

Potential population-level effects of increased haulout-related mortality of Pacific walrus calves

Mark S. Udevitz · Rebecca L. Taylor ·
Joel L. Garlich-Miller · Lori T. Quakenbush ·
Jonathan A. Snyder

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Abstract Availability of summer sea ice has been decreasing in the Chukchi Sea during recent decades, and increasing numbers of Pacific walruses have begun using coastal haulouts in late summer during years when sea ice retreats beyond the continental shelf. Calves and yearlings are particularly susceptible to being crushed during disturbance events that cause the herd to panic and stampede at these large haulouts, but the potential population-level effects of this mortality are unknown. We used recent harvest data, along with previous assumptions about demographic parameters for this population, to estimate female population size and structure in 2009 and project these numbers forward using a range of assumptions about future harvests and haulout-related mortality that might result from increased use of coastal haulouts during late summer. We found that if demographic parameters were held constant, the levels of harvest that occurred during 1990–2008 would have allowed the population to grow during that period. Our projections indicate, however, that an increase in haulout-related mortality affecting only calves has a greater effect on the population than an equivalent increase in harvest-related mortality distributed among all age classes. Therefore, disturbance-related

mortality of calves at coastal haulouts may have relatively important population consequences.

Keywords Bering Sea · Chukchi Sea · Haulout · Mortality · *Odobenus rosmarus divergens* · Pacific walrus · Population dynamics · Projection model · Subsistence harvest · Trampling

Introduction

Pacific walruses (*Odobenus rosmarus divergens*) are important components of the Bering and Chukchi Sea ecosystems (Oliver et al. 1983; Ray et al. 2006) and as a subsistence resource for Alaskan and Chukotkan Natives (Brooks 1953; Garlich-Miller et al. 2006). Walruses use sea ice for calving, nursing, resting, molting, access to offshore foraging areas, and refuge from terrestrial predators and disturbance (Fay 1982). The availability of summer sea ice has been decreasing in the Chukchi Sea during recent decades (Meier et al. 2007), which is causing changes in walrus behavior. Larger numbers of walruses have begun using terrestrial haulouts on the coasts of Alaska and Chukotka in late summer during years when the sea ice has retreated beyond the continental shelf (Fischbach et al. 2009). Young (i.e., smaller) walruses are particularly susceptible to being crushed in these large aggregations during disturbance events that cause the herd to panic and stampede (Kochnev et al. 2008; Fischbach et al. 2009; Kochnev 2010).

Little information is available about walrus demographic parameters and population dynamics. Natural mortality rates for walruses have never been directly estimated, but are generally assumed to be low because walruses are long-lived (~36 years) and have a relatively low reproductive potential (Fay et al. 1997). A few parameters

M. S. Udevitz (✉) · R. L. Taylor
U.S. Geological Survey, Alaska Science Center,
4210 University Drive, Anchorage, AK 99508, USA
e-mail: mudevitz@usgs.gov

J. L. Garlich-Miller · J. A. Snyder
U.S. Fish and Wildlife Service, Marine Mammals Management
Office, 1011 East Tudor Road, Anchorage, AK 99503, USA

L. T. Quakenbush
Alaska Department of Fish and Game, 1300 College Road,
Fairbanks, AK 99701, USA

related to reproduction have been estimated from harvested animals, and it appears that reproductive rates as well as age of first reproduction for Pacific walrus have changed over time (Fay et al. 1997; Garlich-Miller et al. 2006). Range-wide population surveys of Pacific walrus were conducted at 5-year intervals from 1975 to 1990 (Udevitz et al. 2001). Fay et al. (1997) used these surveys for estimating that the population increased to a maximum size of about 300,000 walrus in 1980 before decreasing to about 244,000 walrus in 1985. Using all available data for Pacific walrus, Fay et al. (1997) developed a matrix projection model, incorporating a simple form of density-dependent reproductive rates to match the apparent dynamics of the population during this period. Their analysis provides the best available approximation of the size and structure of the Pacific walrus population up to 1989. The most recent range-wide survey was conducted in 2006 and produced an estimate of 129,000 (95 % CI = 55,000–507,000) walrus, but this estimate is known to be low because the survey only covered about half of the available habitat (Speckman et al. 2011).

