



Tools and Technology

Bayesian Belief Network Models for Species Assessments: An Example With the Pacific Walrus

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ABSTRACT In 2008, the U.S. Fish and Wildlife Service was petitioned to list the Pacific walrus (*Odobenus rosmarus divergens*) under the U.S. Endangered Species Act (ESA). Research into stressors that may be negatively affecting walrus is incomplete. We developed a Bayesian belief network model structured around the ESA 5-factor analysis during a workshop attended by walrus and ESA experts to 1) elicit expert opinion on important stressors and their effects, 2) develop the model, and 3) develop and analyze plausible future scenarios. The listing factors and associated stressors were organized as sub-models, capturing the cumulative effects of the factors through model output, which was the probability of negative, neutral, or positive effects. We found that in a time-constrained workshop, the graphical display of Bayesian belief networks allowed for rapid development, assessment, and revision of model structure and parameters. We modeled up to 3 scenarios (most likely-, worst-, and best-case) for each of 4 time periods (recent past, contemporary, mid-century, and late-century). Model output for the recent past (reference condition) was consistent with observations and provided a baseline for comparison of the outcomes of other periods and scenarios; stressor effects became increasingly negative with time. However, scenario analyses indicated that mitigation of relatively few stressors could reduce the cumulative effects of the listing factors. Uncertainty in model output was lowest for the past but differed by only 7% among the other time periods. We used 4 types of sensitivity analyses to identify explanatory variables that had the greatest influence on model outcomes. Published 2012. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS Bayesian belief network, expert opinion, *Odobenus rosmarus divergens*, Pacific walrus, species status, uncertainty.

Delineation of species conservation needs, including legal protections, requires assessments of the current and predicted status of a population. A number of processes have been developed to place species in legal and conservation status categories, many with unique classification schemes (e.g., International Union for Conservation of Nature Red List, NatureServe Conservation Status, U.S. Endangered Species Act [ESA], U.S. Marine Mammals Protection Act). Species for which status assessments are most important are those that are rare or facing stressors that may result in large population declines. Unfortunately, most of these

species are not well-studied and data are non-existent, sparse, or of low quality.

The U.S. Fish and Wildlife Service (USFWS) received a petition to list the Pacific walrus (*Odobenus rosmarus divergens*) as threatened or endangered under the ESA in 2008 (Center for Biological Diversity 2008). A review of the petition found that it contained information that suggested listing may be warranted (USFWS 2009), which triggered a formal threats assessment that was completed in 2010 (Garlich-Miller et al. 2011). The results of the threats assessment indicated that listing the subspecies was warranted, but precluded by higher priority species (USFWS 2011). The Pacific walrus is currently a candidate for listing under the ESA and is scheduled to either be proposed for listing or removed from the candidate list by 2017.

The Pacific walrus population is wide-ranging, considered panmictic (Fay 1982), and occupies the Bering and Chukchi Seas ($\approx 1,600,000$ km²) in both the Russian Federation and the United States. The basic biological and ecological rela-

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tionships of the subspecies are well-known (Fay 1982), but details are lacking. The Pacific walrus is adapted to exploiting the dynamics and physical characteristics of sea ice, which they use as a resting platform between feeding bouts, passive transportation, parturition, and shelter from storms and predators (Fay 1982). They are most often associated with broken pack ice within 50 km of the ice edge and around persistent polynyas. The entire population winters in the Bering Sea and breeding occurs in January–February. Females with dependent young, sub-adults, and some males migrate with the ice edge into the Chukchi Sea in summer and then return to the Bering Sea in winter. Many mature males stay in the Bering Sea throughout the year. The population is currently large ($\geq 130,000$; Speckman et al. 2011), but population estimates are imprecise (Udevitz et al. 2001, Speckman et al. 2011) and do not allow for assessments of population trend (Garlich-Miller et al. 2011). The age and sex composition of the population and vital rates have been approximated based on several lines of indirect evidence (Fay 1982, Fay et al. 1997), but there are no contemporary estimates. Diets (primarily benthic invertebrates) have been well-documented (Sheffield and Grebmeier 2009), but also need updating and finer taxonomic resolution. Spatial and temporal patterns of prey availability are based on limited sampling (Grebmeier et al. 2006) and the carrying capacity of walrus habitats can only be crudely inferred (Garlich-Miller et al. 2006). One of the most extensive databases available on Pacific walrus comes from monitoring the subsistence harvest (Garlich-Miller et al. 2006, J. Snyder, USFWS, unpublished data), but the biases inherent in those data have not been thoroughly examined. Furthermore, the habitat changes currently underway (accelerating loss of summer sea ice) may make much of the available data based on previous sea-ice dynamics less relevant and also facilitates the expansion of potential stressors currently at low levels (shipping, oil, and gas development) or non-existent (commercial fishing). The current research program is focused on population genetics, movements, foraging energetics, and behavior (<http://alaska.usgs.gov/science/biology/walrus>). Because the available information on nearly every variable that influences the Pacific walrus is either outdated, non-existent, or not of the appropriate temporal and spatial scales (Garlich-Miller et al. 2011), we had to rely heavily on expert opinion in assessing current conditions and predicting the consequences of future projections.

