FLUCTUATING ASYMMETRY AND GENETIC DIVERSITY IN SEA OTTERS (*Enhydra lutris*)

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ABSTRACT

Fluctuating asymmetry (FA) is the measure of minor, random differences between left and right sides in otherwise bilaterally symmetrical organisms. Levels of FA increase with decreasing stability during development and may be related to thermal, chemical, nutritional, genetic and population density factors. Because of the comparative thermal stability in the marine environment, marine mammals may be suitable for studying relations between FA and factors other than temperature. Phylogeographic structuring and population bottlenecks have resulted in differences in genetic diversity among contemporary sea otter populations. Two indices of FA were calculated from ten skull measurements in 442 sea otters from four geographically and genetically distinct populations. We found measurable levels of FA in all populations and FA was a significant source of variation among a sub-sample where repeated measures were made. We found no correlation between FA and haplotype diversity (as a measure of genetic diversity), however, a pattern of increasing FA with decreasing haplotype diversity was discernable with the exception of the California population. The relatively high levels of FA in the California population, where haplotype diversity is also high, may be explained by high contaminant levels. Developmental stress induced by contaminants may override the genetic potential for buffering, leading to increasing FA.

INTRODUCTION

There are three types of asymmetry found in bilaterally symmetrical organisms. Directional asymmetry (DA: characterized by greater development on one side of the organism), antisymmetry (AA: when asymmetry is present but neither side is favored), and fluctuating asymmetry (FA: resulting from organisms' inability to develop perfect symmetry). FA has been used in the past as an estimate of individual as well as population-level fitness. Generally, increasing levels of genetic variability are positively related to increasing fitness among individuals and their populations with increased fitness resulting in lower FA (i.e. greater ability to retain symmetry during development). However, adverse factors during development can result in increasing levels of FA by overriding the benefits incurred by genetic variablity. Previously identified differences in genetic diversity among sea otter populations led us to measure FA in 4 populations, representing the 3 sub-species of sea otters and to test the hypothesis that FA is inversely related to genetic diversity.

METHODS

SKULL COLLECTIONS
Ten metric variables were measured on 442 sea otter skulls from four geographically distinct populations Figure 1. Data were obtained from skulls from Amchitka Island, Alaska (AMC) from 1953-75; Bering Island, Russia (BER) from 1982-85; California (CA) from 1980-91; and Prince William Sound, Alaska (PWS) from 1974-91.

SKULL MEASUREMENTS
Ten paired right and left metric variables were measured from recognizable knobs, condyles or foramen to a tenth of a millimeter using dial calipers Figure 2.

