

Projected status of the Pacific walrus (*Odobenus rosmarus divergens*) in the twenty-first century

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Abstract Extensive and rapid losses of sea ice in the Arctic have raised conservation concerns for the Pacific walrus (*Odobenus rosmarus divergens*), a large pinniped inhabiting arctic and subarctic continental shelf waters of the Chukchi and Bering seas. We developed a Bayesian network model to integrate potential effects of changing environmental conditions and anthropogenic stressors on the future status of the Pacific walrus population at four periods through the twenty-first century. The model framework allowed for inclusion of various sources and levels of knowledge, and representation of structural and parameter uncertainties. Walrus outcome probabilities through the century reflected a clear trend of worsening conditions for the subspecies. From the current observation period to the end of century, the greatest change in walrus outcome probabilities was a progressive decrease in the outcome state of robust and a concomitant increase in the outcome state of vulnerable. The probabilities of rare and extirpated states each progressively increased but remained <10% through

the end of the century. The summed probabilities of vulnerable, rare, and extirpated ($P(v,r,e)$) increased from a current level of 10% in 2004 to 22% by 2050 and 40% by 2095. The degree of uncertainty in walrus outcomes increased monotonically over future periods. In the model, sea ice habitat (particularly for summer/fall) and harvest levels had the greatest influence on future population outcomes. Other potential stressors had much smaller influences on walrus outcomes, mostly because of uncertainty in their future states and our current poor understanding of their mechanistic influence on walrus abundance.

Keywords Status · Walrus · *Odobenus* · Bayesian network · Sea ice

Introduction

Climate warming and reductions in sea ice habitats present a particularly difficult challenge to the conservation of polar marine mammals. Arctic-wide generalizations on species-specific effects of climate change are difficult to make because the sensitivity and response of marine mammals to environmental changes in the Arctic are complex and can vary among and within species (Laidre et al. 2008). The Pacific walrus (*Odobenus rosmarus divergens*) is a large pinniped inhabiting arctic and subarctic continental shelf waters of the Chukchi and Bering seas. Concerns over the future of the Pacific walrus, especially under the stress of climate change, prompted the US Fish and Wildlife Service to initiate a status review in September, 2009, to determine whether listing the subspecies as threatened or endangered is warranted under the Endangered Species Act (US Fish and Wildlife Service 2009). To aid this endeavor, and to focus new research and monitoring efforts, we synthesized

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Fig. 1 Study area used for projecting Pacific walrus status in the twenty-first century



studies and understanding of the Pacific walrus into a knowledge-based model to evaluate possible future influences of anthropogenic stressors and changing environmental conditions on the Pacific walrus population.

The Pacific walrus is currently distributed in Russian and Alaskan waters, and ranges in the north from the eastern East Siberian Sea to the western Beaufort Sea, and in the south from eastern Kamchatka to Bristol Bay (Fay 1982) (Fig. 1). In winter, the entire Pacific walrus population resides in the Bering Sea. Breeding occurs in January and February. Leks are formed where breeding males display and vocalize from water alongside groups of females hauled out on ice, and copulation occurs in water (Fay et al. 1984). Most calving occurs in April–June (15–16 month pregnancy), and mothers care for and nurse their newborn calves on the ice (Fay 1985). Little is known of ice preferences for breeding and calving activities; however, walruses require ice floes large enough to support their weight (Fay 1982; Simpkins et al. 2003). Within its range, Pacific walruses typically occur in areas of unconsolidated ice, open leads, and thin ice where they can create breathing holes, and they avoid areas with very high concentrations of thick ice, such as in the Chukchi Sea in winter (Burns et al. 1980, 1981; Fay 1982).

In spring, most adult female and young walruses follow the receding ice pack northward to summer in the Chukchi Sea, while many of the adult males move toward coastal areas to summer in nearshore areas of the Bering Sea and northern coast of Chukotka. In autumn, female and young walruses migrate with the developing sea ice southward into the Bering Sea, where they are joined by the males in late autumn and winter (Fay 1982).

Walruses are very gregarious and occur in groups of up to ~500 walruses (Fay 1985; Speckman et al. 2010). Group sizes of hauled out walruses tend to be larger when they are on shore than on ice (Fay 1985). Seasonal dynamics of sea ice cover in the Chukchi and Bering seas allow walruses to exploit a wide area of the continental shelf during the year. Adult male walruses have dorsal inflatable pharyngeal pouches, which allow them to sleep at the surface in open water for extended periods (Fay 1960) between foraging trips from land in summer (e.g. Jay et al. 2001).

Reduced summer sea ice over the continental shelf in the Chukchi Sea in the past decade has resulted in increased use of land haul-outs by adult females and young during ice-free periods (Jay and Fischbach 2008; Kavry et al. 2008). This was particularly evident in the summer and fall of 2007 and 2009. During these years, thousands of

walrus hauls out along the coast of northwestern Alaska, and tens of thousands of walrus hauls out along the coast of northern Chukotka when ice disappeared from the shelf. These events led to the trampling and death of hundreds of walrus in Alaska and thousands in Russia (calves are particularly vulnerable), presumably when herds were disturbed from anthropogenic and predator stimuli (Kavry et al. 2008; Kochnev et al. 2008; Fischbach et al. 2009, A. Kochnev, ChukotTINRO, pers. comm. 2009). An unusually high number of walrus hauls out and high levels of mortality occurred on the shores of Wrangel Island, Russia (Ovsyanikov et al. 2008). Increased use of land haul-outs by adult females and young in summer could also result in increased energy expenditures from foraging trips originating from shore and reduced access to preferred feeding grounds.

The Pacific walrus is harvested for subsistence by Alaskan and Russian Native communities. Estimates of walrus harvest levels from 1960 through 2007 range from 3,184 to 16,127 walrus per year (US Fish and Wildlife Service 2010), which includes adult and juvenile walrus (Fay and Bowlby 1994). Estimates of current harvest levels are 4,960–5,457 walrus per year (2003–2007 harvest records). Factors affecting recent harvest levels include cessation of Russian commercial harvests after 1991, changes in political, economic, and social conditions of subsistence hunting communities in Alaska and Russia, and the effects of variable weather and ice conditions on hunting success. Current walrus mortality rates from fisheries interactions and other known human activities (incidental takes) are estimated at about 3 walrus per year (US Fish and Wildlife Service 2010). Thus, the greatest human-caused direct mortality of walrus is from subsistence harvest.

Factors regulating walrus population dynamics are poorly understood, largely because of limited information on walrus vital rates and how vital rates change with population status (Fay 1985; Chivers 1999; Garlich-Miller et al. 2006). The primary non-human predators of walrus are polar bears (*Ursus maritimus*) and killer whales (*Orcinus orca*), and younger walrus are most vulnerable (Fay 1985).

Surveys conducted at 5-year intervals between 1975 and 1990 produced Pacific walrus abundance estimates ranging from 201,039 to 234,020 walrus; however, the estimates have unknown biases and unknown or large variances, and cannot be used for detecting trends in population size (Hills and Gilbert 1994; Gilbert 1999; US Fish and Wildlife Service 2010). A survey conducted in 2006 produced an unbiased estimate of 129,000 individuals within the surveyed area of the population's early spring range, but the estimate had low precision (95% CI: 55,000 to 507,000 individuals). The estimate is considered to be less than the total population size because some areas that were known from past

surveys to contain walrus were unable to be surveyed (Speckman et al. 2010).

Pacific walrus forage on the seafloor of the continental shelves (Fay and Burns 1988; Jay et al. 2001) where benthic production is high (Grebmeier et al. 2006a; Bluhm and Gradinger 2008) and benthic diving is energetically feasible (e.g. Costa and Gales 2003). Walrus feed on a wide variety of organisms including small crustaceans, worms, snails, clams, marine birds, and seals (Fay 1982; Sheffield and Grebmeier 2009), but their diet most frequently consists of clams, snails, and polychaete worms (Sheffield and Grebmeier 2009).

Some of the highest levels of soft-bottom benthic faunal biomass in the world occur in the northern Bering and Chukchi seas (Grebmeier et al. 2006a; Bluhm and Gradinger 2008). In seasonally ice-covered waters, such as the Chukchi and Bering seas, the onset of sea ice melt and the duration of open water have a direct influence on the relative amounts of organic carbon retained in the water column and exported to the sediments (Grebmeier et al. 2010). High primary production, with simultaneously low zooplankton grazing, results in much of the organic matter sinking to the seafloor and enhancing benthic production (Grebmeier and Barry 1991). Reductions in sea ice have the potential to reduce benthic production and increase pelagic consumption in Arctic marine ecosystems; however, detailed biological consequences of reduced sea ice are difficult to predict and depend on regional conditions governing productivity (Piepenburg 2005; Grebmeier et al. 2006a, b; Lalande et al. 2007; Bluhm and Gradinger 2008). Such shifts could result in reduced abundance of benthic prey for walrus.