To help deal with the challenges associated with data quality and incompleteness and inform our ESA threats assessment, we developed a Bayesian belief network model with the following goals: 1) organize, clarify, and graphically display the important stressors and the opinions of the experts on how those stressors operate; 2) define important interactions among the stressors; 3) account for the cumulative effects of the listing factors on the population; 4) identify which stressors had the greatest effect on model outcomes to assist in developing management and research programs; 5) determine how uncertainties in future conditions, and how stressors, alone or in combination, potentially affect the

population through scenario analyses; and 6) ultimately inform a recommendation for an ESA classification (not warranted, threatened, or endangered) for the Pacific walrus.

The purpose of this article is to provide an example of the use of Bayesian belief network modeling in species assessments when information is scarce, and demonstrate how Bayesian belief network models help meet the 6 goals described above.

METHODS

Bayesian belief network models (also known as Bayesian networks, causal probability networks, acyclic directed graphs) have grown in use in the ecological sciences over the past decade (Marcot et al. 2001, Amstrup et al. 2008, Howes et al. 2010, Jay et al. 2011) and descriptions and guidelines for their use and construction have been published (Marcot et al. 2006, Jensen and Nielsen 2007, Kragt 2009, Chen and Pollino 2011). A Bayesian belief network model consists of 3 elements: 1) nodes representing key explanatory variables and one or more response variables; 2) links between nodes that represent cause–effect relationships; and 3) joint probabilities representing the belief that node states will have certain probabilities, given the probabilities of the states of connected nodes (Fig. 1). Nodes are composed of states that are quantified as probabilities, summing to 1. Node states can be the amount, intensity, or categories, etc., of a variable. Nodes representing continuous variables have to be divided into discrete states or categories. Nodes that do not have links to other nodes that influence their prior probabilities are referred to as parent nodes. Nodes that have links to other nodes that influence their prior probabilities are called child nodes. Each node contains a conditional probability table that specifies the relationships among all combinations of the states of the parent node(s), if any, and the states of the child node. Multiple links to a child node can represent interactions among parent nodes and capture the cumulative effects of several variables. A value for each cell of a conditional probability table may be derived from data, or specified by the modeler(s) through a process whereby experts express their certainty about the relationships. The advantages and disadvantages of Bayesian belief network models have been described by Uusitalo (2007) and Kragt (2009). One of the greatest benefits of a Bayesian belief network model is the graphical display of the model, which promotes transparency and understanding among stakeholders (Zorrilla et al. 2010). Another important advantage is that Bayesian belief network models can be easily updated with new data and other types of information. This feature is particularly important for our situation because both governing laws (U.S. Marine Mammals Protection Act, ESA) require an annual review of the status of the Pacific walrus population and any new information can easily be incorporated through updates of nodes, node states, and conditional probability tables.

We conducted a status review for the Pacific walrus that summarized all the available scientific (e.g., research, monitoring, modeling, etc.) and commercial (e.g., fisheries by-catch) data, as well as recent observations of Alaskan and

