

Context-dependent niche variation and fitness consequences in California sea lions

by

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ABSTRACT

Niche variation among sexes and life stages within a population has been documented in many species, yet few studies have investigated niche variation within demographic groups or across ecological contexts. We examined the extent to which pregnant California sea lions (*Zalophus californianus*) at each of three breeding colonies target alternative prey resources and habitats. The three colonies are distributed across distinct regions of the Gulf of California, Mexico and have divergent population dynamics. We compared the nature of niche variation among colonies and investigated the fitness consequences of different foraging strategies within each colony. We analyzed the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from fur collected from 206 suckling pups to characterize relative maternal foraging locations ($\delta^{13}\text{C}$) and trophic levels ($\delta^{15}\text{N}$) during the metabolically demanding late stages of gestation and lactation that occur simultaneously in California sea lions. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were regressed against pup body condition index values to compare the relative individual-level fitness benefits of different maternal foraging strategies. We found that the nature and extent of niche variation differed among colonies. Niche variation was most pronounced at the two largest colonies that appear to experience the highest levels of intraspecific competition and the variation was consistent with habitat features. One colony (Granito) displayed two distinct foraging groups with indistinguishable median pup body condition values, whereas the second (San Jorge) exhibited continuous niche variation and pup body condition varied in relation to maternal foraging location and trophic level, suggesting disparities among alternative foraging strategies. For the smallest colony (Los Islotes), females occupy similar niches with a few outliers. Body condition values of pups at this colony were most variable, but

did not vary with maternal foraging strategy. Our results provide evidence for intrapopulation niche variation among demographically similar individuals during a period of high metabolic stress and reproductive importance. This work suggests possible fitness benefits conferred by alternative foraging strategies, and calls into question the common assumption that members of a population are ecologically equivalent. Future research aimed at understanding animal foraging strategies should consider the nature and extent of niche variation in the context of local ecological conditions.

DEDICATION

To my amazing husband, Daniel, and friends in the Gerber Lab.

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Introduction

Individuals are the foundation of ecological systems and their behaviors influence population dynamics, community structure, ecosystem functioning, and evolutionary processes (Lomnicki 1988; Bolnick *et al.* 2003). However, consideration of individual-level dynamics is relatively uncommon among both population models and management efforts that operate with the assumption that members of a population are ecologically equivalent (Kendall & Fox 2002; Bolnick *et al.* 2003; Chase & Leibold 2003; Dunne 2006). There is growing evidence that persistent inter-individual behavioral differences are ubiquitous in generalist populations, fostering an intensified interest in understanding the nature and extent of intrapopulation niche variation within and across ecological contexts (Van Valen 1965; Chilvers & Corkeron 2001; Bolnick *et al.* 2003; Bolnick *et al.* 2007; Tinker, Bentall & Estes 2008; Chilvers & Wilkinson 2009; Vander Zanden *et al.* 2010; Lowther *et al.* 2011).

Divergent foraging behaviors within a population may be important in the context of wildlife management because such patterns imply inter-individual differences in direct and indirect ecological interactions (Holbrook & Schmitt 1992; Chilvers & Corkeron 2001; Sih, Bell & Johnson 2004; Quevedo, Svanbäck & Eklöv 2009; Votier *et al.* 2010; Bolnick *et al.* 2011). Individuals targeting alternative resources are exposed to different selective pressures and risks (e.g., predation, anthropogenic impacts), and may respond differently to management actions (Bolnick *et al.* 2003). Moreover, fitness consequences associated with an individual's activities may alter the likelihood of their survival and reproduction, directly affecting overall population vital rates (Vindenes, Engen & Saether 2008).

The ecological drivers of fine scale intrapopulation niche partitioning are poorly understood. Controlled experiments and computer simulations indicate that when competition among conspecifics increases, due to prey resource reduction, an increase in predator population size, or other environmental factors, individuals will target new foraging patches or add alternative prey to their diet (Holbrook & Schmitt 1992; Svanbäck & Bolnick 2007; Araújo, Bolnick & Layman 2011). Individuals may target different alternative resources or the same alternative resources in differing proportions, depending upon their preference rankings, optimization criteria, and/or abilities (Araújo, Bolnick & Layman 2011). For example, Tinker et al. (2008) report distinct behaviorally-based consistent variation in foraging that is associated with improved foraging efficiency for individually preferred prey in a high-density subpopulation of California sea otters (*Enhydra lutris nereis*, Linnaeus 1758) within a food-poor environment. In contrast, individual sea otters in a low-density subpopulation within a food-rich environment exhibit similar diets comprised primarily of preferred sea urchin prey (*Strongylocentrotus purpuratus*, Stimpson 1857, and *S. franciscanus*, A. Agassiz 1863).

Within a population, niche variation may be discrete, continuous, or a combination of the two (Bolnick *et al.* 2003; Araújo *et al.* 2010). In cases of discrete variation, individuals can be classified into groups with different ecologies (e.g., groups that use different habitats and/or target different prey). This is typically a consequence of phenotypic differences due to life stage (i.e., ontogenetic shifts, Werner & Gilliam 1984), sex (i.e., sexual dimorphism, Shine 1989), or morphology (i.e., resource use polymorphism, Skulason & Smith 1995; Bolnick *et al.* 2003). In other cases, individuals may occupy unique, but overlapping, portions of a population's ecological niche, which

results in continuous niche variation at the population level (Estes *et al.* 2003; Araújo *et al.* 2010). Continuous niche variation involves varying degrees of individual specialization whereby variation in foraging behavior is greater among individuals than within an individual (Bolnick *et al.* 2003).

Few studies have characterized niche variation among demographically similar individuals (i.e., same sex and life stage). These analyses have primarily focused on pinnipeds and identified persistent inter-individual differences in foraging behavior (Weise, Harvey & Costa 2010; Lowther & Goldsworthy 2011). Within demographic group niche variation can be particularly important among pregnant and nursing female pinnipeds as their foraging success during gestation and lactation has major implications for future population status via its effects on pup post-natal and weaning fitness (Beauplet *et al.* 2005).

To further our understanding of the nature and extent of intrapopulation niche variation among demographically similar individuals and the importance of ecological context as a driver of this phenomenon, we conducted an analysis of foraging strategies of pregnant California sea lions (*Zalophus californianus*) at three breeding colonies in different regions of the Gulf of California, Mexico (Fig. 1 and Table 1). The three colonies differ in population dynamics, habitat features, and prey composition.

It is logistically and financially challenging to observe pregnant sea lions while they are foraging at sea. It is also difficult to collect samples directly from these animals given their size, temperament, and the imperative to avoid handling and/or stressing these animals during an important reproductive period. However, stable isotope analysis of fur from suckling pups provides a unique opportunity to assess maternal foraging ecology.

Stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$, reported as $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$, reported as $\delta^{15}\text{N}$) from animal tissues are commonly used to provide coarse retrospective information about animal movement and foraging ecology (Ben-David & Flaherty 2012), including those of pinnipeds (Kurle & Worthy 2001; Kurle & Worthy 2002; Kurle & Gudmundson 2007; Newsome, Clementz & Koch 2010; Orr *et al.* 2012).

Our approach was three-fold: 1) we used a five-year dataset of pup morphological measurements to develop nested hypotheses about the potential for niche variation at each colony, 2) we used stable isotope analysis of fur collected from suckling pups to determine the nature and extent of niche variation at each colony and to make comparisons among colonies, and 3) we compared the body condition of pups belonging to mothers with different foraging strategies to assess the individual-level fitness consequences of intrapopulation niche variation.

A schematic of our *a priori* hypotheses of the relationships between ecological context, intracolony niche variation, and pup condition is provided in Fig. 2. In particular, we hypothesized that niche variation would be most pronounced at colonies with the least variation in pup body condition as this phenomenon is believed to help stabilize foraging success at the colony level. We hypothesized that the extent of niche variation at each colony would correspond to the colony's population abundance and its proximity to other sea lion breeding colonies, and that the nature of niche variation would depend on local prey and habitat features. Finally, we hypothesized that pup body condition would be comparable among mothers with alternative foraging strategies because niche variation presumably reduces conspecific competition and balances individual foraging success at the colony level when resources are limited.

Materials and methods

SPECIES AND STUDY SYSTEM

California sea lions are widely distributed from Vancouver Island, Canada, along the west coast of the United States and Pacific coast of Baja California, Mexico, and throughout the Gulf of California, Mexico (Reeves *et al.* 2002). In the Gulf of California (hereafter, “Gulf”), California sea lions are distributed among 13 breeding colonies and they are the only resident, breeding pinniped (Szteren, Aurioles & Gerber 2006) (Fig. 1). In 2004, the population size was estimated to include between 24,062 and 31,159 animals, reflecting a 20% decline from the preceding decade, which garnered conservation interest in the Gulf of California sea lion management stock (Szteren, Aurioles & Gerber 2006).

