



Trend in Pacific walrus (*Odobenus rosmarus divergens*) tusk asymmetry, 1990–2014

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ABSTRACT

We used the basal circumference of Pacific walrus (*Odobenus rosmarus divergens*) tusks (upper canine teeth, $n = 21,068$ pairs) to estimate fluctuating asymmetry (FA1 index) from 1990 to 2014. The mean difference in circumference between paired tusks was -0.006 (SEM = 0.002) cm and approximately normally distributed. Measurement error was 0.6 (0.02)%, similar between biologists and lay persons ($P = 0.83$), and $\leq 15\%$ of FA1. Tusk FA1 was greatest in 1990 then declined by 56% ($P = 0.0001$) through 2014. Male and female trends differed ($P = 0.0001$) and male FA1 was 40% greater ($P = 0.0001$) and the rate of decline 28% steeper ($P = 0.3$) than females. A quartic polynomial model ($r^2 = 0.66$, $w_i = 0.685$) fit the trend for female data better than simpler forms, whereas a linear model ($r^2 = 0.55$, $w_i = 0.693$) was a better fit for male data. Walrus tusk FA1 reflected periods when the population was stressed due to food limitations and then recovered, and perhaps when females began to experience the loss of preferred sea ice habitat in summer and FA1 is an easily monitored indicator. More work is needed to confirm the link between FA1, individual fitness, and adaptive potential.

Key words: climate change, carrying capacity, developmental instability, ecological indicator, fluctuating asymmetry, harvest monitoring, population dynamics.

Several lines of evidence indicate that the Pacific walrus (*Odobenus rosmarus divergens*) population was likely at, or above, the nutritional carrying capacity (K_n) of their habitats sometime during the years 1975–1985 (Fay *et al.* 1989, 1997; Garlich-Miller *et al.* 2006, MacCracken *et al.* 2014, Taylor and Udevitz 2015). Density dependent competition for food and space at that time likely stressed individuals and resulted in population level effects (Fay *et al.* 1989). Pacific walruses are long-lived (Fay 1982) and their primary prey (mollusks and worms) would also take several years to recover once the walrus population declined and predation rates on those food items also declined. Taylor and Udevitz (2015) estimated that survival and reproductive rates in Pacific walruses did not begin to increase from lows associated with high population densities until a decade later.

Bilateral traits like walrus tusks (upper canine teeth) are duplicate structures under the influence of the same genome and should develop similarly under optimum conditions (Waddington 1942, Palmer and Strobeck 1986, Klingenberg 2003, Graham *et al.* 2010), and also have some capability to buffer against small random

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perturbations (Palmer and Strobeck 2003). However, disruption of cellular processes (Cánovas *et al.* 2015) can result in developmental instability and deviations from perfect symmetry termed fluctuating asymmetry (FA). Fluctuating asymmetry has been correlated with a variety of environmental and genetic stressors in a variety of taxa (Zakharov *et al.* 1997, Anciães and Marini 2000, Weller and Gazhorn 2004, Serrano *et al.* 2008, Sherman *et al.* 2009, Allenbach 2011, Schmeller *et al.* 2011, Beasley *et al.* 2013, Burghelea *et al.* 2013, Hata *et al.* 2013, Cánovas *et al.* 2015), including pinnipeds, and promoted as an easily monitored indicator of stress providing an early warning of adverse conditions. However, FA has also failed as a biomarker of stress in some species in certain circumstances (Schandorff 1997, Lens *et al.* 2002, Eggeman *et al.* 2009, Allenbach 2011, Vangestel and Lens 2011).

Fluctuating asymmetry is a measure of variation and defined as the difference between right and left sides of a trait ($R - L$) having a mean of 0 and a symmetric distribution (Palmer and Strobeck 2003). Factors that influence the efficacy of FA as an indicator of developmental instability include the function of the trait(s) and their selection history (De Coster *et al.* 2013), measurement error (ME) making up a large portion of FA estimates (which can be subtle), directional asymmetry (data normally distributed, but with a mean other than 0), antisymmetry (data with a mean of 0, but a bimodal or broadly flat distribution), stressor intensity and history, differential wear on one side, and lower survival or reproduction in asymmetric individuals (Palmer and Strobeck 2003). The absolute value, an extension of the mean absolute deviation, of the $R - L$ difference ($|R - L|$, termed FA1), is the most used measure of FA, particularly if only a single trait is measured (Palmer and Strobeck 2003).