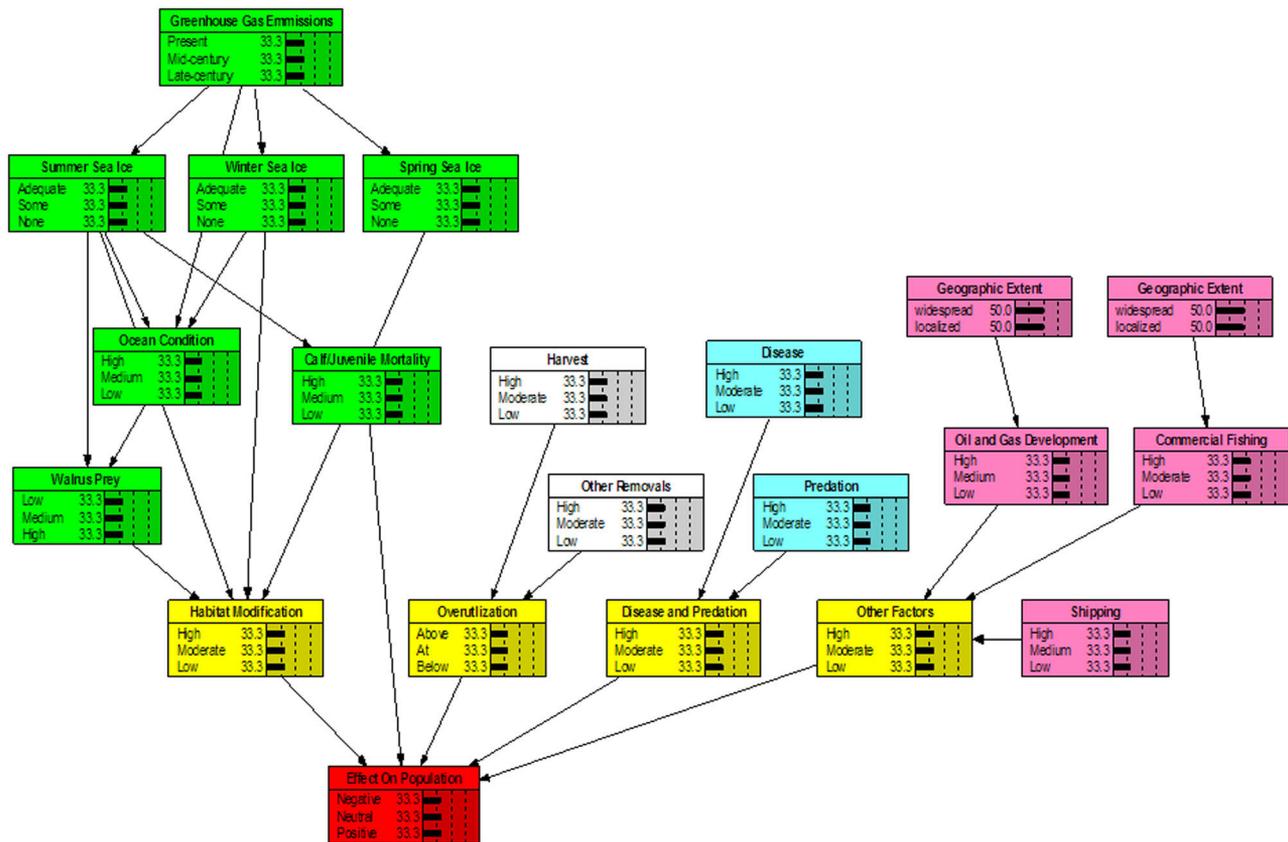


Figure 1. The Bayesian belief network model used to assess the cumulative effects of 4 of the U.S. Endangered Species Act listing factors (habitat modification, overutilization, disease and predation, and other manmade factors [yellow nodes]) on the Pacific walrus population (red node). Green nodes comprise the habitat modification sub-model, white the overutilization sub-model, blue the disease or predation sub-model, and pink the other-factors sub-model. The probabilities of node states were set to unity for illustrative purposes only and do not represent the outcome of any model run.

Russian natives and Russian biologists, to serve as the knowledge base for model building (Garlich-Miller et al. 2011). Because we relied on expert opinion and the assessment had major policy implications, the Bayesian belief network model was developed by a team of 4 walrus and 3 ESA experts during a 5-day workshop in April 2010 (Garlich-Miller et al. 2011) and went through extensive sensitivity analyses and peer review (Marcot et al. 2006, Pollino et al. 2007b). The team specified all the characteristics of the model (nodes and node states, links among nodes, conditional probability tables), as well as time periods (past, current, mid-century, and late-century), and scenarios (most likely, worst-, and best-case) examined. We relied on open negotiations among team members to elicit expert opinions and come to consensus on model structure, node states, and conditional probability table values. The workshop resulted in a working, first approximation of the model. We then solicited open reviews of the model by 4 marine mammal ecologists, 2 ecologists familiar with Bayesian belief network modeling, and 3 upper-level managers. After incorporating those review comments, a blind review was then conducted resulting in further refinements.

The specification of probabilities in a conditional probability table can be difficult and time-consuming for nodes with many states and parents (Marcot et al. 2006, Uusitalo

2007). There are several solutions to this problem (Marcot et al. 2006), but most authors recommend limiting model complexity (no. of nodes and states/node). We followed this advice and also used an automated linear interpolation procedure (G. Wilhere, Washington Department of Fish and Wildlife, personal communication) to complete the more complex conditional probability tables in our model.

Our Bayesian belief network model was structured around 4 of the 5 listing factors of the ESA (Fig. 1) including: A) the present or threatened destruction, modification, or curtailment of habitat or range; B) overutilization for commercial, recreational, scientific, or educational purposes; C) disease or predation; and E) other natural or manmade factors. Listing factor D (adequacy of existing regulations) was assessed in another venue. Garlich-Miller et al. (2011) and expert elicitations identified the stressors faced by the population, trends in those stressors, and walrus response(s) to those stressors. Those stressors were assigned to 1 of the 4 listing factors and became the explanatory nodes in the model (Table 1). The nodes and links associated with each listing factor comprise sub-models that inform the model outcome (response variable); the probability of negative, neutral, and positive effects of the listing factors on the walrus population. Appendix S1 (supplementary materials) contains the values of the conditional probability tables for each node.

Table 1. Node, state definitions, and state weightings (where appropriate) for a Pacific walrus Endangered Species Act (ESA) 5-factor analysis Bayesian belief network model.

