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Variability in the Skull Morphology of Adult Male California Sea Lions and Galapagos Sea Lions

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Introduction

The skull undergoes a complex developmental process during which strong evolutionary forces shape its morphology. In vertebrates, the skull is important because it encompasses several vital organs such as the brain, the senses, the feeding structures, and a large portion of the respiratory system (Webster and Webster 1974, Kardong 2001, Chai and Maxson 2006). The skull facilitates the gathering of information about the surrounding

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environment, allowing individuals to respond to the particular benefits or threats presented to them. Thus, the skull must be strong enough to protect these vulnerable organs, while also facilitating the stimulation of the eyes, ears, and nose, and permitting food and oxygen intake, brain thermoregulation, and the amplification or reduction of sound (Webster and Webster 1974, Kardong 2001, Chai and Maxson 2006).

In order to understand the phenotypic changes that occurred during skull evolution, we must first obtain information on the sequential interactions between genes, cells, tissues, and organs. Important factors include the distinct patterns of tissue growth and differentiation and the various biomechanical interactions occurring during epigenetic development as well as environmental factors (Chai and Maxson 2006, Hallgrímsson et al. 2007a, Richtsmeier and DeLeon 2009).

Species evolution typically occurs as a result of the mutation rate or selection intensity (Barton and Partridge 2000). The intensity of natural selection responds to the rate of change in environmental conditions (Barton and Partridge 2000) and is determined by the interaction of each organism with its environment (Odling-Smee et al. 2003) in the form of behavior (Duckworth 2009). Thus, environmental changes and behavioral variability between individuals are potential causes of evolutionary change as they alter selection pressures (Badyaev 2005). Natural selection pressures mold distinct morphological traits in different environments. Thus, variability in the anatomical, morphological, and functional characteristics of the skull are a good reflection of evolutionary forces (Webster and Webster 1974, Kardong 2001, Chai and Maxson 2006).

Other researchers have used linear morphometrics to assess California sea lion skull morphology (Orr et al. 1970, Zavaleta 2003), identifying differences between colonies on either coast of the Baja California Peninsula and suggesting that the skull plays an important role in male reproductive success with the skull being used as a defense and attack structure (Zavaleta 2003). Linear morphometrics also revealed differences in skull morphology between the western and central colonies of the Galapagos Islands (Wolf et al. 2008).

Behavior and reproduction

California sea lions *Zalophus californianus* (Lesson, 1828) and Galapagos sea lions *Zalophus wolfebaeki* (Sivertsen, 1953) are ideal species for evaluating patterns of phenotypic divergence for several reasons, including differences in their terrestrial habitats and the distribution of females at different colonies. The latter appears to be associated with the territorial behavior

of reproductive males (Heath 1989, Boness 1991, Bohórquez-Herrera et al. 2014). These species exhibit a lek-like polygynous mating system where males fight each other in front of females in order to acquire territories and mate (Heath 1989, Boness 1991, Robertson et al. 2008, Bohórquez-Herrera et al. 2014).

Recent research has shown that differences in the environmental conditions of California sea lion habitats affect the behavioral plasticity of this species' mating system, with males inhabiting high-temperature environments defending their territories while immersed in water as a thermoregulatory strategy. Such a strategy might result in decreased polygyny in the Gulf of California (GC) colonies relative to those on the Pacific coast (PC) of the Baja California Peninsula (Bohórquez-Herrera et al. 2014).

On the other hand, Galapagos sea lions display distinct territorial behavior, with the breeding season being unaffected by male dominance. Combined with the region's drastic environmental conditions, this characteristic has resulted in an extended reproductive season that lasts five to six months during which females choose males based on their permanence in the area rather than dominance *per se*. Thus, male success in aggressive displays does not play an important role in the breeding system for this species (Pörschmann et al. 2010).

Habitat and distribution

The California sea lion is the only pinniped that permanently inhabits the GC; occasionally, other species also have been spotted there, including *Phoca vitulina* Linnaeus, 1758, *Mirounga angustirostris* (Gill, 1866), and *Arctocephalus townsendi* Merriam, 1897 (Aurioles-Gamboa and Zavala-González 1994). This species' habitat range extends from British Columbia on the southwest coast of Canada to the Islas Marias on the southwest coast of Mexico, including both the western and eastern coasts of the Baja California Peninsula (Lowry and Forney 2005).

California sea lions inhabit 29 colonies in the GC (13 reproductive colonies and 16 resting colonies) (Aurioles-Gamboa and Zavala-González 1994). More than 80% of the population in this area is located on small islands with large rocks, clear substrates, and convex coastlines, as part of a strategy used to avoid high temperatures (Aurioles-Gamboa and Zavala-González 1994, González-Suárez and Gerber 2008, Robertson et al. 2008). On the west coast of the Baja California Peninsula, California sea lions inhabit ten colonies, with pups being most abundant on Cedros Island and the San Benito Islands (Lowry and Maravilla-Chavez 2005).

Galapagos sea lions are distributed throughout the archipelago, primarily in colonies on the eastern islands (San Cristobal and Española); the

species coexists with the fur seal (*Arctocephalus galapagoensis* Heller, 1904), which exclusively inhabits the western islands (Isabela and Fernandina). Despite the relatively reduced habitat of this species, population tendencies reflect high variability, with an increase in the fur seal population and a considerable reduction in Galapagos sea lions on the western side of the archipelago in recent years (Páez-Rosas et al. 2014).

Population structure

As is common among pinnipeds, these species exploit extensive feeding areas and are able to travel long distances, allowing them to aggregate and breed at different colonies (Campagna et al. 2001, Westlake and O'Corry-Growe 2002). However, this high level of dispersion is skewed by sex since females exhibit breeding philopatry; thus, males are nearly seven times more dispersed than females (Lawson and Perrin 2007, González-Suárez et al. 2009). The high degree of male dispersion suggests low spatial segregation in the feeding habitats exploited by individuals from the same colony, or a high interconnection between colonies (González-Suárez et al. 2009, Szteren and Aurióles-Gamboa 2011). Clear separation by ecological zones, which cannot be explained by abundance or population growth alone, has been observed for both sea lion species, a pattern confirmed by intraspecific variation in DNA sequences (Aurióles-Gamboa and Zavala-González 1994, Maldonado et al. 1995, Wolf et al. 2008, González-Suárez et al. 2009).

For California sea lions, variability in mitochondrial DNA (maternal inheritance) and nuclear DNA (both maternal and paternal inheritance) reveals a pattern of isolation due to the distance between reproductive colonies. When combined, these methods can be used to distinguish between individuals from the Benitos Islands (Pacific coast) and GC colonies. Within the Gulf, colonies in the CG-South (Los Islotes) can also be distinguished from those in the GC-Central and GC-North. Nuclear DNA does not distinguish between the GC-Central and GC-North colonies (San Jorge, Los Lobos, Granito, and San Esteban); however, mitochondrial DNA does distinguish these populations (Maldonado et al. 1995, González-Suárez et al. 2009, Schramm et al. 2009).

Based on abundance and degree of territory occupation, the GC population includes three distinct regions: north, central, and south. The GC-North colonies include islands with the highest occupation per unit area, representing > 80% of the population; the GC-Central population includes > 15% of the total population, while the GC-South population includes < 3% of the total population (Aurióles-Gamboa and Zavala-González 1994). Other studies have also grouped this species' colonies based on variables like population size, diet, microbial parasites, and skull diseases (Ward et al. 2010, Szteren and Aurióles-Gamboa 2011).