The main objective of this study was to determine if walrus tusk FA was greater during periods when the population was at, or exceeded, K_n and if the magnitude and trend in FA1 differed between males and females. In addition, we suspected that the recent loss of preferred sea ice habitat in summer may differentially affect females as many males remain in the Bering Sea year round where ice normally melts out in May or June (Fay 1982). Ice over the Chukchi Sea continental shelf, which is the summer range of females and young, melted completely in August 2007 ushering in a new open water season regime (MacCracken 2012, Stroeve *et al.* 2014, Wood *et al.* 2015). In 7 of 9 yr between 2007 and 2015, sea ice in the Chukchi Sea was not available to walruses between mid-August and mid-December. We also estimated measurement error (ME) of both experienced and novice observers in relation to indices of FA.

METHODS

Database

Pacific walruses have been harvested for subsistence purposes by Alaska and Chukotka Natives for millennia (Ray 1975) and in Alaska walruses have been managed by the Department of Fish and Game and currently the United States Fish and Wildlife Service (USFWS). Under both entities, successful walrus hunters were required to submit the tusks for tagging and measurement as part of harvest monitoring efforts. The USFWS maintains a database of measured tusks that includes records from 1960–present. However, sample sizes are greatest and the time series most complete from 1990 to the present, comprised of over 21,000 pairs of tusks.

Tusks from harvested walrus or those salvaged from dead animals are required to be tagged within 30 d of acquisition per the U.S. Marine Mammal Protection Act (16 U.S.C. 1361 § 109(i)). To facilitate compliance with the tagging requirement the USFWS has several employees (biologists, law enforcement officers, administrative assistants, *etc.*) at facilities throughout Alaska that processed tusks. However, the majority of tusks were handled by residents of walrus hunting villages in western Alaska that have been recruited to serve as taggers. Village taggers were trained in standard data collection methods and paid a small fee for each tusk processed. Each tusk was measured for basal circumference immediately below the gingiva (gums) and above any medial abrasion associated with the lower mandible. Length of the clinical crown (Fay 1982) was also measured for each tusk from the gingiva to the tip along the convex arc of the tusk. Both measurements were made to the nearest 0.3 cm (1/8 in.) with a cloth tape. Sex, age, and right or left side were recorded for each tusk and paired tusks from the same animal were also identified. Data on circumference and length were thoroughly screened for errors, inconsistencies, and outliers (Palmer and Strobeck 2003). Corrections were made where errors were obvious (*e.g.*, misplaced decimal points, estimates in standard *vs.* metric units, *etc.*). Tusks that were outliers and had unexplainable errors were deleted from the analysis. From this initial screening it was determined that tusk circumference was a more reliable measure than crown length. Physical wear on structures such as tusks can confound estimates of FA. Walrus tusks are occasionally broken, particularly near the tip, but also in various places along the crown length, including near the base and broken tusks are more common in males than females (Fay 1982). Tusk tips may also experience differential wear and breakage as they are used in agnostic interactions, defense from predators, mounting ice floes, and in climbing steep slopes at land haul-outs. In addition, feeding in benthic substrates composed of gravel, and sand may wear the frontal surface of tusks along most of their length (Fay 1982); however, the base of tusks would be protected by the gums and lips (*labia oris*). Thus, basal circumference is less subject to wear and a more precise metric than crown length and all analyses were based on circumference measurements. Canine teeth have also been used to estimate FA by Modi *et al.* (1987) and Cánovas *et al.* (2015).

For our analysis of FA we used data from both males and females and all age classes. We used the FA1 index (Palmer and Strobeck 2003) for those analyses.

