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Determining sex of adult Pacific walruses from mandible measurements

Nathan Taylor,* Casey T. Clark, Nicole Misarti, and Lara Horstmann

College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 2150 Koyukuk Drive, Fairbanks, AK 99775-7220, USA (NT, LH)
Joint Institute for the Study of Atmosphere and Ocean, University of Washington, 3737 Brooklyn Avenue NE, Seattle, WA 98105, USA (CTC)
Water and Environmental Research Center, University of Alaska Fairbanks, 1764 Tanana Loop, Fairbanks, AL 99775-5860, USA (NM)

**Correspondent: nataylor2@alaska.edu*

Pacific walruses (*Odobenus rosmarus divergens*) play a vital role in Arctic marine ecosystems and the subsistence lifestyle of Alaska Native communities. Museum collections contain numerous archaeological and historic walrus specimens that have proven useful in a variety of studies; however, for many cases, the sex of these specimens is unknown. Sexes of adult (> 5 years determined by tooth aging) Atlantic walruses (*Odobenus rosmarus rosmarus*) have been accurately determined in previous studies using mandible measurements. We tested the validity of this approach for Pacific walruses, and used full fusion of the mandibular symphysis to define adults. Using high precision digital calipers (± 0.01 mm), four measurements were taken either on the left or right side of 91 walrus mandibles: 80 modern mandibles (70 known-sex specimens; 10 unknown-sex specimens) and 11 archaeological mandibles of unknown sex. We used linear discriminant function analysis (LDFA) to determine what measurements best distinguished Pacific walrus males from females. Minimum mandible thickness had the most predictive power, whereas mandible length, height, and depth, were less predictive. Posterior probabilities indicated that LDFA classified the known-sex Pacific walruses with 100% accuracy, and unknown sex with ≥ 90% probability. The ability to define the sex of unknown individuals accurately could greatly increase the sample size of future projects dealing with skeletal remains, and will improve future research efforts.

Key words: archaeology, marine mammal, morphometric, *Odobenidae*, *Odobenus rosmarus divergens*, pinniped, sexual dimorphism

Pacific walruses (*Odobenus rosmarus divergens*) are vital to the way of life in many Russian and Alaska Native communities, and are an integral part of Arctic marine ecosystems. The past, present, and future, of walruses therefore is of interest to rural communities, wildlife managers, and researchers. To determine how the changing Arctic is affecting the present-day walrus population, researchers and managers need a better understanding of changes that have occurred in the past. These environmental changes may include loss of sea ice habitat, increased exposure to toxins or contaminants, and changing prey availability due to altered sea ice conditions (Burek et al. 2008). Loss of sea ice likely will have a greater effect on females, because they spend their summers in the Chukchi Sea using ice floes as platforms for hauling out, giving birth, and resting after feeding on the sea floor (Fay 1982).

There are numerous modern and archaeological Pacific walrus specimens in museum collections that have the potential to aid research; however, many of these specimens are of unknown sex. Pacific walruses typically segregate by sex in the summer, and both sexes spend the winter breeding season in the Bering Sea. Following breeding, females, juveniles, and some males (Fay 1982), migrate north with the receding sea ice to summer in the Chukchi Sea, while many males maintain residence in the Bering Sea (Fay 1982; MacCracken and Benter 2016). Males and females have differing energetic demands, as well as other sex-specific physiological differences (Noren et al. 2012, 2014, 2015); identifying walruses by sex thus is important to many research questions. Correctly identifying the sex of specimens therefore can add to previous research and help future investigations result in more informed conclusions.

Correct information as to sex of existing specimens could allow scientists to gain a better understanding of past changes in sex-specific migratory patterns and distribution, as well as Alaska Native harvest patterns through time.

A simple, inexpensive, and effective method for determining the sex of Atlantic walruses (*Odobenus rosmarus rosmarus*) from mandible measurements was developed by Wiig et al. (2007). Our objective here was to test whether this method is transferable to Pacific walruses. For some mammals, such as marmots (*Marmota* sp.), subspecies exhibit substantial morphological differences, particularly in the morphology of the cranium and mandible (Caumul and Polly 2005). Pacific walruses differ from their Atlantic counterparts primarily in their overall size and facial structure (Fay 1982). Atlantic walruses are described as having a narrower and more sloping muzzle when compared to the broader and square snout of the Pacific walrus (Fay 1982). These differences in facial structure and overall body size demonstrate that the size and shape of the mandible differs between the two subspecies, which could affect the application to Pacific walruses of the sex assignment method developed by Wiig et al. (2007).

Determining the sex of a walrus from mandibular measurements has many advantages over genetic sex identification. Typically, to determine the sex of individuals using genetic techniques, DNA is extracted, and the zinc finger protein genes (ZFX and ZFY) are amplified. During electrophoresis, the smaller intron in the Y chromosome results in separation from the X chromosome intron; this separation creates a different banding pattern in males than females (Fischbach et al. 2008). Extracting and analyzing DNA is time-consuming and expensive. Recent work by Robertson et al. (2018) has made this process quicker and less expensive; however, this method only is effective if the DNA is intact enough to examine, making it more useful for modern than archaeological samples. Determining the sex of walruses from mandibles is more cost-effective, and may be especially useful when DNA is too degraded to use genetic methods (Fischbach et al. 2008). In addition, identifying sex based on measurements of mandibles requires relatively little effort and is nondestructive, making this a preferred technique for museum collections. Another inexpensive method to determine the sex of pinnipeds is by the size of canine teeth (Briggs and Morejohn 1975); however, tusks and other teeth are nearly always removed from dead walruses due to the value of ivory, and may not be present in archaeological and beach cast specimens.

