



Latitudinal variation in local productivity influences body condition of South American sea lion pups

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ABSTRACT: In otariids, the condition and growth of offspring are linked to prey availability because females show a strong dependence on local food availability. Thus, it is expected that body condition of sea lion pups will vary spatially and/or temporally as a response to variations in the abundance of prey species on which females feed. The objective of this study was to analyze the geographic and temporal variation in the body condition of South American sea lion *Otaria flavescens* pups in Chile, and to relate it to spatio-temporal variations in prey availability. We captured 340 live pups in 2 distant colonies, Punta Patache/Punta Negra and Cobquecura, along the Chilean coast during consecutive breeding seasons. A morphometric index of pup body condition was estimated by comparing pups in all years using least-squares linear regression of the \log_{10} -transformed measurements of standard length vs. body mass. We analyzed the relationship between this index and estimates of fish biomass (as a proxy of prey availability) at each locality. We found that body condition was significantly different between years and between colonies, suggesting that animals of the central-south area were in better condition than those in the north. A positive relationship between body condition and fish biomass was found, suggesting that differences in body condition may be explained by spatial and temporal differences in prey availability.

KEY WORDS: Body condition index · Body mass · Environmental effects · Morphometrics · *Otaria flavescens* · Southern sea lion

INTRODUCTION

In marine environments, productivity varies both in spatial and temporal scales, influencing marine predator distribution, diet, foraging, diving behavior, and body condition (Lea et al. 2006, Womble et al. 2009). In particular, body condition is one of the main parameters affected by local productivity because it is a

relative measure of the nutritional state or the level of energy reserves of an organism, commonly interpreted as a measure of general well-being of an individual or population (Labocha et al. 2014).

Local productivity is essentially important for colonial species, such as seabirds and otariids (fur seals and sea lions). These species are central place foragers and income breeders that combine foraging

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activity at sea with the raising and provisioning of their young ashore (Lea et al. 2006, Womble et al. 2009). Otariids in particular are characterized by lengthy parental care and nursing periods. As such, the mother must return frequently ashore to provision her pup and is therefore limited to trips lasting from hours to a few days, and to distances from tens to a few hundreds of kilometers from the rookery (Costa & Shaffer 2012). Consequently, for a female, food availability in the area around the rookery is critical for the condition and survival of her offspring, thus creating a direct link between local prey availability and fitness (Womble et al. 2009).

The South American sea lion *Otaria flavescens* (Shaw, 1800), like other otariid species, shows a strong dependence upon local prey availability. Although mainly composed of fish and squid, its diet can be quite variable, as sea lions adapt easily to locally abundant prey (Cappozzo & Perrin 2009). After the birth of her pup, the mother alternates between periods on land nursing the pup and foraging trips in the ocean (Muñoz et al. 2011) and has a lengthy nursing period lasting from 7 mo up to 1 or even 2 yr. Foraging trips usually last 1 or 2 d; the female remains near the rookery and usually does not venture farther than 50 to 100 km (Rodríguez et al. 2013). Considering that growth and maintenance of the pups depends almost exclusively on the ability of their mothers to obtain enough food (Lea et al. 2006), it is expected that the body condition of South American sea lion pups will vary spatially and/or temporally as a response to the distribution and abundance of the prey on which females feed during the nursing period.

The Humboldt Current System (HCS) extends latitudinally from central-south Chile (~42° S) to northern Peru (~4 or 5° S) (Quiñones et al. 2010). The HCS off Chile is one of the most productive ecosystems in the world, with primary production rates of up to 25.8 g C m⁻² d⁻¹ (Daneri et al. 2000). This system, characterized by a south–north flow of surface water of subantarctic origin and by intense upwelling of nutrient-rich/low-oxygen equatorial subsurface waters, is a highly dynamic coastal environment whose primary productivity sustains an extremely high biomass of fish, which in turn supports one of the most productive fishing activities in the world (Daneri et al. 2000). However, although the coastal waters off Chile are in general very productive, significant spatial variations in primary productivity exist along the coast, evident in measurements of chlorophyll *a* (chl *a*) concentration, phytoplankton abundance, analyses of mesozooplankton samples,

and estimates of fish biomass (Daneri et al. 2000). From 2009 to 2012, fish biomass along the central-south coast of Chile averaged 1.4 million t yr⁻¹, and was never less than 850 000 t (www.fip.cl/proyectos.aspx). By contrast, fish biomass in the north averaged 235 000 t yr⁻¹ in the same years, and never exceeded 380 000 t (www.fip.cl/proyectos.aspx). These estimates indicate that the productivity in central-south Chile is notably higher than in the north (Quiñones et al. 2010).