In addition to warming the climate, increased levels of atmospheric CO₂ have led to increased CO₂ loading in the oceans (The Royal Society 2005). Carbon dioxide dissolved in sea water forms carbonic acid, which decreases the amount of calcium carbonate available to marine invertebrates to construct shells or exoskeletons, including those of benthic prey for walrus such as clams and snails. Our current understanding of climate-induced ocean acidification on biological systems is rudimentary, and its long-term consequences on marine ecosystems remain speculative (Orr et al. 2005; Guinotte and Fabry 2008).

Sea ice forms a physical barrier to anthropogenic activities such as shipping, resource development, and commercial fishing. Future summer sea ice losses are likely to lead to increased ship traffic in the Chukchi and Bering seas, including traffic from the transport of goods and from petroleum exploration and development (Arctic Council 2009). Of the potential pollution sources from shipping, perhaps the most significant threat to Arctic ecosystems is the release of oil through accidental or illegal discharge with immediate and long-term consequences (Arctic

Council 2009). The high level of uncertainty associated with the interactions between complex physical, economic, social, and political environments leads to great difficulty in predicting levels of Arctic marine shipping activities in the future (Arctic Council 2009). Regulations in the US Arctic Fishery Management Plan currently prohibit commercial fisheries in the Beaufort and Chukchi seas (National Oceanic and Atmospheric Administration 2009), but sea ice losses could lead to the expansion of fisheries into more northern areas in the future.

Assessing walrus population status in the future requires a method that can accommodate both the complexity of environmental and anthropogenic stressors that may affect the future distribution and abundance of walruses, and the dearth of data on walrus vital rates and demographic response to such stressors. Here, we developed a Bayesian network (BN) model to represent linkages between potential stressors and walrus responses in a probabilistic framework to evaluate potential outcomes of the walrus population through the twenty-first century. The method allowed us to combine various forms of information and uncertainties, including empirical data, modeled sea ice projections, and expert judgment in lieu of missing data (e.g. Choy et al. 2009). We used the BN model to assess potential walrus population outcomes at one past, one near-present, and four future periods.

Materials and methods

Our study area (Fig. 1) was bounded by the edge of the continental shelf (150-m isobath) and the range of the Pacific walrus as delineated by Fay (1982). The Chukchi and Bering seas within the study area span 709,000 and 934,000 km², respectively.

Initial model development

We developed a BN model, using the software Netica® (Norsys, Inc.) and following the guidelines in Marcot et al. (2006), to depict potential effects of environmental conditions and anthropogenic stressors on the future status of the Pacific walrus population. A BN model is a set of variables, referred to as “nodes”, linked by probabilities (Jensen and Nielsen 2007). Our BN model is structured to evaluate the net effects of multiple stressors at various periods. It is neither a population viability analysis nor a time-dynamic demography model because each period is treated independently. Instead, the BN model is a synthesis of expert knowledge, existing studies and sea ice projections by climate models, and as such provides a comprehensive and flexible framework that can be refined as new information becomes available.

The main steps we followed in developing the BN model were to: (1) create an influence diagram (i.e. a causal web) depicting relationships among key factors that may affect walrus distribution and abundance, (2) develop an initial BN model using the influence diagram and comments solicited from walrus experts, (3) revise the model after expert peer review, and (4) test the behavior of the model, using sensitivity analyses on model subsets, and reconcile any unrealistic residual model behavior.

Prior to developing the influence diagram, we independently solicited viewpoints from two Russian and two US walrus experts on potential walrus population stressors. We used their comments to substantiate key factors and interrelationships that were represented in the final influence diagram and subsequent BN model. There was substantial agreement among the experts in the main factors that were identified as important to walrus status in the future.

To guide our development of the initial BN model from the influence diagram, we solicited comments on walrus ecology and potential walrus population stressors from Alaska Native elders during in-person meetings in Savoonga, a prominent Siberian Yupik walrus hunting community on St. Lawrence Island, Alaska. Subsequently, we conducted peer-review interviews with two US walrus experts to solicit concerns or recommendations on the BN model structure including the represented variables, linkages among variables, underlying conditional probabilities, model performance, and sources of data by which to establish values of the model inputs. We documented the content and our reconciliation of each peer review, including subsequent revisions we made to the BN model structure and probability tables.

Overall model structure

In general, our BN model consisted of input, intermediate, and output nodes. Intermediate and output nodes are conditional upon their direct antecedents or “parent nodes;” input nodes are said to be “parentless.” Other nodes that are, in turn, directly linked from a given node are referred to as “child nodes.” Input nodes consisted of anthropogenic stressors and environmental conditions, including sea ice conditions as influenced by climate change. Intermediate nodes were calculations or summaries of environmental and stressor effects and walrus response, expressed by conditional probabilities of multiple influences. Output nodes culminated the collective effect of all conditions and stressors, expressed as conditional probabilities of walrus population outcomes.

We structured our BN model with three seasonal sub-models representing summer/fall (July through November), winter (December through March), and spring (April through June) (Fig. 2), because walruses build energy reserves in summer and fall, breed in winter, and give birth in spring. This enabled us to specifically parameterize input

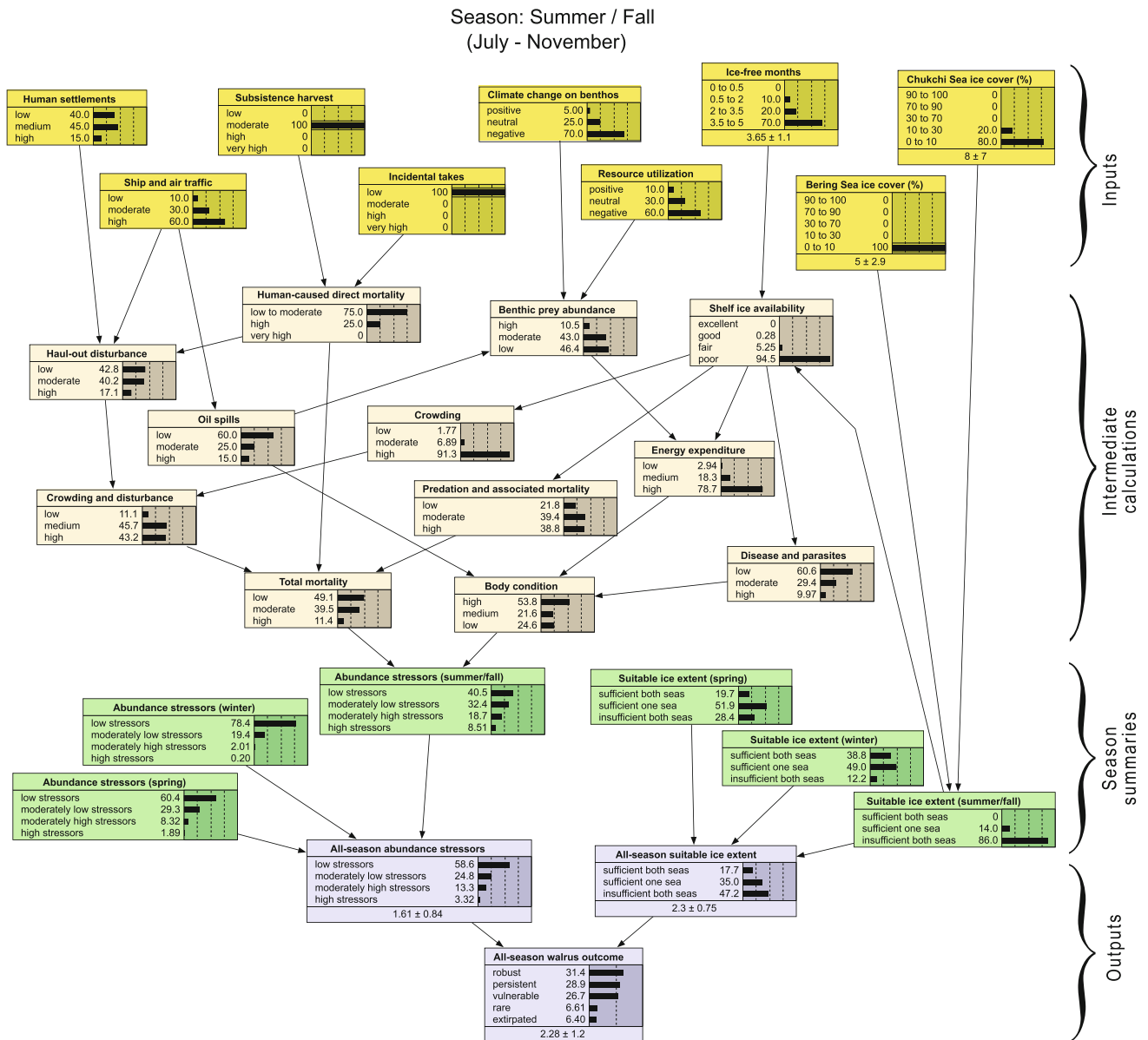


Fig. 2 Influence diagram of a Bayesian network model to project Pacific walrus status in the twenty-first century. This is the submodel diagram for the summer/fall season; similar submodels pertained to winter and spring seasons. The winter submodel included a sea ice “breeding environment” node between “shelf ice availability” and

“abundance stressors”, and the spring submodel included a sea ice “birthing platform” node between “shelf ice availability” and “abundance stressors.” Shown here is the model set to calculate outcome probabilities for period 2095 as depicted in Fig. 3

values (such as sea ice conditions and harvests) by seasons that encompass different and important walrus life history events. All seasonal submodels had similar nodes and links, except for the addition of a sea ice “breeding environment” node in the winter submodel and a sea ice “birthing platform” node in the spring submodel.