In addition to natural mortality, Pacific walrus have been subject to subsistence harvests for thousands of years and to commercial harvests by Russian merchant companies and the American whaling fleet in the 1800's (Bockstoe and Botkin 1982). Since 1930, total reported harvests ranged from 2,300 to 9,500 annually (Fay et al. 1997; Garlich-Miller et al. 2006). Deaths associated with the large terrestrial haulouts that have formed in late summer along the Alaskan and Chukotkan coasts during years of reduced sea ice availability can number in the hundreds per haulout, with the majority of this mortality affecting calves and yearlings (Kochnev et al. 2008; Fischbach et al. 2009; Kochnev 2010).

We used recent harvest data along with the demographic parameters assumed by Fay et al. (1997) to estimate female population size and structure in 2009 and to project these numbers forward with a range of assumptions about future harvests and haulout-related mortality that might result from increasing use of coastal haulouts during late summer. Because calves are the most affected age class and to simplify the analysis, we assumed haulout-related mortality affected only calves. This analysis provides a quantitative basis for evaluating potential population-level consequences of increases in haulout-related mortality.

Materials and methods

Harvest-related mortality 1990–2008

We used the U.S. Fish and Wildlife Service estimates of harvest-related mortality for female walrus 1990–2008.

Estimates for the U.S. harvest were based on data collected in the U.S. Fish and Wildlife Service's Marking, Tagging and Reporting Program (MTRP) and Walrus Harvest Monitor Project (WHMP). Estimates for the Russian harvest were based on data collected in the Chukotka Walrus Harvest Monitoring Program (CWHMP, Chukotka Branch of the Pacific Fisheries Research Center unpublished data). The MTRP is a regulatory program authorized under the Marine Mammal Protection Act requiring subsistence hunters to report each walrus harvested and have the tusks tagged. The WHMP is an observer-based harvest data and sample collection project which has been conducted in the Bering Strait hunting communities of Little Diomedea, Gambell, Savoonga, and Wales. The CWHMP is an observer-based harvest data and sample collection program similar to the WHMP, but conducted by Russian agencies in hunting communities in the Chukotsky and Provideniya districts of Chukotka. All estimates were adjusted to account for a 42 % struck-and-lost rate (U.S. Fish and Wildlife Service unpublished data; Fay et al. 1994). Estimates do not account for calves or yearlings that are not harvested or struck-and-lost but die due to harvest-related loss of their mother. The number of juveniles lost in this way is expected to be relatively small, however.

Population projection to 2009

We based population projections on the demographic parameter values used by Fay et al. (1997). Annual natural mortality rates were 0.050 for calves and 0.015 for ages 1–36, with 36 being the maximum age. The sex ratio of calves was 0.5. The number of females in each age class immediately following births each year was projected as:

$$\begin{pmatrix} n_0(t) \\ n_1(t) \\ n_2(t) \\ \vdots \\ n_{36}(t) \end{pmatrix} = \begin{pmatrix} s_0 m_1(t) & s_1 m_2(t) & \cdots & s_{35} m_{36}(t) & 0 \\ s_0 & 0 & \cdots & 0 & 0 \\ 0 & s_1 & \cdots & 0 & 0 \\ \vdots & \vdots & \cdots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{36} & 0 \end{pmatrix} \times \begin{pmatrix} n_0(t-1) - h_0(t-1) \\ n_1(t-1) - h_1(t-1) \\ n_2(t-1) - h_2(t-1) \\ \vdots \\ n_{36}(t-1) - h_{36}(t-1) \end{pmatrix},$$

where $n_i(t)$ is the number of females in age class i immediately after births in year t , $m_i(t)$ is the reproductive rate (i.e., rate of female calf production) for age i females in year t , $1 - s_i$ is the (assumed constant) natural mortality rate for age i females, and $h_i(t)$ is the additional harvest-related mortality for those females during year t . Harvest mortality was assumed to occur immediately after births so that natural mortality rates applied to all individuals

remaining after accounting for harvest-related mortality. We indexed projections by year of population estimate rather than by year of preceding harvest as was done by Fay et al. (1997) and, in referring to their projections, we translated their indexing to match this convention.

