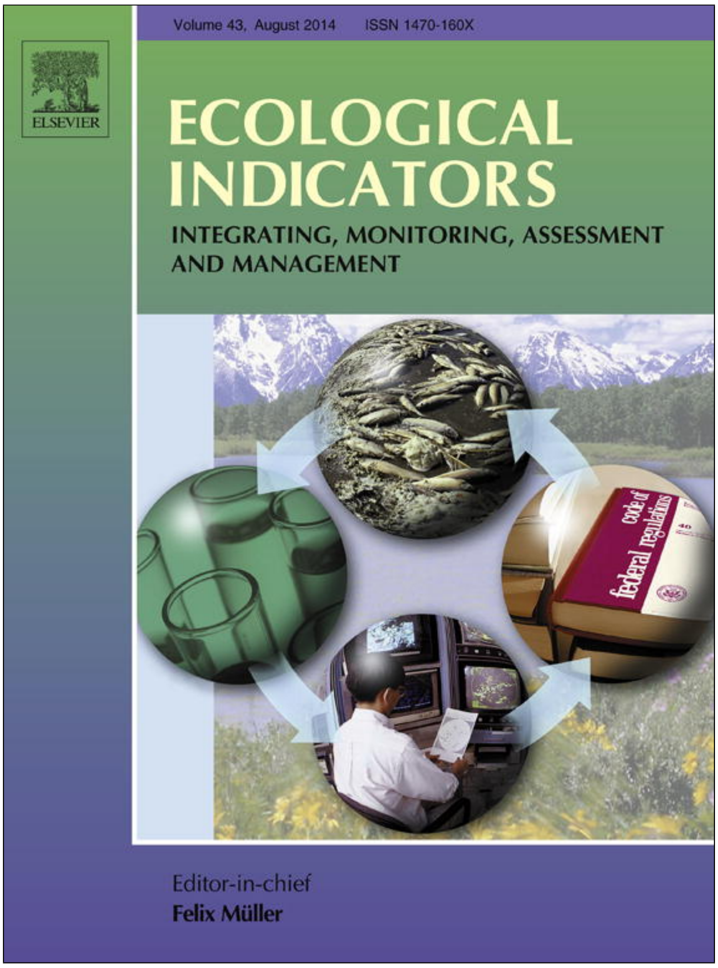
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An index of optimum sustainable population for the Pacific Walrus

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ABSTRACT

The United States Marine Mammal Protection Act of 1972 (MMPA) specified that marine mammal stocks be maintained at an optimum sustainable population level (OSP). However, the information needed to directly estimate OSP for most stocks was not available and indices to OSP were soon proposed but to our knowledge none were fully developed. In 1994, a new management regime was adopted under the MMPA, potential biological removal (PBR), which was specifically developed to assess marine mammal mortalities associated with commercial fisheries. Pacific walruses (*Odobenus rosmarus divergens*) are rarely killed in commercial fisheries, the greatest source of human caused mortality is the subsistence harvest by Alaskan and Russian natives, and PBR estimates have been erroneously used to make inference about the sustainability of the subsistence harvest. It is clear that an index to OSP is needed for the Pacific walrus because PBR as calculated for fisheries is not appropriate. In this study, we explored calf:cow ratios (CCR), estimated from spring harvest data, as an index to population abundance and OSP as a function of habitat carrying capacity (K). Eight of the 10 characteristics of an effective index are applicable to CCRs. Based on abundance estimates when the Pacific walrus population was at or near K and a simulated estimate of maximum net productivity, CCRs of 0.41–0.47 reflect a Pacific walrus population at OSP. The best use of the CCR index will be to inform subsistence hunters of the status of the population and to promote self-regulation of the harvest by hunters. However, because other factors which may be weakly density-dependent such as disease and physical trauma could effect CCRs and the same CCR can be expressed by a declining or increasing population, the index will need to be combined with other information (e.g., habitat change and use patterns, population trend, physical condition of individuals, survival rates, etc.) in a weight of evidence approach in order to have stronger inference. Furthermore, our analyses are based on a data set that included periods when climatic conditions differed from those of recent decades, requiring evaluation of the index into the future.

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1. Introduction

The United States Marine Mammal Protection Act (MMPA) of 1972 (16 U.S.C. 1361), as amended, has the broad goal of maintaining the health and stability of ecosystems that support marine mammals by (1) maintaining marine mammal stocks as significant functioning elements of those ecosystems and (2) not permitting those stocks to diminish below their optimum sustainable population (OSP) levels (MMPA §(2)). Following passage of the MMPA a number of papers were written concerning interpretation and estimation of OSP (Botkin and Sobel 1977; Eberhardt 1977; Eberhardt and Siniff 1977; Gerrodette and DeMaster 1990; Barlow et al., 1995; Wade 1998; Taylor et al., 2000; Robards et al., 2009). The main issues in determining OSP are whether or not the population is regulated by density-dependent mechanisms (Eberhardt 1977) and what fraction of carrying capacity (K) to use in defining OSP. Data on three variables are necessary to estimate OSP directly (1) size of the population, (2) K, and (3) the maximum net productivity level (MNPL) of the population as a function of K (Gerrodette and DeMaster 1990). For most marine mammal populations, accurate estimates of these three variables are not available (Taylor et al., 2000).