Sea lion feeding habits in the Gulf exhibit a regional structure with dietary differences observed among colonies (García-Rodríguez & Aurioles-Gamboa 2004; Porrás-Peters *et al.* 2008). As generalist predators, sea lion populations typically consume a range of species and their diets reflect resource availability (Mellink & Romero-Saavedra 2005). Previous research indicates that sea lions in the Gulf with overlapping ranges may use different foraging areas (García-Rodríguez & Aurioles-Gamboa 2004; Porrás-Peters *et al.* 2008), and recent work has identified dietary differences among life stages and between adult males and females (Elorriaga-Verplancken *et al.* 2012).

We focus on three sea lion colonies in the Gulf: San Jorge, Granito, and Los Islotes (Fig. 1). These colonies represent different subpopulations within the Gulf of California management stock, which exhibit different population sizes and rates of population growth (Table 1) (Ward *et al.* 2010). They are genetically distinct from one

another although there is some movement of individuals, primarily males, among colonies (Ward *et al.* 2010).

Colonies are distributed among two biogeographically distinct regions from north (San Jorge and Granito) to south (Los Islotes) with moderately unique faunal assemblages associated with the physical structures of each region (Walker 1960). A broad shallow, sandy shelf with sill depths of 200-300 m categorizes the northern Gulf, whereas rocky shores and deep basins separated by transverse ridges (sill depth below 1500 m) prevail in the south (Walker 1960). In addition, there are greater annual fluctuations in sea surface temperature and tidal ranges in the north that are thought to be responsible for lower prey diversity in this region (Walker 1960). Despite lower relative diversity, however, there is a high abundance of pelagic fish in the northern region that researchers credit with supporting 82% of the Gulf of California sea lion population (approximately 19,000 individuals) (Aurioles-Gamboa & Zavala-González 1994).

San Jorge, our northernmost colony, represents a large, densely-populated sea lion colony in the Gulf and its population was increasing slightly during the period of this study (Mellink & Romero-Saavedra 2005; Szteren, Aurioles & Gerber 2006) (Table 1). The colony is relatively isolated from other sea lion breeding colonies (Fig. 1), although past research grouped it into a subpopulation with two others (Rocas Consag and Los Lobos) based on geographic distances among the 13 sea lion breeding colonies in the Gulf (Gonzalez-Suarez *et al.* 2006; Ward *et al.* 2010). At the subpopulation level, population dynamics are synchronized among colonies, but each has a unique growth rate (Ward *et al.* 2010).

Prey diversity of San Jorge sea lions includes approximately 40 species (Mellink & Romero-Saavedra 2005). The most important prey are primarily benthic species and include midshipman (*Porichthys* species, Girard 1854), Panama grunt (*Pomadasys panamensis*, Steindachner 1875), and Panama brief squid (*Lolliguncula panamensis*, Berry 1911), species not targeted by local artisanal fisheries (Mellink & Romero-Saavedra 2005).

Granito also supported a relatively large sea lion population at the time of our study, but it declined through the mid-2000s and had less than a quarter of the total abundance of San Jorge (Szteren, Aurióles & Gerber 2006) (Table 1). Granito is part of a subpopulation that includes two other nearby breeding colonies (Los Cantiles and Los Machos). Additionally, another sea lion subpopulation that includes five breeding colonies (El Partido, Rasito, San Esteban, San Pedro Martir, and San Pedro Nolasco) occurs in the region (Gonzalez-Suarez *et al.* 2006; Ward *et al.* 2010) (Fig. 1).

Important prey at Granito are primarily pelagic fish and include Pacific cutlass (*Trichiurus lepturus*, Linnaeus 1758), lanternfish (*Diaphus* species), northern anchovy (*Engraulis mordax*, Girard 1854), shoulderspot (*Caelorinchus scaphopsis*, Gilbert 1890), and Pacific whiting (*Merrucius productus*, Ayres 1855) (García-Rodríguez & Aurióles-Gamboa 2004). Local commercial fisheries target northern anchovy and Pacific sardine (*Sardinops caeruleus*, Girard 1854) (also known as South American pilchard) and interact with sea lions directly and indirectly through trophic interactions (García-Rodríguez & Aurióles-Gamboa 2004).

Los Islotes, the southernmost sea lion breeding colony in our study, is relatively isolated - geographically and genetically - compared to many of the other breeding colonies in the Gulf (Fig. 1). However, it is considered part of a subpopulation that includes one other breeding colony (Farallon de San Ignacio) (Gonzalez-Suarez *et al.* 2006; González-Suárez *et al.* 2009; Ward *et al.* 2010). Los Islotes is one of the smallest sea lions colonies in the Gulf and its population was growing substantially during the time of our study (Table 1) (García-Rodríguez & Auriolos-Gamboa 2004; Szteren, Auriolos & Gerber 2006). The colony is situated in a region with high species and habitat diversity, and important prey species include eastern Pacific flagfin (*Aulopus bajacali*, Parin and Kotlyar 1984), bigeye bass (*Pronotogrammus eos*, Gilbert 1890), threadfin bass (*Pronotogrammus multifasciatus*, Gill 1863), and splittail bass (*Hemanthias* species) (García-Rodríguez & Auriolos-Gamboa 2004; Szteren, Auriolos & Gerber 2006).

Female sea lions give birth, typically to a single pup, between the end of May and middle of July (i.e., the breeding season) with a peak in middle to late June (Garcia-Aguilar & Auriolos-Gamboa 2003). Mothers nurse their pup for 6-12 months, and fifteen to thirty days after parturition, females come into estrus and mate again (Melin *et al.* 2000; Garcia-Aguilar & Auriolos-Gamboa 2003). For the next year mothers endure high energetic expenditures as they both nurture a developing pup *in utero* and nurse their pup from the previous breeding season (Gittleman & Thompson 1988; Garcia-Aguilar & Auriolos-Gamboa 2003; García-Rodríguez & Auriolos-Gamboa 2004). Given their parental role, females are limited to foraging in habitats in proximity to the breeding colony. Movement between distant colonies is rarely observed among female sea lions

and genetic analyses suggest that they are relatively philopatric (Maldonado *et al.* 1995; González-Suárez *et al.* 2009).

BODY CONDITION MEASUREMENTS

We conducted fieldwork for five consecutive summer breeding seasons between 2004 and 2008 when pups were approximately one to two months old (Table 2) (Mellink & Romero-Saavedra 2005; French *et al.* 2011). We captured between 600-700 total pups from each colony, weighed them to the nearest 0.5 kg using a 50 kg capacity Pesola spring scale and measured their total body length and thoracic girth to the nearest cm. Relationships between energy reserves, body condition, growth and health maintenance are well established, so we used a standard body condition index (BCI) for pinnipeds that served as an indicator of individual fitness (French *et al.* 2011). Specifically, we calculated pup condition as $BCI = m/V$, where m = mass (in g) and V = volume (in cm^3), where $V = 0.0265 * L * GT^2$ given measurements of L = length (in cm) and GT = thoracic girth (in cm).

We assumed that BCI values would reflect early post-natal condition, including pre-natal growth and condition at birth given the capturing dates, and higher values of BCI would represent better body condition (French *et al.* 2011). Body size and condition are often important determinants of survival in pinniped species, but the strength of the relationships between survival and different metrics of body condition can vary among species, subpopulations, and sexes (Calambokidis & Gentry 1985; Baker & Fowler 1992; Craig & Ragen 1999; McMahon, Burton & Bester 2000; Baker 2008). Previous work on grey seals (*Halichoerus grypus*, Fabricius 1791) demonstrates that the odds of survival

the first year are increased by a factor of 1.422 (SE = 0.226) with a one standard deviation increase in pup condition at weaning, although pup condition in the grey seal study was calculated as mass/length and mean values for males and females were 0.41 kg/cm and 0.39 kg/cm, respectively (Ailsa, Bernie & Richard 2001). We assume that differences in body condition index values of one standard deviation or greater are biologically meaningful.

In 2006, we captured, weighed, measured, marked, and released pups, recapturing them approximately one month later to estimate post-natal growth rates. We gave unique, identifiable haircuts to pups captured in late June that were less than a month old and marked pups captured in July with unique plastic livestock tags (Dalton I.D. Systems, U.K., Long-Term Jumbo Tags) on each front flipper (French *et al.* 2011). We calculated daily average growth rates (G, in kg/day) as $G = (m_2 - m_1)/T$, where m_2 = weight at recapture (in kg), m_1 = weight at initial capture (in kg), and T = number of days between initial capture and recapture (French *et al.* 2011). An estimate of colony-level growth rate was obtained as the average of the pup-level growth rates, where the averages were computed separately for males and females at each colony (French *et al.* 2011).

For our analyses of pup BCI values, we corrected each pup's weight to account for time of sampling relative to the mid-point of our field season using the following equation: $W_{\text{corrected}} = W_{\text{original}} - 1000(d * G)$, where $W_{\text{corrected}}$ is the weight (i.e., mass) (in g) used in the calculation of BCI values, W_{original} is the pup's original measured weight (in kg), and d is the number of days between the sampling date and the mid-point of our field season, which is positive for sampling dates later in the season and negative for sampling dates earlier in the season. The following growth rates (G) from 2006 were applied to all

years: males (San Jorge = 0.09 kg/d, Granito = 0.11 kg/d, Los Islotes = 0.18 kg/d) and females (San Jorge = 0.09 kg/d, Granito = 0.08 kg/d, Los Islotes = 0.12 kg/d) (Hernández-Camacho, unpublished data). Pup BCI values less than 1.15 g/cm³ and greater than 4.00 g/cm³ were considered outliers in the context of this study and were excluded from our analyses. All field protocols were approved by the Animal Care and Use Committee at Arizona State University, and the American Society of Mammalogists' guidelines were followed at all times (Gannon & Sikes 2007; Sikes & Gannon 2011).