Fay et al. (1997) estimated age-specific reproductive rates based on analyses of reproductive tracts collected during two time periods (Fig. 1a). One set of rates was based on data from 1953 to 1975 corresponding to the period when the population was assumed to be growing and they applied those rates during the years 1950–1978. The second set of rates was based on data from 1979 to 1985 corresponding to the period when the population was assumed to be nearing carrying capacity. They applied those lower rates during the years 1979–1990. This resulted in a density-dependent function for reproductive rates that switched from the higher to the lower set of rates when the population of reproductively mature females (aged >5) increased from 111,000 to 117,000 individuals. We replaced this discrete function with a logistic function of population size that provided a smooth transition between the two sets of rates. The function had the form

$$m_i(t) = a_i + \frac{b_i}{1 + \exp(-d + cN(t - 1))},$$

where a_i is the minimum reproductive rate for age i females (based on data from 1979–1985), $a_i + b_i$ is the maximum reproductive rate for age i females (based on data from 1953–1975), and $N(t)$ is the number of reproductively mature females (>5 years old) in the population at time t (Fig. 1b). We selected values for the other parameters ($c = 0.00015$, $d = 16.3017$) such that the function reached the upper asymptote as the population decreased to the level estimated by Fay et al. (1997) in 1972 and reached the lower asymptote as the population increased to the level estimated by Fay et al. (1997) in 1985 with an inflection point at $d/c = 108,678$ (just slightly less than the transition point used by Fay et al. (1997)). The full transition from one set of rates to the other took 13 years. This produced overall dynamics that were nearly identical to those projected by Fay et al. (1997) but without the abrupt change in population trajectory caused by the discrete form of density dependence (Fig. 2).

We repeated the projections for the female portion of the population from 1950 to 1989 exactly as done by Fay et al. (1997), except we used the smoothed density-dependent function for reproductive rates. We then continued to project this population forward to 2009, in the same manner, using the age-specific estimates of harvest-related mortality for this subsequent period. The average annual population growth rate during this period was calculated as the geometric mean $(N_i/N_j)^{1/(i-j)}$, where N_i is the population size in year i , $i > j$.

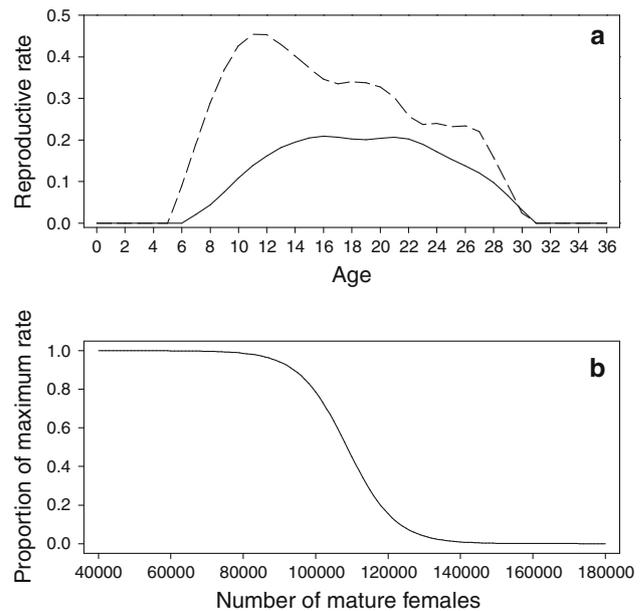


Fig. 1 Maximum and minimum reproductive rates (a) and the density-dependent function used to transition between these rates (b) in the projection model of Pacific walrus population dynamics. Reproductive rates in a were estimated by Fay et al. (1997) based on data from a period when the population was rapidly increasing (1953–1975, dashed line) and a period when the population was approaching carrying capacity (1979–1985, solid line)

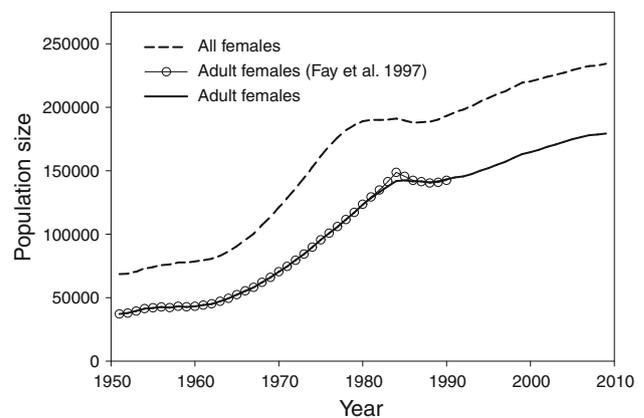


Fig. 2 Estimated population sizes for all female and adult female (≥ 6 years old) Pacific walrus based on a projection model developed by Fay et al. (1997), modified to include smoothly density-dependent reproductive rates, and incorporating more recent estimates of harvest-related mortality. Original values estimated for adult females, 1951–1990, by Fay et al. (1997) are shown for comparison