The specific goals of this research were to: 1) ascertain whether the mandible measurements developed by Wiig et al. (2007) to determine the sex of Atlantic walruses could be used to determine sex of Pacific walruses; 2) to determine whether maturity, as assessed by the full fusion of the mandibular symphysis, is required to accurately determine sex of Pacific walruses; and 3) create a training data set to aid in future walrus studies; that is, a set of published measurements from known-sex animals used to enable the distinction of sex of individuals of unknown sex, thereby allowing researchers without access to known-sex specimens to perform analyses to identify the sex of walruses in the future. In addition, we compared the mandible measurements of Pacific walruses from this study to those reported by Wiig et al. (2007) for Atlantic walruses.

Materials and Methods

Mandibles from 70 known-sex (42 males and 28 females) and 10 unknown-sex walruses of various ontogenetic stages collected during Alaska Native subsistence harvests from 1930 to 2014 were sampled from the Mammal Collection at the University of Alaska Museum (Appendix I; Supplementary Data SD1). Eleven unknown-sex walrus mandibles, collected from archaeological sites in coastal Alaska inhabited 300–1,000 years ago were sampled from the Archaeology Collection at the University of Alaska Museum (Supplementary Data SD1). These mandibles included specimens with fused and unfused mandibular symphyses, reflecting a range of ontogenetic stages. Measurements used in this study (Fig. 1) were directly adapted from Wiig et al. (2007) and taken using digital calipers with an accuracy of ± 0.01 mm. Each set of measurements was collected from the left or right side of the mandible (i.e., the left or right dentary), and was considered to be representative of the mandible as a whole. Although in some instances the term "dentary" might be more technically correct, the term "mandible" is used throughout this paper both for clarity and consistency with previously published research. The four mandible measurements collected in this study are as follows (Fig. 1; abbreviations from Wiig et al. (2007) used for consistency):

1. **Mandible Length (ML):** distance between most anterior and posterior points on one side of the mandible.
2. **Mandible Height (MH)**: distance between most dorsal point on coronoid process and most ventral point on angular process.
3. **Minimum Mandible Depth (MD)**: smallest distance between ventral and dorsal surface of one side of the mandible, posterior to last post-canine. This corresponds to Least Mandible Depth (MD) from Wiig et al. (2007)
4. **Minimum Mandible Thickness (MT)**: smallest distance between lateral and medial surfaces of one side of the mandible, posterior to last post-canine. This corresponds to Least Mandible Thickness (MT) from Wiig et al. (2007)

Whenever possible, all measurements were taken both on the left and right side of the mandible. In instances where one side of the mandible was damaged or incomplete, measurements were collected from the single, complete side. All measurements were repeated three times, on separate days. The mean of the triplicate measurements was calculated for each individual and used in subsequent analyses.

The study undertaken by Wiig et al. (2007) on Atlantic walruses was restricted to individuals 5 years or older, as determined by counts of growth layer groups in teeth collected from analyzed mandibles. Aging animals from tooth cementum growth layers is labor-intensive, and teeth are not always available, particularly for archaeological specimens. We were interested only in classifying animals as adults or nonadults; thus, specific age was not necessary for our purposes. Instead, we assessed the degree of fusion of the mandibular symphysis, as skeletal development can provide coarse estimates of age and maturity (Reitz and Wing 2008). Age-specific data for the development of the walrus skeleton are not available in the literature (Monchot et al. 2013); therefore, we used data on the timing of skeletal development in phocid seals (Storå 2000). The degree of fusion of each individual was recorded along with the measurements of the mandibles. Each specimen was classified as "fully fused," "mostly fused," "partially fused," or "unfused." For the purposes of analyses, mandibles were grouped in two categories: "fully fused," and the other three classifications were lumped as "not fully fused" (Fig. 2).

If complete sets of measurements were available from both sides of the mandible in fully fused specimens (female: $n = 10$; male: $n = 30$), we evaluated mandibular asymmetry as well. Consistent mandibular asymmetry could interfere with this method of sex determination, because measurements from the left and right mandible could not be used interchangeably to determine sex. We compared the means of the left mandible measurements to those of the right mandible measurements using paired *t*-tests. First, asymmetry of each sex was tested to determine if sex-specific asymmetry was evident. Because no sex-based differences in asymmetry were found, paired *t*-tests were then carried out on the pooled (male and female) data. Finally, one-sample *t*-tests were used to determine if the Pacific walrus mandible measurements collected for this study differed significantly from the average measurements reported by Wiig et al. (2007) for Atlantic walruses.