Microsatellite data as well as mitochondrial DNA suggest isolation due to the distance between Galapagos sea lion colonies, including early signs of genetic differentiation (Wolf et al. 2008).

Foraging ecology

Studies analyzing differences in the foraging ecology behavior exhibited by individuals from different California sea lion colonies have also revealed important information regarding their population structure. Based on more than 40 different studies on the species' diet, Espinosa (2007) identified six different groups in USA and Mexico. These six groups included: (1) San Miguel Island (*Merluccius productus*, *Loligo opalescens*, and *Engraulis mordax*), (2) the northwest coast of the Baja California Peninsula to Punta Eugenia (*E. mordax*, *Sardinops sagax caeruleus*, *Trachurus symmetricus*, and *M. productus*), (3) the southwest coast of the Baja California Peninsula from Punta Eugenia to Magdalena Bay (*L. opalescens*, *M. angustimanus*, and *Kathstotoma averruncus*), (4) Los Islotes in GC-South (*Serranus aequidens*, *Aulopus bajacali*, and *Pronotogrammus multifasciatus*), (5) Farallón de San Ignacio, San Pedro Nolasco, San Pedro Martir, Granito, and Los Cantiles Islands in GC-Central (*E. mordax*), and (6) San Esteban, El Pardito, El Rasito, and Los Machos in GC-Central and GC-North (*S. sagax caeruleus*).

Wolf et al. (2008) identified significant differences in niche partitioning among Galapagos sea lions, with animals in the western region using different food sources than those in the central area. Although there appear to be spatio-temporal differences in foraging strategies in terms of which foraging grounds are used (Páez-Rosas and Auriolles-Gamboa 2013), this species feeds exclusively on fish in both regions of the archipelago (Páez-Rosas et al. 2014).

The goal of this study was to assess the genetic, population, ecological, behavioral, and environmental variability between California sea lions and Galapagos sea lions. We assessed patterns of phenotypic divergence in the skulls of adult males from different California sea lion populations and compared them with the Galapagos sea lion population, as the latter have modified their behavior and habitat use in response to environmental conditions (Wolf et al. 2005).

Materials and Methods

Study area

The study area includes California sea lion reproductive colonies along the west coast of California, USA, and both sides of the Baja California

Peninsula, Mexico (Fig. 1). The GC is located on the east coast of Baja California Peninsula (22° and 32° N and 105°–107° W), measuring 1,200 km by 100–150 km and separating the peninsula from the Mexican mainland (Allison 1964, Lluch-Cota et al. 2007). The largest freshwater discharges in the GC derive from rivers in the mountain regions of Sonora and Sinaloa, while the largest sediment discharge comes from the Colorado River (USA) to the north of the GC (Moore and Curray 1982).

The GC is a high evaporation basin that communicates with the Pacific Ocean to the south. The water surface temperature ranges from 14°C to 21°C in February, and from 28°C to 31°C in August; however, the salinity concentration does not vary drastically (35–35.8 UPS) (Roden 1964).

Unlike the GC, the Pacific coast of the peninsula (PCP) has only a few fluvial systems; however, considerable sediments derive from the Magdalena-Santo Domingo coastal plain (Pedrín-Avilés and Padilla-Arredondo 1999). The PCP is a dynamic zone exposed to important oceanographic events like currents, gyres, and blooms. Specifically, the PCP experiences intense coastal upwellings produced by northwesterly winds that intensify in spring (April to May). Thus, deep offshore waters emerge

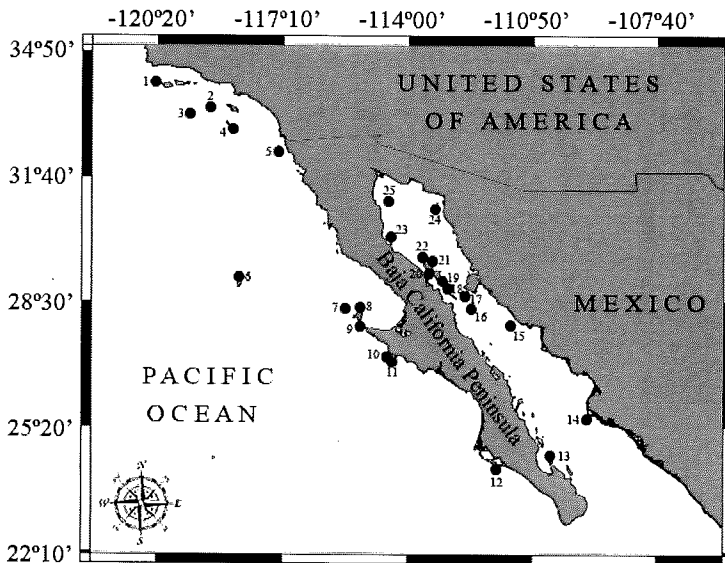


Figure 1. Map showing the location of *Zalophus californianus* reproductive colonies throughout the species' distribution in USA and Mexico. This study compared six population units: PCP-North (1. San Miguel, 2. Guadalupe Island, 7. San Benito Islands, 8. Cedros Island, 9. Natividad Island, 10. San Roque, 11. Asunción Island), PCP-South (12. Santa Margarita Island), GC-South (13. Los Islotes, 14. Farallón de San Ignacio), GC-Central (15. San Pedro Nolasco, 16. San Pedro Mártir, 17. San Esteban, 18. El Rasito, 19. El Partido, 20. Los Machos, 21. Los Cantiles, 22. Granito Island), and GC-North (23. Lobos Island, 24. San Jorge Island, 25. Rocas Consag).

carrying cold waters with a high nutrient concentration to the surface, increasing the phytoplankton population and productivity in the area. The intensity of this phenomenon depends on wind strength, topography, and bathymetry, as well as other oceanographic events like “El Niño” or “La Niña”, which can drastically affect productivity (Espinosa-Carreón et al. 2004, Zavala et al. 2006).

We also analyzed skull samples from Galapagos sea lions *Z. wolfebaeki*. The Galapagos Islands are located in the equatorial Pacific, forming an archipelago (Fig. 2) at the confluence of major ocean currents. Cold waters from the South Equatorial Current circulate from east to west; meanwhile, the Equatorial Counter Current brings subsurface waters from the opposite direction. Moreover, the Panama Current provides warm waters from the northeast; its intensity varies seasonally, and it indirectly influences atmospheric pressure differentials (i.e., “El Niño”) from the Pacific Basin. The affluents of different bodies of water also generate distinct points of upwellings along the continental coast, mostly around the islands located on the western end of the archipelago (Feingold and Glynn 2014).