Population projection beyond 2009

Starting with our estimate of the size and structure of the female population in 2009, we continued to project the population forward in the same manner, but with a range of assumptions about the magnitude of annual harvest-related mortality and annual haulout-related mortality.

We considered levels of total harvest-related mortality ranging from 0 to 8,500 females per year. In general, we assumed that the harvest-related mortality had the same age-specific structure as the estimated total harvest-related mortality from 1990 to 2008. In some cases, however, the number of females in one or more of the older age classes (\geq age 12) was depleted while there were still sufficient numbers of walruses in other older age classes to sustain the total level of mortality being assumed for this group of age classes as a whole. In these cases, the harvest-related mortality was proportionally redistributed, as necessary, to the remaining older age classes.

For simplicity, we assumed that haulout-related mortality only affected calves and occurred immediately after births and any harvests. Thus, in our projections beyond 2009, $h_0(t)$ was replaced by $h_0(t) + z_0(t)$, where $z_0(t)$ represents haulout-related mortality during year t . This formulation is conservative in the sense that if some natural mortality occurred before the haulout-related mortality, the relative effect of the haulout-related mortality would be greater. We considered levels of haulout-related mortality ranging from 0 to 5,500 calves each year.

Projections were continued for 1500 years or until there were not enough older females (\geq age 12) or calves in the population to continue the assumed levels of mortality. We considered the population to be quasi-extinct when assumed mortality levels could no longer be maintained.

For each combination of harvest and haulout-related mortality levels, we categorized the long-term dynamics based on whether they eventually resulted in either an increasing, stationary, or decreasing total population size. Stationary dynamics included stable or dampening oscillations around a constant value. A plot of the categorized points indicated that boundaries between combinations of mortality levels resulting in different dynamic categories were nearly linear. We characterized these boundaries by fitting least-squares regression lines to the boundary points.

Analytical sensitivities

Standard results from matrix theory (e.g., Caswell 2001) are not directly applicable to our full projection model with density-dependent reproductive rates and absolute levels of mortality. However, insight may be gained by considering theoretical results for a simpler model with constant demographic rates. We considered a base model with the same constant natural mortality rates assumed by our full model, no harvest or additional calf mortality, and constant reproductive rates set at the minimum values from our full model. We did not consider higher reproductive rates because they would not be consistent with asymptotic dynamics at the base mortality rates. We calculated the asymptotic population growth rate (λ) for the base model as

the dominant eigenvalue of the associated projection matrix

$$\begin{pmatrix} s_0m_1 & s_1m_2 & \cdots & s_{35}m_{36} & 0 \\ s_0 & 0 & \cdots & 0 & 0 \\ 0 & s_1 & \cdots & 0 & 0 \\ \vdots & \vdots & \cdots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{35} & 0 \end{pmatrix}$$

where we have dropped the reference to year because all rates are constant. We calculated the sensitivity of the asymptotic growth rate to each age-specific survival rate as

$$\frac{\partial \lambda}{\partial s_i} = \frac{v_{i+1}w_i + v_1w_im_i}{\mathbf{v}^T \mathbf{w}}$$

where \mathbf{w} is the right eigenvector (with elements w_i giving the stable age distribution) and \mathbf{v} is the left eigenvector (with elements v_i giving the reproductive values) associated with λ , and T indicates transpose (Caswell 2001).

Results

From 1990 to 2008, female harvest-related mortality ranged from 1,207 to 3,671 walruses per year (mean = 2,179, SE = 146). Seventy-five percent of this mortality was associated with the U.S. harvest (Fig. 3). Most (69 %) of the harvest-related female mortality was for individuals ≥ 12 years old (full body size), but 19 % of this mortality was for 6–11-year-olds (sexually mature but not full size), 1 % was for 1–5-year-olds, and 11 % was for calves (Fig. 4).