Model construct and parameterization

We ran our final BN model for each of six decadal periods: one past and one near-present period of 1979–1988 and

1999–2008 (hereafter referred as 1984 and 2004, respectively), and four future periods of 2020–2029, 2045–2054, 2070–2079, and 2090–2099 (hereafter referred as 2025, 2050, 2075, and 2095, respectively). We used periods of 10 years, as opposed to a single year, to account for the Arctic’s intrinsic inter-annual sea ice variability in the sea ice inputs to the model.

For future periods, we ran the BN model for each of four sets of sea ice projections. The sets of projections were generated from combinations of two CMIP3 general circulation model (GCM) ensembles and two commonly used

Intergovernmental Panel on Climate Change (IPCC) greenhouse gas (GHG) forcing scenarios: A1B and A2 (IPCC 2010). These two GHG scenarios represent alternative paths of resource development and resulting GHG emissions.

Except where noted below for the sea ice and harvest and incidental take variables, values of input nodes and conditional probabilities were assigned by author Jay (walrus specialist) after considering opinions and comments from other walrus experts, formal model reviews, reports, and the scientific literature (Online Resource 1: Tables 1–3). Values of all inputs were estimated under each combination of the three seasons, six periods, and two GHG scenarios. Many of the intermediate and output conditional probabilities address walrus life history responses that are poorly understood, and in these cases, we partially accounted for these uncertainties by assigning moderate to high levels of spread in the conditional probabilities.

Input and intermediate nodes

Input nodes, parameterized for each season, included sea ice projections from the GCMs, indirect climate effects on benthic prey production, anthropogenic stressors including benthic perturbations from resource utilization, effects from ship and air traffic and human settlements, and human-caused mortalities from subsistence harvest and incidental mortalities from fishing, industry, and research activities (Fig. 2, Table 1, and Online Resource 1: Tables 1 and 2).

Sea ice input nodes for each seasonal submodel included three variables: (1) percentage area of the Chukchi Sea covered in ice (“Chukchi Sea ice cover”), (2) percentage area of the Bering Sea covered in ice (“Bering Sea ice cover”), and (3) number of ice-free months in the Chukchi and Bering seas collectively (“ice-free months”). In this way, we expressed both the spatial and temporal extent of sea ice across the two seas and among seasons. These variables represented two important aspects of sea ice relative to its availability to walrus for hauling out. One is the spatial extent of sea ice available to walrus on which to rest and initiate foraging trips across their seasonal range. The second is the duration of time that no sea ice occurs over the entire continental shelf (number of ice-free months), and hence, the duration of time walrus must use terrestrial haul-outs.

Detailed descriptions and methods for deriving the sea ice inputs are presented in Douglas (2010) and briefly described here. We derived sea ice data for the two observation periods (1984 and 2004) from satellite observations of monthly sea ice concentration obtained from the National Snow and Ice Data Center (NSIDC) final data archives for 1979–2007 (Cavalieri et al. 1996) and from preliminary sea ice archives for 2008 (Meier et al. 2006).

We derived sea ice projections for the four future periods (2025, 2050, 2075, and 2095) from combinations of two CMIP3 GCM ensembles and the two GHG scenarios (A1B and A2) (Douglas 2010). The first ensemble of GCMs was comprised of 18 GCMs (hereafter referred as the GCM_18 set, Online Resource 1: Table 4) that had monthly twenty-first century sea ice projections derived under each of the two GHG scenarios available in the CMIP3 data archive (Meehl et al. 2007). We selected the second ensemble of GCMs from the GCM_18 ensemble based on each model’s ability to simulate the extent and seasonality of sea ice during the past 30 years of satellite observations (hereafter referred as the GCM_SD2 set) and was comprised of 11 GCMs for the Bering Sea and 10 GCMs for the Chukchi Sea (Online Resource 1: Table 4).

We averaged monthly values of ice extent from the observation periods and monthly projections of ice extent from each GCM model, within season and year, then averaged the within-season averages within each decadal period. For each GCM, we summed the number of ice-free months within season and year then averaged the within-season sums within each decadal period. For each BN model run of future periods, we assigned a probability to each state within a sea ice input node that was equal to the proportion of models that projected a sea ice value within the state’s interval. This allowed us to capture the variability (i.e. uncertainty) of ice projections among GCMs directly into the BN model.

We calculated average sea ice extent separately for the Chukchi and Bering seas in each season as a metric to describe the potential range of seasonal walrus movements and occupancy in the two seas (“suitable ice extent”) (Fig. 2, Table 1, and Online Resource 1: Table 1). There is considerable uncertainty as to the lower threshold of sea ice needed to sustain walrus offshore. From radio-tracking studies, walrus have been observed using very sparse, remnant ice during summer in the Chukchi Sea (Jay and Fischbach 2008), and during these conditions, walrus may need to travel greater distances to reach favorable foraging areas. In contrast, walrus are not able to penetrate and effectively utilize areas with very high ice concentrations (Fay 1982), such as current conditions in winter in the Chukchi Sea where ice concentrations of >90% commonly occur (Douglas 2010). Although we recognize that total ice extent can be comprised of many ice concentrations, we used ice extent in the two seas as a proxy for the availability of suitable ice habitat for walrus. We considered very high or very low ice extent to be less-suitable walrus habitat. We used suitable sea ice extent from all three seasons to indicate the annual potential range of walrus movements and occupancy. We also used suitable ice extent with “ice-free months” to inform seasonal “shelf ice availability” in the model.

Table 1 Title and description of input, intermediate, and output nodes used in a Bayesian network model of Pacific walrus status (unless otherwise indicated, the same states are used for all three seasons in the model; see Online Resources 1: Table 1 for more detailed node descriptions)

Node title	Node description	States
Input nodes		
Ice-free months	Mean number of months within a season with no sea ice to support walrus for hauling out over the continental shelf of the Chukchi and Bering Seas	0.0 to 0.5, 0.5 to 2.0, 2.0 to 3.5, 3.5 to 5.0 (Summer/Fall) 0.0 to 0.5, 0.5 to 2.0, 2.0 to 3.0 (Spring) 0.0 to 0.5, 0.5 to 2.0, 2.0 to 4.0 (Winter)
Chukchi Sea ice cover	Extent of sea ice in the Chukchi Sea, expressed as a percentage of the Chukchi Sea shelf within the study area	90–100%, 70–90%, 30–70%, 10–30%, 0–10%
Bering Sea ice cover	Extent of sea ice in the Bering Sea, expressed as a percentage of the Bering Sea shelf within the study area	90–100%, 70–90%, 30–70%, 10–30%, 0–10%
Climate change on benthos	Cumulative impact of various factors related to climate change on the production of benthic prey. Reduced sea ice and ocean acidification are assumed to potentially have the greatest influence on benthic prey production	Positive, neutral, negative
Resource utilization	Impact of benthic prey production from activities that can perturb the seafloor from extraction of natural resources, such as from commercial fishing and oil and gas development	Positive, neutral, negative
Ship and air traffic	Amount of ship and air traffic from commercial shipping, tourism, and fishing, and oil and gas development	Low, moderate, high
Human settlements	Density of humans along the coasts of Alaska and Russia	Low, medium, high
Subsistence harvest	Number of walrus killed by Native subsistence hunting in Russia and Alaska	Low, moderate, high, very high
Incidental takes	Number of walrus killed from illegal activities and incidentally from fishing, industry, and research activities in Russia and Alaska	Low, moderate, high, very high
Intermediate nodes		
Suitable ice extent	Potential range of walrus movements in the Chukchi and Bering Seas as a function of the nodes “Chukchi Sea ice cover” and “Bering Sea ice cover”	Sufficient both seas, sufficient one sea, insufficient both seas
Abundance stressors	Stressors to the abundance of the Pacific walrus population as a function of the nodes “body condition” and “total mortality” (and “breeding environment” in the winter submodel, and “birthing platform” in the spring submodel)	Low stressors, moderately low stressors, moderately high stressors, high stressors
Shelf ice availability	Availability of sea ice to walrus for hauling out during the season as a function of the nodes “ice-free months” and “suitable ice extent”	Excellent, good, fair, poor
Benthic prey abundance	Abundance of benthic prey as a function of the nodes “climate change on benthos”, “resource utilization”, and “oil spills”	High, moderate, low
Energy expenditure	Energy expended by walrus on foraging and swimming as a function of the nodes “shelf ice availability” and “benthic prey abundance”	Low, medium, high
Disease and parasites	Incidence of disease and parasites in the walrus population as a function of the node “shelf ice availability”	Low, moderate, high