Measurement Error

Fluctuating asymmetry estimates are typically small relative to trait size and in some cases ME can make up a substantial portion of the estimate and needs to be assessed (Palmer and Strobeck 2003). The tusks of Pacific walrus develop from the apex of the clinical root where an internal layer of dentin is overlain with cementum in annual increments (Fay 1982). Overlap in the annual increments is greatest at the gum line where tusk circumference measurements were taken. Thus, natural variation in circumference is likely additive, facilitating the detection of FA. Circumference measurements of each tusk were made only once by village taggers or USFWS personnel, precluding a direct assessment of ME for the majority of tusks. However, we were able to assess ME based on a subsample of 28 individual tusks and 11 pairs of tusks that are also part of the larger database. This analysis had three objectives: (1) estimate ME, (2) determine if ME varied substantially between observers that were trained scientists and lay persons, and (3) for paired tusks estimate ME relative to FA following procedures outlined in Palmer and Strobeck (2003).

To meet those objectives, we recruited three biologists experienced in measuring tusks as well as three laypersons with no experience measuring tusks or wildlife in general as surrogates for village taggers. Each person was instructed in how and where to measure tusk circumference and to make two measurements of each tusk with at least 4 h separating the two measurements. Tusks were laid out on a laboratory counter in random order, including eight pairs that were not in the skull to insure that the measurement of one tusk of a pair did not influence the measurement of the second tusk. However, three pairs of tusks were still in the skull and observers were instructed to avoid any bias in measurements that this might create.

For single tusks, the absolute difference between the first and second measurements (ME1 of Palmer and Strobeck [2003]) was estimated and compared between experienced and lay persons with a *t*-test. For paired tusks, we followed the applicable procedures in Palmer and Strobeck (2003) to assess the effects of ME on FA estimates except we used a repeated measures general linear model (GLM) because of unequal sample sizes among observers. Side, observer, animal, and the animal*side interaction were fixed effects, testing for directional asymmetry (DA), observer experience, and the contribution of between sides variation to ME, respectively. We also calculated two other indices of ME as described in Palmer and Strobeck (2003) using the partitioned mean squares from the GLM:

$$\text{ME3 (proportional error)} = 100 \times \frac{\text{MS}_{\text{error}}}{\text{MS}_{\text{side*animal}}} \text{ and}$$

$$\text{ME4 (repeatability)} = \frac{\text{MS}_{\text{animal}} - \text{MS}_{\text{error}}}{\text{MS}_{\text{animal}} + (N - 1)\text{MS}_{\text{error}}}.$$

Measurement error as a portion of FA can also be directly assessed using two FA indices, *i.e.*, FA4a – FA10a (Palmer and Strobeck 2003) where:

$$\text{FA4a} = 0.798\sqrt{\text{MS}_{\text{side*animal}}}, \text{ and}$$

$$\text{FA10a} = 0.798\sqrt{\text{MS}_{\text{side*animal}} - \text{MS}_{\text{error}}}.$$

See Palmer and Strobeck (2003, p. 286) for the derivation of the constant in both equations.

Fluctuating Asymmetry Analyses of all Tusks

Directional asymmetry and antisymmetry (AS) can confound estimates of FA1 (Palmer and Strobeck 2003) and need to be assessed. We evaluated DA and AS by examination of distribution plots of signed R – L tusk circumference estimates. Directional asymmetry is characterized by a normal distribution with a mean other than 0. To further assess DA we also conducted a 1-tailed *t*-test to determine if the mean of signed R – L circumference differed statistically from 0. Antisymmetry is defined as either a bimodal or broad flat distribution with a mean of 0 (Palmer and Strobeck 2003, Hata *et al.* 2013), which would be apparent in the distribution plot. The data were also tested for departures from normality with the Anderson-Darling test (Anderson and Darling 1954).

Fluctuating asymmetry analyses are also confounded if trait size and FA are strongly correlated. We examined this relationship with Spearman's rank correlation

(r_i) between FA1 for a pair of tusks and mean circumference of the pair (Palmer and Strobeck 2003).