Our projections indicated that if the assumptions about demographic parameters remained constant, then at levels of harvest that occurred during 1990–2008, the population would have continued to grow during that period (Fig. 2).

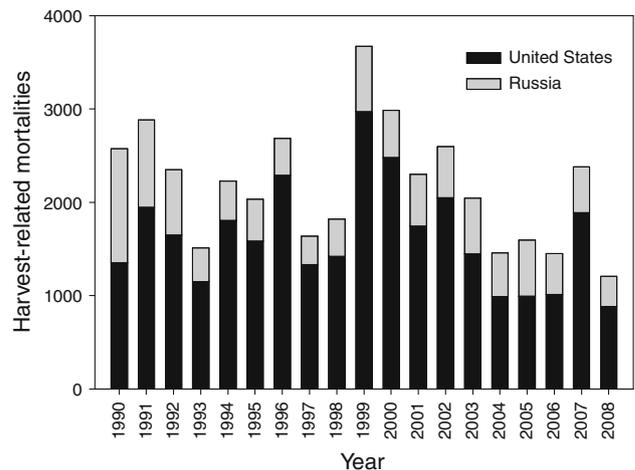


Fig. 3 Total number of female walrus mortalities associated with harvests in the United States and Russia, 1990–2008

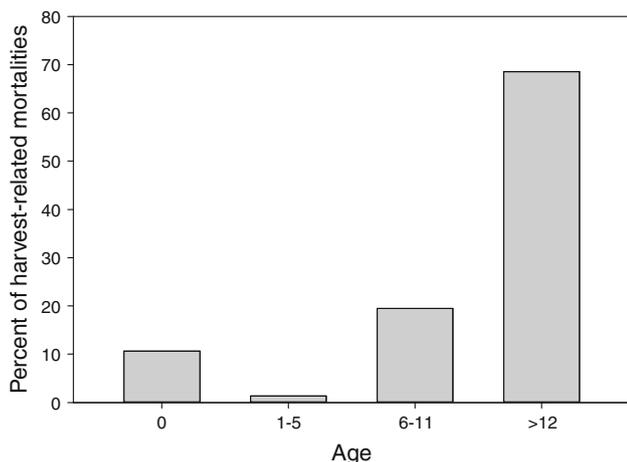


Fig. 4 Age distribution of female walrus mortalities associated with combined harvests in the United States and Russia, 1990–2008

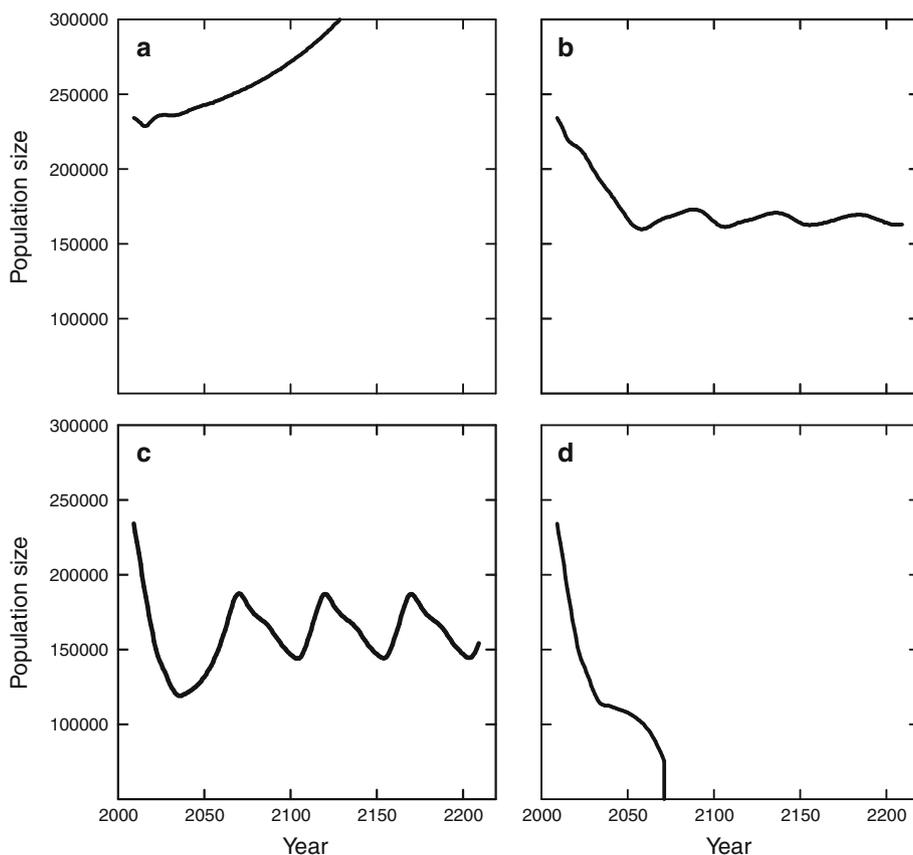
Our estimates of total female population size were 193,000 in 1990 and 234,000 in 2009, resulting in an average annual population growth rate of 1.010 for those 19 years.