Table 1 continued

Node title	Node description	States
Oil spills	Regularity and severity of hydrocarbons released into the water as a function of the node “ship and air traffic”	Low, moderate, high
Body condition	Amount of body reserves possessed by animals in the population, particularly in the form of fat and muscle, as a function of the nodes “energy expenditure”, “disease and parasites”, and “oil spills”	High, medium, low
Predation and associated mortality	Number of walrus killed by predators (excluding humans), which are primarily polar bears and killer whales, as a function of the node “shelf ice availability”	Low, moderate, high
Haul-out disturbance	Level of disturbances to hauled out walrus on ice, and particularly, on terrestrial haul-outs as a function of the nodes “ship and air traffic”, “human settlements”, and “human-caused direct mortality”	Low, moderate, high
Crowding	Number of walrus at a haul-out as a function of the node “shelf ice availability”	Low, moderate, high
Crowding and disturbance	Intensity of a disturbance on a haul-out as a function of the nodes “crowding” and “haul-out disturbance”	Low, medium, high
Human-caused direct mortality	Total number of walrus directly killed by humans in Russia and Alaska as a function of the nodes “subsistence harvest” and “incidental takes”	Low to moderate, high, very high
Total mortality	Total number of walrus killed as a function of the nodes “predation and associated mortality”, “crowding and disturbance” and “human-caused direct mortality”	Low, moderate, high
Breeding environment (node in winter submodel only)	Adequacy of ice habitat for breeding as a function of the node “shelf ice availability”	Superior, adequate, inferior
Birth platform (node in spring submodel only)	Adequacy of ice habitat for birthing, nursing, and providing protection to newborn calves during severe storms as a function of the node “shelf ice availability”	Superior, adequate, inferior
Output nodes		
All-season suitable ice extent	Overall suitable ice extent throughout the year, which reflects the potential range and occupancy of walrus movements in the Chukchi and Bering seas, as a function of “suitable ice extent” in summer/fall, winter, and spring	Sufficient both seas, sufficient one sea, insufficient both seas
All-season abundance stressors	Overall stressors on walrus abundance throughout the year as a function of “abundance stressors” in summer/fall, winter, and spring	Low stressors, moderately low stressors, moderately high stressors, high stressors
All-season walrus outcome	Walrus population overall outcome as a function of the nodes “all-season suitable ice extent” and “all-season abundance stressors”	Robust, persistent, vulnerable, rare, extirpated

In the model, we linked lower shelf ice availability to greater walrus predation (particularly from polar bears), walrus crowding, and incidence of disease and parasites in the population, by increasing the size and concentrating the locations of walrus haul-outs. High levels of crowding and disturbances at terrestrial haul-outs (and perhaps large haul-outs on ice floes) can lead to mortalities (particularly of juvenile walrus) from intraspecific trampling events (e.g.

Kavry et al. 2008; Kochnev et al. 2008). In the model, we also linked lower shelf ice availability to greater amounts of energy walrus expend on foraging and on swimming to preferred feeding grounds. This might be especially true when walrus (particularly females and young) are forced to use terrestrial haul-outs when ice is completely unavailable over the shelf during summer and must swim to and from offshore prey patches between resting periods on

shore. We also linked greater energy expenditure, and incidence of disease and parasites, to lower walrus body condition and their ability to store energy.

We combined subsistence harvest and incidental takes into overall human-caused direct mortality, which in turn contributes to haul-out disturbances. In our model, levels of subsistence harvest and incidental takes are gauged relative to sustainable levels of removal from the population. We considered low and moderate harvest levels to be below a sustainable level of removal and high and very high harvest levels to be above a sustainable level of removal.

Harvest levels that might be expected in future periods are speculative. It is possible that spring hunting in the Bering Strait region may become more difficult because of increases in open water and increased rates of ice melt, so we assigned a moderate level of walrus harvest for spring through the end of century. Harvest in the summer/fall season could increase due to greater access to walruses when they haul-out on shore in fall in the absence of offshore sea ice, so we assigned a moderate harvest for summer/fall through the end of century. Harvest is typically low in winter, and sea ice conditions in this season are projected to change only slightly through the century, so we assigned a low level of harvest for winter through the end of century. Assigning a constant state of harvest through the end of century implies that harvest levels will vary with population size. We also investigated how lower or higher levels of harvest might affect walrus outcomes with “influence runs” of the BN model.

For the two observation periods (1984 and 2004), we estimated low, moderate, high, and very high harvest levels from Alaskan and Russian harvest statistics (USFWS, Marine Mammals Management Office, Anchorage, AK, USA) and estimated potential biological removal for four different rates of maximum theoretical net productivity (Online Resource 1: Table 1).

The amount of ship and air traffic associated with commercial shipping, tourism, and fishing, the levels of oil and gas development, and the density levels of humans along the coasts of Alaska and Russia could add to disturbances to walruses hauled out on ice and shore. We presumed that future sea ice losses, and associated longer ice-free periods during summer and fall, would lead to increased ship traffic in the Chukchi and Bering Seas. In addition, with increasing resource development and tourism, decreasing summer sea ice, and an overall increase in world population, some increase in the number and size of coastal settlements might be expected. We linked increases in ship traffic to increased risks of oil spills, which could adversely affect walrus body condition by direct contact or indirectly from bioaccumulation through the food chain and into walrus prey.

Various factors related to climate change, including reduced sea ice and ocean acidification, and benthic pertur-

bations from activities associated with the extraction of natural resources, such as from commercial fishing and oil and gas development, could influence benthic prey abundance. Although the realization of these conditions in the future is difficult to predict, we linked them to negative effects on benthic prey production. We linked levels of benthic prey abundance, in turn, to the amount of energy expended by walruses while foraging and hence to body condition. We then linked walrus body condition and total walrus mortality to overall levels of stress on population abundance, because poor body condition can lead to decreased reproductive rates and juvenile survival.

Output nodes

Output nodes consisted of “all-season suitable ice extent,” “all-season abundance stressors,” and “all-season walrus outcome” (Fig. 2, Table 1, and Online Resource 1: Tables 1 and 3). All-season suitable ice extent combined the effects of suitable ice extent from the three seasonal submodels to express overall suitable ice extent throughout the year, reflecting the potential range of walrus movements and occupancy throughout the two seas during the year. All-season abundance stressors represented the overall stressors on walrus abundance throughout the year. We considered high levels of abundance stressors from more than one season to have a greater negative influence than high levels of abundance stressors from a single season.

The all-season walrus outcome combined effects of all-season suitable ice extent and all-season abundance stressors into relative probabilities that the Pacific walrus population would be robust, persistent, vulnerable, rare, or extirpated, which we defined as:

- *robust* the Pacific walrus occurs in numbers and distribution robust enough for the population to use available habitat, for individuals to relocate if possible and needed, and for the population to fully withstand anthropogenic stressors and adverse environmental conditions without significant declines in abundance or distribution;
- *persistent* the Pacific walrus occurs in numbers and distribution adequate enough for the population to use available habitat, although locally adverse conditions of anthropogenic stressors and environmental conditions may lead to some declines in abundance or occupancy in some areas;
- *vulnerable* the Pacific walrus occurs in numbers and distribution that is likely to make the population susceptible to locally adverse conditions of anthropogenic stressors and environmental conditions resulting in declines in abundance or occupancy in some areas;
- *rare* the Pacific walrus occurs in numbers and distribution that is likely to make the population highly susceptible

to locally adverse conditions of anthropogenic stressors and environmental conditions resulting in a population with greatly reduced abundance and occupancy that is more or less restricted to isolated pockets;

- *extirpated* the Pacific walrus population is absent through all, or nearly all, of the Chukchi and Bering Sea region.

Model outcomes, sensitivity analysis, and influence runs

We compared model outcomes, consisting of probabilities of the five walrus population response states, among each combination of period, GCM set, and GHG scenario to evaluate differences and trends. These results were based on our modeled best estimates of walrus outcomes and are referred to here as “normative” outcomes under each combination. The distribution of probabilities among outcome states indicates the degree of uncertainty in projected outcomes. Total uncertainty would be represented by uniform probabilities among all outcome states, total certainty by 100% probability in one state and 0% probability in all other states, and intermediate levels of certainty by the distribution of probabilities among multiple states.

We conducted sensitivity analyses of the BN model to determine the sensitivity of outcomes to the input nodes. Sensitivity was calculated in the modeling shell Netica[®] as entropy reduction (reduction in the disorder or variation) of the walrus outcome node relative to the information represented in the input nodes (see Marcot et al. 2006 for method and equation). Sensitivity tests indicated how much of the variation in the selected node is explained by each of the other nodes considered and is conducted by setting all nodes to their default conditions. In our model, we set all prior probabilities of the input nodes for the sensitivity analyses to uniform distributions, reflecting total uncertainty among states. Sensitivity results provide information on the inherent underlying conditional probability structure of the model, not on the sensitivity of particular model outcomes to input conditions specified under given model runs.