Linear discriminant function analysis (LDFA) was carried out using the R package *MASS* (Venables and Ripley 2003) to assess whether the sex of a walrus specimen can be assigned from the four mandible measurements, and to evaluate the predictive value of each measurement for distinguishing between males and females. Leave-one-out cross-validation was used to determine whether the training data set (Supplementary Data SD1) can be used to assign the sex of unknown-sex individuals. To do

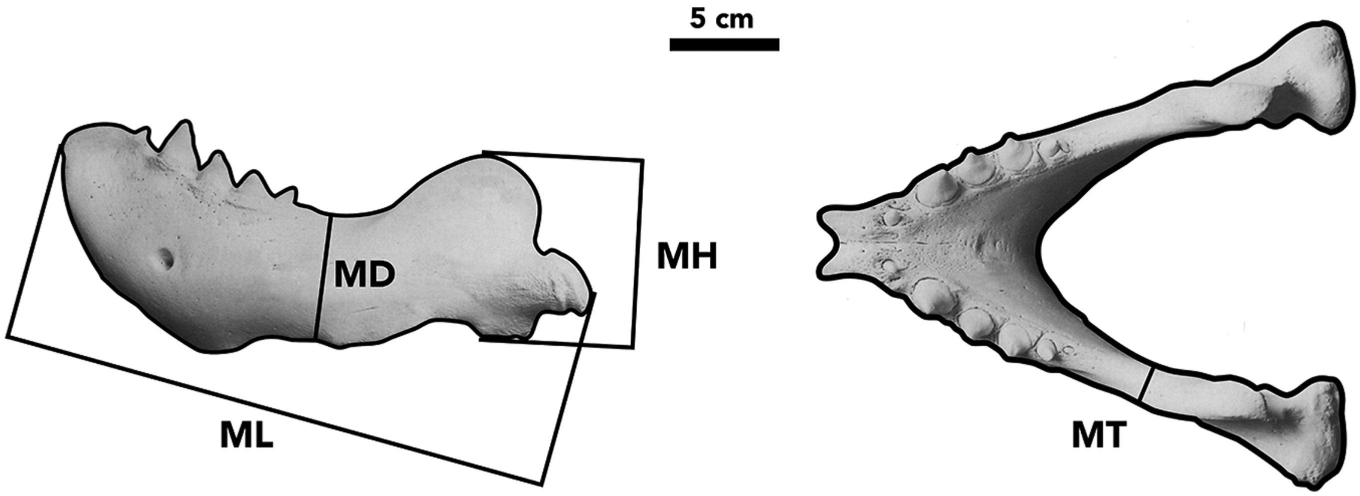

Fig. 1.—Diagram of four measurements taken on Pacific walrus (*Odobenus rosmarus divergens*) mandibles: mandible length (ML), minimum mandible depth (MD), mandible height (MH), and minimum mandible thickness (MT). Measurement abbreviations are named for consistency with Wiig et al. (2007). Adapted from Kastelein and Gerrits (1990).

Fig. 2.—Degree of fusion of mandibular symphysis in Pacific walruses, *Odobenus rosmarus divergens* (left to right: University of Alaska Museum [UAM] Catalog Number, sex, and fusion state): UAM:Mamm:11684, female, fully fused; UAM:Mamm:11690, male, mostly fused; UAM:Mamm:11515, female, partially fused; and UAM:Mamm:11521, female, unfused. All fusion states other than "fully fused" were classified as "not fully fused" for sex determination analyses. Images are for illustrative purposes only and are not to scale.

this, measurements of known-sex individuals were run through the LDFA, with one individual isolated from the group and treated as an unknown-sex animal. The LDFA then attempted to determine the sex of the isolated individual based on the remaining data set. Posterior probabilities were examined to assess the robustness of the predictions made by the LDFA (Supplementary Data SD2).

Values from the left mandible were used for this analysis, except in instances where the complete set of left mandible measurements was not available, in which case the right mandible was used. The LDFA assumes multivariate normality and equal variances across groups (Hair et al. 1998). To test for multivariate normality, we carried out a Royston's H test for multivariate normality (Royston 1983) using the *MVN* package in R (Korkmaz et al. 2014). A Box's M test (Box 1949) was run using the *heplots* package in R (Fox et al. 2009) to assess whether variances were equal across all groups. These assumptions were tested prior to running the LDFA. All statistical analyses were conducted in RStudio version 1.1.456 (RStudio Team 2015) using R version 3.5.1 (R Core Team 2020). Significance was assessed using an alpha value of 0.05.

RESULTS

The average precision for triplicate measurements taken in this study was: Left ML: ± 0.44 mm; Left MH: ± 0.48 mm; Left MD: ± 0.45 mm; Left MT: ± 0.47 mm; Right ML: ± 0.59 mm; Right MH: ± 0.42 mm; Right MD: ± 0.56 mm; Right MT: ± 0.40 mm. Complete sets of all measurements taken from both sides of the mandible were available for 40 individual walruses: 10 females and 30 males. There was no significant, consistent asymmetry between the left and right sides of the mandible (Table 1). Asymmetry also was examined within males and females. Neither males nor females exhibited significant, consistent asymmetry (Table 2). Pacific walrus mandibles were significantly larger than those of Atlantic walruses recorded by Wiig et al. (2007) (Table 3). Both Pacific walrus males and females were larger than their Atlantic counterparts in all four dentary measurements (Table 3). This is consistent with the overall larger body size of Pacific walruses compared to Atlantic walruses (Fay 1982).

Fusion state of the mandibular symphysis was used to estimate the maturity of individuals. Visual examination of the data revealed that fusion state is an appropriate tool for evaluating maturity of walrus specimens when using mandible measurements to determine sex of individuals (Fig. 3). Males with mandibles that were not fully fused tended to have measurements similar to females with fully fused mandibles. Similarly, females with mandibles that were not fully fused tended to have measurements that were smaller than fully fused males and females. Only one male and one female in the "not fully fused" group had measurements that likely would have resulted in accurate sex assignment (Fig. 3). We therefore conclude that sex of a walrus cannot accurately be determined when mandibles are not fully fused. In our sample, 16.8% of individuals did not exhibit full fusion of the mandibles, and consequently were not used. Only individuals with fully fused mandibles were used in the remaining analyses: 67 modern specimens (33 male, 24 female, and 10 unknown sex); 11 archaeological (all unknown sex; Supplementary Data SD1).