Gerrodette and DeMaster (1990) described two methods to estimate population size relative to K; back calculation and dynamic response analysis. Back calculation assumes that the population size prior to human exploitation would be at or near K and then uses estimates of demographic parameters and harvest levels to reconstruct population trends back to that point in time. Unfortunately, this also requires information that is generally

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not available for marine mammals (population size, vital rates, and harvest estimates). The dynamic response method estimates other parameters (i.e., indices) that are related to population status relative to *K* and MNPL. Many of these parameters are relatively easily measured, but require an understanding of the relationship between the index and population status. Furthermore, it is unlikely that an index can stand alone (Caughley 1974; McCullough 1994) and it may need to be combined in a weight of evidence approach (Robards et al., 2009) with other metrics such as body condition, population trend, habitat characteristics, etc.

Because estimating OSP was not possible for most marine mammals, a human-caused mortality limit for marine mammal populations was set that would be more practical and the concept of potential biological removal (PBR) was developed (Wade 1998). The PBR model is a very conservative approach designed to eliminate marine mammal mortalities associated with commercial fisheries (MMPA §118(f)(8)). Although the MMPA is clear that PBR is intended for fishery-related mortalities, the PBR estimate is often incorrectly compared to subsistence harvest levels of Pacific walruses (*Odobenus rosmarus divergens*) (Robards et al., 2009; Marine Mammal Commission 2012). Because the annual harvest often exceeds the PBR estimate (USFWS (United States Fish and Wildlife Service), 2013), some may view the harvest as unsustainable. However, PBR is not well suited to the Pacific walrus population because: (1) fisheries-related mortalities are minor (0–3/year; USFWS, 2013), (2) a reliable estimate of the minimum population size, a key parameter in PBR estimation is unavailable, and (3) management options are limited because the subsistence harvest is exempt from most of the provisions of the MMPA. Thus, PBR has little to no practical application with respect to managing walruses at a sustainable population level and furthermore, the MMPA (§ 119) specifies that harvest management is to be addressed through co-management programs.

The data needed to directly estimate OSP for walruses are not available, but development of an index to OSP is possible. If a reliable index can be developed, a more appropriate management regime could be established. Eberhardt and Siniff (1977) identified 12 variables within four broader categories (behavioral, body condition, reproductive rates, and demographics or habitat measures) that have potential as an index to OSP for marine mammals in general. In addition, Eberhardt (1977) described a likely sequence of changes in vital rates as populations approached *K*, starting with a decline in juvenile survival, followed by an increase in age at first reproduction (AFR), then a decline in adult female reproductive rates, and finally a decline in adult survival, noting that changes in reproductive rates were the most sensitive. Through simulations, Chivers (1999) found that birth rates of Pacific walruses declined as population abundance approached *K*; consistent with the assumptions of density-dependence.

It is generally believed that the Pacific walrus population was held below *K* prior to 1960 due to hunting. Hunting restrictions imposed from 1960 to 1979 resulted in the population reaching *K* between 1975 and 1985, when a decline in the reproductive rate occurred, as would be expected under the influence of density-dependence. When hunting quotas were lifted in 1980 the population again dropped below *K* by 1990 (Fay et al., 1989; Fay et al., 1997; Garlich-Miller et al., 2006).

One of the most comprehensive databases available for Pacific walruses comes from harvest monitoring (Garlich-Miller et al., 2011). Three reproductive performance measures are potentially available from these data including pregnancy rates, AFR (Fay et al., 1997; Garlich-Miller et al., 2006), and calf:cow ratios (CCR). Fay et al. (1989) and Garlich-Miller et al. (2006) found that trends in AFR estimated from the examination of walrus reproductive tracts were consistent with the historic changes in population size, but pregnancy rates were not consistent with those changes, most likely due to the selection of older females with larger tusks by hunters (Garlich-Miller et al., 2006).

Although female reproductive tracts accompanied by reliable age data can provide good estimates of AFR, the correct parts and the required data are not always provided (Alaska Department of Fish and Game, undated), and the tracts are large, difficult to handle, and store. Examination of uteruses and ovaries is time consuming and requires substantial expertise and training. Furthermore, AFR estimates for walruses based on hunter collected samples may be inaccurate due to the underrepresentation of younger females in the harvest (Chivers 1999). Because of these issues, we examined the utility of CCRs derived from annual enumeration of harvested animals as an index to abundance and OSP as a function of *K*. Calf:cow ratios have long been used as a measure of productivity in ungulates (Harris et al., 2007) and some marine mammals (Kenyon et al., 1954; Carrick et al., 1962; Garrott et al., 2012), are reflective of population status relative to *K* (Picton 1984; Harrington et al., 1999; Lubow et al., 2002), and were identified by Fay and Kelly (1989), Robards et al. (2009), and Citta et al. (2013) as a potential useful metric for determining the status of the Pacific walrus population.