We also conducted “influence runs” of the model where we assigned selected input nodes best-case and worst-case scenarios while holding all other input nodes to their original values for future periods (Table 2). The purpose was to examine the effect of prescribing selected stressors at high and low bounds when all other inputs remained at their normative values. In this way, influence runs differ from sensitivity analyses in that influence run inputs are set according to each condition of period, GCM set, and GHG scenario. The influence runs provided insights into the relative influence of climate change on benthic prey abundance, ship and air traffic, sea ice, walrus harvest, and overall anthropogenic stressors, and indicated the degrees to which adverse (or beneficial) effects on walrus populations from each

stressor could be altered by improving (or worsening) its level of stress. We qualitatively compared walrus population outcomes generated from the influence runs to the normative model outcomes.

Results

Model outcomes

Only small differences in all-season walrus outcomes resulted from sea ice projections derived from combinations of the GCM_18 and GCM_SD2 GCM sets and the A1B and A2 GHG scenarios (Online Resource 1: Table 5). Walrus outcomes were nearly the same with the somewhat narrower spread sea ice projections from the GCM_SD2 subset as with the spread of projections from the GCM_18 set of models. The high similarity in walrus outcomes between the two GCM sets was probably due to the high similarity in the central tendency of sea ice input values between the two sets (Douglas 2010) and from how sea ice values were binned into discrete ranges in the BN model. Walrus outcomes under the A2 GHG scenario were also qualitatively similar to those under the A1B GHG scenario. Hereafter, for simplicity, we refer to outcomes from model runs using only the GCM_SD2 models and A1B GHG scenario.

Walrus outcomes were similar between the two observation periods (1984 and 2004). From the current observation period to the end of century, the greatest change in walrus outcome probabilities was a progressive decrease in the outcome state of robust and a concomitant increase in the outcome state of vulnerable. The probabilities of rare and extirpated states each progressively increased at a similar rate, but remained <10% through the end of the century. Probabilities of persistent changed only slightly through the end of century, (Fig. 3 and Online Resource 1: Table 5).

Walrus outcome probabilities can be summed in different combinations to aid interpretation. For example, the summed probabilities of robust and persistent—representing the marginal probability of being in one of those two states—decreased from a current level of about 90% in 2004 to 78% by 2050 and 60% by 2095. In contrast, the summed probabilities of vulnerable, rare, and extirpated ($P(v,r,e)$) increased from a current level of 10% in 2004 to 22% by 2050 and 40% by 2095.

The degree of uncertainty among walrus outcome states increased monotonically over future periods (Fig. 3). This was evidenced by an increasing spread of probabilities among the outcome states, as probabilities of robust and persistent states declined and probabilities of vulnerable, rare, and extirpated states rose. Under all periods, however, probabilities of rare or extirpated states remained individually

Table 2 Groups of input nodes and their forced state used in influence runs of a Bayesian network model of Pacific walrus status

Influence runs	Input nodes and their forced state in each run
(A) Influence of overall anthropogenic stressors	
Compare results on the response variables from influence runs IA1 and IA2, with those from the “normative” run. The difference will be the potentially mitigating or adverse influence of maximal protection guidelines on anthropogenic stressors (other than climate change)	
(IA1) Influence of minimal anthropogenic stressors and low harvest, under projected climate change effects	RUsummer/fall, RUwinter, RUspring → positive SATsummer/fall, SATwinter, SATspring → low HUMsummer/fall, HUMwinter, HUMspring → low HVSTsummer/fall, HVSTwinter, HVSTspring → low
(IA2) Influence of maximal anthropogenic stressors and very high harvest, under projected climate change effects	RUsummer/fall, RUwinter, RUspring → negative SATsummer/fall, SATspring → high SATwinter → moderate HUMsummer/fall, HUMwinter, HUMspring → high HVSTsummer/fall, HVSTspring → very high HVSTwinter → low
(B) Influence of harvest	
When compared with influence runs IA1 and IA2 above, influence runs IB1-IB3 would reveal the incremental positive influence of regulating harvest only (and not resource utilization, ship and air traffic, and human settlements)	
(IB1) Influence of low harvest	HVSTsummer/fall, HVSTwinter, HVSTspring → low
(IB2) Influence of high harvest	HVSTsummer/fall, HVSTspring → high HVSTwinter → low
(IB3) Influence of very high harvest	HVSTsummer/fall, HVSTspring → very high HVSTwinter → low
(C) Influence of ship and air traffic	
(IC1) Influence of minimal ship and air traffic	SATsummer/fall, SATwinter, SATspring → low
(IC2) Influence of maximal ship and air traffic	SATsummer/fall, SATspring → high SATwinter → moderate
(D) Influence of climate change on benthos	
(ID1) Influence of positive effects of climate change on benthos	CCBsummer/fall, CCBwinter, CCBspring → positive
(ID2) Influence of negative effects of climate change on benthos	CCBsummer/fall, CCBwinter, CCBspring → negative

Table 2 continued

Influence runs	Input nodes and their forced state in each run			
(E) Influence of sea ice				
	Period			
	2025	2050	2075	2095
(IE1) Influence of maximal sea ice (the assigned state for each input variable was based on the value from the GCM_SD2 A1B model that projected the highest sea ice condition for that variable in the indicated season and period)	IceMsummer/fall → 0 to 0.5	IceMsummer/fall → 0.5 to 2	IceMsummer/fall → 0.5 to 2	IceMsummer/fall → 0.5 to 2
	IceMwinter → 0 to 0.5	IceMwinter → 0 to 0.5	IceMwinter → 0 to 0.5	IceMwinter → 0 to 0.5
	IceMspring → 0 to 0.5	IceMspring → 0 to 0.5	IceMspring → 0 to 0.5	IceMspring → 0 to 0.5
	IceCsummer/fall → 30 to 70	IceCsummer/fall → 30 to 70	IceCsummer/fall → 30 to 70	IceCsummer/fall → 10 to 30
	IceCwinter → 90 to 100	IceCwinter → 90 to 100	IceCwinter → 90 to 100	IceCwinter → 90 to 100
	IceCspring → 90 to 100	IceCspring → 90 to 100	IceCspring → 90 to 100	IceCspring → 90 to 100
	IceBsummer/fall → 0 to 10	IceBsummer/fall → 0 to 10	IceBsummer/fall → 0 to 10	IceBsummer/fall → 0 to 10
	IceBwinter → 70 to 90	IceBwinter → 30 to 70	IceBwinter → 30 to 70	IceBwinter → 30 to 70
IceBspring → 30 to 70	IceBspring → 30 to 70	IceBspring → 30 to 70	IceBspring → 30 to 70	
(IE2) Influence of minimal sea ice (the assigned state for each input variable was based on the value from the GCM_SD2 A1B model that projected the lowest sea ice condition for that variable in the indicated season and period)	IceMsummer/fall → 2 to 3.5	IceMsummer/fall → 3.5 to 5	IceMsummer/fall → 3.5 to 5	IceMsummer/fall → 3.5 to 5
	IceMwinter → 0 to 0.5	IceMwinter → 0 to 0.5	IceMwinter → 0 to 0.5	IceMwinter → 0 to 0.5
	IceMspring → 0 to 0.5	IceMspring → 0 to 0.5	IceMspring → 0 to 0.5	IceMspring → 0 to 0.5
	IceCsummer/fall → 10 to 30	IceCsummer/fall → 0 to 10	IceCsummer/fall → 0 to 10	IceCsummer/fall → 0 to 10
	IceCwinter → 90 to 100	IceCwinter → 70 to 90	IceCwinter → 70 to 90	IceCwinter → 30 to 70
	IceCspring → 90 to 100	IceCspring → 70 to 90	IceCspring → 70 to 90	IceCspring → 70 to 90
	IceBsummer/fall → 0 to 10	IceBsummer/fall → 0 to 10	IceBsummer/fall → 0 to 10	IceBsummer/fall → 0 to 10
	IceBwinter → 30 to 70	IceBwinter → 10 to 30	IceBwinter → 0 to 10	IceBwinter → 0 to 10
IceBspring → 10 to 30	IceBspring → 0 to 10	IceBspring → 0 to 10	IceBspring → 0 to 10	

RU Resource utilization, *SAT* Ship and air traffic, *HU* Human settlements, *HVST* Subsistence harvest, *CCB* Climate change on benthos, *IceM* Ice-free months, *IceC* Chukchi Sea ice cover, *IceB* Bering Sea ice cover, *summer/fall* summer/fall submodel node, *winter* winter submodel node, *spring* spring submodel node