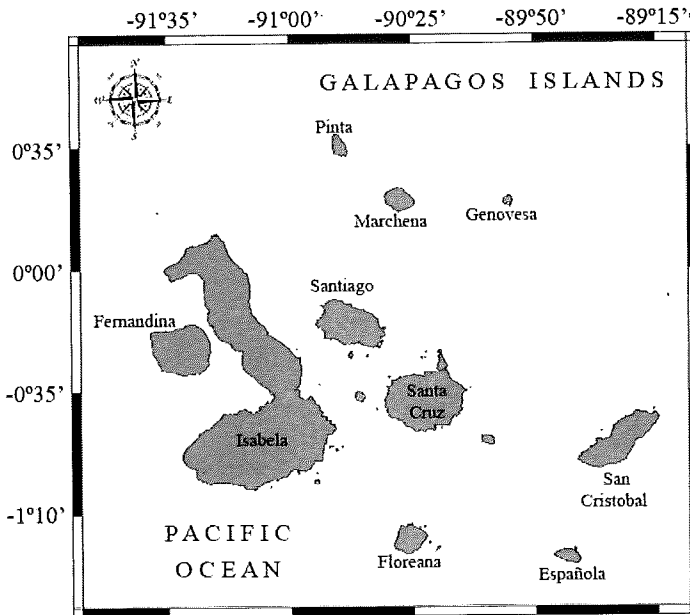


Figure 2. Map showing the *Zalophus wolfebaeki* reproductive colonies on the Galapagos Islands (Equatorial Pacific).

Skull morphology

Photographic collection

For the morphological characterization, photographs were taken from the dorsal, ventral, and lateral views of the adult male skulls. The PCP-North California sea lion skulls (see Fig. 1) are from the Mammalogy Department at the Natural History Museum of Los Angeles County in California, USA. Skulls from the populations inhabiting Mexican coasts are from the Laboratorio de Ecología de Pinipedos "Burney J. Le Boeuf" at the Centro Interdisciplinario de Ciencias Marinas (CICIMAR, Interdisciplinary Center for Marine Sciences) of the Instituto Politécnico Nacional (IPN, National Polytechnic Institute) located in La Paz, Baja California Sur, Mexico. We obtained photographs of Galapagos sea lion skulls from the Ornithology and Mastozoology Collection at the California Academy of Sciences in San Francisco, California, USA. We only performed the morphological analysis on skulls with complete structures in order to ensure that the landmarks could be located; thus, the sample number for each view varied depending on how damaged the visible structures of a particular view were (Table 1).

Table 1. Skull sample size for each view of each population analyzed.

Region	Dorsal view	Ventral view	Lateral view
PCP-North	51	50	52
PCP-Central	8	7	10
PCP-South	54	39	54
GC-North	4	0	5
GC-Central	65	56	68
GC-South	16	6	15
<i>Z. wollebaeki</i>	8	8	7
TOTAL	206	166	211

Geometric morphometrics

Skull morphology was assessed using geometric morphometrics (GM), one of the newest methods for studying shape variation; it is also considered the most suitable methodology for cephalometrics studies (Bookstein 1991, Rohlf and Marcus 1993, McIntyre and Mossey 2003). This technique

evaluates morphological information using landmarks on anatomical structures that adequately describe the design of those structures; the locations of these landmarks are then translated to Cartesian coordinates in two- or three-dimensional space (Van der Molen et al. 2007).

The use of GM eliminates differences in the size, position, and orientation of each object; thus, the resulting information refers only to its geometric configuration (Rohlf and Slice 1990). This permits the use of a wide range of statistical tools that not only ensure the correct interpretation of morphological variation but also facilitate identification of its causes (Adams et al. 2013b). Thus, the combination of GM and multivariate statistics (the essence of this technique) allows us to characterize structural morphology completely and without redundancy (Klingenberg 2013a).

GM takes into account the spatial relationships between landmarks without the need to predefine the set of features to sample (Klingenberg 2013a). Thus, GM facilitates analysis of biological forms, preserving physical structure, maintaining geometric relationships, and permitting analysis of morphological variation from a global perspective. Moreover, this technique enables us to make statistical comparisons of morphology, generating graphical representations that facilitate visualization of the direction, location, and magnitude of each morphological variation (Adams and Funk 1997, Van der Molen et al. 2007, Adams et al. 2013a, Klingenberg 2013b).

Two types of marks are used for this procedure: landmarks and sliding landmarks (Fig. 3). Landmarks are homologous variables on particular structures with common ancestral origin that can be easily identified on the phenotype (Bookstein 1991, Adams et al. 2004, Polly 2008). Sliding landmarks are homology-free variables applied to the phenotype using a mathematic algorithm "homologous" in its orientation relative to other landmarks. This permits us to include in morphological analysis those areas of each structure that are defined by curves or surfaces that cannot be delimited with landmarks, permitting comparison of morphological variations that have been gained or lost as part of evolutionary processes (Adams et al. 2004, Slice 2007, Polly 2008).

We used TPS software for image processing. Digitized landmarks were translated to two-dimensional coordinates, then a Generalized Procrustes Analysis (GPA) was applied, using geomorph package using R statistical computing environment (Adams et al. 2013a). The GPA makes rotational adjustments, overlapping one landmark over another, and optimizes a goodness of fit measure where the specimens are translated, scaled, and rotated until all position, size, and orientation data have been removed and the only variable remaining is morphology (Rohlf and Slice 1990, Van der Molen et al. 2007).

Sliding landmarks go through an additional process that "slides" them over a curve edge until they fits as closely as possible the position of a reference specimen (Green 1996, Bookstein 1997, Adams et al. 2004). Thus,