Node	Definitions and quantification
Greenhouse gas (GHG) emissions	CO ₂ atmospheric concentrations at 3 time periods; current (≈ 400 ppm), and projections for mid-century (2045–2054, ≈ 500 ppm) and late-century (2090–2099, ≈ 800 ppm) based on A1B and A2 2007 Intergovernmental Panel on Climate Change scenarios
Summer sea ice	The spatial distribution of ice over the outer continental shelf of the Chukchi Sea (709,000 km ²) during Jul–Nov. Adequate was defined as the presence of the ice edge (≈ 50 -km-wide strip of broken pack ice) over the continental shelf. Some ice was defined as the presence of remnant broken pack ice ($\leq 15\%$ cover) over the continental shelf as observed in 2008, but with the ice edge over the Arctic basin. None was no ice over the continental shelf. Probabilities for current conditions were based on observations from 2001 to 2010, where 6 of those summers had no ice (inadequate). Sea-ice projections were made by Douglas (2010)
Winter sea ice	The spatial distribution of sea ice during the Dec–Mar breeding period in the Bering Sea (934,000 km ²). Adequate was defined as the ice edge extending south of traditional breeding areas in the northern Bering Sea in Dec and some as ice over those breeding areas by Jan. None is no ice in these areas during the breeding period
Spring sea ice	The spatial distribution of sea ice during the Apr–Jun birthing, foraging, and migrating season in the Bering Sea and the Chukchi Sea. Adequate was defined as the presence of ice in Apr in traditional breeding areas, and some as ice cover in those same areas in Jun. None is no ice in these areas during this period
Ocean condition	Change in ocean acidification and temp as affected by ice conditions, currents, and GHG emissions. Low was defined as relatively small changes based on current observations (0.1 pH unit decline, 2° C increase), medium was defined as another 0.2 pH unit decline and 3° C, and high 0.3 pH units, 3–6° C increase. In developing the conditional probability table for this node, both factors were weighted equally
Calf and juv mortality	Due to trampling events at summer–autumn terrestrial haulouts along the Chukchi Sea coast. Low was equal to levels in the past (100–1,000 deaths) that occurred infrequently (1 of 5 yr), medium was $\geq 1,000$ deaths more frequently (1 of 3 yr), and high was current observations of $\geq 3,000$ deaths every other yr
Walrus prey	The amount of prey (mass) as affected by ocean conditions and access to prey via sea-ice platforms. Low was a decline in prey due to 0.3 pH unit decline, no summer ice as defined for the summer ice node, and limited to foraging from the coast. Medium was a decline in prey mass due to 0.3 pH unit decline and some summer ice. High was levels of adequate prey mass and adequate ice based on the recent past. In developing the conditional probability table for this node, all inputs were weighted equally
Habitat modification	ESA listing factor A, integrating the effects of seasonal ice conditions, ocean condition, and walrus prey. Low was defined as levels observed in 1990s that correspond to low levels for each input node, moderate was levels observed in 2000–2010, and high was levels forecast for the future (mid- and late-century as defined above). In developing the conditional probability table for this node, all factors were weighted equally
Harvest	Subsistence harvest rates. Based on percent of assumed population size (200,000), modeled max. growth rate (0.8/yr), and past harvest levels (3,000–16,000/yr). Low was $\leq 2\%$ of the population, moderate 3–4%, and high $\geq 5\%$ annual harvest
Other removals Overutilization	0–30 calves/yr for zoos and aquaria and 0–3 ad/yr in fishing bycatch. States are defined the same as for the harvest node above ESA listing factor B. The cumulative effects of harvest and other removals. States were relative to sustainable levels as defined in the harvest node in terms of percent of the population. Current levels are assumed to be moderate and as harvest or other removals increase or decrease, the states change as per the conditional probability table. In developing the conditional probability table for this node, harvest was weighted 1,000× more important than other removals
Disease	The cumulative effects of both disease and parasitism as both are expected to change in similar ways with climate change. Current levels are considered to be low. It was not possible to quantify these states because there is no to little information on current infection or infestation levels, rates of change, or mortalities due to disease or parasites
Predation	The effect of predation by polar bears (<i>Ursus maritimus</i>), brown bears (<i>U. arctos</i>), and killer whales (<i>Orcinus orca</i>). Current levels of predation were considered to be low. It was not possible to quantify these states because there is no to little information on predation rates or mortalities due to predation
Disease and predation	The cumulative effects of both disease and predation. Current conditions define the low state. The other states are relative to current conditions as defined in the conditional probability table. In developing the conditional probability table for this node, predation was weighted twice as important as disease and/or parasitism
Geographic extent	The spatial extent (km ²) of commercial activities. These nodes capture the potential for expanded activities in the future, and put the scope of current activities in context of the range of the Pacific walrus. Currently the geographic extent of oil and gas development is localized relative to the summer distribution of walrus (the lease area is about 10% of the Chukchi Sea). Activities may be considered widespread if they become $\geq 50\%$ of the area. There is a single, small salmon fishery in Kotzebue Sound of the Chukchi Sea and trawl fishing is restricted to the southern Bering Sea on the edge of the walrus distribution. Current activities are considered localized. Activities may be considered widespread if they become $\geq 50\%$ of the area
Oil and gas development	The cumulative effects of the geographic (spatial) extent and intensity (type) of activities. This node is the intensity of development. Seismic exploration only was low intensity, exploratory drilling medium intensity, and full development and well production high intensity
Commercial fishing	The cumulative effects of geographic extent and amount of activities. This node is the amount of activity occurring in the range of the Pacific walrus. Current fishing levels (1 of 21 Bering Sea and/or Aleutian Island fisheries within the walrus range, and a salmon fishery in Kotzebue Sound) were considered low. We did not quantify moderate and high levels other than how those states would be affected based on the conditional probability table
Shipping	Domestic shipping along the Alaskan and Chukotkan coasts and emerging international commercial shipping originating in the Northwest Passage or Northern Sea Route transiting through the Bering Strait and further south. The states of this node represent the levels of shipping traffic (vessel transits/yr) along defined shipping lanes. Current levels of shipping (277–338 transits/yr) for all purposes are considered low. We had no data to quantify and define medium and high states, other than incremental increases over current conditions (e.g., 50% and 100%, respectively)
Other factors	ESA listing factor E. The cumulative effects of oil and gas development, commercial fishing, and shipping. The low state represents current conditions; medium and high states were defined as indicated above for each activity. In developing the conditional probability table for this node, oil and gas was weighted 2× more important than fishing or shipping
Effect on population	The cumulative effects of the 4 ESA listing factors in terms of the probability of negative, neutral, and positive outcomes on the Pacific walrus population. Changes in the probabilities of each state were defined to reflect changes in the intensity of stressors with each time period (past, current, mid-century, and late-century). Although stressors are primarily negative, because their effects and walrus response to those effects are largely hypothetical they may also be neutral, and there is a chance that positive interactions could occur

Time Periods and Scenario Analyses

To assess model accuracy, provide context for interpretation of model results, and assess the future, 4 decadal periods were modeled: the past (1979–1988), which served as a reference condition, current conditions (1989–2010), projections for mid-century (2045–2054), and late-century (2090–2099; Table 2). The past was a period when habitat conditions were favorable for walrus, the population was large, subsistence harvests were considered sustainable, and many looming stressors were inconsequential. For current conditions, the states of many stressors were unknown or poorly documented, and for mid-century and late-century periods could only be guessed at. As a result, we identified several combinations of plausible states for each node, excluding greenhouse gas emissions, for each time period.