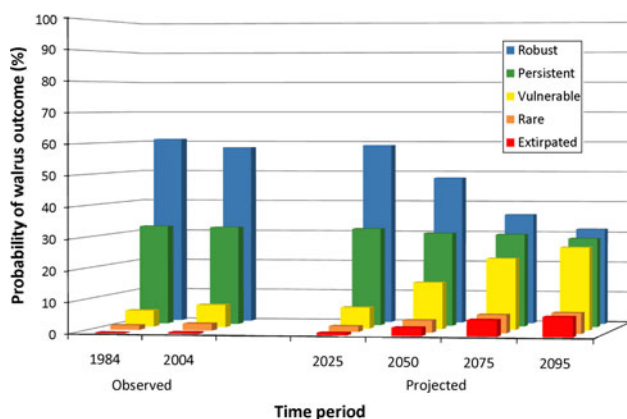


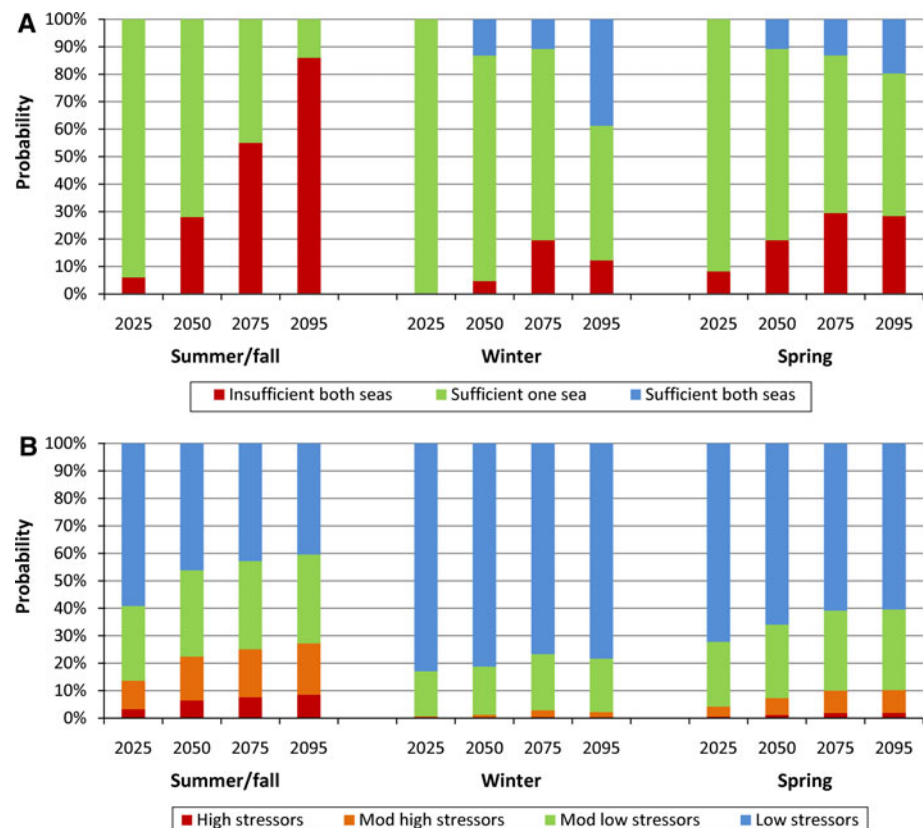
Fig. 3 Probabilities of walrus outcomes projected from a Bayesian network model of Pacific walrus status for 6 periods and using sea ice projections from the GCM_SD2 set and A1B GHG emission scenario (“normative” run)

low even at the end of the century; hence, uncertainty among the model outcomes was spread primarily across the robust, persistent, and vulnerable states.

In our BN model, changes in walrus outcomes (Fig. 3) reflected changes in the parent nodes: all-season suitable ice extent and all-season abundance stressors (Fig. 2). All-season suitable ice extent was derived from suitable ice extent in each of the three seasons. Suitable ice extent grew increasingly insufficient in both seas for walrus movements and occupancy through end of century in all three seasons, but most sharply in summer/fall (Fig. 4). In summer/fall, suitable ice extent was determined from sea ice extent in the Chukchi Sea. In winter and spring, probabilities of insufficient ice extent in both seas occurred when there was some probability of very high ice extent in the Chukchi Sea, a condition making it difficult for walruses to occupy the area, together with some probability of low ice extent in the Bering Sea. Projected sea ice extent in the Chukchi Sea never reached low levels in winter or spring through the end of century.

All-season abundance stressors were influenced by variables linked to shelf ice availability, which was determined by both suitable ice extent and number of ice-free months (Fig. 2). In a trend similar to that of suitable ice extent,

Fig. 4 Probabilities of “suitable ice extent” (a) and “abundance stressors” (b) by future periods and seasons from a Bayesian network model of Pacific walrus status using sea ice projections from the GCM_SD2 set and A1B GHG emission scenario



stressors on walrus abundance increased through end of century in all seasons, but most notably in summer/fall (Fig. 4). Abundance stressors increased only slightly in winter.

Sensitivity analyses

Sensitivity analyses suggested that the inherent probability structure (i.e. not specified for any particular scenario or period) of the BN model renders the all-season walrus outcome to generally being more sensitive to sea ice and harvest levels than to other factors (Table 3). Walrus outcome was somewhat more sensitive to ice-free months in winter and spring than in summer/fall. This is likely due to the added “breeding environment” and “birthing platform” nodes in the winter and spring submodels, respectively, which affected abundance stressors and provided an additional path for ice-free months to influence the outcomes. A full analysis of sensitivity of the outcomes to every node in the BN model (Online Resource 1: Table 6) suggested that factors in each season played a role in determining walrus outcomes, with a greater overall sensitivity to all-season abundance stressors than to all-season suitable ice extent.

Influence runs

Influence runs of the BN model, in which we varied selected stressors to extreme values and compared the

walrus outcomes to those from the normative model run, suggested that sea ice stressors had substantial influence on walrus outcomes (Fig. 5, Table 2). Setting sea ice habitat (number of ice-free months and ice extent) to GCM-projected maximal sea ice conditions at each future period, while leaving all other input nodes unchanged at their normative values, resulted in projected $P(v,r,e)$ values 6–24% below the normative values through end of century. In contrast, setting sea ice habitat to GCM-projected minimal sea ice conditions resulted in projected $P(v,r,e)$ values 1–19% above the normative values through end of century. The slight decrease in $P(v,r,e)$ in 2095 under the minimal sea ice influence run was due to improved sea ice conditions in the Chukchi Sea from decreased sea ice cover in winter.

The influence runs suggested that “climate change on benthos” and “ship and air traffic” had negligible influence on walrus outcomes (Fig. 5, Table 2). That is, minimizing and maximizing the values of these stressors resulted in very little difference from the normative values of $P(v,r,e)$.

Minimizing harvest had little positive influence on walrus outcomes compared to the normative $P(v,r,e)$ values (Fig. 5), but high and very high harvest had progressively higher adverse influence on walrus outcomes. High harvest led to an increase in $P(v,r,e)$ of 13–17% over normative values through end of century. Very high harvest resulted in an increase in $P(v,r,e)$ of 30–35% over normative values.

Table 3 Results of sensitivity analysis results of the Bayesian network model, sorted by season. Entropy reduction refers to the degree to which the final all-season walrus outcome probabilities are sensitive to each input node in the model, listed here in decreasing order of effect

Summer/Fall		Winter		Spring	
Node name	Entropy reduction	Node name	Entropy reduction	Node name	Entropy reduction
Incidental takes	0.00856	Ice-free months	0.01417	Ice-free months	0.01832
Subsistence harvest	0.00856	Incidental takes	0.00574	Subsistence harvest	0.00426
Bering Sea ice cover	0.00567	Subsistence harvest	0.00574	Incidental takes	0.00426
Ice-free months	0.00382	Bering Sea ice cover	0.00516	Bering Sea ice cover	0.00381
Chukchi Sea ice cover	0.00287	Chukchi Sea ice cover	0.00256	Chukchi Sea ice cover	0.00187
Ship and air traffic	0.00127	Ship and air traffic	0.00101	Ship and air traffic	0.00085
Human settlements	0.00009	Human settlements	0.00006	Human settlements	0.00004
Climate change on benthos	0	Climate change on benthos	0	Climate change on benthos	0
Resource utilization	0	Resource utilization	0	Resource utilization	0

Similar to the harvest influence runs, minimizing overall anthropogenic stressors (which included harvest, Table 2) had little positive influence on walrus outcomes compared to the normative walrus outcomes, but maximizing anthropogenic stressors imparted a high degree of adverse influence. Maximizing overall anthropogenic stressors resulted in an increase in $P(v,r,e)$ of 35–45% over normative values through end of century.

In summary, the influence runs suggest that changes in sea ice habitat and harvest could have the greatest influence on future walrus outcomes. In the normative run, harvest was set to a constant state through the end of century (moderate for spring and summer/fall and low for winter); therefore, most of the increase in $P(v,r,e)$ through end of century in the normative run was due to projected declines in sea ice habitat. Since the harvest influence runs were identical to the normative run but with varying levels of harvest settings, the influence of harvest could be largely additive to the influence of sea ice on future walrus outcomes. Of the anthropogenic stressors that might be mitigated (other than climate change), harvest had the greatest influence on walrus outcomes.