Depending on assumptions about mortality rates beyond 2009, the population could either continue to grow, stabilize around a constant value via dampening or non-dampening oscillations, or decline to eventual extinction (Fig. 5). Oscillating dynamics occurred when mortality

rates were at intermediate levels—low enough to allow a decline in population size to be turned around by the associated increase in reproductive rates, but high enough to cause the population to decline again as the density-dependent reproductive rates went back down.

The population continued to grow if the sum of harvest-related mortalities and $1.1 \times$ additional calf mortalities was $<2,900$ per year, so the population would continue to grow if, for example, harvest was less than 2,900 females per year with no additional calf mortality or with an additional mortality of less than 2,600 calves and no harvest (Fig. 6). The population declined to extinction if the sum of harvest-related mortalities and $1.6 \times$ additional calf mortalities was $>8,400$ per year, so the population would decline to quasi-extinction if, for example, harvest was more than 8,400 females per year with no additional calf mortality or with an additional calf mortality of more than about 5,300 female calves per year and no harvest (Fig. 6). At these harvest and calf mortality rates, the population became quasi-extinct during the years between 2025 and 2133 (i.e., 16–124 years after 2009). For mortality rates that did not result in continued growth or eventual extinction, the population always initially declined, but then eventually either converged to or oscillated around a value of between 135,000 and 169,000 total females. The minimum population size reached during the initial decline before

Fig. 5 Examples of the four basic categories of population dynamics for female Pacific walrus resulting from various levels of additional annual mortality. Examples illustrate increasing (a), stationary (b, c), and decreasing (d) population trajectories. Stationary trajectories include dampening (b) and stable (c) oscillations



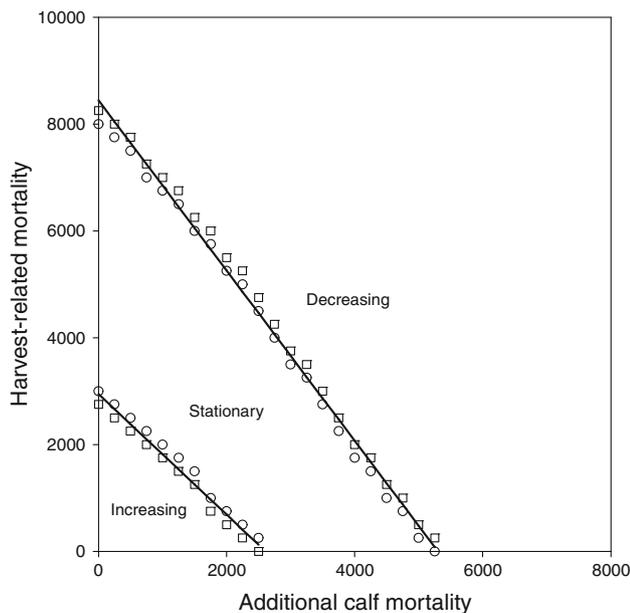


Fig. 6 Types of long-term population dynamics projected for female Pacific walrus subject to different annual levels of harvest-related and additional calf mortality. The boundary between increasing and stationary populations is given by $y = 2,900 - 1.1x$ ($R^2 = 0.98$), where y is total harvest-related mortality, and x is additional calf mortality. The boundary between stationary and decreasing populations is given by $y = 8,400 - 1.6x$ ($R^2 = 0.99$). Circles indicate boundary points for the stationary region. Squares indicate boundary points for the decreasing and increasing regions

trajectories stabilized ranged from 89,000 to 168,000 total females.