Considering the marked differences in primary productivity between the north and central-south coast of Chile, it is expected that body condition of sea lions pups from central-south Chile should be better than that of pups from the less productive coast in the north. The aim of this study was to analyze spatial and temporal variation in the body condition of the South American sea lion pups in Chile by using a morphometric index, and to relate this variation to spatial and temporal changes in prey availability.

MATERIALS AND METHODS

Study area

This study was carried out in 2 areas of the Chilean coast, separated by a distance of about 1730 km. One of the areas is located in the north of Chile and is formed by 2 rocks, Punta Patache (20° 48' S, 70° 12' W) and Punta Negra (20° 50' S, 70° 10' W), both sustaining breeding colonies of the South American sea lion. Hereafter, this area will be referred as PP/PN. The rocks are both located about 50 to 100 m off the coast of mainland Chile (Fig. 1). Colony sizes at PP/PN were estimated by Bartheld et al. (2008) to be 950 and 1245 animals, respectively. The second study area (Cobquecura; 36° 07' S, 72° 48' W) is a rocky island located about 80 to 100 m off the central-south coast of Chile. This represents the most important breeding colony along the coast of central Chile, with approximately 2900 animals (Sepúlveda et al. 2011) (Fig. 1). The pupping season for the South American sea lion in the Chilean coast occurs during January and February (austral summer months). According to Acevedo et al. (2003) and Quiñones et al. (2011), the birth peak is similar in the 2 localities, extending from late January to early February. A recent study based on mtDNA and microsatellite analyses showed that no spatial genetic structure occurs in *Otaria flavescens* along the Chilean coast from 18 to 42° S (Weinberger 2013), suggesting a low

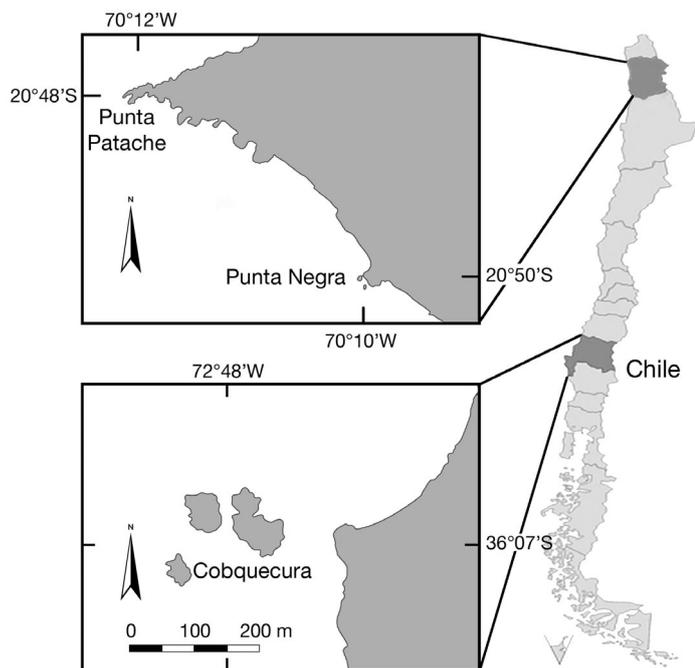


Fig. 1. Breeding colony study sites for South American sea lions in the north zone (Punta Patache/Punta Negra, PP/PN) and central-south zone (Cobquecura) of Chile

genetic differentiation and a high gene flow between sea lions from the 2 studied areas.

During the breeding season, high waves frequently sweep away healthy pups from these colonies and transport them, alive, to adjacent continental beaches. While some of these pups are capable of returning to the colony by themselves, others die on the beach from hunger and dehydration. We based our results on live pups that were captured immediately after stranding on the beach. This method has the advantage of not causing disturbances to the colony that could disrupt nursing behavior and/or reduce pup survival by trampling or abandonment of the pup (Green et al. 2010). However, it should be noted that our sampling method could be biased because not all the pups have the same probability of being swept away from the colony. This could be the case if the distribution of older and more experienced females versus younger females in the colony is not homogeneous. However, we assume that all pups have a similar probability of being stranded on the beach based on 3 criteria: (1) a similar bias operates in both colonies; (2) high waves frequently hit in different zones of the colonies; and (3) pups from different parts of the colonies are swept away from the colony to the beach. The latter has been observed during storms.