Discussion

Dominant effects of sea ice and harvest

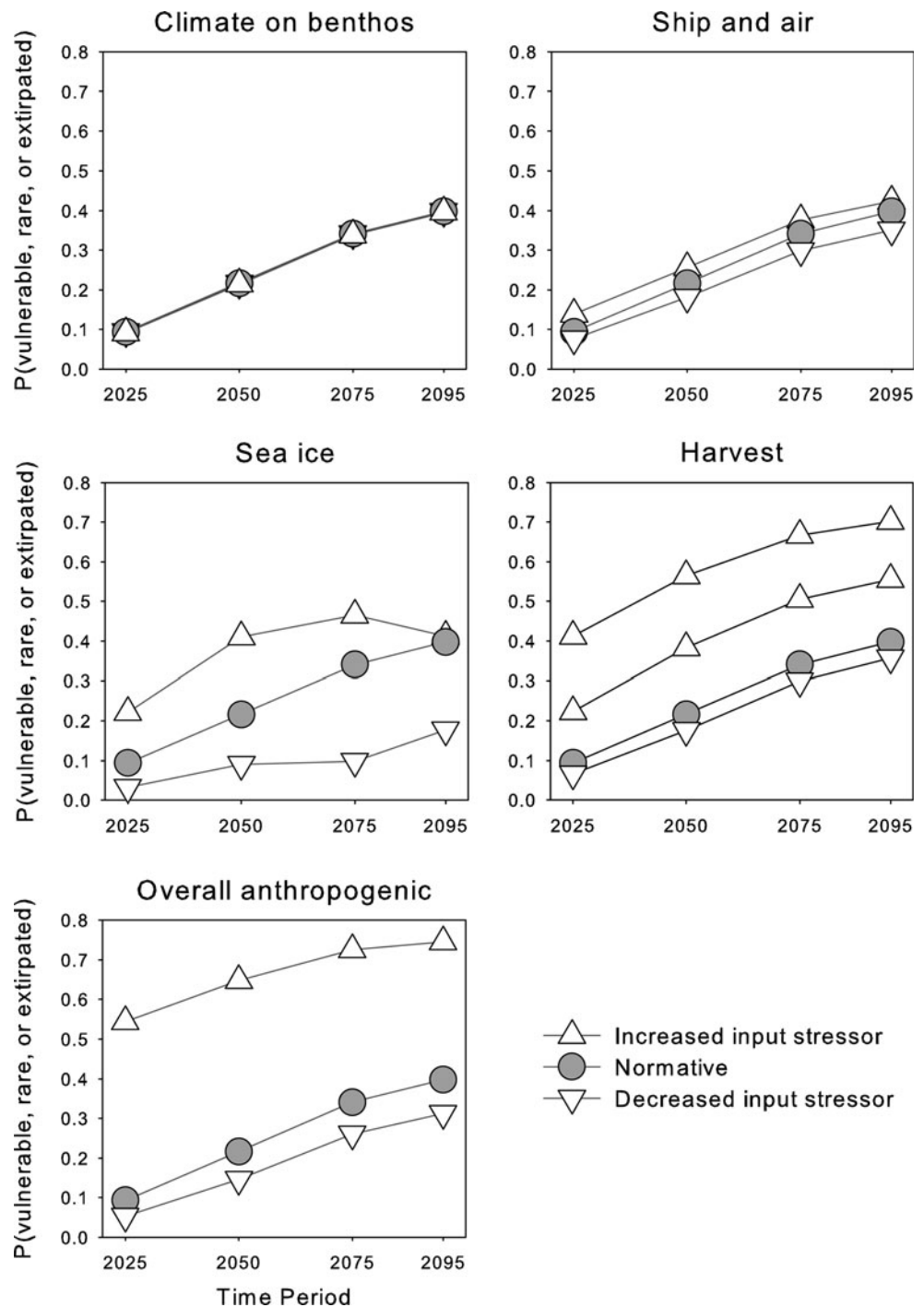
The projected decreases in the walrus outcome states of robust and persistent from the current observation period to the end of century (and concomitant increases in the outcome states of vulnerable, rare, and extirpation) reflected a trend of worsening conditions for the Pacific walrus. The trends in outcomes were accompanied by increasing uncertainty among the robust, persistent, and vulnerable states.

Sensitivity analyses and influence runs indicated that sea ice habitat and harvest could have the greatest influence on future walrus outcomes. The progressive increase over time in probabilities of vulnerable, rare, and extirpation suggests that perhaps there will be no thresholds that trigger accelerated population change, given that future sea ice change adheres to the GCM projections and that future harvest rates are proportional to walrus population size.

Sea ice projections indicate that ice-free conditions over the entire shelf will occur during August, September, and October (during summer/fall) by the end of the century and will be accompanied by an earlier sea ice melt in spring and delayed sea ice freeze-up in late fall (Douglas 2010). We assumed that the geographic location of breeding and birthing can shift without consequence to the population, but if this assumption proves false, then adverse influences on walrus may be greater than indicated by our BN model.

In our model, sea ice habitat decreased most in summer/fall (Fig. 4) due to decreased sea ice extent in the Chukchi Sea and increased number of ice-free months over the continental shelf. The decreased sea ice habitat was linked to decreased body condition from poorer ice availability and increased total mortality from increased crowding and disturbance mortalities on the haul-outs. This, together with the moderate setting of harvest we specified through end of century for summer/fall, resulted in the summer/fall season having the greatest influence on all-season walrus outcomes. Abundance stressors projected for spring were less than those projected for summer/fall because sea ice conditions in spring are not projected to degrade as greatly as in summer/fall. Sea ice and other conditions through end of century in winter (including low harvest level settings) had only small adverse influences on all-season walrus outcomes.

Fig. 5 Summed probabilities of vulnerable, rare, and extirpated derived from “influence runs” of a Bayesian network model of Pacific walrus status. Influence runs consisted of individually varying specified input conditions (e.g. sea ice, harvest, and other human activities) while holding other input conditions constant at their normative levels for that period, and using sea ice projections from the GCM_SD2 set and A1B GHG emission scenario. Harvest influence runs included two levels of increased input stressors (see Table 2)



We incorporated uncertainty of modeled sea ice projections into our BN model runs by having each GCM model provide an observation for each run under each combination of period, GCM set, and GHG scenario. However, summer Arctic sea ice extent could decline more rapidly than forecasted by many GCMs (Stroeve et al. 2007; Wang and Overland 2009). If sea ice continues to decline more rapidly in the future than is projected by most GCMs, changes in the status of the walrus population could occur more rapidly

than indicated by our model's normative run. Our minimum sea ice influence run used sea ice input values that represent a composite of the most extreme minimal sea ice projections (Table 2). For the early twenty-first century, these projections portrayed a trajectory of ice loss that was actually faster than observed, and for subsequent decades, it would not be unreasonable to consider the results of the minimum sea ice influence run (Fig. 5) as exemplifying a worst-case trajectory of ice loss under the A1B forcing scenario.

Results of the influence runs suggest that although minimizing harvest from current levels may have little positive effect on population outcomes in the future, harvests of high and very high levels (above the moderate harvest levels set in the normative conditions) could add significantly to the adverse effects of future sea ice conditions. If in the future, the walrus population declines, but a constant number of walruses continue to be harvested, the level of stress by the harvest would effectively increase, as exemplified in our high or very high harvest influence runs (Fig. 5). Also, increased access to walruses on terrestrial haul-out sites in Alaska and Russia during progressively longer ice-free periods in summer/fall could result in higher harvest levels and disturbances, leading to higher mortality levels. The net effect of harvest on walrus outcomes in the future will likely depend on the level of stress imparted by future sea ice change and the ability of walruses to cope with those changes. The potential influence of very high harvest on walrus outcome in our model is consistent with the observed response in walrus distribution and abundance after high levels of harvest in past centuries. Very high levels of commercial harvests of Pacific walruses in late nineteenth through mid-twentieth century led to depleted population levels and dramatic reductions in population range (Fay et al. 1989; Garlich-Miller et al. 2006).

Implications of uncertainties of the marine ecosystem

The negligible influence that “ship and air traffic” and “climate change on benthos” had on walrus outcomes in the BN model was likely due to the low influence these factors imparted on body condition, combined with the relatively low influence of body condition on seasonal abundance stressors. The probabilities we assigned to these relationships in the model (Online Resource 1: Tables 2 and 3) reflected our current poor understanding and uncertainty of their future conditions and the mechanisms and processes by which they will affect walrus prey abundance and body condition and their ultimate ramifications on walrus vital rates and abundance. However, the relatively low influence these factors had on walrus outcomes in our model does not reflect certain knowledge that these factors are trivial. Rather, their low influence reflects our uncertainty in the magnitude and timing in which the factors might be expressed and the degree of stress that the factors could impart on the Pacific walrus population.