STABLE ISOTOPE ANALYSIS

We used the stable carbon and nitrogen isotope values from sea lion pup fur to make inferences about the diets and foraging locations of sea lion mothers in this study (Aurioles-Gamboa *et al.* 2009). Stable nitrogen isotope values ($\delta^{15}\text{N}$) indicate a consumer's trophic position as $\delta^{15}\text{N}$ values increase predictably with increasing trophic level (Porrás-Peters *et al.* 2008; Newsome, Clementz & Koch 2010). Stable carbon isotope values ($\delta^{13}\text{C}$) reflect sources of primary production, which can vary geographically, thus making it possible to track animals as they forage in isotopically distinct foraging regions (Newsome, Clementz & Koch 2010). Patterns in the $\delta^{13}\text{C}$ values in marine systems include higher $\delta^{13}\text{C}$ values in nearshore and benthic areas relative to offshore and pelagic areas, respectively (Hobson, Piatt & Pitocchelli 1994; Porrás-Peters *et al.* 2008).

The stable isotope values of metabolically inert tissues such as hair represent an average of an individual's foraging behavior over the period of tissue formation (Kurle 2009). The advantage of analyzing the stable isotope values from fur is that they provide

long-term averages of the prey ingested by the predator. Given sea lions' delayed embryonic implantation and the timing of hair development that occurs during the later months of gestation in mammals (Atkinson 1997; Ramsdell & Zabka 2008; Saladin 2010), we assumed that the stable isotope values of fur collected from suckling pups represented their mother's diet during the late winter to early summer (i.e., the gestation period) previous to the time of tissue collection. The stable isotope values from pup fur, while indicative of the mothers' diets, are not exact replicates of maternal isotope values because pup fur would reflect an elevated trophic level relative to the mother as pups are consuming maternal tissue throughout gestation (Aurioles, Koch & Le Boeuf 2006; Habran *et al.* 2010; Lowther & Goldsworthy 2011).

We collected fur samples from a subset of pups at each colony over several years (Table 3). We cleaned each fur sample three times with petroleum ether (PE) to remove lipids, rinsed them with water, then dried them in a drying oven for 24 to 48 hours at 80 °C. We cut the fur into very small pieces with sharp scissors, homogenized the samples, and loaded ~0.7 mg of each into a tin capsule for stable isotope analysis in a magnetic sector gas source mass spectrometer (Thermo Delta Plus Advantage) coupled to an elemental analyzer at the W.M. Keck Foundation Laboratory at Arizona State University in Tempe, Arizona. Ten percent of the samples from each colony were analyzed in triplicate to measure within-sample variation. The standard deviation (SD) of $\delta^{13}\text{C}$ for our triplicate samples was 0.09‰ and the SD of $\delta^{15}\text{N}$ for our triplicate samples was 0.07‰. We calculated the precision of our data as the SD of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from a set of standards and they were 0.12‰ and 0.21‰, respectively.

STATISTICAL ANALYSES

To assess our hypotheses regarding niche variation at each colony, we compared median pup BCI values from the five-year morphological dataset among colonies, years, and years within each colony using a series of Kruskal-Wallis tests and Mann-Whitney *U* post-hoc tests (Dytham 2011) (Fig. 3). We used non-parametric tests because the data exhibited non-transformable deviations from normality. We compared colony BCI value variances and year BCI value variances within each colony using Brown-Forsyth tests (Brown & Forsythe 1974). We hypothesized that there was a negative relationship between variation in pup BCI values and the extent of niche variation at each colony. Therefore, if a colony exhibited little variation in pup BCI values, we expected some level of niche variation.

To compare the extent of niche variation among colonies, we tested for homogeneity of the variances using pair-wise Brown-Forsyth tests for the $\delta^{13}\text{C}$ values and Bartlett's tests for the $\delta^{15}\text{N}$ values (Brown & Forsythe 1974; Zar 2010). The nature of niche variation at each colony was identified using biplots of the stable isotope values of the pup fur (Fig. 4). Additionally, we quantified covariance between the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values within each colony using the Pearson product-moment correlation analysis when assumptions for the parametric test were met (Dytham 2011). Otherwise, the Spearman rank-order correlation test was implemented (Dytham 2011).

We used a hierarchical cluster analysis to identify distinct foraging groups within a colony. In our hierarchical cluster analysis, points were classified based on their dissimilarities as measured by the Bray-Curtis index, and clusters were connected to one another or points were connected to existing clusters using the UPGMA average linkage

method that establishes the distance between two clusters as the distance between cluster centroids. The R *vegan* package was used to conduct the hierarchical cluster analysis.

Where groups were delineated and the assumptions or sample size requirements for parametric tests were violated, we used a Mann-Whitney *U* test to compare median $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between groups, and group variances for each isotope were compared using a Bartlett's test (Zar 2010; Dytham 2011).

We determined whether there are fitness consequences associated with alternative maternal foraging strategies by regressing the pup-level BCI values at each colony on their corresponding covariate-centered $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Additionally, a one-way ANOVA was used to compare mean BCI values among distinct foraging groups within a colony when such groups were identified (Dytham 2011). All statistical analyses were conducted in R (version 2.15.2). Statistical significance was inferred at a p-value of 0.05 or less.

Results

BODY CONDITION COMPARISONS

Median BCI values were significantly different between colonies (San Jorge = 2.046 g/cm³, Granito = 2.020 g/cm³, and Los Islotes = 2.105 g/cm³) and varied annually (Fig. 3). Over the five-year study period, Granito pups exhibited the lowest median BCI value and Los Islotes pups exhibited the highest. Granito also contained the smallest BCI values variance (0.134), while Los Islotes contained the greatest (0.177), and the differences were statistically significant. These patterns were mirrored among the pups from which we sampled fur for our stable isotope analysis (Table 4).

STABLE ISOTOPE VALUES AND BODY CONDITION RELATIONSHIPS

The nitrogen isotope value ($\delta^{15}\text{N}$) variances were homogeneous among colonies, whereas the $\delta^{13}\text{C}$ variances were only homogeneous between San Jorge and Granito (Table 4).

The variance of the $\delta^{13}\text{C}$ values was significantly lower at Los Islotes, suggesting greater spatial niche variation at San Jorge and Granito relative to Los Islotes (Table 4). At San Jorge and Los Islotes, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values demonstrated significant positive covariation, a pattern not observed at Granito (Figs. 4a, b, c). Granito was the only colony in which distinct groups were identified. There were two, which differed significantly in median $\delta^{13}\text{C}$ values and $\delta^{15}\text{N}$ variances, but median $\delta^{15}\text{N}$ values and $\delta^{13}\text{C}$ variances were indistinguishable between the groups (Fig. 4b, Fig. 5).

Variation in BCI values among fur-sampled pups from Granito was tightly constrained at the lower end of the BCI values range in our study (Table 4 and Figs. 6b1, 2). Conversely, variation in BCI values was greatest among the fur-sampled pups at Los Islotes and most values were in the upper end of our BCI values range (Table 4 and Figs. 6c1, 2). The median and variance of BCI values among fur-sampled pups at San Jorge were intermediate among the three colonies.

There were no significant relationships between stable isotope values and pup BCI values at Granito or Los Islotes (Figs. 6b, c). Additionally, median pup BCI values and variances did not differ significantly between the two groups at Granito. In contrast, at San Jorge there was a significant negative relationship between the $\delta^{13}\text{C}$ values from the pup fur and pup BCI values, and a significant, but small, positive relationship between the $\delta^{15}\text{N}$ values from the pup fur and pup BCI values (Figs. 6a1, 2).

Discussion

Our work shows that niche variation is a dynamic species characteristic that can exist among demographically similar individuals and occur during important reproductive periods. Our intent was not to explicitly characterize the degree of individual specialization or describe the foraging behaviors of individual females at each of our study colonies, but to highlight the complexities of a species' ecological niche and the potential need for greater consideration of these nuances. Below, we provide a discussion of the relationships between ecological context, the nature and extent of intracolony niche variation, and the fitness consequences of alternative maternal foraging strategies at each of our study colonies. For sea lion mothers in the Gulf, niche variation occurs spatially and takes different forms at three colonies, reflecting local ecological context. Local ecological conditions vary with respect to the size of the sea lion colony, proximity of other breeding colonies, availability of prey resources, and habitat heterogeneity. At two of our colonies (Granito and Los Islotes), niche variation corresponds to a leveling out of pup body condition at the colony level, whereas it leads to fitness disparities at the other (San Jorge).