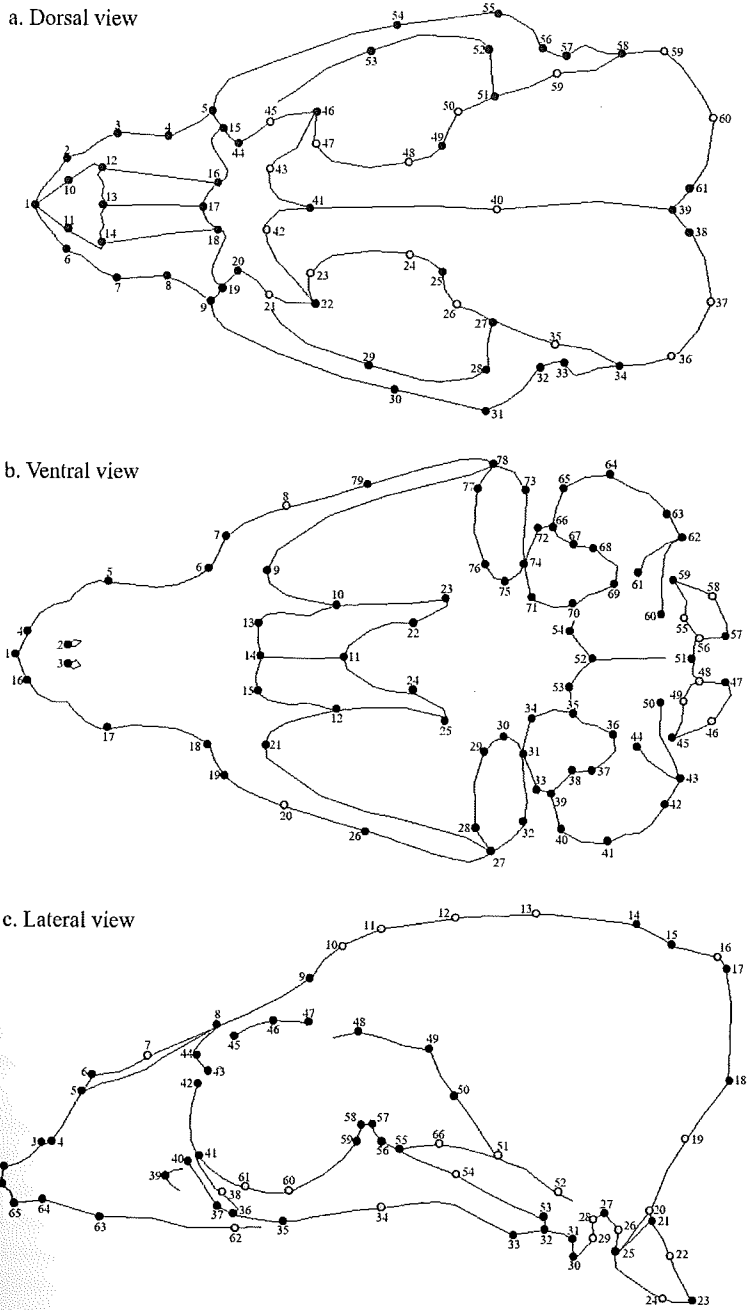


Figure 3. Schema of the (a) dorsal, (b) ventral, and (c) lateral views of the adult male skulls, showing the location of landmarks (black dots) and sliding landmarks (gray dots).

a sliding landmarks can slide along the local direction parallel to the same edge in order to minimize the bending energy needed to produce the relative change of the curve area relative to the reference specimen (Bookstein 1997, Adams et al. 2004, Pérez et al. 2006).

Statistical analyses

We assessed the variation in the GPA data using Principal Component Analysis (PCA). PCA does not take into account the global structure, which is why it does not necessarily reveal groups even when they are present. However, PCA facilitates the identification of changes in morphology associated with the greatest variation; thus, it identifies which aspects of morphology are particularly variable, or particularly constant.

We used multivariate analysis of variance (MANOVA) with posthoc paired tests in order to assess whether there were significant differences between geographically neighboring population. To graphically represent the relationships among population means, we performed an additional PCA of the mean skull shape for each population. Morphological differences were then represented graphically with thin plate splines, which express changes in landmark configuration (morphological changes) as deformations of the tissues in which the landmarks are embedded (Bookstein 1991, Slice et al. 1998, Slice 2007). These procedures were done using geomorph package using R statistical computing environment (Adams et al. 2013a).

Results

We carried out a PCA of all specimens analyzed in order to identify general variation between the California and Galapagos sea lion populations. Because PCA does not consider group structure, none of the resulting figures reflects different population groups (Figs. 4–6). However, these graphic representations enable us to identify changes associated with the greatest variation in order to identify the morphological features that are particularly variable.

The morphological variables responsible for the greatest variation (first component) include the anteroposterior elongation of the dorsal zone of the upper jaw and the frontal zone of the skull (Figs. 4 and 6), the lateral elongation of the zygomatic arches and mastoid process (Figs. 5 and 6), the height of the sagittal crest, the anterior position of the zygomatic arch, and the dorsal process of the temporal apophysis of the zygomatic bone (Fig. 6).

In addition, some other features made a lesser contribution (second principal component), explaining a considerable amount of variation. These included the posterior elongation of the braincase, the posterolateral

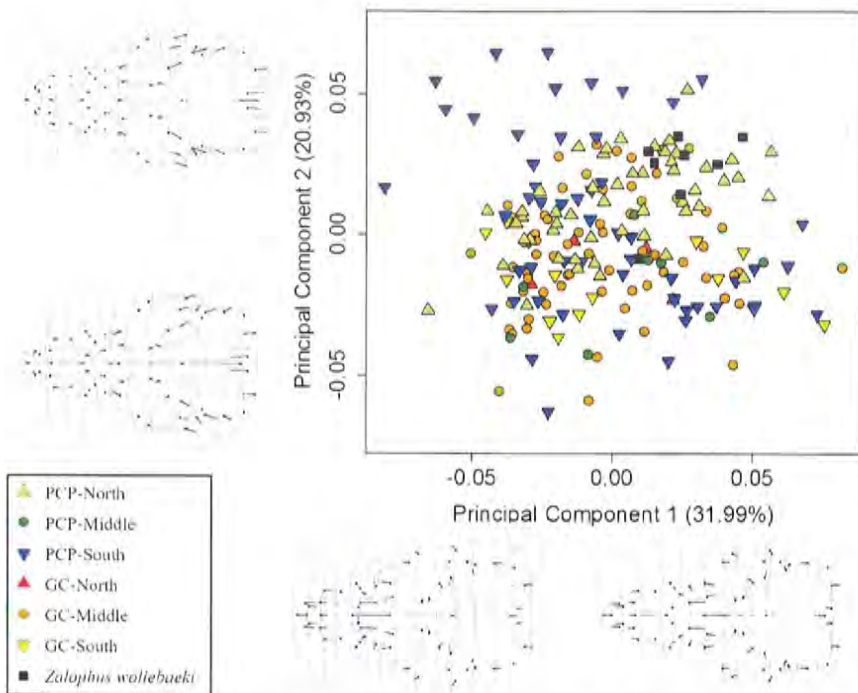


Figure 4. Principal component analysis and thin plate splines of the maximum and minimum values for each component; *dorsal view* of the skulls of all individuals analyzed.

elongation of the zygomatic apophysis of the temporal bone (Fig. 4), the anterolateral elongation of the mastoid apophysis and the tympanic bullae, the anterior elongation of the upper jaw, the anterior position of the occipital condyles (Fig. 5), and the elevation of the zygomatic arches (Fig. 6).

In contrast, some morphological features show more stability, with little variability between sea lion populations. These include the morphology of the nasal bones (Fig. 4), the width of the upper jaw (Figs. 4 and 5), the morphology of the dorsal lamina of the palatine bone, the base of the occipital bone (Fig. 5), the dorsal end of the orbital edge above the temporal apophysis of the zygomatic bone, and the zygomatic apophysis of the frontal bone (Fig. 6).

The MANOVA revealed significant differences between California sea lions and Galapagos sea lions for all of the skull views analyzed (Table 2). The paired comparisons for each view (dorsal, ventral and lateral) showed similar tendencies, with specific differences being explained by the variability of different skull modules. Fewer significant differences were observed between populations based on the ventral view of the skull, while the dorsal and lateral views more clearly separate nearly all neighboring

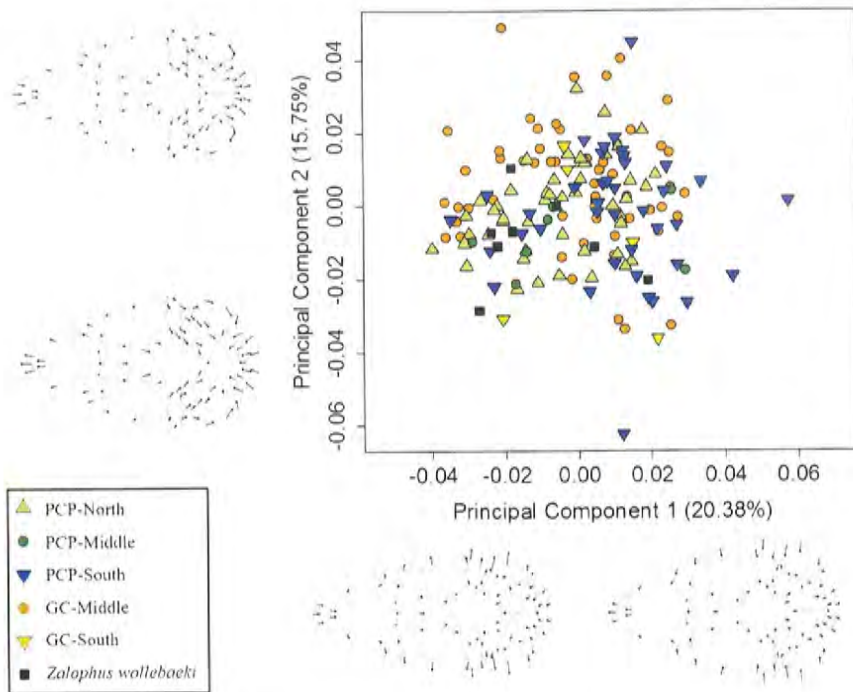


Figure 5. Principal component analysis and thin plate splines of the maximum and minimum values for each component; *ventral view* of the skulls of all individuals analyzed.