We used a linear mixed effects model (Zuur *et al.* 2009) estimated by restricted maximum likelihood to test for differences in FA1 among years (1990–2014) and between males and females. Year and sex and their interaction were modeled as fixed effects and individual walruses as a random effect. Model fit was assessed by examination of a residuals plot. The importance of contrasts among the fixed factors was evaluated using Tukey's Honestly Significant Difference test. Due to the large sample size, we set alpha at 0.001 to reduce the false discovery rate (Colquhoun 2014) in addition to Bonferroni adjustments. We expected FA1 estimates to be relatively large early in the time series, reflecting the effects of the population exceeding K_n and then to decline in subsequent years.

A significant year*sex interaction term in the mixed effects model would indicate disparate trends between male and female walruses and those trends would be further examined using a model selection approach (Burnham and Anderson 2002) by estimating null (intercept only), linear, and nonlinear (polynomial) ordinary least squares regressions for each sex and assessing model fit with r^2 and Akaike's Information criteria (AIC_c). To guard against overfitting (Burnham and Anderson 2002, Fieberg and Johnson 2015), polynomial models were limited to those that improved fit based on subsequent differences in r^2 and AIC_c estimates (both >5 units). Akaike weights (w_i), and evidence ratios (Burnham and Anderson 2002) were used to assess the relative importance of each model for males and females. Models within two AIC_c units were considered equivalent in describing the trend. For these analyses, the mean FA1 (y) was regressed against year (x^n) for 1990–2014.

RESULTS

Measurement Error

The mean circumference for all tusks of the subsample used to assess ME was 17.4 (SEM = 0.15) cm and average ME1 was 0.10 (0.05) cm or 0.6%. The difference in ME1 estimates between biologists and lay persons for all tusks was 0.03 (0.001) cm (10%, $P = 0.83$). For paired tusks, the mean difference in ME1 measurements between biologists and lay persons was 0.01 (0.002) cm. The mean difference between right and left tusks was -0.04 (0.03) cm ($P = 0.68$) indicating no DA. However, tests for AS were inconsistent as signed R - L data were approximately normally distributed ($P = 0.08$), but the leptokurtosis estimate was 1.55 (0.63; $P = 0.03$). The significant side*animal interaction ($P = 0.0001$) indicated that an analysis of FA would be not be confounded by ME (Schandorff 1997; Palmer and Strobeck 2003, appendix V). The estimate for ME3 was 28% and ME4 was 0.98. The estimates for FA4a and FA10a were 0.58 and 0.49, respectively, indicating that the contribution of ME to FA was 0.09 or 15.5%.

Fluctuating Asymmetry Analyses

A plot of signed R - L tusk circumference estimates for male and female data sets suggested a slight leptokurtic departure from normality (Fig. 1). Skew was estimated as -0.12 (0.02), leptokurtosis at 9.36 (0.03), the Anderson-Darling test for normality