All assumptions of the LDFA were tested prior to analysis and were met (Box's $M = 16.12$, $d.f. = 10$, $P = 0.10$; Royston's H: [females] $H = 6.40$, $P = 0.18$, [males] $H = 2.54$, $P = 0.65$). The LDFA correctly predicted sex for all the known-sex individuals, as determined by leave-one-out cross-validation (Fig. 4; Supplementary Data SD1). It also assigned sex to unknown-sex individuals with posterior probabilities of ≥ 90% (Fig. 4; Supplementary Data SD2). The coefficients of the LDFA indicated that minimum mandible thickness (MT) and mandible length (ML) had the highest predictive power (MT: 0.17; ML: 0.05; MH: 0.01; MD: −0.02; Figs. 3, 5, and 6). MT showed the greatest separation, with the least amount of overlap between sexes. ML had the second highest predictive power, with good separation bar two individuals. Minimum mandible depth (MD) and mandible height (MH) both exhibited less separation between sexes, as reflected by their lower predictive power in the LDFA (Fig. 5).

Plotting the mandible measurements that contributed most strongly to the linear discriminant functions, MT and ML, reveals a substantial difference between male and female walruses, both modern and archaeological (Fig. 6). The sexes show strong separation, with females clustering together in the smaller MT and ML values, whereas males grouped together based on larger MT and ML measurements. The unknown-sex individuals fell squarely in the two different groups, showing that this method is applicable both to modern and archaeological unknown-sex individuals (Fig. 6).

DISCUSSION

For Pacific walruses with fully fused mandibular symphyses, this method accurately assigned sex to specimens—with some limitations. This method of sex determination only is useful for mature walruses. Female Pacific walruses reach sexual maturity

Table 1.—Mean measurements (in mm) of Pacific walruses (*Odobenus rosmarus divergens*) with fully fused mandibular symphyses; ML: mandible length; MH: mandible height; MD: minimum mandible depth; MT: minimum mandible thickness (± 1 *SD*) for the left and right sides of the mandible, and mean differences between the two sides for individual walruses, where complete sets of all measurements were available for both dentaries ($n = 40$). The t-statistic ($d.f.$: 39) and the P-value for the paired t-test of the difference between left and right sides of the mandible are included.

	Left side mean (mm)	Right side mean (mm)	Mean diff.	t_{39}	P-value
ML	278.69 ± 29.76	281.71 ± 29.09	−1.53	−1.53	0.13
MH	97.27 ± 12.12	96.93 ± 12.06	0.34	0.94	0.35
MD	69.72 ± 11.22	69.28 ± 10.85	0.44	1.31	0.20
MT	33.77 ± 10.04	33.47 ± 10.17	0.30	−0.82	0.15

Table 2.—Mean measurements (in mm) of female and male Pacific walruses (*Odobenus rosmarus divergens*) with fully fused mandibular symphyses; ML: mandible length; MH: mandible height; MD: minimum mandible depth; MT: minimum mandible thickness (± 1 *SD*) for the left and right walrus dentaries, and mean differences between the two sides for individual walruses, where complete sets of all measurements were available for both dentaries (female: $n = 8$, male: $n = 26$). The *t*-statistic (female: *d.f.* = 7, male: *d.f.* = 25), and the *P*-value for the paired *t*-test of the difference between left and right walrus dentaries are included.

Female	Left side mean (mm)	Right side mean (mm)	Mean difference	t_7	*P*-value
ML	237.05 ± 13.39	237.23 ± 12.26	–0.18	–0.19	0.86
MH	80.00 ± 4.67	79.460 ± 4.40	0.44	0.47	0.65
MD	53.53 ± 3.66	53.72 ± 4.13	–0.19	–0.59	0.57
MT	18.78 ± 2.05	18.56 ± 2.16	0.23	0.78	0.46
Male	**Left side mean (mm)**	**Right side mean (mm)**	**Mean difference**	t_{25}	***P*-value**
ML	283.65 ± 30.73	284.37 ± 31.39	–0.73	–1.27	0.93
MH	98.98 ± 11.91	98.62 ± 12.11	0.35	1.01	0.91
MD	71.69 ± 10.08	71.09 ± 9.93	0.61	1.67	0.81
MT	35.80 ± 8.54	35.60 ± 8.58	0.20	0.87	0.93

Table 3.—Comparison of mean mandible measurements (in mm; ± 1 *SD*) of Pacific walrus (*Odobenus rosmarus divergens*) and Atlantic walrus (*O. r. rosmarus*). Pacific walrus values are from this study, and Atlantic walrus values are taken from Wiig et al. (2007). The *t*-statistic (*d.f.*: male: 32, female: 23), and the *P*-value for the paired *t*-test of the difference between Pacific and Atlantic walrus mandible measurement means are included, as is the sample size (*n*).