populations. The PCP-Central and PCP-South populations were not significantly different, nor were the GC-North and GC-Central populations (Table 2). It is important to note that PCP-Central and GC-North are the populations with the smallest sample size, which may explain the lack of significant differences.

The PCA of the mean skull shapes for each population allowed us to identify morphological variations between sea lion populations. For the dorsal and ventral views (Figs. 7–8), the greatest variation was explained by a strong separation between the *Z. wollebaeki* and *Z. californianus* populations. This difference derives from the posterior elongation of the frontal bone and the braincase in Galapagos sea lions (Fig. 7) and the fact that the smaller occipital condyles and the lateral contraction in the zygomatic apophysis of the temporal bone, the mandibular fossa, and the mastoid process together produce a much thinner skull compared to California sea lions. The dorsal and ventral views also reveal that *Z. californianus* incisors are closer to the tip of the face, and that the bases of the canine teeth are larger than in *Z. wollebaeki* (Figs. 7 and 8).

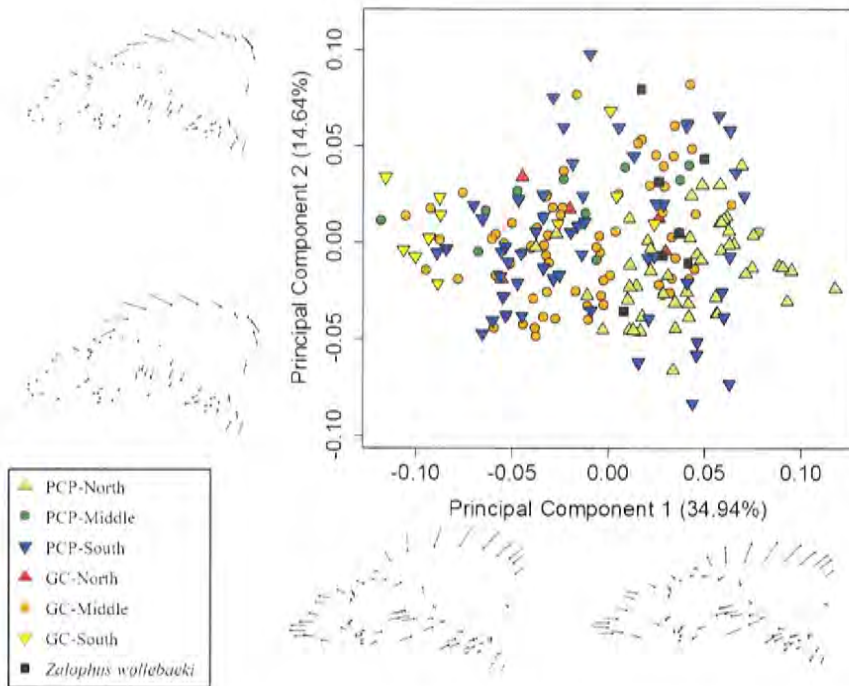


Figure 6. Principal component analysis and thin plate splines of the maximum and minimum values for each component; lateral view of the skulls of all individuals analyzed.

Table 2. MANOVA results and paired comparison (Euclidean distances) for neighboring populations of *Z. californianus* and the *Z. wollebaeki* population for each of the skull views analyzed. Values in bold correspond indicate populations with no significant differences between them.

Paired comparison		Dorsal view		Ventral view		Lateral view	
		$F_{(6,205)} = 3.030$ $p = 0.001$		$F_{(5,168)} = 3.012$ $p = 0.001$		$F_{(6,210)} = 6.283$ $p = 0.001$	
		d	p	d	p	d	p
PCP-North	PCP-Central	0.036	0.013	0.019	0.323	0.069	0.001
PCP-Central	PCP-South	0.030	0.068	0.022	0.095	0.029	0.246
PCP-South	GC-South	0.025	0.029	0.021	0.273	0.040	0.007
GC-South	GC-Central	0.024	0.039	0.027	0.021	0.037	0.015
GC-Central	GC-North	0.024	0.768	-	-	0.031	0.543
PCP-North	<i>Z. wollebaeki</i>	0.043	0.001	0.025	0.013	0.035	0.213
PCP-Central	<i>Z. wollebaeki</i>	0.059	0.002	0.029	0.091	0.067	0.012
PCP-South	<i>Z. wollebaeki</i>	0.049	0.001	0.032	0.001	0.059	0.009
GC-North	<i>Z. wollebaeki</i>	0.062	0.006	-	-	0.070	0.029
GC-Central	<i>Z. wollebaeki</i>	0.053	0.001	0.030	0.001	0.062	0.002
GC-South	<i>Z. wollebaeki</i>	0.055	0.001	0.030	0.089	0.082	0.002

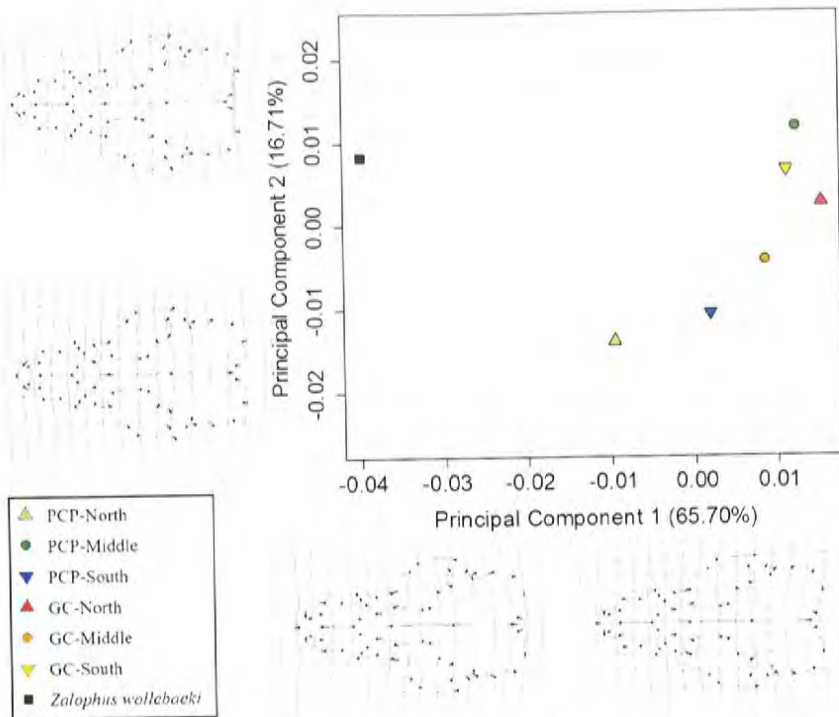


Figure 7. Principal component analysis and thin plate splines of the maximum and minimum values for each component; dorsal view of the mean skull shape for each region.