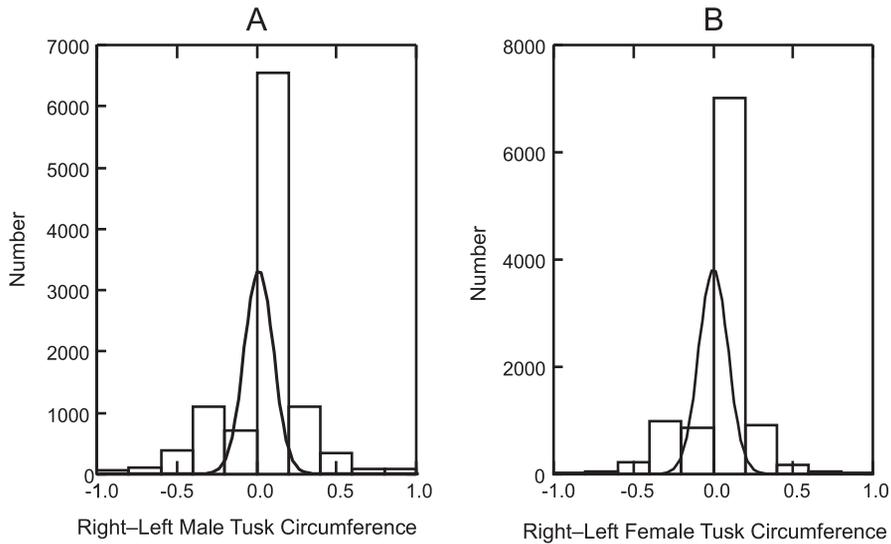


Figure 1. Normal curve density plot overlain on a histogram of male (A) and female (B) Pacific walrus (*Odobenus rosmarus divergens*) signed right minus left tusk basal circumference sampled from 1990 to 2014 illustrating the possibility of directional asymmetry ($H_0: = 0$, $t = 2.00$ and 3.00 , $P = 0.04$ and 0.003 , respectively) and lack of antisymmetry. Note difference in y axes.

was equivocal ($P < 0.01$), and the mean (-0.006 [0.002]) was statistically different from zero ($t = 3.34$, $P < 0.001$), indicating that DA may be present. However, AS was not evident in Fig. 1. Mean FA1 for the full data set was 0.13 (0.001) cm and tusk circumference was weakly correlated ($r_s = 0.11$) with FA1.

Mean FA1 for males and females combined declined monotonically by $3.2\%/yr$ from 1990 to 2014 ($P = 0.0001$). In general, FA1 estimates for the early 1990s were greater than those of the mid-1990s to 2014, the late 1990s estimates were greater than those for the 2000s to 2014, the mid- to late 2000s were greater than those of 2010–2014, and differences among 2010–2014 were small ($P > 0.001$). Mean male FA1 was 40% larger ($P = 0.0001$) than female mean estimates and the rate of decline in FA1 for males was 28% steeper ($P = 0.3$; Fig. 2, 3). The year*sex interaction term ($P = 0.0001$) indicated that the trend in male and female FA1 differed.

Null, linear, quadratic, and cubic models were estimated for males. Linear and cubic models ranked the best but differed by 2.716 AIC_c units, with w_i and ER estimates (Table 1) indicating that the linear model was the better of the two (Fig. 2). For males, the trend in mean FA1 was monotonically negative and year to year variation was low (coefficient of variation [CV] = 0.16).

Null through quartic polynomial models were estimated for females and AIC_c estimates indicated that quartic and cubic models were close ($AIC_c = 2.040$), but w_i and ER estimates (Table 1) indicated that the quartic model was the better of the two. The negative trend in FA1 for females was steepest in the 1990s, much less steep from 2000 to 2010, then became positive (Fig. 3). Year to year variation in mean female FA1 was also low (CV = 0.21)

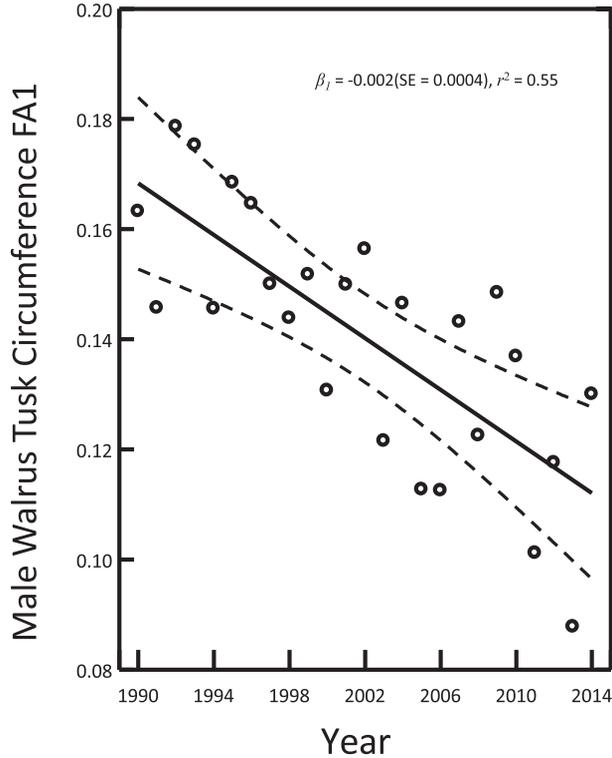


Figure 2. Trend in mean male Pacific walrus (*Odobenus rosmarus divergens*) tusk basal circumference fluctuating asymmetry (indexed as FA1 = $|R - L|$) from 1990 to 2014. Open circles are annual means (annual n was 318–656), the solid line is the estimate of a least squares linear regression and the dashed lines the 95% confidence interval.