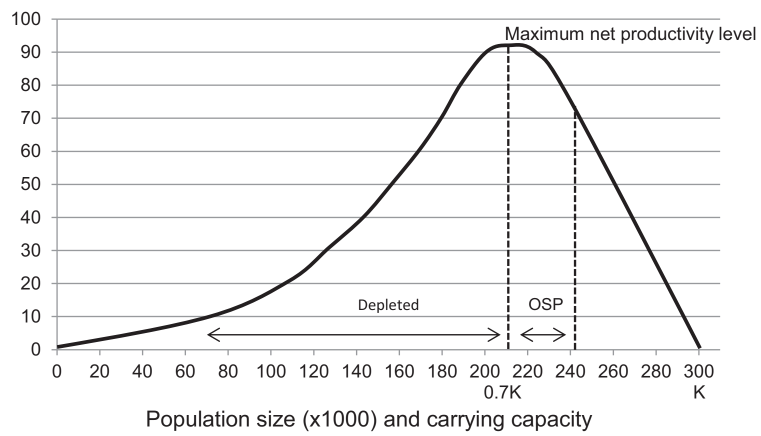

Fig. 1. Theoretical relationships among population size, habitat carrying capacity (*K*), net productivity of the population, and the classification of populations as depleted and at an optimal sustainable population (OSP) level under the Marine Mammal Protection Act as applied to the Pacific walrus (*Odobenus rosmarus divergens*) population.

2. Methods

To define OSP a lower and upper bound need to be established. The National Marine Fisheries Service and U.S. Fish and Wildlife Service (50 C.F.R. § 216.3) suggested that the lower bound occurs when the population is at MNPL and the upper bound occurs at *K*. However, different MNPLs have been proposed. Eberhardt and Siniff (1977) suggested that MNPL is greater than 0.5 K, the theoretical expectation, and Barlow et al. (1995) used 0.6 K as MNPL. Wade (1998) modeled three density-dependent net productivity curves resulting in MNPLs ranging from 0.45 to 0.70 K.

The upper bound of OSP has been defined as *K* (50 C.F.R. § 216.3) even though net productivity typically declines before populations reach *K* (Eberhardt 1977). We used a more biologically realistic estimate for the upper bound of OSP as a fraction of *K*. Wade's (1998), Fig. 1) simulations indicate that a 20% decrease in MNPL occurs at 0.55, 0.7, and 0.8 K, depending on whether the relationship has positive skew, is linear, or has a negative skew, respectively. In this paper we use MNPL (as a fraction of *K*) as the lower bound and 0.8 K as the upper bound (Fig. 1).

We used the annual cumulative total of adult females and calves harvested to provide an estimate of the CCR for each year. The U.S. Fish and Wildlife Service (USFWS), maintains a Pacific walrus harvest database that includes a time series of CCR estimates from 1960-present (Garlich-Miller et al., 2011). Early data collection was administered by the Alaska Department of Fish and Game and more recent efforts by the USFWS (Garlich-Miller et al., 2006). These data included the number of males, females, and calves harvested during April–June in the villages of Gambell, Savoonga, and Diomede in the Bering Strait region of Alaska. Monitors meet hunters on the beach as they return from hunting trips and record the number of adult males, females, and calves in each boat. The accuracy of this method is dependent of the ability of observers and hunters to identify adults by sex and calves by age (sex of the calves is not necessary); we assume that both hunter and field crew identification is very accurate for adult females and calves. Since 2002, the harvest has continued to be monitored with the sex and age of the harvest recorded (Garlich-Miller et al., 2011). No data were available for 1990 and 1991.

To be useful, an index of OSP should meet a variety of conditions and assumptions (Gerrodette and DeMaster 1990) (Table 1). Importantly, Gerrodette and DeMaster (1990) noted that the overriding goal of any index should be to indicate, in a quantifiable way, whether a population is near or far from *K*.

Calf:cow ratios from harvested walruses are easily quantified and trends are readily interpreted based on population regulation theory and simulations of walrus population dynamics (Chivers 1999). Estimates derived from harvest data are biased, but the primary component of that bias, hunter preference, is likely constant (Garlich-Miller et al., 2006). Eberhardt's (1977) analysis indicated that changes in CCRs should be more detectable than indices based on population demographics.

The relationship between CCRs and population size should be inverse, consistent, and strongly correlated if CCRs are to be a useful index to OSP. To assess this requirement, we plotted CCR and population size estimates from 1960 to 2009 and calculated the rank-order correlation. Population estimates were made infrequently and sporadically between 1960 and 1975 (Fay et al., 1997). Beginning in 1975, population estimates were made at 5-year intervals until 1990 (Udevitz et al., 2001). The next available estimate was in 2006, which is known to be biased low but the magnitude of that bias is not known (Speckman et al., 2011). Thus, at least one estimate is available for each decade from 1960 to 2009. To estimate the correlation and graph the relationship, we averaged both population size and CCR estimates for each decade from 1960 to 2009 ($n = 5$).