Because the future is unknowable, surprises are common (Doak et al. 2008), and past trends may not provide reliable predictions (Kass et al. 2011), scenario analysis is increasing in use (Peterson et al. 2003, Gray 2011, Kass et al. 2011). For our scenario analyses, node states were set to conditions defined by a scenario (often a probability of 1.0 for either the high or low state), and we assessed how those scenarios affected model output for best-case, worst-case, and most-likely case scenarios. However, a most-likely case scenario could not be developed for the late-century period because of a high level of uncertainty in the states for most explanatory nodes that far into the future. For the past, the habitat modification sub-model was disabled and levels for the other nodes were set consistent with observations from that time period. Best-case scenarios were based on setting node states to reflect conditions that would occur through successful mitigation of threats associated with overutilization, disease or predation, and other manmade factors (Garlich-Miller et al. 2011). Most-likely case scenarios were based on setting node states to those reflecting little change from current conditions. The worst-case scenarios for each time period were modeled by setting node states to reflect increasing,

unmitigated effects on the population. In evaluating the results of these analyses we focused on the dominant 2 states as defined by the posterior probabilities of the response variable node.

Sensitivity Analyses and Model Evaluation

We used four methods to evaluate model effectiveness: peer review, scenario analyses, diagnostic analyses, and sensitivity analyses (Marcot et al. 2006, Pollino et al. 2007b, Kragt 2009; Chen and Pollino 2011). In addition, we also assessed the relative uncertainty of response variable states for each time period and scenario combination with entropy estimates (H), the degree to which the probability of the outcome is spread out over the 3 different states, as $H = -\sum[P_{ix} \times \log_3(P_i)]$, where P_i is the probability of each state.

The Netica[®] software (Norsys Software Corp., Vancouver, British Columbia) used to build our model contains 2 sensitivity analyses that are based on entropy calculations—entropy reduction and mutual information (see Pollino et al. 2007b for details). For those analyses, explanatory (input) nodes were set to current conditions. In addition, we conducted 2 additional sampling-based empirical sensitivity analyses. For the first (state sensitivity), we systematically varied the prior probabilities of the states of one explanatory node, while holding the prior probabilities of the states of all other explanatory nodes constant, and quantified changes in the posterior probabilities of the states of the response node (Table 3). Due to the large number of possible combinations of nodes and node states we only evaluated the extreme cases for each node. For example, in assessing the influence of the harvest node on model responses, we set the probability of the states of the other parent nodes at 1.0 for high (other states = 0), set the states of the harvest node at 1.0 high, and recorded the probability associated with each state in the response (effect on population) node. We then set the harvest node states to 1.0 low and recorded the outcome. For the next iteration, we then set the

Table 2. Model node state specifications for each of 4 time periods for the walrus Bayesian belief network model threats assessment.

Node	Past (1979–1988)	Current (1989–2010)	Mid-century (2045–2055)	Late-century (2090–2099)
Explanatory nodes				
Greenhouse gas emissions	Not applicable	Low ^a	Moderate	High
Harvest	High	Low or moderate	Low, moderate, and high	Low, moderate, and high
Other removals	Low	Low	Low	Low
Disease	Low	Low	Low or moderate	Low or moderate
Predation	Low	Low or moderate	Low or moderate	Low or moderate
Geographic extent	Not applicable	Local	Local or widespread	Local or widespread
Shipping	Low	Low	Low or moderate	Low, moderate, and high
Intermediate nodes				
Summer sea ice	Adequate	Predicted ^b	Predicted	Predicted
Winter sea ice	Adequate	Predicted	Predicted	Predicted
Spring sea ice	Adequate	Predicted	Predicted	Predicted
Ocean conditions	Low	Predicted	Predicted	Predicted
Oil and gas development	Low	Predicted	Predicted	Predicted
Commercial fishing	Low	Predicted	Predicted	Predicted

^a For each state listed, the prior probability was set to 1.0 for that time period. For nodes and period with multiple states, the probability for each was set to 1.0, depending on the scenario under consideration.

^b The probabilities of the states of these nodes are a function of the states of connected nodes higher in the network and the conditional probability tables of each node.

Table 3. Results (mean [SE] percent change in model outcome) of 2 sampling-based sensitivity analyses of a Bayesian belief network model used to assist in a U.S. Endangered Species Act 5-factor analysis for the Pacific walrus (*Odobenus rosmarus divergens*). In the node-states analysis we systematically varied the states of the explanatory (parent) nodes (subsistence harvest, greenhouse gas emissions, predation, disease, international commercial shipping, extent of oil and gas development and commercial fishing, and other removals), and in the conditional probability tables (CPT) analysis we varied the conditional probabilities of all nodes. Mean rank is the average rank (descending order) of each node based on these results and the sensitivity analyses performed by the Netica software.