While greater areas of open water and a longer growing season from changes in sea ice conditions in the future could lead to increased primary production in Arctic waters (Arrigo et al. 2008), the biological processes that govern pelagic and benthic productivity at regional scales are complex, and therefore, the effect of future sea ice losses on ecosystem structure in the Chukchi and Bering seas is

uncertain (Grebmeier et al. 2010). Earlier sea ice melt and reductions in sea ice extent have the potential to reduce benthic production and increase pelagic consumption in Arctic marine ecosystems and thus result in decreased food supply to walrus benthic prey; however, dependencies on regional conditions make detailed biological responses difficult to predict (Piepenburg 2005; Grebmeier et al. 2006a, b; Lalande et al. 2007; Bluhm and Gradinger 2008).

In addition to the potentially large effects that reduced sea ice may have on lowering production of walrus prey, increasing levels of dissolved CO₂ in the world's oceans and associated increase in ocean acidification could ultimately have profound adverse effects on shell-producing organisms (Bates et al. 2009). Since walruses feed largely on clams, this phenomenon could have larger effects on the walrus outcomes than we projected. Forecasts are uncertain for saturation levels of carbonate minerals in the Chukchi Sea and broader Arctic Ocean because of challenges in predicting future changes in sea ice cover, temperature, stratification and nutrient supply, inputs of freshwater and terrestrial organic carbon, and complex physical and biological feedbacks in the region (Bates et al. 2009).

Paleobiogeography and the potential of walruses to adapt to future stressors

Biogeographical studies can provide important contextual information to management and conservation issues and are particularly relevant in the Arctic where rapid environmental change is projected to occur (Murray 2008). The extant Pacific and Atlantic walrus (*O. r. divergens* and *O. r. rosomarus*), and at least 20 fossil species within 14 genera and three subfamilies, are members of the monophyletic Odobenidae. Phylogenetic and stratigraphic data suggest that odobenids first evolved in the North Pacific sometime before 18 Ma (late early Miocene) (Kohno et al. 1995; Deméré et al. 2003). These small-bodied archaic walruses gave rise during the middle and late Miocene to larger-bodied, but non-tusked lineages of imagotariine and dusignathine walruses (Deméré et al. 2003; Arnason et al. 2006). More recent records of walrus fossils from Japan and California suggest that the lineage containing the modern walrus evolved in the North Pacific near the Miocene–Pliocene boundary about 5–7 Ma. An early, large-bodied, tusked member of this odobenine lineage dispersed northward from the North Pacific during a pre-glacial event of the early Pliocene through the Bering Strait perhaps 4–5 Ma, into the ice-free Arctic Ocean, and eventually into the North Atlantic in an east-to-west direction (Kohno et al. 1995; Deméré et al. 2003). These Pliocene North Atlantic walruses went extinct without any descendants (Kohno and Ray 2008).

It is hypothesized that *Odobenus* evolved in the North Pacific during the early Pleistocene and apparently moved

northward during interglacials and southward during glacials (Harington and Beard 1992); however, they were periodically isolated in the North Pacific from the Arctic Ocean and North Atlantic from the cyclical closing of the Bering Strait from glacio-eustatic oscillations (Davies 1958; Deméré et al. 2003). Since the start of the current ice age about 2.6 Ma, through to the present Holocene interglacial period (started 12,000 ka), glacio-eustatic oscillations have occurred at regular intervals, initially on about 40,000-y time scales and then later on about 100,000-y time scales (Augustin et al. 2004). Walrus evolved tusks and shifted toward benthic-molluscivory (Adam and Berta 2002) about 5 Ma (Miocene-Pliocene boundary) (Kohn et al. 1995; Deméré et al. 2003). The evolution of the extant *O. rosmarus* Pacific and Atlantic subspecies sometime during the Pleistocene probably arose from the splitting of the species' former Holarctic range from extensive sea ice in the Canadian Arctic during an early glacial phase (Kohn et al. 1995; Deméré et al. 2003). Thus, the extant Pacific and Atlantic walrus have apparently been exposed to repeated opening and closure of the Bering Strait and glacial cycles (Augustin et al. 2004), with potentially ice-free marginal seas during interglacial periods (Davies 1958), since the Pleistocene (~2.5 Ma).

The persistence of the Pacific walrus in the geologic past, apparently during periods without sea ice, or with much more limited sea ice than now, suggests a likelihood that walrus will persist through the current century, albeit in perhaps reduced numbers. The pharyngeal pouches of the walrus are an apparent adaptation to resting offshore (Fay 1960) in the absence of sea ice, and the wide taxonomic range of walrus prey (Fay 1982) suggests plasticity in the walrus diet. These characteristics may help walrus withstand some of the future sea ice-related stressors they may encounter in the face of rapid environmental change. However, the degree to which their potential ecological flexibility would also provide a buffer against additional anthropogenic-related stressors in the future cannot be gauged by the historic or prehistoric record alone.

Next steps in continuing research and model refinement

Climate change and the rapid loss of sea ice raise concerns for conservation of the Pacific walrus and other arctic species (e.g. Amstrup et al. 2008). Forecasting the response of arctic species to their complex and rapidly changing environment requires consideration of a number of potential stressors, often with very limited information. This study was a first step in developing a comprehensive framework to integrate the various linkages and multiple influences of environmental and anthropogenic stressors that may affect the future distribution and abundance of the Pacific walrus. This framework also allowed for the integration of various

sources of data and expert knowledge, including the paucity of data on walrus vital rates and demographic response to stressors, and to represent structural and parameter uncertainties explicitly through probabilities of influence. Such an approach is an appropriate means of evaluating potential future cumulative effects of multiple stressors, particularly in light of uncertainties and incomplete data (Robards et al. 2009). The walrus BN model can help focus new research and monitoring efforts. Updates of model structure and probability values can easily include new data or knowledge as they become available, a distinct advantage of the Bayesian approach (e.g. see Marcot et al. 2006). Similarly, another suite of sea ice projections will become available within the next few years from the IPCC 5th assessment report and can be incorporated into the BN model.

The energetic costs associated with modified walrus behaviors in response to environmental changes are presently unknown. New research to address this information gap, such as studies of walrus bioenergetics relative to sea ice availability and distribution of benthic prey, could be coupled with models of walrus population dynamics to better understand and quantify the linkages between energy expenditure, body condition, and walrus demography. In addition, monitoring the levels of mortality associated with use of land haul-outs by females and young during adverse sea ice conditions will enable better estimation of the likely influence of future sea ice changes to walrus abundance.

Conclusions

We used a BN model to represent linkages between potential stressors and walrus responses in a probabilistic framework to evaluate potential outcomes of the walrus population through the twenty-first century. Model outcomes reflected a clear trend of worsening conditions for the Pacific walrus. From the current observation period to the end of century, the greatest change in walrus outcome probabilities was a progressive decrease in the outcome state of robust and a concomitant increase in the outcome state of vulnerable. The probabilities of rare and extirpated states each progressively increased but remained <10% through the end of the century. The summed probabilities of vulnerable, rare, and extirpated ($P(v,r,e)$) increased from a current level of 10% in 2004 to 22% by 2050 and 40% by 2095. The degree of uncertainty in walrus outcomes increased monotonically over future periods.

Sensitivity analyses and influence runs from our BN model indicated that sea ice habitat and harvest could have the greatest influence on future walrus outcomes. Most of the increase in $P(v,r,e)$ through end of century in the normative run of the BN model was due to projected declines in sea ice habitat in summer/fall.

Results of the influence runs suggested that, of the anthropogenic stressors that might be mitigated (other than climate change), harvest had the greatest influence on walrus outcomes. High and very high harvest levels could add significantly to the projected adverse effects of future sea ice conditions. Minimizing harvest from current levels may have minor positive effect on population outcomes in the future; however, improvements to multiple environmental factors and anthropogenic stressors together could provide greater benefit.

The negligible influence that “ship and air traffic” and “climate change on benthos” had on walrus outcomes mostly reflects uncertainty in future states of these variables and our current poor understanding of the processes and mechanisms by which changes in ship traffic, reduced sea ice, and atmospheric carbon loading in the oceans may affect walrus prey abundance and its ultimate ramifications on walrus vital rates and abundance. The relatively low influence that these factors had on walrus outcome in our model does not reflect certain knowledge that these factors are trivial. Rather, their low influence reflects our uncertainty in the magnitude and timing in which the factors might be expressed and the degree of stress that the factors could impart on the Pacific walrus population.

This study is a first step in developing a comprehensive framework to incorporate the various complex linkages of environmental and anthropogenic stressors that may affect the future distribution and abundance of walruses. This framework also allowed for the integration of various sources of data and expert knowledge, including the paucity of data on walrus vital rates and demographic response to these stressors. Future efforts to build on our current work should include monitoring the response of walruses to changing arctic conditions, research on specific aspects of walrus life history pertaining to climate change effects on the benthos and prey production, and development of walrus bioenergetics models relative to changes in sea ice availability and benthic prey coupled with models of walrus population dynamics.

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Conflict of interest The authors declare that they have no conflict of interest.

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