The paired comparisons of the dorsal view showed significant differences between neighboring populations of California sea lions and the Galapagos sea lion population (Table 2). The exceptions are the PCP-Central and PCP-South ($d = 0.030$, $P = 0.068$), and the GC-North and GC-Central ($d = 0.024$, $P = 0.768$) populations, as no significant differences were identified between them. As mentioned above, these results may be influenced by small sample sizes.

The second component of the dorsal view PCA reveals that the variation between PCP populations is much greater than that between GC populations (Fig. 7). This variation is explained by the posterior elongation of the nuchal crest, the lateral elongation of the zygomatic apophysis of the temporal bone, and the space between incisive teeth being defined by a lateral external bulge (on each side) (Fig. 7). The GC populations are concentrated in the center of this component; meanwhile, the PCP populations show greater variation with PCP-North and PCP-South being located at the negative end of the axis, while PCP-Central is located at the positive end along with Galapagos sea lion population.

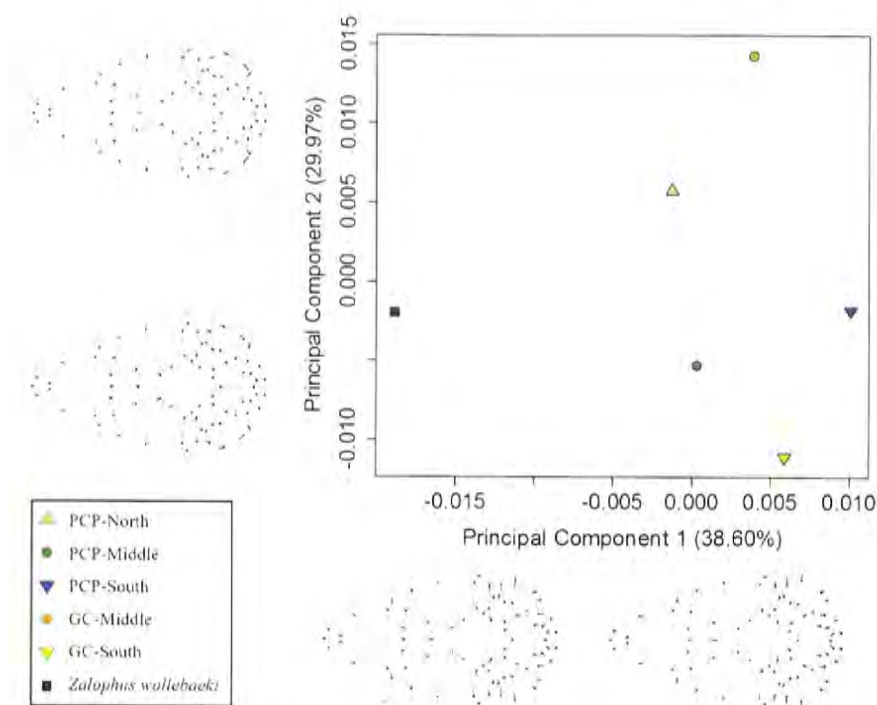


Figure 8. Principal component analysis and thin plate splines of the maximum and minimum values for each component; ventral view of the mean skull shape for each region.

The paired comparisons of the ventral view did not show significant differences between PCP populations (PCP-North vs. PCP-Central, PCP-Central vs. PCP-South), or between PCP-South populations and the GC. Likewise, the Galapagos sea lion population did not differ significantly from the PCP-Central or GC-South populations (Table 2). The Galapagos sea lion population and the PCP populations are located in the center of the axis, indicating less variation in their ventral view features, while the GC-Central and GC-South populations are located on opposing ends of the axis, suggesting considerable variation (Fig. 8). The variability explained by this second component is due to the anterolateral elongation of the mastoid process, the position of the palate fissures, and the lateral elongation of the zygomatic process of the temporal bone (Fig. 8).

Based on the results of the lateral view, the PCP-Central and PCP-South populations were not significantly different from one another nor were they significantly different from the GC-North and GC-Central populations. The Galapagos sea lion population also was not significantly different from the PCP-North population (Table 2). These similarities are represented graphically in the PCA of the lateral view (Fig. 9), where the

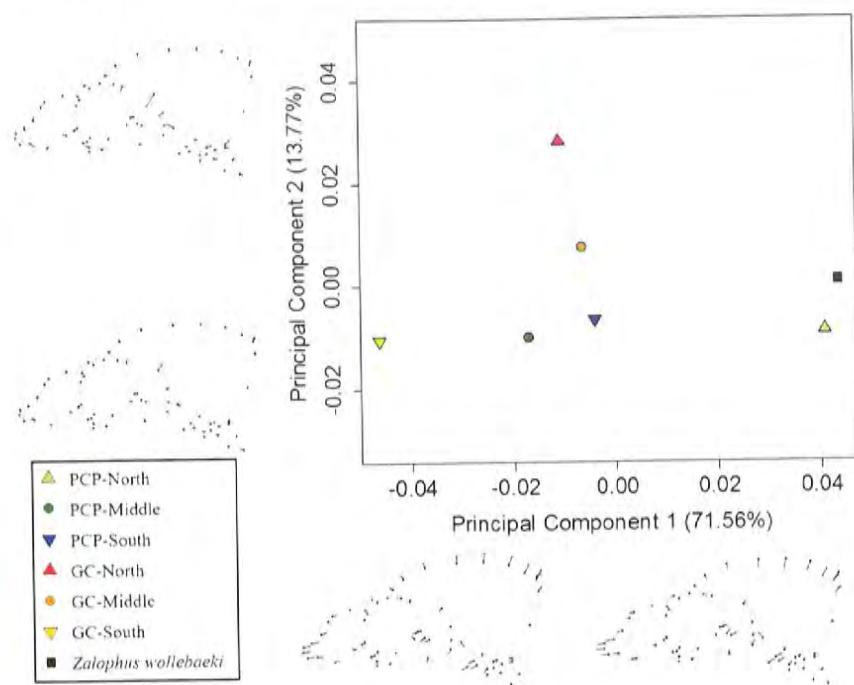


Figure 9. Principal component analysis and thin plate splines of the maximum and minimum values for each component; lateral view of the mean skull shape for each region.

first axis of variation includes the GC-South population at its negative end, while the PCP-North population and the Galapagos sea lion population are located at the positive end. The variability summarized by this axis is associated with the height of the sagittal crest, the anterior elongation of the nasal, incisive, and maxilar bones, and the anteroventral elongation of the zygomatic arches (Fig. 9). The second component explains the variability in GC-North individuals as deriving from the ventral inflection point of the frontal bone where it joins the parietal bone; as well as the position of the infraorbital foramen, and the inflection point of the occipital bone where it joins the mastoid process in the posterior area of the skull (Fig. 9).

Discussion

The skull is composed of several integrated components, the development, functioning, and evolution of which occur simultaneously (Webster and Webster 1974, Kardong 2001, Chai and Maxson 2006, Klingenberg 2013a).