DISCUSSION

Measurement Error

Measurement error was a small proportion of tusk basal circumference and FA1 estimates and our FA analyses were not compromised by ME. Persons with little or no experience measuring tusks were as competent as trained scientists. Positioning a cloth tape around the base of a tusk and reading the graduated ruler is not a very complex or technical task and is highly repeatable within and among observers. This finding increases confidence in the efficacy of village taggers and other novice lay persons in measuring tusk characteristics as well as the validity of our FA analyses. However, it is possible that the people we enlisted to measure tusks were more diligent in their efforts than village taggers due to the laboratory setting and other circumstances even though the objectives of the exercise or use of the data were not conveyed to them.

Statistical tests suggested that DA was present; however, the departure from a normal distribution was so small that it was likely due to developmental instability rather than DA (Palmer and Strobeck 2003). Furthermore, the small P -values

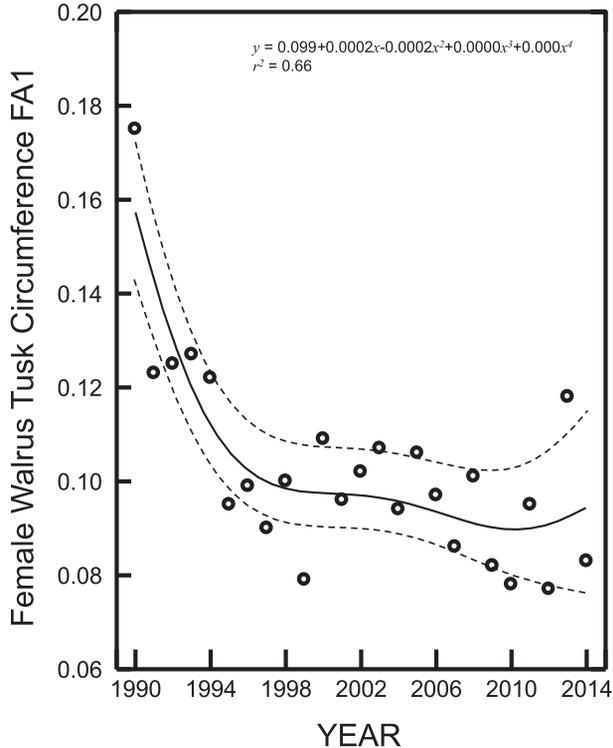


Figure 3. Trend in mean female Pacific walrus (*Odobenus rosmarus divergens*) tusk basal circumference fluctuating asymmetry (indexed as $FA1 = |R - L|$) from 1990 to 2014. Open circles are annual means (annual n was 41–972), the solid line is the estimate of a quartic polynomial least squares regression and the dashed lines the 95% confidence interval.

associated with test statistics for normality are due to the large sample size in this study as even small effect sizes result in small P -values in such instances. Palmer and Strobeck (2003) suggested as a rule of thumb that if DA is no larger than $FA4a$ then subsequent analyses of FA are valid. We cannot estimate $FA4a$ for the full data set, but assuming that the subset of tusks for which $FA4a$ was estimated is representative; then DA is orders of magnitude less than $FA4a$ (0.58).