To define OSP with CCRs, and by extension define CCR values around MNPL, we needed an estimate of population size at *K* (N_K), an estimate of population size at MNPL (N_{mnpl}), an estimate of population size at the point where density-dependent mechanisms reduce the net productivity level ($N_{<K}$), and a model that predicts CCRs at the N_is listed above. Fay et al. (1997) estimated the Pacific walrus population to be 290,700–310,700 when it was at *K* in 1975–1985, therefore we used an N_k of 300,000 in our analyses. Through simulation, Chivers (1999) estimated MNPL for Pacific

Table 1
Twelve criteria proposed by Eberhardt and Siniff (1977) that may be useful in estimating the status of a marine mammal population relative to the carrying capacity of the habitats and the applicability and feasibility of those criteria to Pacific walruses (*Odobenus rosmarus divergens*).

Criteria	Applicability	Monitoring feasibility and needs
Behavioral attributes		
Antagonistic/displacement behavior	Not likely, highly gregarious species	Highly feasible.
Activity budgets	Likely	Highly feasible, requires development of methods.
Diet changes	Likely	Feasible but samples limited to harvested animals, need food quality estimates, and finer taxonomic resolution of prey.
Individual responses		
Body condition (energy stores)	Highly applicable	Highly feasible, need to calibrate current metrics (blubber thickness, % fat in blubber).
Growth rates	Highly applicable	Not feasible to repeatedly capture and measure individuals.
Incidence of disease/parasitism	Unknown	Highly feasible, samples limited to harvested animals.
Reproductive characteristics		
Age of females at 1st reproduction	Highly applicable	Highly feasible, samples limited to harvested animals, biased due to few young adults in harvest, requires examination of reproductive tracts.
Reproductive rates of females	Highly applicable	Highly feasible, samples limited to harvested animals, biased due to age structure of harvest, requires examination of reproductive tracts for some measures.
Population aspects		
Age structure	Highly applicable	Highly feasible, current methods need calibration.
Survival of young	Highly applicable	Feasible, methods need development and calibration.
Occupancy of marginal rage	Unknown	Feasible, marginal range undefined,methods need development.
Rate of change in population size	Unknown	Feasible, requires more precise population estimates.
Effects on habitat/prey	Unknown/highly applicable	Questionable/not feasible, prey estimates likely too sparse and imprecise.

walruses at 0.66 K, resulting an N_{mnpl} = 198,000 used here. Because Chivers' (1999) MNPL estimate suggests a positive skew, we used Wade's (1998, Fig. 1) positive skewed relationship to estimate the fraction of *K* where a 20% decline in net productivity occurred, or 0.8 K. This resulted in $N_{<K}$ = 240,000. To predict CCRs at N_{mnpl} and $N_{<K}$, the lower and upper bounds of OSP respectively, we conducted a linear regression analysis with CCR estimates as the response variable (*y*) and population size as the explanatory variable (*x*) from the 1960–2009 data set. Due to the several orders of magnitude difference in the two data types, the data were standardized as calves/1000 cows and *N*/1000. We averaged both population and CCR estimates for each decade from 1960 to 2009 and used SYSTAT v.13 to estimate the regression equation with the least squares method.

A desirable characteristic when using an index is a small variance (Gerrodette and DeMaster 1990). No within year estimates of precision can be calculated, but year to year variation was moderate (Fig. 2, coefficient of variation [SD/mean = 0.67). To reduce the annual variation in CCR estimates we used a 5-year moving average. In addition, a 5-year moving average is likely more reflective of the population dynamics of Pacific walruses given their long reproductive life span, low reproductive rates, and high survival (Fay 1982).

To effectively track changes in CCRs, the rate of change should be greatest around MNPL (Gerrodette and DeMaster 1990). To assess this we calculated the absolute percent change in CCRs from one year to the next, calculated the 5-year moving average of the absolute percent change for the time series, and then calculated the mean of those 5-year moving average estimates for the 10 years bracketing three time periods; (1) when the population was at MNPL when it was increasing, (2) when the population was at MNPL when it declined, and (3) when the population was furthest from *K* at either end of the time series. We compared the mean rate of change for each of the three time periods with a Kruskall–Wallis one-way ANOVA followed by the Conover–Iman method for pairwise comparisons (Table 2).

3. Results

The trend in CCRs for 1960–2009 is consistent with theoretical expectations of density-dependent demographics (i.e., CCRs were highest when the population was below *K* and lowest when it was at *K* (Fig. 2)). The quadratic polynomial regression as presented in Fig. 2 fits the data better (Akaike's Information Criteria (AIC_c) = −29.4) than either a linear model (AIC_c = −11.8), or cubic polynomial (AIC_c = −28.2). The relationship between the size of the Pacific walrus population and CCRs from harvest data is inverse and strongly correlated (Fig. 3, r_s = − 0.91). The regression equation relating CCRs to population size is CCR = 743.7–1.4(SE = 0.4)**N* (R^2 = 0.76, *P* = 0.03). Calf:cow ratios that correspond to OSP based on our calculations ranged from 408 to 466 calves/1000 cows (or 0.41–0.47) and the population was at OSP from about 1972 to 1979 when it was increasing and again from 1993 to 1999 as it declined (Fig. 4). A CCR of 0.47 is indicative of MNPL which occurred in 1972 and 1999.

Applying a 5-year moving average to the CCR time series reduced the coefficient of variation 10-fold from 0.67 (Fig. 2) to 0.06 (Fig. 4). This made the trend more visible without effecting the time periods when the walrus population was at OSP or not at OSP.