However, this integration is not absolute as the skull is composed of different modules that are relatively independent (Klingenberg 2008, 2010, 2013a).

The cranium, jaws, and teeth are structures that respond differently to environmental and natural selection processes as they are subjected to different genetic, developmental, and functional controls (Caumul and Polly 2005, Rychlik et al. 2006, Hallgrímsson et al. 2007a, b). The amount of time required for the ontogenetic development of each structure is one factor that contributes to morphological variation (Hillson 1986, Kardong 2001, Hallgrímsson et al. 2007a, b). Thus, we divided the skull into three partially independent and embryologically distinct modules: 1. The basicranium, which derives from the chondrocranium; 2. The neurocranium, which is composed of the dermal bones of the cranium; and 3. The face, which derives initially from the splanchnocranium with a posterior development of elements from the dermal bones of the cranium (Hallgrímsson et al. 2007a, b) (Fig. 10).

The cranial base is considered the central integrative structure of the skull (Lieberman et al. 2000, Hallgrímsson et al. 2007a, b) as it is in the center of the skull structure, located under the brain and neurocranium and below and behind the face. As such, the cranial base indirectly acts as a transmitter between the face and the neurocranium (Hallgrímsson et al. 2007a, b). Likewise, the cranial base is the first zone of the skull to reach adult size and shape, primarily growing by endochondral ossification, in which bone tissue is produced from cartilage. The neurocranium fully develops next, followed by the face; unlike the cranial base, these structures develop through intramembranous ossification of sutures, wherein a membrane facilitates bone formation (periosteum). This bone can shape and reabsorb bone tissue, undergoing continuous self-remodeling (Hallgrímsson et al. 2007a, b).

Skull module integration has been the subject of several evolutionary biology studies involving these species and taxonomical groups. Other researchers have employed a variety of statistical techniques to address fundamental biological questions regarding evolutionary, genetic, and functional integration (Klingenberg 2013a). Although we did not evaluate skull structure modularity here, the PCAs provide us with general information on skull structure integration and modularity (Klingenberg 2013a).

Thus, we can infer integration between the described modules (Fig. 10) based on general morphological variations (reflected in the first four principal components) for each skull view (Figs. 4–6). In all cases, there was greater similarity within each module of morphological variation (measured by the direction and magnitude of the vectors) than between them. However, the direction and magnitude of the change varied for different skull modules (Fig. 10). Thus, we infer that each of the

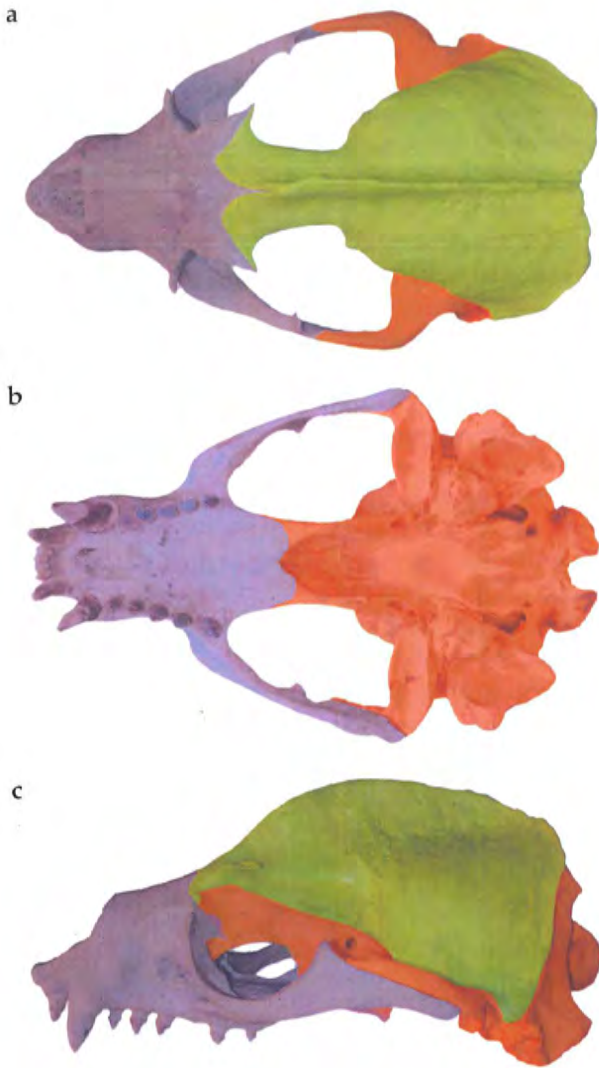


Figure 10. Developmental modules shown on the (a) dorsal, (b) ventral, and (c) lateral views of a *Zalophus californianus* skull (blue: face, green: neurocranium [braincase], red: cranium base).

skull modules develops independently. This has been reported for other mammal species, with modularity reflecting complex integration in skull development (Hallgrímsson et al. 2007a, b). However, our interpretations are based on general patterns of variability in skull integration and modularity. Additional and more specific analyses should be undertaken in order to answer these important biological questions at established levels of confidence (Klingenberg 2013a).

Overall, the greatest morphological variations between California and Galapagos sea lions occurred in the dorsal zone of the upper jaw, the frontal area of the skull, the zygomatic arches, the mastoid process, and the sagittal crest. The braincase reaches adult size relatively early because it serves as a supportive and protective structure for the brain; however, its growth continues as mechanical forces act on it and regulate transcription factors in the sutures (Moss and Young 1960, Opperman et al. 2005). The sagittal crest is a simple bone extension in the central line of the braincase that serves as the adherence point for the temporal muscles; thus, its development is directly associated with the growth of this muscle (Washburn 1947) and the higher sagittal crest, the more developed the temporal muscle. The sagittal crest is a feature with high phenotypic plasticity due to its importance in mastication, defining bite pressure as the movement and force of the mandible is defined largely by the size of the temporal muscles and sagittal crest (Searfoss 1995, Holbrook 2002, Cameron and Groves 2004).

On the other hand, the frontal zone of the face, particularly the jaws and the zygomatic bone, reach adult size after the base and braincase have done so; thus, their somatic growth patterns continue in accordance with the muscles inserted into those bones (Moss and Young 1960, Cheverud 1995, Opperman et al. 2005, Hallgrímsson et al. 2007a, b). As bones that extend on each side of the skull, the zygomatic arches are of great importance as their size and distance from the central skull body are indicators of the relative size of the temporal bones passing through them. They also connect the posterior part of the mandible to the cranium; thus, the larger the aperture of the zygomatic arches, the stronger and larger the temporal muscles, as is the case for most carnivores (Searfoss 1995).

These structures also offer support to the temporal muscles, anchoring the masseter muscles, which are responsible for raising the lower jaw (Searfoss 1995). Several studies have shown that zygomatic arch morphology varies during growth, adjusting to feeding changes that occur during different life stages (Rafferti et al. 2000, Usami and Itoh 2006). The frontal zone of the skull, which includes the zygomatic arches and the dorsal zone of the upper jaw, exhibited greater phenotypic plasticity, reflecting the influence of the environment on the organisms' ontogeny (Cheverud 1995, Opperman et al. 2005). The morphological variability of the skulls of different sea lion populations reflects the diversity and availability of feeding resources throughout their distribution.