SAN JORGE

Given the size of the sea lion population at San Jorge (Table 1), we predicted considerable intracolony competition in nearby marine habitats. We found that niche variation takes on a continuous form at this colony (Figs. 2b, 4a). This suggests, that to mitigate competitive interactions among colony residents, pregnant females occupy different, but overlapping niches (i.e., niches comprised of some of the same resources,

but in different proportions) that range from nearshore or benthic habitats, indicated by higher $\delta^{13}\text{C}$ values from pup fur, to more offshore or pelagic habitats that are indicated by lower $\delta^{13}\text{C}$ values (Hobson, Piatt & Pitocchelli 1994; Porras-Peters *et al.* 2008).

The habitats surrounding San Jorge are relatively homogeneous, comprised of sandy substrate and shallow water depths in all directions. Large areas between the island and nearby coast to the east are less than 20 m deep, whereas waters to the west only reach depths of 45 m (Mellink, Dominguez & Luévano 2001; Mellink & Romero-Saavedra 2005). The shallowness of San Jorge's surrounding marine habitats generate uncommon ecological characteristics that researchers have credited with facilitating the prolonged breeding season and residency of the Eastern Pacific brown booby (*Sula leucogaster brewsteri*, Goss 1888) population on the island (Mellink 2000) and the unexpected increase in the local sea lion population with no changes to pup production during the 1997-1998 El Niño Southern Oscillation event (Mellink 2003). We suspect that the continuous nature of niche variation at San Jorge corresponds to available habitat.

Individuals at San Jorge that are foraging closer to the shore or in more benthic habitats are foraging on higher trophic level prey than individuals foraging further offshore or in pelagic habitats. This is demonstrated by the positive correlation between the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from pup fur (Fig. 4a). A similar pattern of niche partitioning has been observed among female Australian sea lions (*Neophoca cinerea*, Péron 1816) (Lowther & Goldsworthy 2011) and is consistent with offshore foragers targeting pelagic schooling fish such as sardines that are high quality and feed on plankton (Aurioles-Gamboa *et al.* 2009).

The linear relationships between the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and BCI values at San Jorge indicate that alternative maternal foraging strategies confer dissimilar fitness benefits to suckling pups (Figs. 5a1, 2). Mothers foraging on higher trophic level prey have healthier pups as indicated by their higher BCI values. Additionally, mothers that forage in more offshore or pelagic habitats have pups with better body condition than mothers foraging in more nearshore or benthic areas. Resources in nearshore or benthic areas may be of sufficient quality, but may be limited by high residual levels of intracolony competition as all sea lions coming and going from the colony may capture prey opportunistically in the immediate vicinity of the colony.

As proposed by central place foraging theory, longer foraging trips must be suitably rewarding for animals to undertake them (Orians & Pearson 1979). Foraging in offshore or pelagic habitats may provide some San Jorge females opportunities to capture higher quantities of prey (e.g., schooling fish), but catching these types of prey may require more experience and/or honing of prey-specific strategies that limit some females' access to these resources. Another possibility is that fisheries and tourism activities in nearshore areas around San Jorge constrain the benefits of foraging close to the colony. We draw our conclusions regarding the statistically significant relationships between isotope values and pup BCI values at San Jorge with care and note that these relationships may be insignificant if we were to account for the uncertainty in our isotope values when conducting our regression.

GRANITO

In contrast to San Jorge, the $\delta^{13}\text{C}$ values from pup fur indicate that niche variation takes a discrete form at Granito where females adopt one of two conspicuous foraging strategies that we hypothesize are: (1) more nearshore or benthic and (2) more offshore or pelagic (Fig. 4b). Females that employ the more nearshore/benthic strategy also appear to target more trophically diverse prey given that the $\delta^{15}\text{N}$ values from their pups are more variable than those from the pelagic group (Fig. 4b).

Like San Jorge, Granito is situated in the northern Gulf, which is generally comprised of a shallow sandy shelf and is characterized as species depauperate (Walker 1960). However, there is a 1000 m trench to the west of Granito (Fig. 1) that introduces habitat heterogeneity and opportunities for females to target different foraging habitats (Walker 1960). This may contribute to the two alternate foraging strategies observed.

Given the size of the colony's sea lion population (second in abundance among our study colonies, Table 1) and its location in a region with many other sea lion breeding colonies (Fig. 1), such niche partitioning could be advantageous (Tinker, Bentall & Estes 2008). Foraging opportunities for Granito sea lions may be reduced by intraspecific competition with other sea lions at the colony as well as sea lions from nearby breeding colonies (Gonzalez-Suarez *et al.* 2006; Ward *et al.* 2010).

Consistent with our hypothesis, niche variation at Granito is associated with low levels of variation in pup body condition (Fig. 2d and Figs. 6b1, 2). Pups belonging to mothers employing either of the two foraging strategies have indistinguishable BCI values. We conclude that niche partitioning may effectively reduce competition at this colony leading to more equivalent foraging success among pregnant females. This may

be of biological significance because median pup BCI value is lowest at Granito, particularly in 2008 when fur samples were collected (Table 4 and Fig. 3d). Low average BCI values suggest that food quality or quantity may be limited at this colony. However, this cannot be confirmed without prey data. Furthermore, the low pup BCI values may be symptomatic of other ecosystem dynamics that are affecting Granito sea lions. In the decade preceding our study, Granito experienced a significant population decline and exhibited the most variable population growth rate among our study colonies as indicated by its confidence limit (Table 1).

In general, the northern Gulf, while not as species diverse as the southern Gulf, is very productive and supports large populations of pelagic fish (Aurioles-Gamboa & Zavala-González 1994). Pacific sardine is a key component of Granito's regional ecosystem (Szteren, Aurioles & Gerber 2006), and its importance in the sea lions' diet has been correlated to their distribution (García-Rodríguez & Aurioles-Gamboa 2004). Sharp declines in sardine fishery landings have coincided with decreasing trends in the sea lion subpopulations in this region (Szteren, Aurioles & Gerber 2006). During periods when the concentration of prey such as the sardine are low, the sea lion population is vulnerable (García-Rodríguez & Aurioles-Gamboa 2004) and employing different foraging strategies may stabilize individual fitness at the colony level. Granito also experiences the greatest inter-annual fluctuations in pup BCI values (Fig. 3d), which might be representative of local fisheries having a significant impact on sea lion foraging opportunities, although more data are needed.

LOS ISLOTES

At Los Islotes, the smallest and southernmost of our study colonies (Fig. 1 and Table 1), niche variation is least pronounced, indicated by the lowest variance in the $\delta^{13}\text{C}$ values from pups as well as a relatively tight clustering of a majority of the isotope values in the biplot (Table 4 and Fig. 4c). Females from Los Islotes appear to be feeding over a smaller spatial range than females at the other two colonies. Given the high level of habitat heterogeneity (i.e., rocky topography and quick drops in ocean depth off the coast), it is possible to access more pelagic, deep water habitats in shorter distances from shore. Additionally, there is a positive relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that suggests lower trophic level foraging occurs further from the colony or in more pelagic habitats relative to nearshore/benthic foraging, similar to the pattern observed at San Jorge.

We suspect that there is little need for mothers to specialize on different resources given the small size of the sea lion population at Los Islotes and its geographic isolation from other colonies (Fig. 1) (Gonzalez-Suarez *et al.* 2006; Ward *et al.* 2010). Sea lion abundance at Los Islotes is limited by the space available on the island. Its small size (0.046 km²) constrains carrying capacity and keeps the population relatively small compared to some of the larger colonies (i.e., San Jorge = 0.602 km², Granito = 0.249 km²) (Hernández-Camacho, unpublished data). We believe this reduces intracolony competition and allows a majority of females to target the optimal diet.

The prey base at Los Islotes is diverse with 75 taxa of bony fishes recorded among sea lion scats at this colony (Auriolles-Gamboa *et al.* 2003). Yet, in spite of such prey richness, five species comprise the principal components of the colony's diet

(Aurioles-Gamboa *et al.* 2003). The five principal species consumed at Los Islotes include the eastern Pacific flagfin, bigeye bass (*Pronotoqrammus eos*, Gilbert 1890), threadfin bass (*Pronotoqrammus multifasciatus*, Gill 1863), *Hemanthias* species, and other members of the sea bass family, Serranidae (Aurioles-Gamboa *et al.* 2003). If females are targeting the same preferred prey (5 taxa) and randomly sampling a smaller proportion of secondary prey (70 taxa) from what is available, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from their pups, which represent their mother's average diet over a period of months, are not likely to be significantly different.

During the winter, subadult males make up the dominant stage class at Los Islotes and they account for 60-80% of the prey consumption at the colony (Aurioles-Gamboa *et al.* 2003). Subadult males are thought to target *A. bajacali*; therefore, the low level of niche variation observed among the majority of our females may be attributed to constrained foraging opportunities resulting from competition with subadult males during the period of study in our animals. Alternatively, mothers may be specializing on different individual species of the five principal prey taxa targeted at the colony level, but because these taxa are all found at depth, their stable isotope values may be similar and indistinguishable among our fur samples (Aurioles-Gamboa *et al.* 2003; Matthews & Mazumder 2004; Flaherty & Ben-David 2010).

While most of our study animals appear to share an ecological niche, there are several distinct outlying individuals among the Los Islotes dataset that may represent individuals with divergent foraging strategies (i.e., true specialists). These individuals must consistently sample distinct foraging resources to have unique stable isotope values given that our data represent a several-month average of each individual's diet. The

diverse prey base in the Los Islotes ecosystem may make it feasible for some mothers to target a separate suite of resources not consistently exploited by other colony members. These alternative strategies may not be uncommon at the colony level, but their limited occurrence in our dataset may be an artifact of our sample size.