Node	Analysis		Mean (SE) rank
	Node states	CPT	
Habitat modification	Not applicable	32 (13)	1 (0)
Calf and juv mortalities	Not applicable	16 (7)	2 (0)
Summer sea ice	Not applicable	31 (8)	3 (1)
Harvest	13 (3)	16 (7)	4 (0.4)
Prey abundance and access	Not applicable	8 (2)	4 (0.6)
Greenhouse gas emissions	6 (1)	Not applicable	4 (3)
Winter sea ice	Not applicable	10 (3)	5 (1)
Ocean condition	Not applicable	4 (2)	6 (1)
Spring sea ice	Not applicable	6 (2)	7 (1)
Other removals	Not applicable	0.3 (0.3)	7 (1)
Disease or predation	1 (0.6)	Not applicable	9 (0.4)
Disease	1 (0.2)	3 (1)	10 (2)
Oil and gas	Not applicable	1 (0.1)	11 (0.3)
Predation	Not applicable	5 (1)	12 (3)
Commercial fishing	Not applicable	1 (0.1)	12 (0.3)
Oil and gas extent	0.1 (0.02)	Not applicable	14 (3)
Shipping	0.4 (0.1)	1 (0.1)	14 (2)
Commercial fishing extent	0.1 (0.03)	Not applicable	15 (3)

states of the harvest node back to 1.0 high, changed a different parent node (e.g., predation), set the states to 1.0 low, recorded the outcome, then set the harvest node to 1.0 low, recorded the outcome; and repeated the process until all possible combinations of parent nodes and states were completed. We then calculated the mean percent change in the response probabilities associated with the change in each parent node.

In the second sampling based analysis (conditional probability table sensitivity), we systematically varied the parameters of the conditional probability tables (Coupé and van der Gaag 2002, Pollino et al. 2007b) of nodes in a similar manner as described above, with the states of all parent nodes reflecting current conditions, which served as the baseline for calculating changes in model output due to conditional probability table changes. Again, due to the large number of possible combinations of conditional probabilities, particularly for nodes with many parents, we limited that analysis to the extreme cases of complete uncertainty (equal probabilities across states) and complete certainty (e.g., 1.0 high or low) of each state for each node. Other potential combinations of node states and conditional probabilities would fall within these extremes and provide relatively little additional information to these analyses. We quantified the results of the state and conditional probability table sampling analyses as the mean percent change in model output for each node. To combine the results of the 4 sensitivity analyses, we ranked each node in descending order based on the associated percent change in the response node and calculated the mean rank for each.

RESULTS

Reviewers of the model provided a variety of comments and suggestions, ranging from agreement with model structure

and results, to suggested structural changes and addition of new objectives. The majority of suggestions made by reviewers were incorporated into the model and model documentation. We did not add other objectives to our modeling effort and did not incorporate structural changes that deviated from the ESA 5-factor analysis.

The model output for the past had a probability of neutral effects ($P_{=}$) of 0.74 (Fig. 2), which was in agreement with observations from that time period. That is, because the model was developed to address relatively recent and emerging stressors, one would expect a largely neutral outcome for the past. In addition, because the model structure and parameters were based on current conditions and uncertain relationships among stressors and walrus response, the outcome for the past indicated that our model accurately depicted known conditions, should perform well for other time periods, and set a baseline for judging model output for other time periods and scenarios.

The probability of negative (P_{-}) effects increased 16–29% over the past (reference condition) with a 23–28% decrease in $P_{=}$ for current conditions (Fig. 2). Those changes were lowest for the best-case scenario. Under current conditions, $P_{=}$ was greater than P_{-} by 7–22%, and there was little difference in model output between the most-likely case scenario and the worst-case scenario (Fig. 2).

For mid-century projections, P_{-} increased 21–42% and $P_{=}$ declined 24–35% compared with the past (Fig. 2). There was no difference between most-likely and worst-case conditions for mid-century, with P_{-} being greatest (0.55), followed by $P_{=}$ (0.39). However, under the best-case scenario, $P_{=}$ was greatest (0.50) and the probability of positive (P_{+}) effects increased 10%.

Due to uncertainties in forecasting stressor levels and walrus response to the end of the century, any scenario within