For a given level of total mortality, additional calf mortality had a greater effect on population dynamics than harvest-related mortality (Fig. 6). Harvest mortality had to be increased 1.1 times the required increase in additional calf mortality to cause a growing population to become stationary. Harvest mortality had to be increased 1.6 times the required increase in additional calf mortality to cause a stationary population to decline.

The asymptotic population growth rate was 1.014 for the non-density-dependent base model with only natural mortality and minimum reproductive rates. Sensitivity of population growth rate to survival was a non-increasing function of age, with sensitivities strictly and rapidly declining for ages >6 , until becoming negligible at age 30 (Fig. 7).

Discussion

Subsistence and commercial harvests have been assumed to be the primary mortality factor affecting the Pacific walrus population (Fay 1982; Fay et al. 1989). Our work represents the first attempt to quantify the potential effect

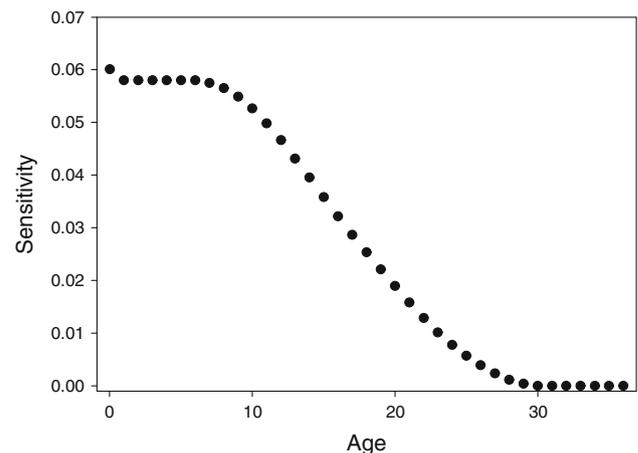


Fig. 7 Sensitivities of asymptotic population growth rate to age-specific survival rates in a base model of female Pacific walrus population dynamics with only natural mortality and minimum reproductive rates

of increased haulout-related mortality relative to harvest-related mortality. In terms of demography, the important difference between harvest and haulout-related mortality is age structure. Our analysis essentially considers the effect of concentrating a higher proportion of the mortality in the youngest age class. Projections from the full density-dependent model indicated that an increase in haulout-related mortality affecting only calves would have a greater effect on the population than an equivalent increase in harvest-related mortality distributed among all age classes. This is consistent with the pattern of age-specific sensitivities calculated for the base model with constant demographic rates (Fig. 7). Sensitivity of population growth rate to survival is lowest for the oldest age classes. Harvest affects all age classes, but mostly ages >1 , with 68 % of harvest-related mortality affecting ages >11 (Fig. 4). Thus, the largest portion of harvest-related mortality is focused on the age classes with the lowest sensitivities. Calves, on the other hand, are the age class with the highest sensitivity, so mortality focusing on this age class will have a relatively larger effect on population dynamics.

This may seem contrary to the common observation that, for long-lived vertebrates, changes in adult survival rates have larger effects on the population than changes in juvenile survival rates (e.g., Eberhardt 2002). Survival rates of adults tend to be more important in these cases because populations of long-lived species are comprised mostly of adults, so changes in adult survival rates affect more year-classes and more individuals than do changes in juvenile rates. Survival rates of individual year-classes of adults, however, are not necessarily more important than individual year-classes of juveniles (Caswell 2001). Moreover, our study considers the effect of taking a fixed number of individuals from the population each year,

resulting in smaller changes in survival rates when that number is distributed among a larger portion of the population.

Although we did not specifically consider the potential effect of increased haulout-related mortality of yearlings, they also are relatively small in size and are susceptible to trampling during disturbance events at coastal haulouts (Kochnev et al. 2008; Fischbach et al. 2009; Kochnev 2010). Yearlings comprise a smaller portion of the harvest than calves (Fig. 4) and sensitivity of population growth rate to their survival is almost as high as that for calves (Fig. 7). Thus, we would expect increased haulout-related mortality for yearlings to also have a relatively large effect on overall population dynamics.