The mean annual rate of change in CCR estimates was about 54% greater (*P* = 0.003) when the population was near MNPL and increasing than when it was near MNPL and deceasing or far from MNPL (Table 3). Rate of change estimates were nearly identical when the population was declining and at MNPL or far from MNPL.

4. Discussion

Both the strong negative correlation between CCRs and population size, and the trend in CCRs are consistent with density-dependent population responses. The trend in CCRs derived from harvest records from 1960 to 2009 are consistent with the historic trends in the walrus population (Fay 1982; Sease 1986; Fay et al., 1989; Fay et al., 1997; Garlich-Miller et al., 2006) and illustrate the utility of CCRs as an index of OSP (Fig. 4). In addition, the ease of estimating CCRs, their interpretability, and the fact that they possess many of the other desirable characteristics identified by Gerrodette and DeMaster (1990) provide additional support for using CCR estimates as an index of OSP. Given the potential complications associated with the collection and handling of reproductive tracts and the effort needed to estimate AFR, CCR estimates as quantified from spring harvest records are a viable alternative.

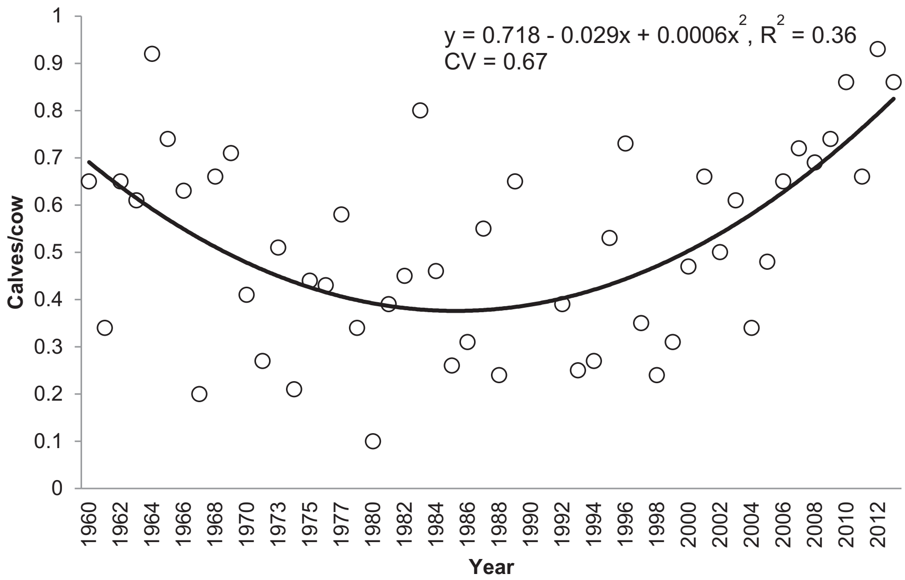

Fig. 2. Trend in calf:cow ratios for Pacific walruses (*Odobenus rosmarus divergens)* estimated from harvest data collected from the native villages of Gambell, Savoonga, and Diomede, Alaska from 1960 to 2013. The trend line is based on the least squares regression at the top of the plot. CV is the coefficient of variation (standard deviation/mean).

Table 2
Desired characteristics of a useful measure of the optimum sustainable population (OSP) for marine mammals (from Gerrodette and DeMaster 1990), as applied to calf:cow ratios of Pacific walruses (*Odobenus rosmarus divergens*) estimated from harvest data in terms of whether the metric has been assessed and the method of assessment.

Desirable characteristic	Assessed	Assessment methods
Easily measured	Yes	Field studies (Fay and Kelly 1989; Citta et al., 2013), this study
Readily interpretable	Yes	Population regulation theory
Unbiased or constant bias	Partially	Qualitatively (Garlich-Miller et al., 2006)
Defined in terms of OSP quantitatively	Yes	Regression, this study
Consistent relationship to population size	Yes	Simulation (Fay et al., 1977; Chivers 1999), correlation this study
Small variance	Yes	Coefficient of variation, smoothing, this study
Uninfluenced by other conditions	No	Field studies of disease, predation, accidents, etc.
Changes are easily detectable	Yes	Simulation (Eberhardt and Siniff 1977), this study
Rate of change greatest near MNPL[a]	Yes	Annual percent change, this study
Values above and below MNPL known	Yes	Regression, this study

[a] Maximum net productivity level.