	Female					
	Pacific		Atlantic			
	n	Mean ± *SD*	*n*	Mean ± *SD*	t_{23}	*P*-value
ML	24	235.74 ± 10.27	28	225.74 ± 9.14	5.00	< 0.001
MH	24	81.26 ± 5.19	29	75.27 ± 4.37	5.67	< 0.001
LMD	24	54.73 ± 4.26	29	47.36 ± 3.0	8.00	< 0.001
LMT	24	19.95 ± 2.71	29	15.31 ± 2.17	8.95	< 0.001
	Male					
	Pacific		Atlantic			
	n	Mean ± *SD*	*n*	Mean ± *SD*	t_{32}	*P*-value
ML	33	292.31 ± 16.25	43	262.64 ± 12.82	14.4	< 0.001
MH	33	102.18 ± 7.55	43	88.61 ± 5.21	12.6	< 0.001
LMD	33	73.82 ± 7.10	43	59.20 ± 3.52	14.9	< 0.001
LMT	33	38.37 ± 5.56	43	24.24 ± 3.0	18.30	< 0.001

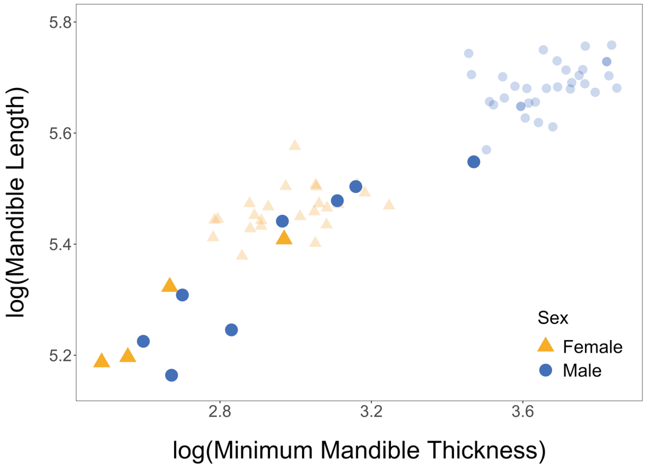

Fig. 3.—Log-log plot of minimum mandible thickness (MT) against mandible length (ML) for all measured Pacific walrus (*Odobenus rosmarus divergens*) mandibles to highlight the difference between individuals with fully fused mandibles and those without. Females with fully fused mandibles are represented by small orange triangles, males by small blue circles. Individuals without fully fused mandibles are represented by larger colored data points (females: orange triangles; males: blue circles).

between 4 and 7 years of age (Fay 1982; Garlich-Miller et al. 2006). Males are able to produce sperm (i.e., are "mature") before they are physically able to compete for a mate with other males (around 15 years of age—Fay 1982). The mandibular symphysis in male and female walruses likely is fully fused at an age prior to full maturity, such that they are able to feed effectively (Fay 1982). Our results suggest that visually examining the fusion of the mandibular symphysis is useful for estimating the degree of skeletal maturity necessary to accurately determine sex (Fig. 3). This approach can be used when there are no teeth available for age estimation, when destructive analysis is not an option, or the research budget does not allow for tooth aging. Although using the fully fused mandibular symphysis is not as accurate as using tooth cementum layers to age walruses (Garlich-Miller et al. 1993), it provides an effective way to gauge maturity for determining sex from mandible measurements.

There is no published information about mandibular fusion with age in walruses. Data from other pinnipeds, however, support the use of bone fusion to estimate maturity (Storå 2000; Jones et al. 2013; Monchot et al. 2013). The variability in the degree of fusion among individuals and between the sexes of walruses is

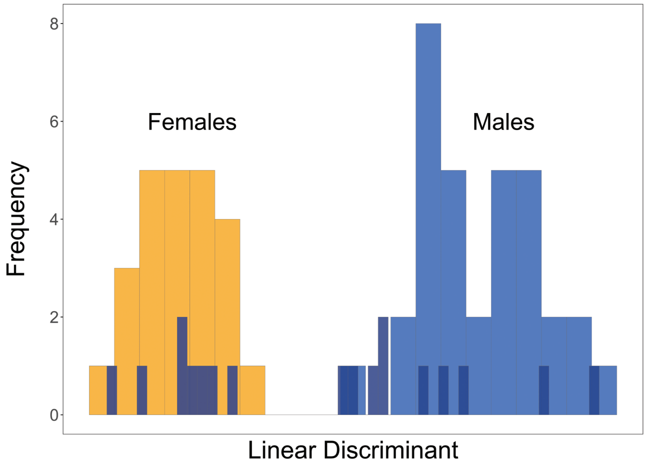

Fig. 4.—Histogram of the linear discriminant values for Pacific walruses (*Odobenus rosmarus divergens*) used in this study. Females are represented by orange, males by blue, and unknown-sex individuals in smaller indigo columns.

not well-documented, but it is likely that some variation exists. The strong sexual dimorphism of walruses explains the differences in mandible measurements observed between the sexes. This has been well-documented in the skulls of otariids (sea lions and fur seals), with larger species having more pronounced sexual dimorphism (Brunner et al. 2004). In the present study, two out of 12 walruses with mandibles that were not fully fused (one male and one female) had measurements similar to mature animals, and likely would have been correctly identified to sex if included in the LDFA (Fig. 3). None of the walruses with fully fused mandibles grouped with the wrong sex or with immature animals, suggesting that this approach is slightly conservative.