FA CALCULATIONS
We followed the methods detailed in Palmer and Strobeck (1986) to calculate measurement error and FA. We corrected for DA when necessary but found there was no need for size scaling within or among populations. A Bonferroni adjustment to the significance of p-values was used within each population's array of tests (Tsubaki 1998, Rice 1989, Sokal and Rohlf 1995). Two FA indices were calculated. Table 1. To test for FA differences among populations a 2-way (Index 5) or a one way (Index 11) Anova was performed. Tukey's multiple comparisons procedure and Kendall's concordance test were also performed. Haplotype diversities were obtained from Cronin et. al. 1996. Spearman correlations were calculated for each FA index versus mtDNA haplotype diversity.
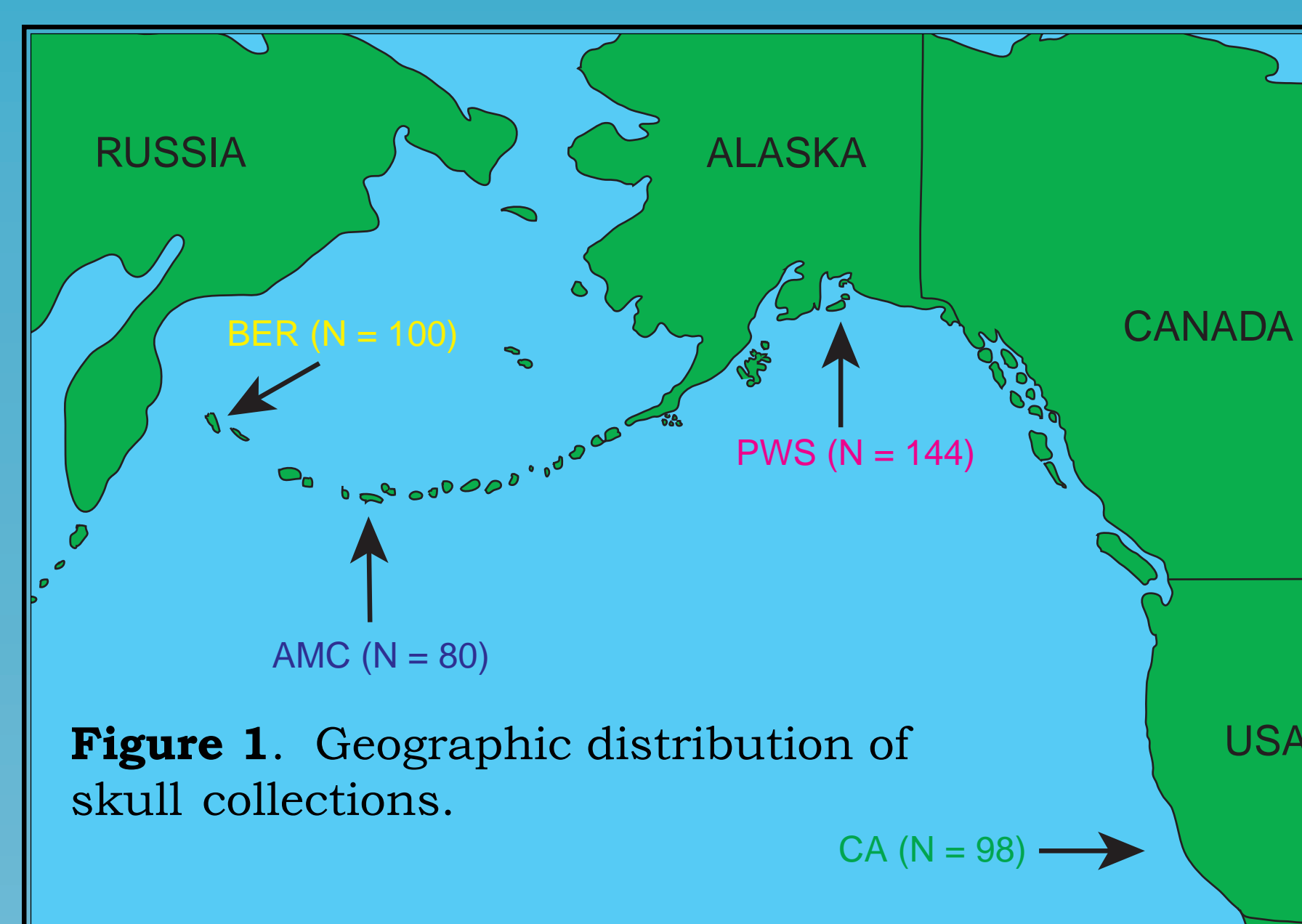

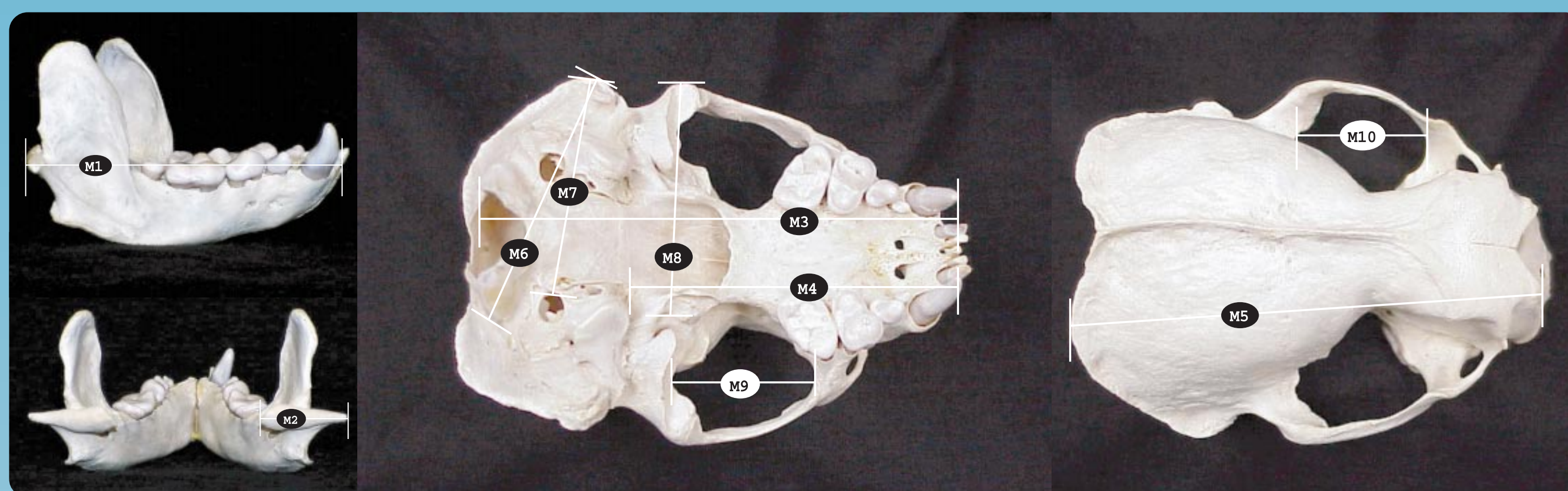**Figure 1**. Geographic distribution of skull collections.