In contrast, the cranial base is less affected by the environment during ontogenetic development as it is the first region of the skull to reach adult size, it acts as a base that supports the brain structure, and it is the confluence of many nerves and blood vessels (Cheverud 1995, Lieberman et al. 2000, Opperman et al. 2005). The morphological variations observed on the ventral view were associated with the components previously

mentioned (zygomatic arches and upper jaw), as well as the mastoid process. Considering the early development of the cranial base, the variability present in the mastoid process may reflect directional selection rather than phenotypic plasticity.

The mastoid apophysis is a rounded projection of the temporal bone located behind the ear canal. It is important as an area of adherence for the muscles associated with head movements like the splenius capitis, longissimus capitis, and sternocleidomastoid. The sternocleidomastoid muscle originates in the manubrium extending from the medial third of the clavicle to the mastoid process and superior nuchal line of the occipital bone; it is responsible for controlling lateral flexion (nodding) and rotation (turning the head left and right). The splenius capitis originates in the first dorsal vertebrae in the dorsal cervical ligament of the neck; inserted in the occipital bone and the mastoid process, it permits unilateral tilting and rotation of the head in the same direction. Finally, the longissimus capitis refers to the "minor complex" (semispinalis) and originates in the sixth thoracic dorsal vertebra and extends to the occipital bone and the mastoid process; its function is focused on extension, tilt, and rotation movements (Tate 2009).

Recently, Bohórquez-Herrera et al. (2014) reported a significant change in the behavior of individuals in terms of where they spend most of their time. This study highlighted how the *Z. californianus* mating system was affected by changing environmental conditions, with males inhabiting high temperature environments in the GC spending most of their time immersed in the water as a thermoregulatory strategy. This change in mating behavior was exhibited even when males were defending their territories, displaying aggression toward male competitors by chasing (swimming) them, biting them, and destroying their fins. This behavior is a complete behavioral transformation of the mating system originally described for this species (Heath 1989, Boness 1991), which is still present in the PCP populations where males defend their territories on land (Bohórquez-Herrera et al. 2014).

The lateral elongation of the mastoid process in the sea lions populations analyzed here implies that there is an important variation in the adhesion areas of these muscles; thus, when the area of articulation increases, the length of the lower arm of the head muscles also increase (Antón and Galobart 1999), providing greater contraction power (Salesa et al. 2005). Following Bohórquez-Herrera et al. (2014), we argue that morphological variation in the mastoid process is related to variation in neck movements, and differences in the force of gravity acting on individuals who spend most of their time in the water versus those that remain on land.

We also observed variation in the development of different skull modules between the different populations of California sea lions and the Galapagos sea lion population. The ventral view, which is mainly

composed of the cranial base module (Fig. 10), includes the fewest significant differences between populations (Table 2). This view only allowed us to discriminate between the GC-Central and GC-South populations, as well as between the Galapagos sea lion population and the PCP-North, PCP-South, and GC-Central populations.

Despite the small size of the Galapagos sea lion population (Table 1), the cranial base is significantly different from the California sea lion populations. The lack of significant differences between the Galapagos population and PCP-Central and GC-South California sea lion populations might be related to the small sample size.

The different skull views analyzed allowed us to differentiate each California sea lion population from the Galapagos sea lion population based on the first PCA component of variation. These analyses showed that *Z. wolfebaeki* is characterized by a thin skull due to the lateral contraction of the zygomatic apophysis of the temporal bone, the mandibular fossa, and the mastoid process. This equatorial population also exhibited a reduced area at the base of canine teeth and smaller occipital condyles. The front area and braincase are posterior elongated, while the nasal, incisive, and maxillary bones are anterior elongated. The species also presents a low sagittal crest and thin, dorsal elongated zygomatic arches.

The separation between the Galapagos sea lion population and the California sea lion populations is based on variation in the development of three skull modules. The cranial base is responsible for many of these differences (zygomatic process of the temporal bone, mandibular fossa, mastoid process, and occipital condyles), reflecting the fact that skull features separate the two species at the evolutionary level. Moreover, variations in the modules of the face and the braincase likely represent the influence of environmental factors.

Using linear morphometrics, Zavaleta (2003) analyzed the skull morphology of adult males of these two species, finding that the principal differences were in the face area (condyle-canine length, upper jaw length, palate length, incisor foramen length, and interorbital minimum width), with only one difference being associated with the cranial base (length of the posterior lacerate foramen). This is in contrast to our study, in which the cranial base included many significant differences that distinguish these two species.

The morphological variations identified in the face module are associated with the variability of the Galapagos population; a low, but significant genetic and morphological differences have been reported between populations on western versus central islands (Wolf et al. 2008). Morphological variations in the dorsal and lateral zones of the mandible and face separate these populations (Wolf et al. 2008). Finally, the morphological variability in the braincase is likely due to environmental factors.

Since the first axis of variation of the PCA clearly separated the two species, the morphological variability within California sea lion populations was observed mostly on the second axis of variation. In the ventral view, the separation between GC populations was based mostly on variation in the mastoid apophysis; in the GC-Central they are posterior elongated, while in the GC-South they are anterior elongated (PC2, Fig. 8). The cranial base is the first module that reaches adult size and shape; thus, morphological variations are generally associated with processes of natural selection, rather than phenotypic plasticity. As a result, the minimal morphological variability in the cranial base of PCP populations may be due to a normalizing selection. In contrast, selection does not seem to favor mean shapes among the GC populations; thus, we argue that disruptive or directional selection processes are at work in this region.

In contrast, for the dorsal view we observed greater variability between the PCP and CG populations (shorter distance between the third incisor and the tip of the face, posterior elongation of the nuchal crest, and lateral elongation of the temporal zygomatic process) (CP2, Fig. 7). Variability in this view mainly derived from two modules that reach adult size and shape late in individual ontogeny (face and braincase); thus, variability is likely a reflection of environmental factors.

Despite the fact that face and braincase variability of California sea lion populations was relatively low in the dorsal view, the lateral view revealed considerable variation in these two modules associated with environmental factors. In the lateral view, the PCP-Central and -South populations did not show significant differences as they have little morphological variability (defined by the first two components of variation in the PCA) relative to other populations. Likewise, the GC-North and GC-Central populations showed little variation in the main axis of morphological variation, and both are separated from the GC-South population as the latter presents skulls with high sagittal crests, posterior compressed frontal zones, and wide zygomatic arches. The PCP-North population presented opposing features, and was more similar to Galapagos sea lions.

Thus, the lateral view of the skull showed a high variability in the three skull modules for the different California sea lion populations; the GC-North and GC-Central populations in particular stand out as they exhibit anteroventral elongated braincases. The high morphological variability indicates that the lateral view of the skull best reflects the influence of environmental variability during ontogenetic development. This is observed in sea lion skull morphology in the form of higher sagittal crests.

The skull morphology analysis previously carried out by Zavaleta (2003) identified one PCP population of California sea lions and two GC

populations. In the present study, we identified a clear segregation of the PCP-North population from the PCP-Central and PCP-South populations. Likewise, the GC-South population we separated from the GC-North and GC-Central populations present in the Gulf of California.

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Keywords: pinniped skull, morphology, sagittal crest, basicranium, zygomatic arches, evolution, California sea lion, Galapagos sea lion

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TROPICAL PINNIPEDS

Bio-Ecology, Threats and Conservation

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