For archaeological specimens, which can spend hundreds or thousands of years buried in the ground, damage to bones may make data collection difficult or impossible (Hedges et al. 1995). Most of the damage to the archaeological walrus specimens measured for this study was minimal and did not interfere with data collection. In some instances, however, damage to the

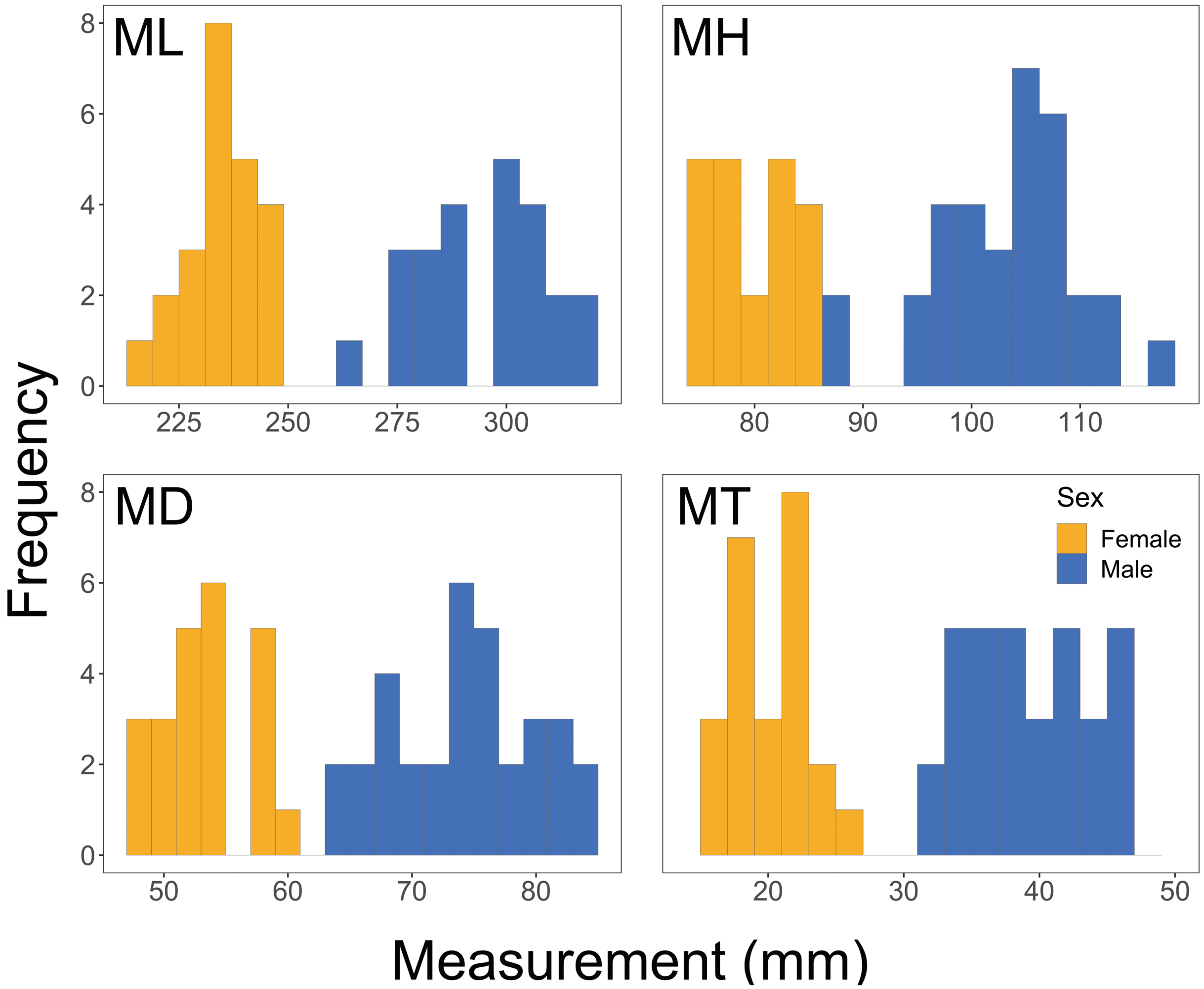

Fig. 5.—Histograms showing the distributions of four mandible measurements (in mm) MH: mandible height; MD: minimum mandible depth; ML: mandible length; MT: minimum mandible thickness, taken on fully fused Pacific walrus (*Odobenus rosmarus divergens*) mandibles. Females in orange, males in blue.

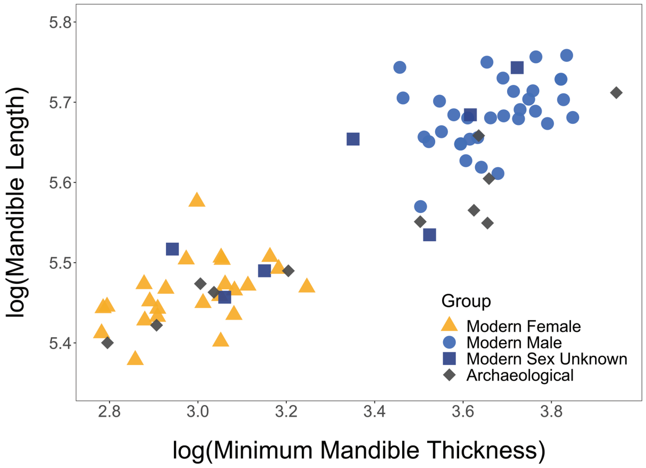

Fig. 6.—Log-log plot of minimum mandible thickness versus mandible length for all sampled Pacific walruses (*Odobenus rosmarus divergens*). Modern female individuals are shown as orange triangles, modern male individuals are shown as blue circles, modern sex unknown individuals are shown as indigo squares, and archaeological walruses as dark gray diamonds.