Figure 2. Sea otter skull with 10 traits measured for FA analysis. Each trait was measured on the right and left sides of the skull.

Table 1. FA indices calculated in this study.

Index[a]	Formula[b]	Advantages	Disadvantages
5	$\sum (R - L)^2 / N$	• More power than other indices.	• Difficult to compute. • Biased by DA and AA. • More sensitive to outliers than other indices.
11[c]	$A_i = \sum |R - L|$; $11 = \sum A_i / N$	• Summarizes FA of multiple traits.	• Biased by DA and AA in any trait. • May be biased by one or a few traits.

[a]Palmer, A.R. 1994; Palmer, A.R. and Strobeck, C. 1986.
[b]R = measure of trait on right side. L = measure of trait on left side.
[c]Index 11 was calculated for skulls with a complete set of measurements, thus A_i is a sum of asymmetry per skull.

RESULTS

FA Calculations: Fluctuating asymmetry was found to be measurable and to be a significant source of the observed variation in all but one trait. Distributions characteristic of FA and DA were apparent in all traits. Table 2. No traits in any group had distributions characteristic of AA. M3 displays FA in one, DA in one, and neither form of asymmetry in two populations; therefore this trait was eliminated from further analysis.

AMC consistently had the lowest FA values while the highest FA was split among BER, CA, and PWS (Figure 3). Figure 4 shows FA (Index 5) per trait per population and FA (Index 11) per population. M4 has the largest FA while no one trait has the smallest FA across populations.. AMC has the lowest and CA the highest FA. Table 3.

FA vs Haplotype Diversity: There were no significant correlations between any of the two FA indices and mtDNA haplotype diversity. Excluding the CA population there did appear to be a pattern of decreasing FA with increasing mtDNA haplotype diversity, however this was not significant, Figure 4 shows FA versus mtDNA haplotype diversity for Index 5 and 11.

TRAIT	FA	DA	AA	NONE
M1	3	1	0	0
M2	2	2	0	0
M3	1	1	0	2
M4	4	0	0	0
M5	2	2	0	0
M6	2	2	0	0
M7	3	1	0	0
M8	2	2	0	0
M9	4	0	0	0
M10	4	0	0	0

Table 2. Results of univariate statistics showing the number of populations with the type of asymmetry listed. For example, M1 displayed FA in 3 populations and DA in one. See Figure 2 for traits.

Index	Min (Trait/Loc)	Max (Trait/Loc)	W	p-values
5	0.5571 (M10/AMC)	3.0763 (M4/BER)	0.51	pop: p = 0.01 trait: p = 0.0001 pop * trait: p = 0.05
11	6.9937 (NA/AMC)	8.4184 (NA/CA)	NA	Difference at p < 0.06