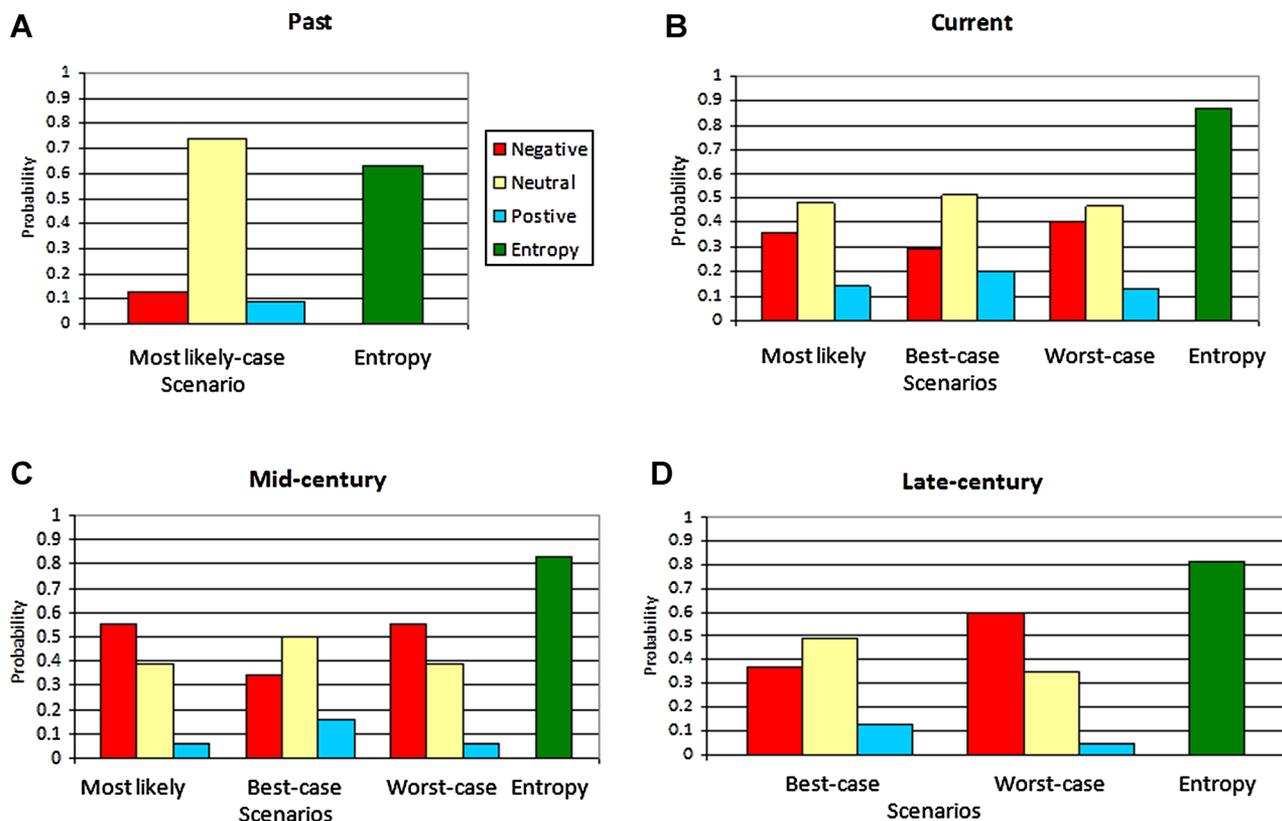


Figure 2. Bayesian belief network model outcomes (probability of negative [red], neutral [yellow], positive [blue] cumulative effects, and entropy [green]) for 1–3 scenarios (most-likely case, best-case, and worst-case) at 4 time periods (A = past [1979–1989], B = current [1999–2010], C = mid-century [2045–2055], and D = late-century [2090–2099]). The model was used to assist in a U.S. Endangered Species Act 5-factor analysis for the Pacific walrus (*Odobenus rosmarus divergens*).

the bounds of the model input was judged to be equally probable and the worst-case and best-case scenarios represented those bounds (Fig. 2). Under the worst-case scenario, P_{-} increased 47% compared with the past with a 39% decline in P_{+} . The best-case scenario output was similar to that for the other time periods.

Uncertainty in model output as measured by entropy (Fig. 2) was lowest for the past, consistent with the available information. Entropy estimates among current, mid-century and late-century periods differed by only 7%, but uncertainty in model output for those time periods was 29–38% greater than for the past. The best-case scenario was consistently the most uncertain when compared with the other scenario(s) at each time period (Fig. 2).

The entropy reduction and mutual information sensitivity analyses performed by Netica indicated that model output was most influenced by the habitat modification node (9.2%) followed by calf mortalities (1.3%), prey (0.7%), summer ice (0.6%), and overutilization (0.2%). The sampling-based sensitivity analysis where the states of explanatory nodes were systematically varied (state sensitivity) indicated that the mean magnitude of change in model output was greatest for the harvest node followed by greenhouse gas emissions, predation, disease, shipping, oil and gas development, and commercial fishing (Table 3). In contrast, systematically varying the conditional probability tables of each node (con-

ditional probability table sensitivity) indicated that habitat modification, summer sea ice, calf and/or juvenile mortalities and harvest (tied), winter sea ice, and prey nodes influenced model output the most. Taken together, the 4 methods of sensitivity analysis indicated that habitat modification, calf mortalities, summer sea ice, harvest, prey, and greenhouse gas emissions (the latter 3 were tied) had the greatest effects on model outcomes (Table 3).

DISCUSSION

Efforts to assess the legal and conservation status of a species are often hindered by a lack of information or poor quality information because these species are often rare or difficult to study. For example, the International Union for Conservation of Nature Red List process includes a data-deficient category for such species, which currently includes the Pacific walrus. The ESA and other processes do not have that option and more definitive categories must be used. For many cases, expert opinion provides the basis for species assessments and Bayesian belief network modeling is appropriate for eliciting and quantifying expert opinion (Marcot et al. 2006, Jensen and Nielsen 2007).

We found the Bayesian belief network model to be invaluable in conducting an ESA 5-factor analysis where expert opinion was relied on to compensate for a lack of data. The greatest advantage in our situation was the graphical display

of a complex system that helped organize and clarify interactions among sets of related stressors. This was particularly advantageous in the time-constrained workshop of our threats assessment because participants could rapidly assess and revise model structure and parameters, explore different scenarios, and see how uncertainty affected model outcomes. In addition, the automation of the interpolation procedure to complete large conditional probability tables was instrumental to the timely evaluation and refinement of the model.