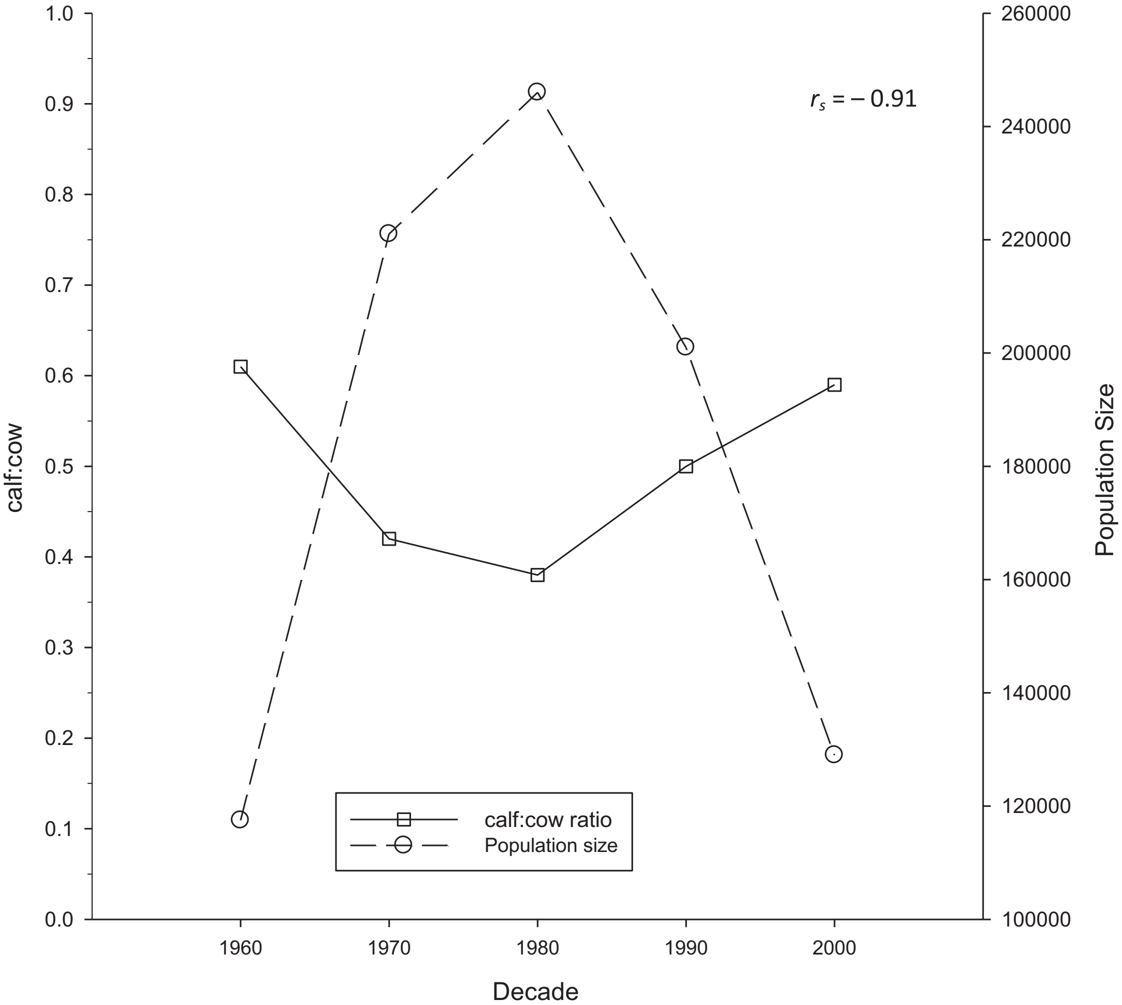

Fig. 3. Trends in mean calf:cow ratios from harvest data and population size from aerial surveys for the Pacific walrus (*Odobenus rosmarus divergens*) averaged by decade from 1960 to 2010. The 2006 population estimate is known to be biased low, but the magnitude of the bias is unknown and there is no consensus on how to correct the estimate.

The efficacy of our analyses hinges on two important assumptions: (1) the population was at *K* from 1975 to 1985, and (2) the population was about 300,000 at that time. As previously noted there are several lines of evidence supporting the first assumption (Fay et al., 1997; Garlich-Miller et al., 2006; MacCracken 2012). Unfortunately, walrus population estimates are imprecise (Hills and Gilbert 1994; Udevitz et al., 2001; Speckman et al., 2011) creating uncertainty in their application and interpretation. For example, the 2006 estimate of 129,000 is known to be biased low and adjustments to that figure (e.g., applying the density of walruses in the surveyed area to the area of suitable habitat not surveyed) could increase the estimate to 200,000+ which would significantly alter the relationship between *N* and CCRs. However, there is currently no consensus among walrus researchers and managers on the most appropriate method to adjust the 2006 estimate (MacCracken, pers. observ.)

The annual variation in CCRs was substantially reduced by calculating a moving average, a common technique with time series