FA1 and Habitat Carrying Capacity

The K_n of the Bering and Chukchi Seas for walrus has never been known and population estimates are imprecise. However, there are several lines of evidence consistent with the presumption that the population was at, or exceeded, K_n around 1980. Fay *et al.* (1997, p. 546) stated "...estimates indicated that the population reached its asymptote around 1980, consistent with changes in fertility, distribution, food habits, and increasing numbers on the more southerly haulouts..." Fay *et al.* (1989) also noted the associated declines in blubber thickness, productivity (also noted by Garlich-Miller *et al.* [2006] and MacCracken *et al.* [2014]), calf survival, and the size of bivalves eaten (their preferred prey). At the same time, alternate food

Table 1. Results of model selection procedures to describe the trend in mean Pacific walrus (*Odobenus rosmarus divergens*) tusk basal circumference fluctuating asymmetry (indexed as FA1 = |R - L|) for males and females from 1990 to 2014. Null to quartic polynomial models were estimated. Akaike's information criteria (AIC_c), Akaike weights (w_i), and evidence ratios (ER) were used to determine which model(s) fit the data the best for each sex.

Sex and model	K^a	r^2	AIC _c	ΔAIC_c^b	w_i	ER ^c
Male						
Linear	2	0.55	-132.394	0	0.693	
Quadratic	3	0.53	-129.970	2.424	0.258	2.686
Cubic	4	0.51	-127.023	5.321	0.070	14.438
Null	1	0.00	-114.384	18.010	0.000	n/a ^d
Female						
Quartic	5	0.66	-137.906	0	0.685	
Cubic	4	0.60	-135.862	2.040	0.247	2.733
Quadratic	3	0.51	-133.146	4.760	0.093	114.167
Linear	2	0.36	-127.828	10.078	0.006	171.25
Null	1	0.00	-118.231	19.675	0.000	n/a ^d

^aNumber of model parameters.

^bAIC₁ - AIC_j.

^c W_1/W_j .

^dNot applicable.

items in stomachs (seals and fish) increased as did age at first reproduction (also seen by Garlich-Miller *et al.* [2006]) and the mean age of harvested animals, all to be expected when a population has reached or exceeded K_n (Eberhardt 1977).

Some of the same lines of evidence are also consistent with a Pacific walrus population below K_n from 1990 to the present. Recent observations indicate that the majority of animals are in good condition, productivity has increased (MacCracken *et al.* 2014), stomach samples are dominated by bivalves, gastropods, and marine worms (Sheffield and Grebmeier 2009), numbers of animals at southern haul-outs has declined, as well as the mean age of harvested animals (Garlich-Miller *et al.* 2006).

Population estimates based on aerial surveys are available from 1975 to 1990 at 5 yr intervals (Hills and Gilbert 1994, Fay *et al.* 1997) with another survey conducted in 2006 (Speckman *et al.* 2011). The magnitude and rate of population change cannot be reliably determined from these surveys due to the imprecision of the estimates and sampling issues (Hills and Gilbert 1994, Udevitz *et al.* 2001, Taylor and Udevitz 2015). However, Taylor and Udevitz (2015) integrated the aerial survey population estimates (recalculated based on a log-normal distribution) and ship-based age and sex composition counts that were conducted annually in 1981–1984, 1998, and 1999 (Citta *et al.* 2014) with Bayesian methods. This effort increased the precision of the aerial survey population estimates and resulted in a population trend indicating a large population in 1975 ($\approx 380,000$) with a subsequent decline to 2003 with the rate of decline greatest in the 1980s. This population trend, as well as, the age composition of females, and model derived reproductive rates and calf survival rates are also consistent with expectations based on the Pacific walrus population reaching or exceeding K_n early in the time series. The negative trend in FA1 for males and females combined and males alone from 1990 to 2014 is consistent with the modeling results of Taylor and Udevitz (2015) and other evidence (Fay *et al.* 1997, MacCracken *et al.* 2014) that the Pacific walrus population was still expressing the effects

a decade or more later of exceeding K_n and that those effects diminished as the population subsequently declined.