Most of the outliers at Los Islotes have higher $\delta^{13}\text{C}$ values, indicating more nearshore/benthic foraging. These females may be younger mothers that are less experienced, which limits their foraging to familiar areas near the colony. Lower success rates and higher foraging costs often influence the selection of prey and foraging habitats among less experienced predators (Burns *et al.* 2006). Alternatively, nearshore foragers may be smaller mothers that are unable to access deeper, offshore resources because diving ability is positively correlated with body mass in air-breathing marine vertebrates (Halsey, Butler & Blackburn 2006). This pattern has been observed among male California sea lions off the Pacific coast of the United States (Weise, Harvey & Costa 2010).

In general, median pup BCI value is highest at Los Islotes, which suggests foraging opportunities are greater here than at our other study colonies. This may be due to the small size of the sea lion colony. However, BCI values are also most variable at Los Islotes, suggesting inter-individual differences in maternal foraging success. In a system in which a majority of mothers generally target the same optimal habitats and prey, this is representative of mothers' competitive performance for preferred prey.

TEMPORAL AND SPATIAL NICHE VARIATION

Trophic level appears to be a species-level characteristic in California sea lions that is relatively consistent across contexts. The $\delta^{15}\text{N}$ values from the pups ranged from $\sim 20.5\%$ to $\sim 22.5\%$, a span covering less than one trophic level (Kurle & Worthy 2002). Inter-seasonal consistency of sea lion trophic level has been documented in the Gulf via stable isotope analysis by other researchers, although sea lions at Granito demonstrate greater trophic diversity during the non-breeding season (García-Rodríguez & Aurióles-Gamboa 2004; Villegas-Amtmann *et al.* 2011).

At all of our colonies, intrapopulation niche variation occurs primarily via spatial segregation as indicated by differences in the $\delta^{13}\text{C}$ values from the pups. We anticipate that the spatial niche variation we observed over the late winter to early summer of our study is maintained across years given the relative stability of pup BCI values in our five-year morphological dataset (Figs. 3b, c, d, e). However, the nature of niche variation at each colony is not necessarily maintained across seasons within a year (Aurióles-Gamboa *et al.* 2003). Prior research found greater foraging specialization and individual variability in sea lion diets in the Gulf during the breeding season. These behavioral disparities resulted from changes in individuals' spatial distribution and diving behavior in response to greater intracolony competition during warmer periods when the shallow marine habitats around the colony are less productive (Villegas-Amtmann *et al.* 2011). These patterns are less pronounced at some colonies during the colder, non-breeding season that our data represents (Villegas-Amtmann *et al.* 2011).

Animals at San Jorge change their diet between seasons, seemingly diversifying their diet in the winter when their preferred prey is unavailable (Mellink, Dominguez &

Luévano 2001; Garcia-Aguilar & Auriolles-Gamboa 2003). When midshipman, Panama grunt, and Panama brief squid are absent from sea lion scats at San Jorge, weakfish (*Cynoscion* species), a benthic taxa that inhabits coastal nearshore areas and is a year-round resident of the local ecosystem, becomes more important in the population's diet (Allen & Ross Robertson 1994; Mellink & Romero-Saavedra 2005; Chao *et al.* 2010). When preferred prey are not abundant and diet diversity declines, pelagic species such as Pacific anchoveta (*Centengraulis mysticetus*, Gunther 1867) and northern/California anchovy also become more abundant in sea lion scat with anchovy becoming more important in March (Mellink & Romero-Saavedra 2005).

A similar pattern is observed at Granito. Scat analysis revealed that in January prey diversity at the colony level is relatively high and species such as Pacific sardine (*Sardinops caeruleus*, Girard 1854) are a key component of the colony's diet along with smaller portions of midshipman (*Porichthys* species, Girard 1854) and chub mackerel (*Scomber japonicas*, Houttuyn 1782) (Garcia-Aguilar & Auriolles-Gamboa 2003). During this time of greater population diet diversity, Pacific cutlass (*Trichiurus nitens*, Garman 1899), which is the dominant species in the fall when diet diversity is low (Garcia-Aguilar & Auriolles-Gamboa 2003; García-Rodríguez & Auriolles-Gamboa 2004), is nearly absent from sea lions' diets.

The diet of sea lions at Los Islotes also varies seasonally, although differences may reflect changes in the demographic structure of the colony more than changes in females' diets (Auriolles-Gamboa *et al.* 2003). Given the low level of intracolony competition at Los Islotes, seasonality is not expected to significantly alter the structure of niche variation among pregnancy females. If seasonality affects niche variation, it may

do so by influencing the outlying individuals because the productivity of nearshore areas where they appear to forage are more vulnerable to seasonal changes than more offshore areas, although more data are necessary.

CAVEATS

Our focus on pregnant California sea lions provides an example of niche variation among individuals that are experiencing inflated physiological stress relative to other demographic groups at our colonies. The mothers in our study are in the process of gestation and most are also nursing a pup from the previous breeding season. To acquire the resources necessary to maintain a growing fetus and lactate, our focal animals are perhaps more driven to ensure foraging success. At San Jorge and Granito, where we presume females are experiencing higher intrapopulation competition, this may drive the patterns of niche variation we observed. Previous work has documented niche partitioning among sex- and stage-classes of California sea lions in other regions (Elorriaga-Verplancken *et al.* 2012), however, we do not expect niche variation, if it exists, to be as pronounced within other demographic groups given their lower metabolic demands relative to pregnant and lactating females.

We focused primarily on the influence of intraspecific competition, and abundance and diversity of available prey resources and foraging habitats, on the nature and extent of niche variation at our colonies. Other ecological factors may be responsible for the patterns we observed and deserve future research attention. Differences in interspecific competition among our study colonies may be important. The presence of other species with similar ecological niches tends to reduce the degree of individual

specialization in some contexts (Araújo, Bolnick & Layman 2011). This may be important in the more species diverse southern Gulf where the incidence of other predators may constrain the niche width of females at Los Islotes. Additionally, the presence of other predators such as sharks that target sea lions as prey may influence the nature of niche variation at our colonies because the spatial distribution of predation risk and individual differences in risk aversion can affect individuals' foraging decisions (Araújo, Bolnick & Layman 2011). Finally, human disturbance may be contributing to our results as people can act as sea lion competitors (e.g. via fisheries) and predators. Additional data on sea lion-human interactions will elucidate the mechanisms by which people may affect sea lion foraging decisions in the Gulf.

CONCLUSIONS AND BROADER RELEVANCE

Within-population heterogeneity can have ecological and evolutionary consequences. Specifically, intrapopulation niche variation can impact ecological processes by altering the spectrum of direct and indirect interactions that occur among individuals and with their surroundings (Miner *et al.* 2005). Persistent inter-individual behavioral differences can expose some individuals to diet-specific risks, including predators and parasites (Bolnick *et al.* 2003; Johnson *et al.* 2009), and can affect the ways in which wildlife interacts with humans (Yeakel *et al.* 2009; Votier *et al.* 2010; Graham *et al.* 2011; Donaldson *et al.* 2012). In addition, depending on the heritability and temporal consistency of specializations, inter-individual differences may translate to trait evolution (Bolnick *et al.* 2003).

With this understanding, it is ill advised to continue operating under the simplifying assumption that intrapopulation niche variation is nonexistent or of no consequence. In the context of marine management, where many conservation measures are spatial in nature, ignoring inter-individual differences in habitat use may equate to insufficient protection or wasted management resources. Additionally, accounting for intrapopulation heterogeneity can inform risk evaluations because heterogeneous populations may be more robust to extinction due to demographic stochasticity, environmental change, and other threats (Fox 2005). For example, consistent superior performance of some individuals can reduce extinction risk as much as increasing the population size, in some cases (Conner & White 1999; Kendall & Fox 2002). Additional research is recommended to identify the conditions under which a more detailed understanding of a population's ecology is warranted to ensure management success.

Table 1. The subpopulation characteristics (location, population size, and growth rate) for each colony in this study.

Colony ^a (latitude, longitude)	N ^b (2004 N, % change: period) ^c	λ ^d (0.1% confidence limits)
San Jorge (31°01'N, 113°15'W)	3,434 (3,833, 12.3%: 1985 - 2004)	1.009 (0.983-1.035)
Granito (29°34'N, 113°32'W)	1,235 (848, -49.0%: 1991 - 2004)	1.025 (0.934-1.126)
Los Islotes (24°35'N, 110°23'W)	565 (439, 50.6%: 1993-2004)	1.043 (0.990-1.098)

^a (Porras-Peters *et al.* 2008)

^b Population size in 2008 (Hernández-Camacho, unpublished data). A correction of 50% for pups and 54% for females was applied following (Szteren, Aurióles & Gerber 2006).

^c (Szteren, Aurióles & Gerber 2006).