Analysis of several scenarios and 4 time periods was useful in setting a benchmark (the past) for judging the outcomes at other time periods, and identifying uncertainties. Model results for the past were more than trivial because the model was developed and parameterized to reflect current conditions—the past served as a check on model accuracy in the absence of data (Pollino et al. 2007*b*). Furthermore, as we specified node states for current and future decades, greater uncertainties emerged. For example, due to the potential response of walrus to some stressors (e.g., density-dependent mortality) and possible implementation of mitigation measures of unknown efficacy, etc., many alternative scenarios of node states were equally plausible. These difficulties precluded identifying a most-likely case scenario for the late-century decade, which represented a measure of uncertainty in and of itself.

Scenario analyses can be used as an early warning of major changes in ecological trajectories and regime shifts. Scenario analyses along with sensitivity analyses can identify what variables to monitor, when to monitor, and where to monitor. As the future develops managers can track outcomes, relate observed outcomes to predicted outcomes, and implement the appropriate mitigation and monitoring programs. For example, loss of sea ice in the summer and the subsequent use of coastal haulouts by Pacific walrus females with calves and young animals create several stressors with unknown long-term effects (Garlich-Miller et al. 2011). Models project more frequent and longer ice-free summers and managers can track trends in ice cover on a daily basis (National Snow & Ice Data Center; <http://nsidc.org/arcticseaicenews/>), begin monitoring coastal areas for haulout formation based on ice characteristics, and implement haulout-protective measures as needed. A more long-term concern is the depletion of prey near coastal haulouts (Garlich-Miller et al. 2011). This may occur if large haulouts repeatedly form in the same area each year and tracking haulout formation along with a measure of animal condition will alert managers to potential prey depletion.

An unexpected result of our uncertainty analysis was the slightly lower entropy estimate for the late-century model predictions, particularly given the fact that we could not develop a most-likely case scenario for that time period. This could be the result of not having a third scenario for that time period, or our failure to adequately capture those uncertainties in the conditional probability table. The latter case seems most likely because sea-ice modeling was based on the combination of 2 of 6 greenhouse gas emissions scenarios (Douglas 2010), thus narrowing the range of possible outcomes; and because those outcomes were invariant with

respect to other scenarios, they were portrayed as having greater certainty than an assessment of all plausible futures.

We found that the sensitivity analysis employed by the Netica software emphasized model structure and conditional probability table specifications. In contrast, the sampling-based analyses we conducted identified additional variables (e.g., subsistence harvest) as the most influential factors. Our results suggest that for models of complex situations it may be necessary to conduct several types of sensitivity analyses to insure that important issues are not overlooked. Pollino et al. (2007*b*) also noted that both entropy reduction and mutual information analyses should be considered in model evaluations.

The states of our response variable node (negative, neutral, or positive effects on the population) were, as one reviewer put it, less than satisfying. However, the model displayed and quantified the probabilities, and by our definition, the intensity of the cumulative effects of the stressors on the population, not population status. We felt that attempting to link the effects of the listing factors to population status at this time was too uncertain, potentially misleading, and ultimately unnecessary. As population status changes as a result of listing decisions, modifications of the model output will be relatively easy to make. Our modeling effort was only one of many considerations in making an ESA status recommendation, and as stated above was most valuable in organizing and clarifying a complex situation and providing guidance for management and research programs.

At the time of model development, we decided that the evaluation of regulations (listing Factor D) would be best handled in another forum. However, given the multiple laws/regulations of varying effectiveness associated with each stressor, it may be advantageous, particularly in terms of organization and clarity, to also incorporate Factor D into a Bayesian belief network model.

Many modeling exercises are continuous and iterative (Marcot et al. 2006; Pollino et al. 2007*a, b*; Howes et al. 2010). One of the strengths of Bayesian belief network models is that they are easily updated (Marcot et al. 2001, 2006; Chen and Pollino 2011). Our model will be updated and refined over time because USFWS policy requires the annual review of ESA candidate species and the U.S. Marine Mammals Protection Act and ESA require a review of the status of species listed as strategic and threatened or endangered every 1–5 years, respectively. Our model was subject to some evaluation and validation, but we do not have the data to formally update and test the model. In addition, Marcot (2012) recently presented several other metrics for Bayesian belief network evaluation that we could use in the future. There are a number of research and monitoring projects underway that will provide the types of data needed to update the model in the future and perhaps make the use of data-intensive population models or population-viability models feasible.

MANAGEMENT IMPLICATIONS

Managers routinely make decisions with incomplete and imperfect information about complex and politically charged

situations. Climate disruption in the Arctic is outpacing other regions of the globe (Blunden et al. 2011), and this will intensify the need for rapid decision-making and likely outpace the generation of reliable knowledge, placing a premium on expert opinion. Bayesian belief network models are useful for clarifying complex situations, quantifying expert opinion, assessing uncertainties, quantifying cumulative effects, and conducting scenario analyses. These exercises are in turn useful for identifying data gaps and research priorities, tracking trends and predicting their outcomes, and identifying potentially useful management and monitoring programs. Scenario analyses can identify management actions that can be applied immediately, no matter how the future develops. For example, when Pacific walrus are hauled out on the coast, they are easily disturbed and will flee *en mass* to the water, often trampling calves and younger animals. Preventing disturbances at haulouts is a mitigation measure that can be implemented under all scenarios of haulout formation, now and in the future, and will facilitate the potential adaptation of Pacific walrus to the loss of summer sea ice.

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