The larger FA1 estimates for males may simply reflect the sexual dimorphism of walrus; mean mass of 54 adult males was 45% greater than the mean mass of 34 adult females (Fay 1982). In addition, the range in circumference of male tusks was 22.7 cm and females 15.2 cm. The greater inherent variation in male tusks may result in larger FA1 estimates. In addition, the fact that the entire Pacific walrus population winters in the Bering Sea (Fay 1982), but in the spring females with dependent young, barren females, immature females as well as relatively few immature and adult males move north with the receding sea ice and summer in the Chukchi Sea. In contrast, many subadult and adult males remain year round in the Bering Sea, which becomes completely ice free by May or June, and use coastal haul-outs to rest. Walrus prey may have been depleted at a faster rate and greater amount in the Bering Sea than in the Chukchi Sea and males likely experienced a larger year round energy deficit than females (Coltman *et al.* 1998, Crocker *et al.* 2012). Compounding the decline in prey is the greater energy expenditures likely experienced by males associated with feeding trips from summer coastal haul-outs in contrast to females resting on ice floes in the Chukchi Sea, which may be directly over, or much closer to areas of high prey abundance.

Fluctuating Asymmetry and Habitat Change

The difference in the trend in FA1 between males (linear) and females (curvilinear) suggests that some environmental condition is affecting them differentially. The most likely cause is the decline in sea ice habitats in summer in the Chukchi Sea which has become most pronounced since 2007 (MacCracken 2012, Maslowski *et al.* 2012, Stroeve *et al.* 2014, Xia *et al.* 2014). There are several potential stressors acting on females associated with this change in preferred habitats such as a reliance on coastal haul-outs for 2–3 mo for resting which may result in increased feeding costs and periodic disturbance-related flight behaviors and subsequent mortalities. In addition, economic development activities such as oil and gas exploration, commercial shipping, and tourism in the Chukchi Sea are also on the rise (Jay *et al.* 2011, MacCracken *et al.* 2013). The quartic model indicates that the stresses associated with the population exceeding K_n were diminishing in the 1990s, but in the early 2000s the negative trend in female FA1 became less steep, and then leveled out and became positive about 2011.

The relationship between tusk FA and individual or population performance is unknown. The primary functions of tusks are in threat displays, communicating the rank of individuals, as weapons, and in mounting ice floes or hanging from the edge while resting (Fay 1982). Tusks may also serve as secondary sexual characters as there are features (width, length, base to tip convergence, *etc.*) that are indicative of male or female animals and dominance. Breeding males use tusks as weapons when defending breeding display positions near groups of estrous females. However, male displays are primarily vocal (Fay 1982) and given the more obvious characters of tusks such as length, diameter, breakage, curvature, and divergence or convergence along the crown length it seems unlikely that subtle differences in R – L basal circumference would provide much of a clue to male fitness in female mate choice. However, tusk circumference FA may be strongly correlated with some other trait such as age, size, and social rank that may be important.

Monitoring FA1 of walrus tusks appears to be useful in detecting when individuals may be under increased stress due to food limitation and habitat changes and could provide an indication of the occurrence, frequency, and intensity of these stressors. Ocean acidification associated with increasing CO₂ absorption by the Arctic Ocean and subsequent declines in the saturation state of calcium carbonates has the potential to reduce the abundance of the main prey of walruses; bivalves, gastropods, and polychaetes (Kroeker *et al.* 2010, Waldbusser *et al.* 2014), which could lead to food shortages and nutritional stress in the future (Mathis *et al.* 2015).

Wild animals face a number of biotic and abiotic factors that challenge their well-being throughout their lives (Wingfield *et al.* 1998, Hoffman and Hercus 2000, Boonstra 2013). The role of stress and subsequent adaptive responses that promote fitness in wild animals is becoming better understood (Boonstra 2013, Jessop *et al.* 2013, Love *et al.* 2013, Wingfield 2013). Glucocorticoid stress hormones influence a variety of physiological, morphological, and behavioral processes under normal as well as acute and chronic stress conditions (Jessop *et al.* 2013). These hormones could promote developmental instability as they redirect resources to mitigating stress, but substantial uncertainty exists in the processes. Nonetheless, this may be one mechanism by which phenotypic plasticity based on standing genetic diversity is expressed, which could be adaptive if selected for (Gilbert 2006, Woods 2014, Nishizaki *et al.* 2015). Thus, linking FA to an individual's potential to adapt to changing environments may be a useful area of inquiry in both short-term and evolutionary adaptive developmental plasticity (Nettle and Bateson 2015).

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