^d Population growth rate (mean annual rate of increase) obtained from a count-based population viability analysis (PVA) conducted from 1976-2004 based on census data (Szteren, Aurióles & Gerber 2006). $\lambda > 1$ does not guarantee the population will increase as the confidence limits indicate a chance that each population could decline and become extinct.

Table 2. Sampling schedule and number of individual pups sampled for morphological measurements at each colony.

Island	Sampling Date	Male	Female	Total
San Jorge	June 18-20, 22-23, 2004 July 13-15, 2004 June 20-21, 2005 July 20-22, 2005 June 17-19, 2006 July 14-16, 2006 August 11-13, 2006 June 24-26, 2007 July 27-29, 2007 June 21-23, 2008 July 21-23, 2008	363	331	694
Granito	June 30-July 1, 2004 July 24-26, 2004 June 20-21, 2005 July 18, 20-21, 2005 June 16, 20-21, 2006 July 14-16, 2006 August 11-12, 2006 June 24-26, 2007 July 27-28, 2007 July 28-30, 2008	330	287	617
Los Islotes	July 3-5, 2004 July 20-26, 2004 June 23, 25-27, 2005 July 23-27, 2005 June 21-25, 2006 July 11-14, 2006 August 7-10, 2006 June 22-25, 2007 July 26-29, 2007 June 19-22, 2008 July 19-22, 2008	392	291	683

Table 3. Sampling schedule and number of individual pups sampled for fur collection for stable isotope analysis at each colony.

Island	Sampling Date	Male	Female	Total
San Jorge	July 14-16, 2006 August 11-12, 2006 July 27-29, 2007	40	43	83
Granito	July 28-30, 2008	26	26	52
Los Islotes	June 21-24, 2006 July 11-14, 2006 August 8-9, 2006	43	28	71

Table 4. The $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and body condition index (BCI) values from fur-sampled pups at each colony. Bold values denote a significant difference from other values in a column. Median $\delta^{13}\text{C}$ values and median BIC values were compared using Kruskal-Wallis tests and Mann-Whitney U post-hoc tests. Mean $\delta^{15}\text{N}$ values were compared using a one-way ANOVA and Fisher Least Significant Difference post-hoc tests. The variances of $\delta^{13}\text{C}$ values were compared using Brown-Forsyth tests, and BCI and $\delta^{15}\text{N}$ variances were compared using the Bartlett's test. Statistical significance evaluated at $p \leq 0.5$.

Colony	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)		BCI (g/cm^3) *	
	Mean [Median] (SE)	σ^2 (SD)	Mean [Median] (SE)	σ^2 (SD)	Mean [Median] (SE)	σ^2 (SD)
San Jorge (N=83)	-15.2 [-15.1] (0.052)	0.23 (0.48)	21.6** [21.6] (0.047)	0.19 (0.44)	1.85 [1.88] (0.027)	0.062 (0.25)
Granito (N=52)	-14.7 [-14.9] (0.073)	0.28 (0.53)	21.8** [21.8] (0.061)	0.19 (0.44)	1.76 [1.76] (0.017)	0.015 (0.12)
Los Islotes (N=71)	-15.0 [-15.0] (0.043)	0.13 (0.36)	21.7 [21.8] (0.049)	0.17 (0.41)	2.43 [2.45] (0.049)	0.161 (0.40)
Sites combined (N=206)	-15.0 [-15.0] (0.034)	0.23 (0.48)	21.7 [21.7] (0.030)	0.19 (0.44)	2.02 [1.92] (0.029)	0.168 (0.41)

* Sample excludes outliers ($\text{BCI} > 3.5 \text{ g}/\text{cm}^3$, $< 1.15 \text{ g}/\text{cm}^3$) (San Jorge, N=1; Los Islotes, N=3)

** Significant differences in mean $\delta^{15}\text{N}$ values at San Jorge and Granito are statistically significant, but not biologically significant, meaning that the isotopic difference was not large enough to indicate foraging at different trophic levels.

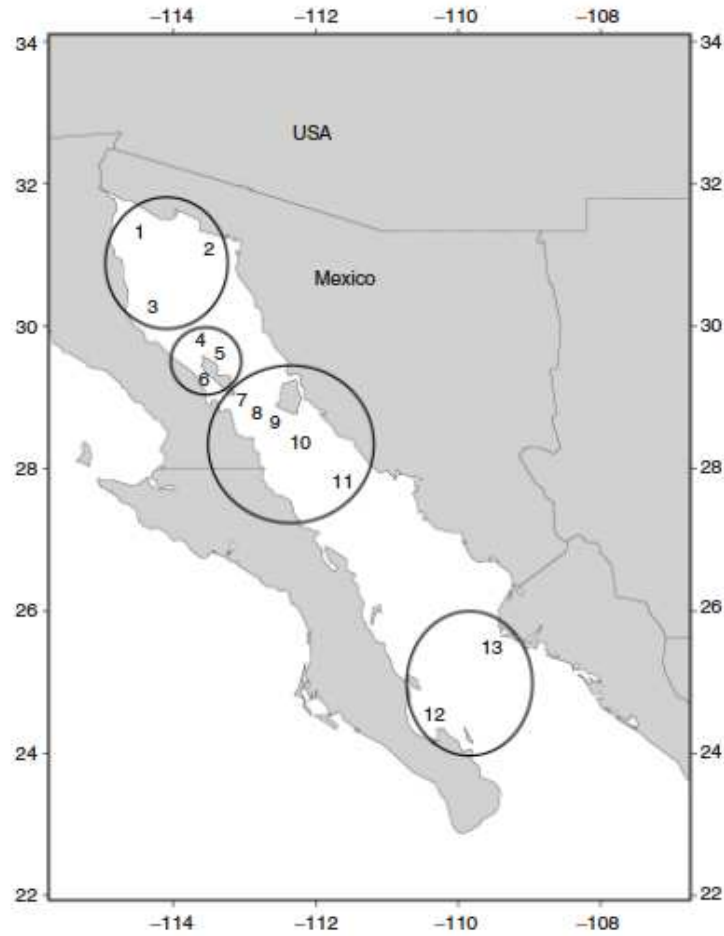


Fig. 1. Map of the Gulf of California, Mexico. California sea lion breeding colonies: 1. Rocas Consag, 2. San Jorge, 3. Los Lobos, 4. Granito, 5. Cantiles, 6. Machos, 7. Partido, 8. Rasito, 9. San Esteban, 10. San Pedro Martir, 11. San Pedro Nolasco, 12. Los Islotes, and Farallon de San Ignacio. Circles represent subpopulations delineated in Gonzalez-Suarez *et al.* (2006). Map taken from Gonzalez-Suarez *et al.* (2006).