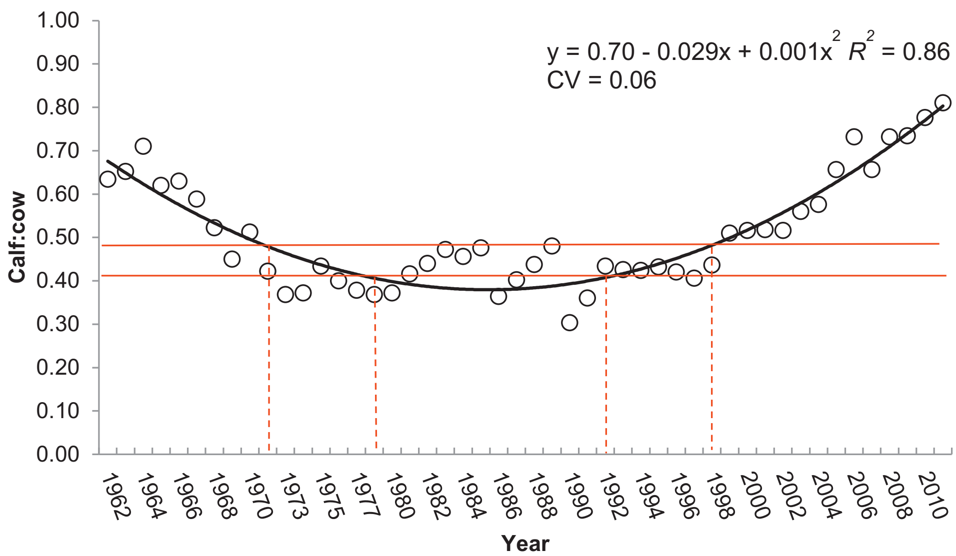

Fig. 4. Trend in calf:cow ratios (CCR), 5-year moving average, of Pacific walruses (*Odobenus rosmarus divergens*) estimated from harvest data collected from the native villages of Gambell, Savoonga, and Diomede Alaska from 1960 to 2013. The black trend line is based on the least squares regression at the top of the plot. CV is the coefficient of variation (standard deviation/mean). Red horizontal lines are the estimated range of the optimum sustainable population (OSP) as indexed by CCRs. Red vertical dashed lines bound the years the population was at OSP during the time series (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

Table 3
Mean(SE) absolute percent change between subsequent years in calf:cow ratios of the Pacific walrus (*Odobenus rosmarus divergens*) estimated from harvest data for 3 periods based on population trend relative to maximum net productivity level (MNPL). Estimates followed by the same letter are significantly different (Kruskal–Wallis test, $P = 0.003$).

Period	Percent change
Population at MNPL and increasing	63(4)[a,b]
Population at MNPL and decreasing	41(2)[a]
Population far from MNPL, either trend	40(5)[b]

data (Chatfield 2004). However, a drawback to this approach is end-effects, in this case the loss of two data points on either end of the time series. This is not a problem with the retrospective analysis presented here, but it does result in a 2-year time lag in detecting a future change. However, the lack of differences in the periods when the population was within OSP between the raw and smoothed data and the delayed population response to a management action lessens this concern and also suggests that reducing variance may not be that important.

The annual rate of change in CCRs was 54–58% greater when the walrus population was near MNPL and increasing compared to when the population was near MNPL but declining. This suggests that the annual rate of change in CCRs could indicate population trend. There are two major factors influencing the rate of change in CCRs: (1) variation in female productivity and (2) variation in harvest patterns. Productivity as measured by CCRs when the population was increasing toward *K* may be more variable due to competition for food among adult females resulting in reduced pregnancy rates, aggressive interactions resulting in trauma and abortions, low survival of fetuses and newborns, etc.

The observed population trends were primarily the result of changes in hunting regulations and it is not clear how the regulations influenced the taking of calves. Records indicate that during the initial years when adult female quotas were in effect, calf harvests did not count against the quota (Alaska Department of Fish and Game, undated) and in later years only "orphaned calves" were legal (Hinman 1980) without regard to sex. This change in policy could account for increased variation in CCRs because the orphaned calf provision required hunters to determine calf maternal status which can be difficult when in large groups of walruses. Hunting without restrictions occurred when the population was declining and near MNPL and when it was furthest from MNPL. It is conceivable that hunting pressure at those times could have reduced and equalized the variation in CCRs that we observed.

Biases in harvest data occur from 3 sources: (1) hunter selection for a preferred age and sex, (2) differential vulnerability by age and sex, and (3) regulations dictating which age and sex can be taken. For the Pacific walrus, we know that hunters select for animals with larger tusks and certain villages prefer adult females and calves (Sease 1986; Garlich-Miller et al., 2006; Kochnev 2010). There is little information on differential vulnerability (Sease 1986), but Fay and Kelly (1989) noted that calf:cow pairs may be closer to the ice edge while other demographic groups may be further into the ice. Presumably, there is a tendency for hunters to take animals along the ice edge, rather than travel into the pack ice where navigation is more difficult and shifting floes can be dangerous.

There are currently no regulations governing the composition or amount of harvest of Pacific walruses in the United States, but from 1960 to 1979 the take of females was limited to 5–7/hunter/year. In Russia, there is an annual quota, but no rule regarding age or sex that can be harvested and the quota have not been reached in recent years (Kochnev 2012, pers. comm.). For this analysis, we assumed that biases in the harvest data are constant over time as suggested by Garlich-Miller et al. (2006).