posterior section of the bone made measuring mandible length and height difficult. Some specimens were too damaged for reliable data collection, most commonly as a result of damage to the coronoid or condylar processes. Erosion or shrinkage of bones can occur when exposed to the elements for extended periods (Hedges 2002). If minor erosion occurred in our archaeological specimens, it apparently did not interfere with sex determination, as these animals clustered closely with bones of known-sex male and female walruses (Fig. 6). There was no indication of bone shrinkage in the selected bones, because there were no split lines or fissures (Tappen 1969); however, heavily eroded mandibles could prove difficult to accurately measure and might not be appropriate for use in this type of study.

Measurements of Pacific walrus mandibles with fully fused symphyses provided accurate determination of sex in known-sex animals, and predicted sex with high confidence (> 90%) in modern and archaeological specimens of unknown sex (Fig. 6). This method allows for sex to be determined for archaeological samples and museum preparations with DNA that is too degraded for analysis, thereby improving the interpretability of past research and informing future studies. This technique is faster and more cost-effective than other methods (i.e., DNA—Fischbach et al. 2008). There was no consistent asymmetry observed in the walrus mandibles (Table 1), making it possible to measure either side of the mandible for classification. This method can be used as long as one side of the mandible is intact, and the mandibular symphysis is fully fused. Additional methods for estimating maturity also may be useful; however, fusion of the mandibular symphysis appeared effective for the specimens in this study.

The ability to assign sex accurately to modern and archaeological Pacific walruses of unknown sex will provide larger sample sizes for studies using cranial material, where sex is important. Female and male walruses have different physiological needs and display strong sexual dimorphism (Fay 1982; Noren et al. 2012, 2014, 2015). Determining sex from mandibles also may allow past research on Pacific walruses to be revisited to increase sample size and improve the interpretations of analyses (e.g., stable isotope, trace element, and hormone analyses) carried out on bones of unknown-sex walruses (e.g., Charapata et al. 2018; Clark et al. 2019).

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Mean of triplicate measurements (in mm) taken from left and right Pacific walruses (*Odobenus rosmarus divergens*) mandibles with fully fused mandibular symphysis. Catalog numbers (UAM ID) were assigned by the researcher (NT) when UAM ID was unavailable. Time period was abbreviated as: MOD: modern; ARC: archaeological. Sex was noted as: F: female; M: male; U: unknown. Measurements are abbreviated as: LML: left mandible length; LMH: left mandible height; LMD: left minimum mandible depth; LMT: left minimum mandible thickness; RML: right mandible length; RMH: right mandible height; RMD: right minimum mandible depth; RMT: right minimum mandible thickness. female: $n = 28$, male: $n = 42$, unknown sex: $n = 21$.

Supplementary Data SD2.—Posterior probabilities of sex assignments from linear discriminant function analysis (LDFA) for Pacific walruses (*Odobenus rosmarus divergens*) with fully fused mandibles. Individual identification numbers were assigned by the researcher (NT) when UAM ID was unavailable. female: $n = 24$, male: $n = 33$, unknown sex: $n = 19$.

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APPENDIX I

Sex and locality information of Pacific walruses (*Odobenus rosmarus divergens*) with fully fused mandibles. University of Alaska Museum catalog numbers (UAM catalog number) were used to identify specimens. For those without UAM catalog numbers, an identifier was assigned by the authors. Time period was abbreviated as: MOD: modern; ARC: archaeological.