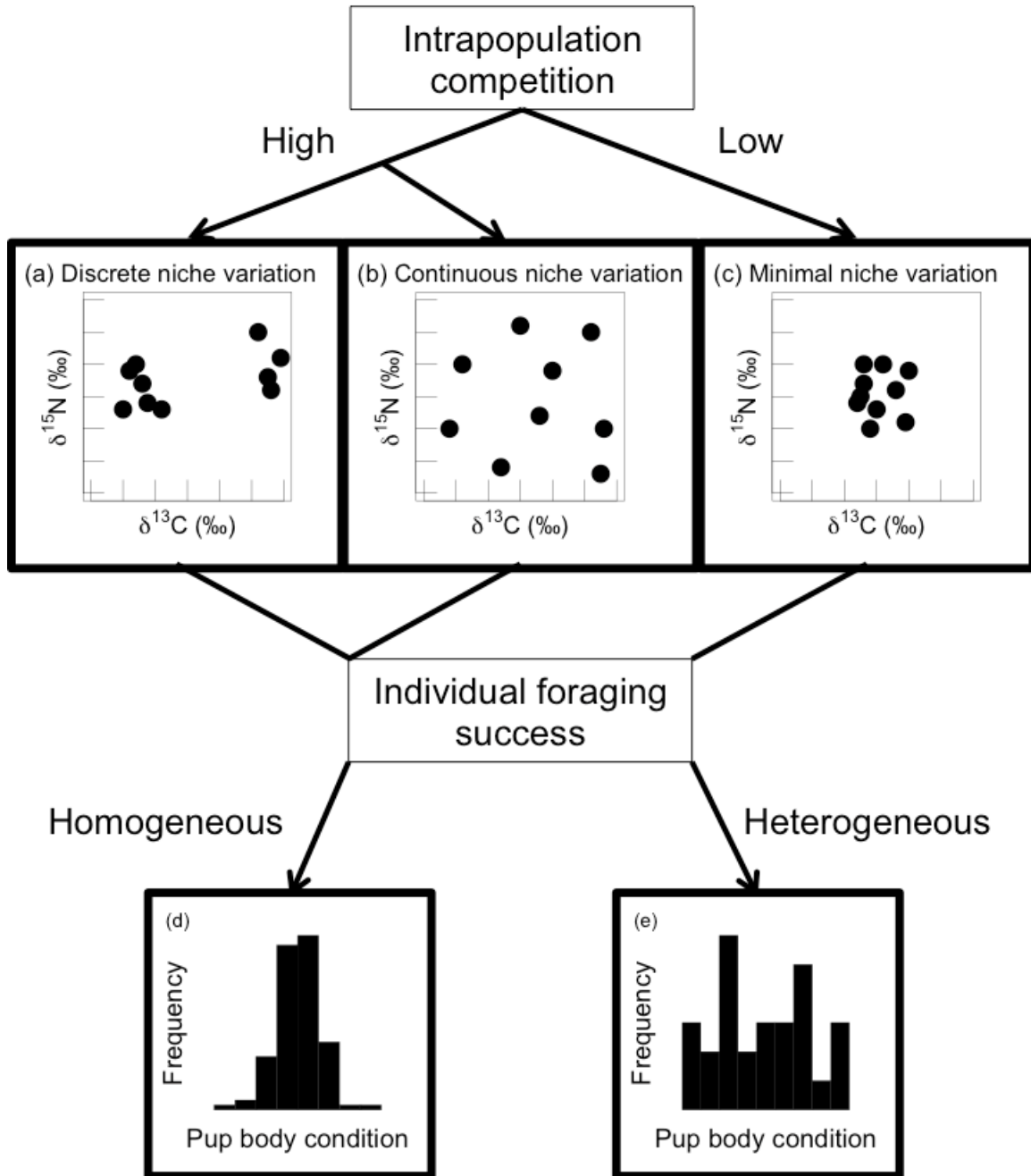


Fig. 2. Conceptual framework of hypothesized relationships between intrapopulation competition, the nature of niche variation, and resulting fitness consequences. Bold boxes represent data evaluated in our study. We hypothesized that when intrapopulation competition is high due to a large population size, competition with nearby colonies, or a

decline in prey abundance, the population will exhibit niche variation. The nature of niche variation may be discrete (a) or continuous (b). The presence of niche variation enables poorer competitors to achieve greater foraging success as they target alternate prey types for which there is presumably less competition. This reduces disparities in foraging success among individuals leading to less variation in the distribution of body condition values of individuals' offspring (d). In contrast, we hypothesized that when intrapopulation competition is low, individuals will target the same set of preferred prey resources or foraging habitats (c). Better competitors or more experienced individuals will have greater foraging success, leading to greater variation in the distribution of pup body condition values at the population level (e).

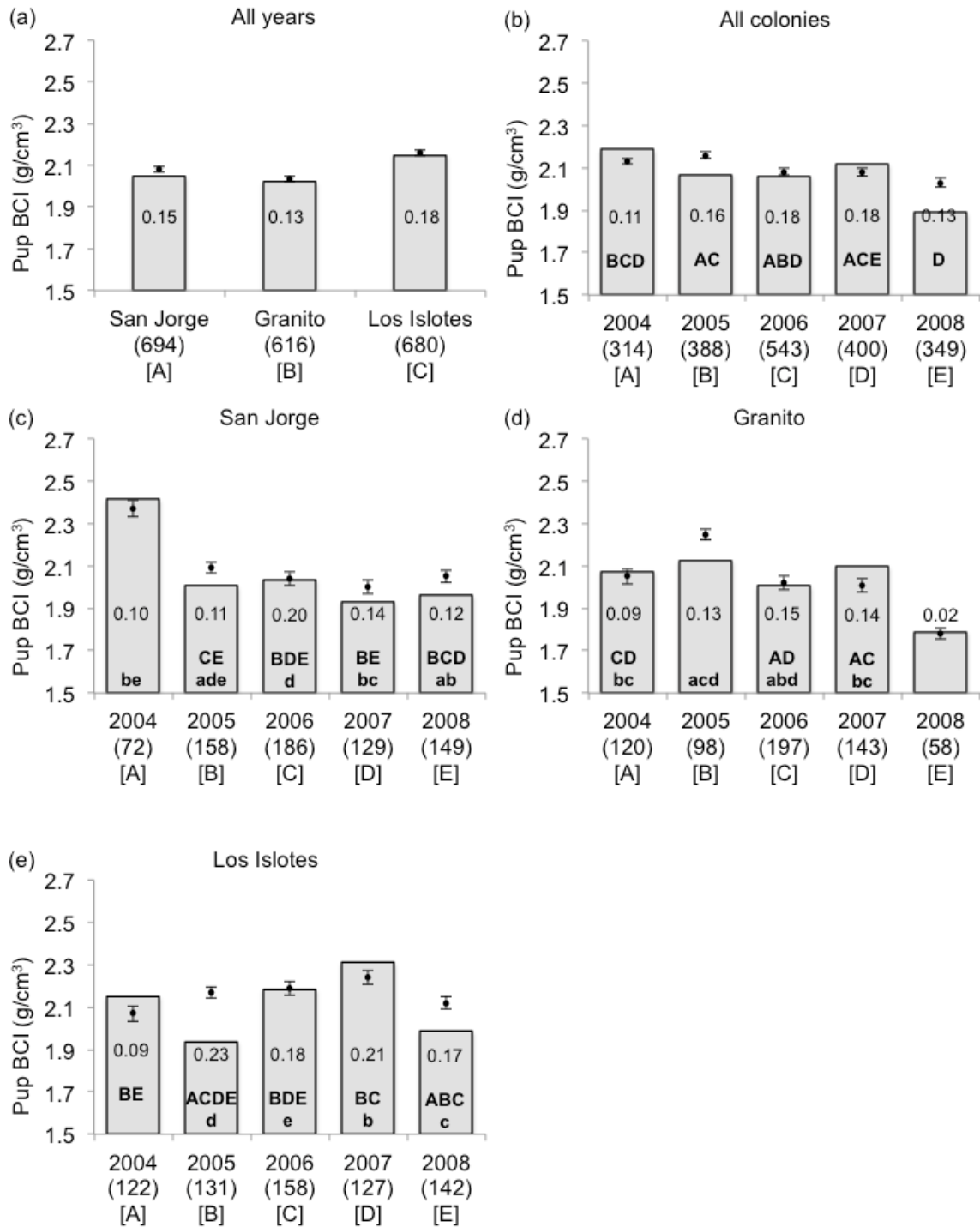


Fig. 3. Comparison of median pup body condition index (BCI) values at the three study colonies for the five-year dataset. The graphs include pup BCI comparisons: (a) among

colonies (summed across years), (b) among years (summed across colonies), and (c-e) among years within each colony (i.e., inter-annual variation). Under each bar is the sample description: name or year, sample size (in parentheses), and identifier for statistical analysis [in square brackets]. The capital letters at the base of each bar indicate the sample medians that are not significantly different. The lowercase letters at the base of each bar indicate sample variances that are homogeneous. The sample variances are displayed by the number labels in each bar, and the points with error bars portray the sample means and standard errors. Median values indicated by the bars were compared using a Kruskal-Wallis test and Mann-Whitney *U* post-hoc tests. Variances were compared for (a, c-e) using Brown-Forsyth tests. Statistical significance was evaluated at $p \leq 0.5$.

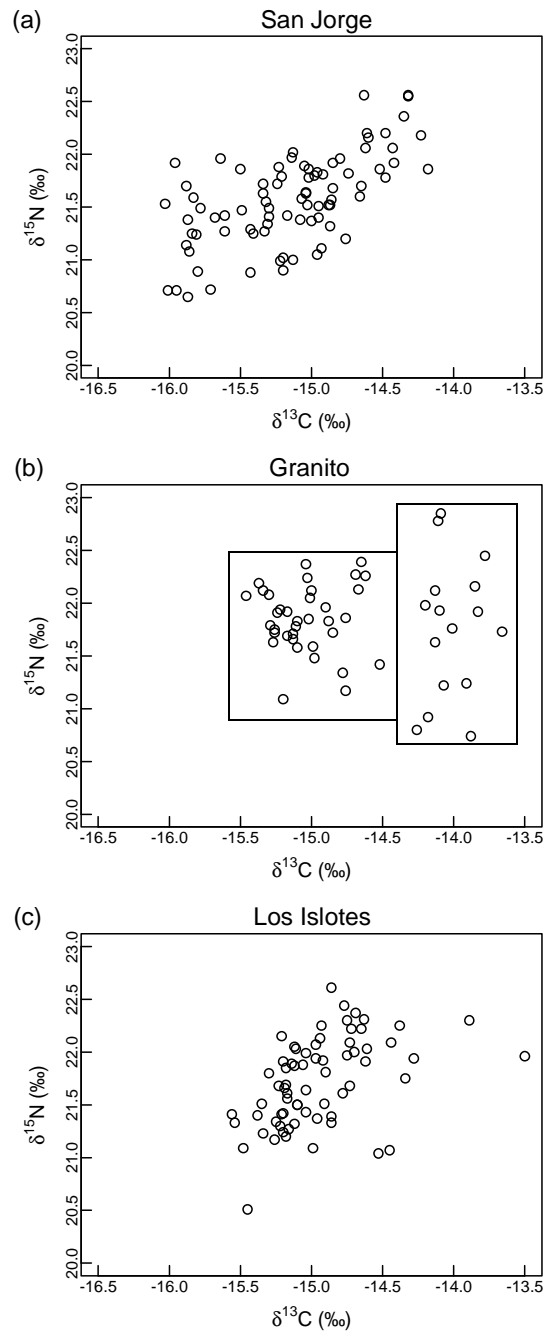


Fig. 4. Biplots of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values at: (a) San Jorge; (b) Granito; and (c) Los Islotes. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are positively correlated at San Jorge (Pearson correlation: $r = 0.626$, $p < 0.01$) and at Los Islotes (Spearman correlation: $r = 0.509$, $p <$

0.01), but there is no correlation at Granito (Spearman correlation: $r = -0.011$, $p = 0.938$).