Fay and Kelly (1989) reported CCR estimates for Pacific walruses ranging from 0.02 to 0.27 based on the sex and age composition of live animals visually inspected from ships in late-summer. Several other papers also provide CCR data with estimates of 0.34 (Fay 1982), 0.03–0.15 (Sease 1986; including some of the data of Fay and Kelly (1989)), 0.05–0.44 (Fay et al., 1977; a summary of various data sets), 0.57–0.73 (derived from harvest data compiled by Garlich-Miller et al., 2006; including near-term fetuses in harvested females), 0.04–0.25 (Kochnev 2010; from September to November harvest records), 0.03–0.17 (Citta et al., 2013; summer counts of walruses on sea ice in the 1980s [including those of Fay and Kelly (1989)] and 1990s), and 0.25 for land-based counts (Monson et al., 2013). Most of these estimates are much smaller than our spring harvest records (Fig. 2). This discrepancy is undoubtedly due to hunter-selection bias in the spring but also loss of calves prior to surveys conducted later in the year (Citta et al., 2013). The mean and standard error, in parentheses, of the CCR estimates presented above is 0.28(0.08) and the mean from the 1960–2009 harvest database is 0.49(0.03). Theoretically, the maximum CCR for Pacific walruses for any year would be 0.50 (Garlich-Miller et al., 2006), only 2% larger than the long-term average from hunter harvest records. It is also noteworthy that CCRs indexing OSP are near the theoretical maximum as would be expected if CCRs are reflective of net productivity levels.

Calf:cow ratios can be estimated using other methods than harvest records including direct observations of walruses on the ice or land (Fay and Kelly 1989; Citta et al., 2013) and high-definition aerial photography-videography (Monson et al., 2013). Surveys during and shortly after the spring birthing pulse would be required to reduce potential biases associated with calf mortalities as the summer progressed (Citta et al., 2013). However, if CCRs from sources other than harvest records are to be used as an index to OSP, the relationship between those sources and harvest records will need to be evaluated. On the other hand, CCRs estimated from other methods may stand alone as a measure of productivity and potential recruitment.

Given the uncertainties described above, this exercise is most useful as an example of developing and evaluating a potential index of OSP, using an OSP index, and illustrating the difficulties of managing marine mammal populations for OSP. Populations are likely to fluctuate in and out of OSP no matter how intensive the management program because of the narrow range of OSP and the time lags involved among management actions, population changes, density-dependent responses in vital rates, and potential subsequent adjustments to management programs. For example, using the CCR index over the 1960–2009 time series the population would have been classified as "depleted" (i.e., below OSP) under the MMPA (§ 3) from 1960 to 1973, "at OSP" from 1972 to 1979, above OSP from 1980 to 1992, at OSP from 1993 to 1999, and then depleted from 2000 to 2009. In addition, officially changing the status of the population under the MMPA is a complex legal and political process requiring stakeholder notifications, administrative hearings, rule proposals, public comment, and rule finalization. By the time the process is complete ($\geq$3 years) the population status could change and the process would need to start again to change it back. Such a process further increases the time lag between population change, management actions, subsequent population response, and adaptive management, not to mention the erosion of public confidence. However, by increasing the upper bound of OSP to *K*, the management regime would be less sensitive to the short-term fluctuations in the CCR index and a more stable management regime (at OSP from 1972 to 1999 in this example) would be established avoiding the problems of constantly changing management regulations that cannot keep up with the changes in the index. In addition, the risk of overharvesting by subsistence hunters during this period would be small. Our choice of a 20% deviation from *K* as the upper boundary for OSP is somewhat arbitrary and should be determined by incorporating the level of risk that managers are willing to accept (Taylor et al., 2007).

The most effective way to adjust harvest levels, if needed, is through the co-management process as specified in the MMPA (§ 119), promoting voluntary actions of self-regulation by walrus hunting communities (Robards et al., 2009; MacCracken 2012). The CCR index developed here along with other measures of population status (e.g., habitat characteristics and use, individual physical condition, survival rates, observations of hunters, population trend, etc.) may be best used through a weight of evidence approach as a guide to native hunters informing them when hunting limits are advisable, how long they need to be in place, and when they can be relaxed. In addition, because the same CCR can be expressed when populations are increasing or declining, an independent measure of abundance or status will be needed as part of the weight of evidence approach (Caughley 1974; McCullough 1994) when population trend is uncertain.

Other than density-dependent reproductive processes, factors that could also influence CCRs are predation, disease, parasitism, accidents, malnutrition, trampling due to disturbances, etc. (Garlich-Miller et al., 2011; MacCracken 2012). However, the influence of most of these factors is time-dependent, i.e., the longer the time interval between birthing and CCR estimation, the greater the likelihood of these other factors influencing calf survival. Stressors that could influence CCRs that are not primarily density-dependent, include, among others, diseases or physical trauma that may cause abortions. These factors could reduce CCRs and indicate that the population is at OSP when it is not. Without additional information on population size and trend such a situation would be difficult to recognize, further emphasizing the importance of a weight of evidence approach when using an index to assess population status.

The near 50-year data set that we used to develop the CCR index spans periods of relative climate stability as well as more recent rapid climate changes. Climate changes over the last few decades have resulted in changes in sea-ice habitat dynamics, changes in Pacific walrus distribution, increased use of terrestrial habitats, and lower harvest levels (MacCracken 2012). These changes are predicted to intensify in the future and other stressors such as ocean acidification may come into play (MacCracken et al., 2014). These changes could reduce the efficacy of CCRs as an index to OSP. Theoretically, the relationship between CCRs and *K* should be stable, but changes in sea-ice dynamics and weather that alter hunting opportunities, practices, and success have the greatest potential to influence the CCR index, requiring evaluation into the future.

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