consensus scoring metrics (e.g., median versus mean ratings), and different research or management prioritization scores. Such testing provides transparency about the robustness or weakness of modeling conclusions when prioritizing system components for management or research. Finally, prioritization scores can be custom-tailored to address specific objectives in conducting a conceptual modeling exercise. For example, the Chinook salmon case study included a prioritization score that incorporated both state of knowledge and state of management or research efforts currently being devoted to a given model component, highlighting system components that fall within a knowledge and management gap. Addressing these gaps would lead to a strategy of complementing extant research and management efforts for Chinook salmon management.

A potentially useful extension to the conceptual modeling approach outlined above is to include ratings for the cost and feasibility of successfully implementing research or management efforts to address a given system component. If available, monetary cost information could be directly incorporated into the conceptual modeling process, for example, by identifying costs for specific research or management projects to address a system component. Alternatively, subjective ratings by modeling participants could be used to provide relative rankings of system components based upon cost or feasibility. By including cost or feasibility considerations, conceptual modeling can support cost-benefit evaluation of alternatives and calculations of value of information in a structured decision analysis framework, facilitating research and management planning in both near- and long-term timeframes (Schmoldt and Peterson, 2000). For example, participants in the Chinook salmon case study rated both habitat connectivity and disease as high-priority stressor–life stage combinations during the spawning freshwater migration (low state of knowledge, low state of management or research attention, and high strength of impact). In general, habitat connectivity restoration efforts such as fish passage barrier removal are costly, and implementing them may require long-term planning for staff and funding (e.g., the State of Washington estimates approximately $3.9 million USD per culvert mitigation project within the state; WSDOT, 2014). Alternatively, research on disease dynamics may be more readily addressed given extant funding and staffing levels in the near term. Thus, when faced with limited budgets, decision makers may choose to prioritize lower-cost, disease-related research in the near term, and work towards expensive habitat connectivity projects in long-term planning.

Respondent critique common to both case studies indicated that experts felt constrained by starting with prior models. While prior models are not necessary, we note that the conceptual modeling exercises would likely not have been achievable in one-day workshops without them. Indeed, we found that group discussions began quickly when we presented a starting model, and while prior conceptual models guided the process, groups successfully updated the starting model and reached an agreed-upon consensus model (e.g., see the Chinook salmon strategic planning case study). Conceptual models larger than the case studies presented here can quickly become time-intensive, presenting a practical limit to what can be achieved in a one- or two-day workshop. In such cases, larger systems could be broken into submodels, with smaller groups working in parallel, or analysts could rely more heavily on literature, as opposed to in-person group participation, to inform models (e.g., Radomski and Goeman, 1996; Harwell et al., 2010). The provision of additional time for conceptual model generation without the use of a prior model, when possible, allows participants to become familiar with the modeling process, establish relationships, and identify communication issues, benefiting later stages of the conceptual modeling process, including use of the model for prioritization, communication, or decision making (M.A. Harwell, pers. comm. 2015). In practice, efforts involving multiple stakeholder groups often use a series of modeling workshops to provide sufficient time to develop a conceptual model and familiarize participants with the modeling process (Ogden et al., 2005 and related articles in the special issue of *Wetlands*, Vol. 25).

We achieved success with quantitative scoring of conceptual model component attributes with a group of relatively well informed and like-skilled participants for the marine and freshwater case studies presented above. We caution, however, against over-interpretation of quantitative metrics, particularly in cases where participants may not have adequate understanding or experience to make informed ratings. In such cases, quantitative metrics may portray false precision, and simpler qualitative ratings approaches, such as a two-category "high" or "low" rating approach, may better reflect participants' abilities to rate model components, while still allowing for the ability to organize and prioritize model components. Indeed, another common modeling extension indicated by respondents during modeling feedback was the inclusion of participant self-ratings to accommodate varying degrees of expertise about system components. As indicated earlier, respondent self-ratings could be used to create weighted averages of system-attribute ratings. The suggestion at least serves as a reminder that the quality of any model reflects the inputs used to construct it, and whenever possible, conceptual modeling participants need to encompass relevant knowledge about the given system to be explored.

Conceptual models provide a transparent way to prioritize research and management objectives among diverse groups of stakeholders and can provide an effective communication tool for informing stakeholders or funders about progress in addressing system components through research or management (e.g., Ogden et al., 2005 and related articles in the special issue of *Wetlands*, Vol. 25). Changes in system uncertainty over time resulting from management or research efforts can be visualized using conceptual maps, for example, by employing color shades or intensities to represent the state of knowledge about a system component. In an analogous scheme, color or shading-coded conceptual maps can illustrate changes in allocation of management or research resources in response to an identified management or research priority. In effect, conceptual models can provide a visualization of a business plan to help organizations make the best use of their limited resources.

In addition to synthesizing systems understanding, conceptual models present a practical operations tool to address the challenges of implementing cross-disciplinary and cross-organizational management and research efforts to address socioecological systems. Reviews of large systems research and management collaborations have demonstrated that communication of objectives and results among collaborators, stakeholders, and funders is critical for success (Alberti et al., 2011; Sievenan et al., 2012). Conceptual models provide a condensed body of information that can be transferred among organizations, facilitating sharing of knowledge and highlighting commonalities and differences in beliefs about a system (e.g., Heemskerk et al., 2003). By their visual nature, they provide succinct representations of complex systems that can be shared with both technical and non-technical stakeholders involved in decision making and management of the modeled system. Formalization of stakeholder priorities through quantitative scores can also provide a unified framework for identifying and addressing conflicting interests in making management decisions about natural resource systems. Once developed, conceptual models can aid decision making and management of complex systems by providing a simulation tool to explore management options and consider future scenarios (i.e., "scenario planning"; e.g., Radomski and Goeman, 1996; Peterson et al., 2003).

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APPENDICES

The following appendices are available in a supplementary file to the online version of this article at:
http://arctic.journalhosting.ucalgary.ca/arctic/index.php/arctic/rt/SuppFiles/4521/0

APPENDIX 1. Linkage ratings exercise for zooplankton-herring-whale conceptual ecological model.

APPENDIX 2. Chinook salmon conceptual model stressor–life history stage impact ratings exercise.

APPENDIX 3. Chinook salmon stressor–life history stage impact consensus ratings.

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