The two boxes in (b) indicate that there are two isotopically distinct foraging groups at Granito that are significantly different with regards to median $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variances.

Group 1 (left): median $\delta^{13}\text{C}$ is -15.1‰ and $\delta^{15}\text{N}$ variance is 0.10, Group 2 (right): median $\delta^{13}\text{C}$ is -14.1‰ and $\delta^{15}\text{N}$ variance is 0.42. Medians were compared using a Mann-

Whitney U test and variances were compared using a Bartlett's test. Significance was evaluated at $p \leq 0.5$.

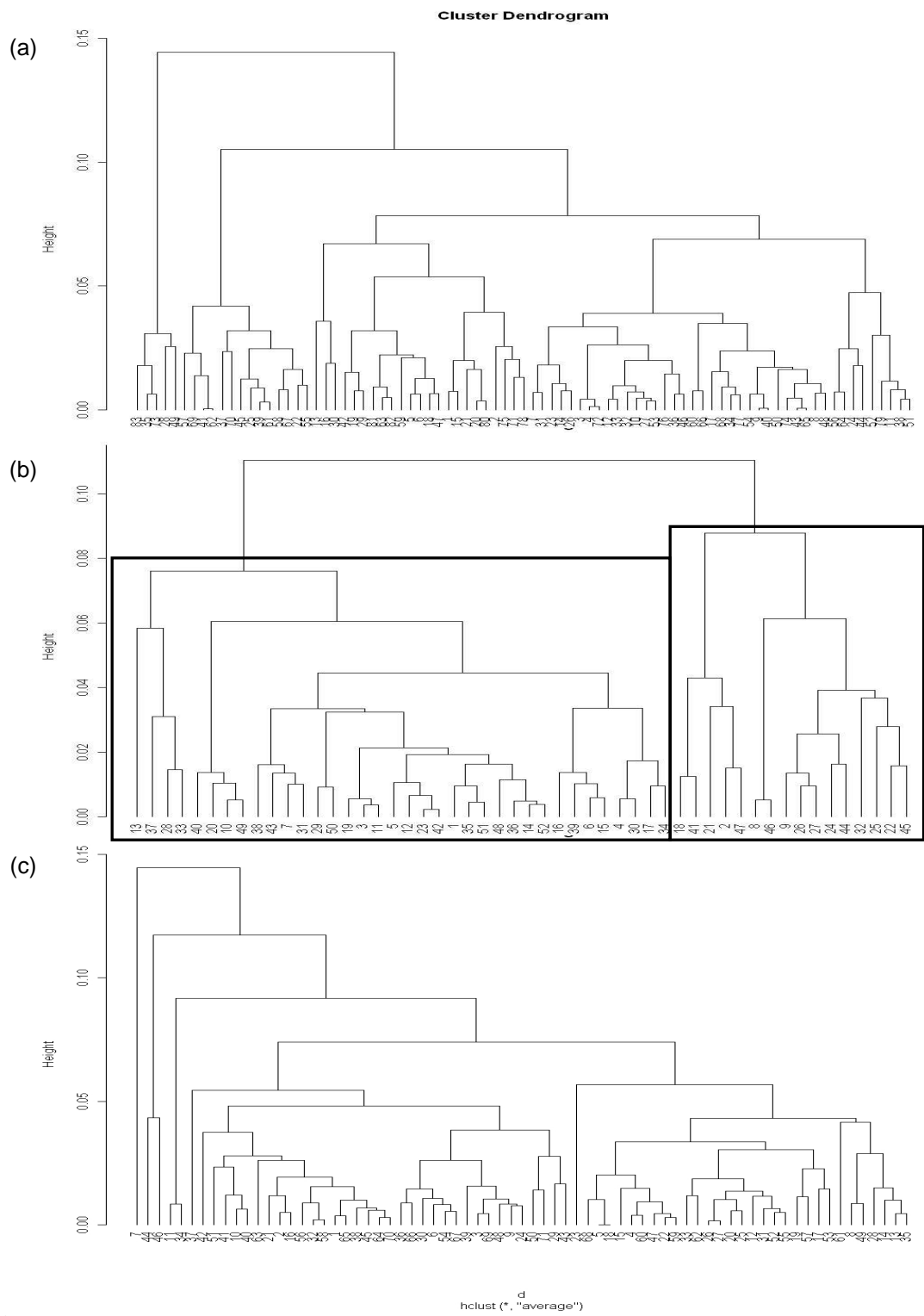


Fig. 5. Dendrograms produced by hierarchical cluster analysis showing similarities between sea lion pups based on their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values at: (a) San Jorge; (b) Granito;

and (c) Los Islotes. The two boxes in (b) indicate the two distinct foraging groups at Granito.

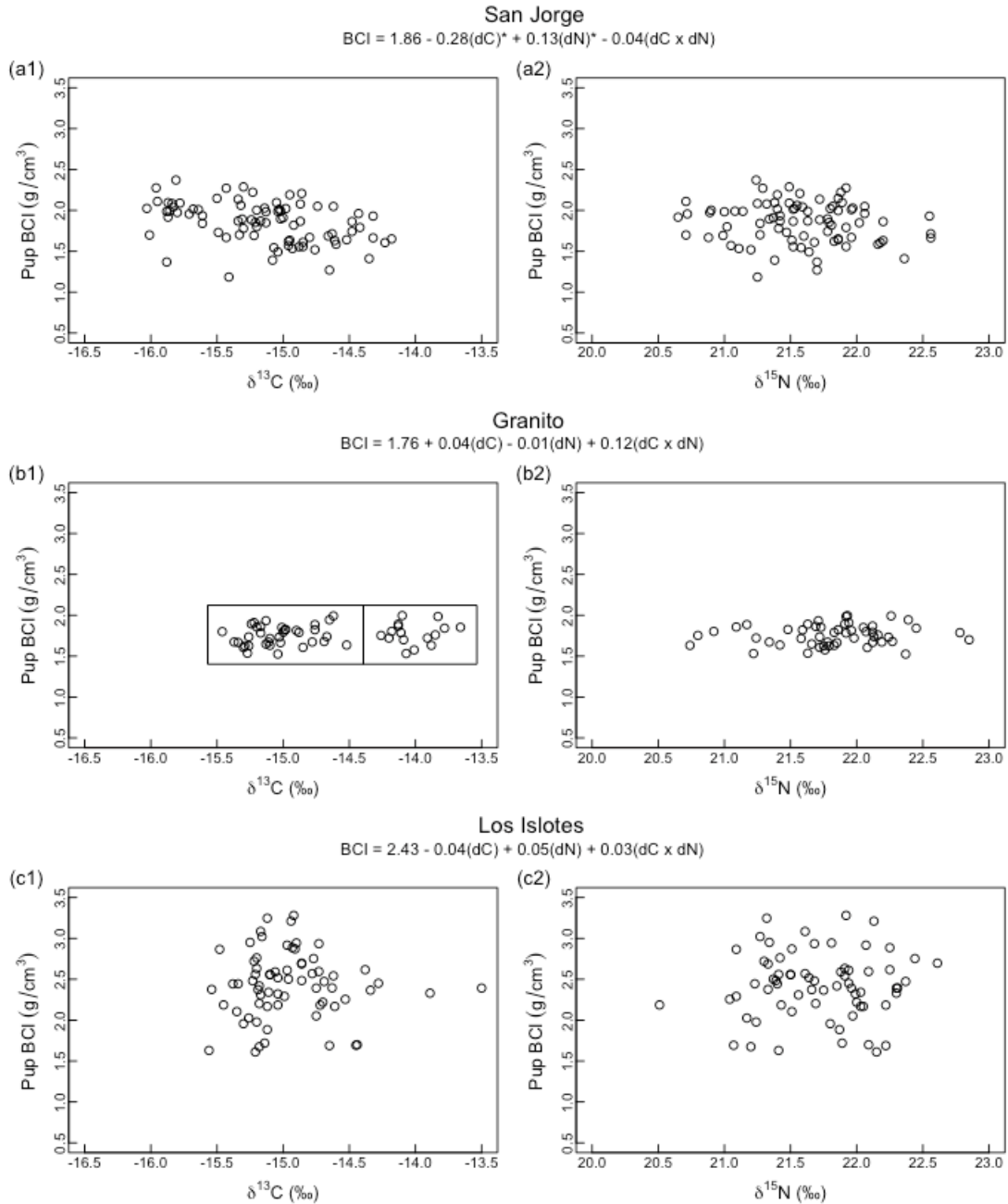


Fig. 6. Relationships between covariate-centered $\delta^{13}\text{C}$ (dC) and $\delta^{15}\text{N}$ (dN) values and pup body condition index (BCI) values at each colony. The parameter values for the linear regressions that are statistically significant are shown with a *. Significance was evaluated at $p \leq 0.5$. The two boxes in (b1) indicate the two foraging groups at Granito.

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