Asymptotic dynamics of the base model with constant demographic rates are essentially the same as the long-term dynamics of the full density-dependent model in cases where the population continued to grow because, in these cases, the reproductive rates remained constant at their minimum values. The long-term dynamics are identical in the case with no harvest and no haulout-related mortality. In the other cases, the levels of harvest and haulout-related mortality we considered eventually become negligible as the population continues to grow. Thus, the asymptotic growth rate of 1.0143 analytically determined for the base model is also the long-term growth rate projected by the density-dependent model in all of the cases where the population continued to grow. Maximum short-term growth rates projected by the density-dependent model are greater and occurred when population sizes were low enough for reproductive rates to be at their maximum levels.

Our long-term projections are theoretical because it is unlikely that demographic parameters have remained constant since Fay et al. (1997) completed their analysis, and these parameters will likely continue to change in direct or indirect response to changes in climate and sea ice availability, as well as other factors. This is particularly true of the cases projecting continued population growth because it would not be possible for the population to grow without limit. In cases where the population continued to grow, demographic rates were held constant, with reproductive rates set at values that were estimated from data associated with conditions during 1979–1985 (Fay et al. 1997). As the projected population continued to increase, however, it quickly reached levels well beyond the level associated with conditions in 1979–1985, and it is unreasonable to assume demographic rates would remain constant as the population continued to increase much beyond that level.

Mortality rates at coastal haulout sites are poorly known and difficult to quantify or predict. Coastal haulouts occur in remote geographic locations, and there are no systematic

range-wide surveillance programs to quantify haulout mortality. Even where surveys are possible, it is difficult to count carcasses while the haulout is active and often storm surges disband the herd and remove the carcasses before they can be counted. Nevertheless, it is apparent that there is considerable inter-annual variation in the mortality associated with use of coastal haulouts. For example, in 2007, sea ice receded far beyond the continental shelf break and large herds of walrus occupied coastal haulouts in Chukotka and Alaska for a period of several months (Garlich-Miller et al. 2011). Russian investigators estimated that 3,000–10,000 animals died at these haulouts from trampling during disturbance events (WWF 2010). In 2008, scattered areas of sea ice persisted over the continental shelf, fewer walrus used coastal haulouts, and associated mortality was low (Garlich-Miller et al. 2011).

Factors thought to influence the susceptibility to trampling-related mortality include herd size and demographics, weather, spatial and geomorphic characteristics of the haulout, how long animals have been out of the water, and disturbance (Nikulin 1941; Salter 1979; Miller 1982). Future mortality rates at coastal haulouts are likely to be influenced by the efficacy of efforts to minimize disturbance. Some of the largest coastal haulouts in Chukotka have formed in close proximity to villages. Several communities have developed local management programs to help reduce disturbance-related mortalities at the haulouts. These efforts have been quite successful and although some disturbances and mortalities are likely unavoidable; the number of mortalities has been considerably reduced in just a few years (WWF 2010). Minimizing disturbances at haulouts along the Arctic coast of Alaska has also become a priority, and Alaskan communities are working with managers to protect walrus when they are on shore (Garlich-Miller 2012).

Other sources of mortality, in addition to trampling, may be associated with increased use of coastal haulouts and some of these may affect walrus of all ages. Prey availability near haulouts may be low because the haulouts are in less productive areas or because local prey is depleted by walrus using the haulouts so that walrus may have to travel greater distances to forage with less time to rest between trips (Jay et al. 2011). Increased duration of use of the haulouts may result in greater accumulation of waste products, increasing the potential for spreading diseases and parasites (Burek et al. 2008). Coastal haulouts also allow contact with terrestrial and domestic animals and their waste products, further increasing the potential for transmission of new diseases.

This study quantifies potential population dynamics and relative impacts of harvest and haulout-related mortality implied by the most widely accepted assumptions regarding Pacific walrus demographic parameters. Our analysis

suggests that disturbance-related mortality of calves at coastal haulouts may have relatively important population consequences. Future research should focus on estimating demographic parameters under more recent conditions, incorporating other factors that may affect demographic rates, and quantifying uncertainty in the model. This might be accomplished by embedding the model in a Bayesian framework like that used by Witting and Born (2005) for Atlantic walrus, incorporating all available data.

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