UAM Catalog Number	Time Period	Sex	Location	Region
UAM:Mamm:10538	MOD	Female	Kotzebue Sound	Chukchi Sea
UAM:Mamm:11684	MOD	Female	Unknown	Bering Sea
UAM:Mamm:11685	MOD	Female	Unknown	Bering Sea
UAM:Mamm:11691	MOD	Female	St. Lawrence Island	Bering Sea
UAM:Mamm:11692	MOD	Female	St. Lawrence Island	Bering Sea
UAM:Mamm:11696	MOD	Female	St. Lawrence Island	Bering Sea
UAM:Mamm:11700	MOD	Female	St. Lawrence Island	Bering Sea
UAM:Mamm:11705	MOD	Female	St. Lawrence Island	Bering Sea
UAM:Mamm:11707	MOD	Female	St. Lawrence Island	Bering Sea
UAM:Mamm:11708	MOD	Female	St. Lawrence Island	Bering Sea
UAM:Mamm:11709	MOD	Female	St. Lawrence Island	Bering Sea
UAM:Mamm:11710	MOD	Female	St. Lawrence Island	Bering Sea
UAM:Mamm:16586	MOD	Female	Nushagak Bay	Bering Sea
UAM:Mamm:16587	MOD	Female	St. Lawrence Island	Bering Sea
UAM:Mamm:16588	MOD	Female	St. Lawrence Island	Bering Sea
UAM:Mamm:16589	MOD	Female	St. Lawrence Island	Bering Sea
UAM:Mamm:16590	MOD	Female	St. Lawrence Island	Bering Sea
UAM:Mamm:16591	MOD	Female	St. Lawrence Island	Bering Sea
UAM:Mamm:16592	MOD	Female	St. Lawrence Island	Bering Sea
UAM:Mamm:16593	MOD	Female	St. Lawrence Island	Bering Sea
UAM:Mamm:99597	MOD	Female	Hagemeister Island	Bering Sea
UAM:Mamm:125957	MOD	Female	Point Lay	Chukchi Sea
UAM:Mamm:130619	MOD	Female	Chukchi Sea	Chukchi Sea
UAM:Mamm:130620	MOD	Female	Chukchi Sea	Chukchi Sea
UAM:Mamm:130625	MOD	Female	St. Lawrence Island	Bering Sea
UAM:Mamm:134799	MOD	Female	Nome	Bering Sea
UAM:Mamm:4861	MOD	Male	Barrow Quad	Chukchi Sea
UAM:Mamm:5220	MOD	Male	St. Lawrence Island	Bering Sea
UAM:Mamm:7277	MOD	Male	St. Lawrence Island	Bering Sea
UAM:Mamm:11649	MOD	Male	St. Lawrence Island	Bering Sea
UAM:Mamm:11711	MOD	Male	St. Matthew Island	Bering Sea
UAM:Mamm:11694	MOD	Male	St. Lawrence Island	Bering Sea
UAM:Mamm:12069	MOD	Male	Round Island	Bering Sea
UAM:Mamm:12070	MOD	Male	Round Island	Bering Sea
UAM:Mamm:12071	MOD	Male	Round Island	Bering Sea
UAM:Mamm:12073	MOD	Male	Round Island	Bering Sea
UAM:Mamm:12074	MOD	Male	Nushagak Bay	Bering Sea
UAM:Mamm:12075	MOD	Male	Nushagak Bay	Bering Sea
UAM:Mamm:12076	MOD	Male	Round Island	Bering Sea
UAM:Mamm:12077	MOD	Male	Round Island	Bering Sea
UAM:Mamm:12078	MOD	Male	Round Island	Bering Sea
UAM:Mamm:12079	MOD	Male	Round Island	Bering Sea
UAM:Mamm:12080	MOD	Male	Nushagak Bay	Bering Sea
UAM:Mamm:12081	MOD	Male	Nushagak Bay	Bering Sea
UAM:Mamm:12082	MOD	Male	Nushagak Bay	Bering Sea
UAM:Mamm:12083	MOD	Male	Nushagak Bay	Bering Sea
UAM:Mamm:12084	MOD	Male	Nushagak Bay	Bering Sea
UAM:Mamm:12085	MOD	Male	Nushagak Bay	Bering Sea
UAM:Mamm:12086	MOD	Male	Nushagak Bay	Bering Sea
UAM:Mamm:14793	MOD	Male	Nushagak Bay	Bering Sea
UAM:Mamm:87001	MOD	Male	Hagemeister Island	Bering Sea
UAM:Mamm:87003	MOD	Male	Hagemeister Island	Bering Sea
UAM:Mamm:87004	MOD	Male	Hagemeister Island	Bering Sea
UAM:Mamm:87006	MOD	Male	Bristol Bay	Bering Sea
UAM:Mamm:87009	MOD	Male	Bristol Bay	Bering Sea
UAM:Mamm:87329	MOD	Male	Nushagak Bay	Bering Sea
UAM:Mamm:87330	MOD	Male	Hagemeister Island	Bering Sea
UAM:Mamm:99578	MOD	Male	Nushagak Bay	Bering Sea
UAM:Mamm:99586	MOD	Male	Nushagak Bay	Bering Sea
UAM:Mamm:99596	MOD	Male	Hagemeister Island	Bering Sea
UAM:Mamm:134798	MOD	Male	Nome	Bering Sea
UAM:Mamm:5218	MOD	Unknown	Point Hope	Chukchi Sea
UAM:Mamm:99584	MOD	Unknown	Bristol Bay	Bering Sea
UAM:Mamm:125513	MOD	Unknown	Hagemeister Island	Bering Sea
UAM:Mamm:125515	MOD	Unknown	Bristol Bay	Bering Sea

APPENDIX I. Continued

UAM Catalog Number	Time Period	Sex	Location	Region
"Elephant Point"	MOD	Unknown	Unknown	Unknown
"House 1"	MOD	Unknown	Unknown	Unknown
"Newspaper"	MOD	Unknown	Unknown	Unknown
"Orange bone"	MOD	Unknown	Unknown	Unknown
"No ID #1"	ARC	Unknown	Gambell	Bering Sea
"No ID #2"	ARC	Unknown	St. Lawrence Island	Bering Sea
UAM:Arc:UA72-060-0018	ARC	Unknown	St. Lawrence Island	Bering Sea
UAM:Arc:UA72-065-0521	ARC	Unknown	St. Lawrence Island	Bering Sea
UAM:Arc:UA72-065-0522	ARC	Unknown	St. Lawrence Island	Bering Sea
UAM:Arc:UA72-065-0525	ARC	Unknown	St. Lawrence Island	Bering Sea
UAM:Arc:UA72-065-0526	ARC	Unknown	St. Lawrence Island	Bering Sea
UAM:Arc:UA72-065-0529	ARC	Unknown	St. Lawrence Island	Bering Sea
UAM:Arc:UA72-065-0530	ARC	Unknown	St. Lawrence Island	Bering Sea
UAM:Arc:UA72-065-0534	ARC	Unknown	St. Lawrence Island	Bering Sea