Table 3. Minimum and maximum (also the trait and population with each value) fluctuating asymmetry values for each index; Kendall's W statistic showing the degree of concordance between asymmetry and trait across populations. Resulting p-values from 2-way ANOVA (Index 5: pop * trait); 1-way ANOVA (Index 11: pop).
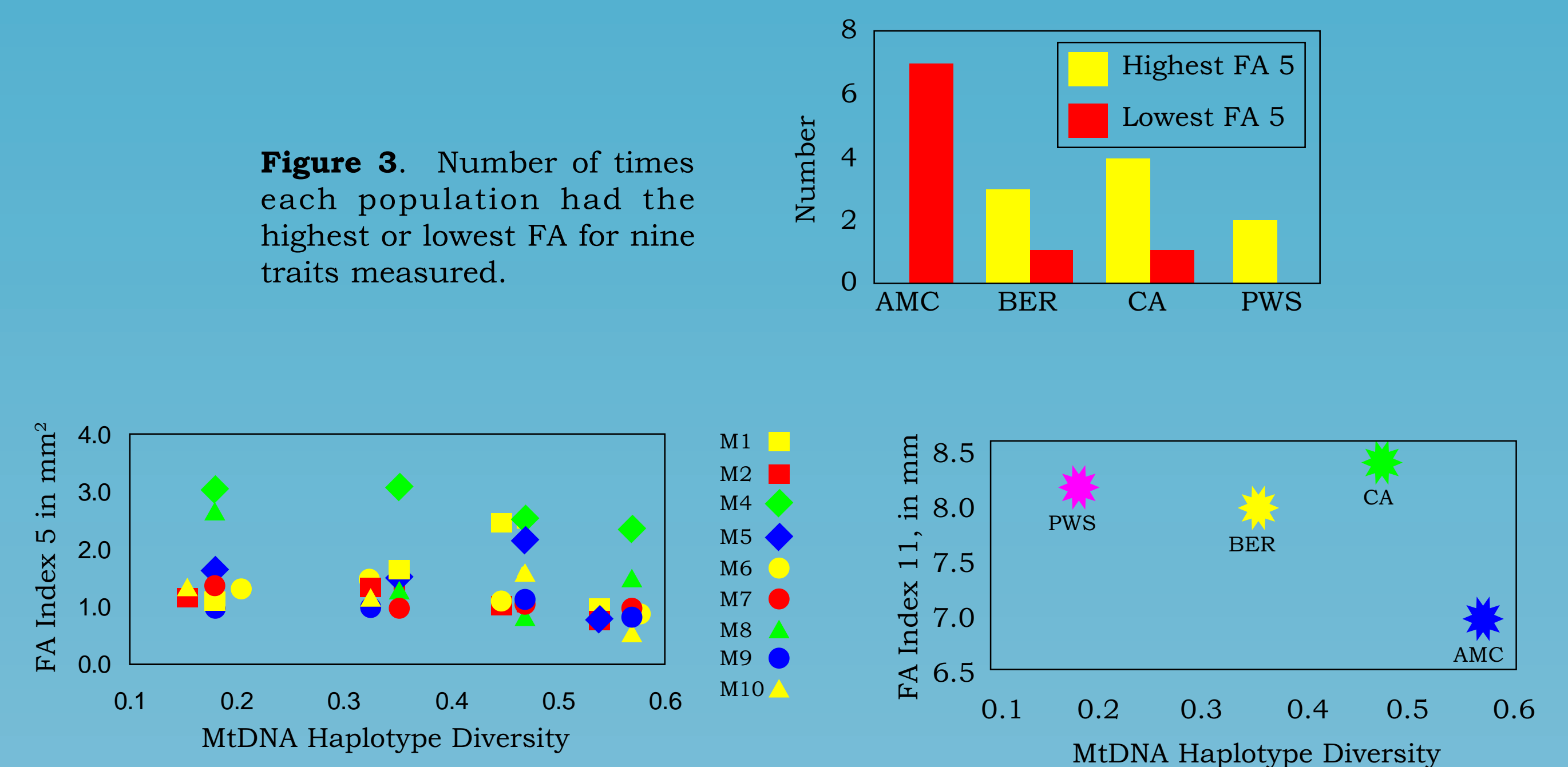

Figure 3. Number of times each population had the highest or lowest FA for nine traits measured.

Figure 4. Fluctuating asymmetry (Index 5 and 11) versus mtDNA haplotype diversity in four populations. Index 11 is a summary index thus there is only one point per population rather than one per trait per population as in Index 5. See Figure 2 for explanations of traits.

CONCLUSIONS

FA is measurable in sea otters and differences exist among populations.

FA in CA is higher than expected based on mtDNA haplotype diversities.

Populations varied in genetic diversity and FA, but not as expected and factors such as contaminants or parasites may have contributed to the patterns we observed.