Capture and measurements of sea lion pups

In the PP/PN area, a total of 202 live pups (86 females and 116 males) in 2011 ($n = 48$; 17 females and 31 males), 2012 ($n = 98$; 44 females and 54 males) and 2013 ($n = 56$; 25 females and 31 males) were captured. During all years, 2 observers remained in front of the colony from 09:00 to 18:00 h for 1 mo (from the third week of January to the third week of February). Visits to the colony were done every other day, regardless of meteorological conditions. In the Cobquecura area, a total of 138 pups (56 females and 82 males) in 2009 ($n = 11$; 4 females and 7 males), 2010 ($n = 36$; 18 females and 18 males), 2011 ($n = 72$; 29 females and 43 males) and 2012 ($n = 19$; 5 females and 14 males) were captured. In this colony, 2 or 3 observers were placed in front of the colony from 09:00 to 18:00 h for 2 mo (1 January to 28 February). Visits to this colony were done on a daily basis. No other breeding colonies are close to the studied colonies, so it was assumed that all pups captured came from the studied rookeries.

To evaluate body condition, standard length (L , straight-line nose to tail, dorsal view) to the nearest 0.01 m, and body mass (M) to the nearest 0.1 kg was recorded for each pup. Pups were marked with water-resistant paint on one front flipper to avoid measuring the same individual again and set free. Body mass is proportional to body length (Bradshaw et al. 2000). In order to control for any possible effect of body size on individual variation in mass, a condition index was calculated by regressing $\log_{10}M$ against $\log_{10}L$ (Bradshaw et al. 2000). Male and female pups were analyzed separately. Applying the regression equation to $\log_{10}L$ gives \log_{10} predicted mass (M_p):

$$\log_{10} M_p = a + b \times \log_{10}L \quad (1)$$

where a is a constant and b is the regression coefficient. The ratio of observed mass (M_o) to M_p gives an index of relative condition (CI_m):

$$CI_m = M_o/M_p \quad (2)$$

Because we sampled the pups over a 1 or 2 mo period during each year, it is possible that pup condition was subject to bias resulting from asynchrony in the date of capture (Bradshaw et al. 2000). To examine the amount of variation in pup condition that could be explained by sampling date, we used a least-squares regression of CI_m for pups from each sex–locality combination against the day of the year each pup was measured. Generalized linear models (GLMs) were used to examine the effect of colony and year of pup capture on the variation of CI_m . For a

better comparison, only pups captured in 2011 and 2012 in the 2 colonies ($n = 146$ from PP/PN and $n = 91$ from Cobquecura) were used in this analysis. All statistical analyses were run in Statistica 7.0 software (StatSoft) with a significance level of $\alpha = 0.05$.

Estimation of prey availability

We also examined the relationship between fish biomass (as a proxy of prey availability) within each area and pup CI_m using a linear regression model. Data were \log_{10} transformed for analysis. We analyzed the biomass of 2 pelagic clupeid species: anchovy *Engraulis ringens* and common sardine *Strangomera bentincki*, which are considered to be the most economically important resources for both industrial and small-scale fisheries in north and central-south Chile (Gutiérrez-Estrada et al. 2007, Castillo-Jordán et al. 2010), and commonly reported as one of the most important prey species in the diet of the South American sea lion in Chile, both in the north (>90% of diet composition; Sielfeld 1999) and in the central-south (30 to 60% of diet composition; Muñoz et al. 2013). Density and fish biomass data were obtained from acoustic surveys carried out onboard the RV 'Abate Molina', a stern trawler 43.2 m long and with 1400 HP. Two study areas were used to examine fish biomass, a northern area located between Arica ($18^{\circ} 22' S$) and Punta Buitre ($24^{\circ} 40' S$) extending from 1 nautical mile (nmi) to 20 nmi along the coast (Fig. 2a), and a central-south area located between $33^{\circ} 40' S$ and $40^{\circ} 00' S$ (Fig. 2b). The surveys in the north were carried out during December from 2010 to 2013, and during January from 2010 to 2013 in the central-south. In both zones, systematic acoustic sampling was performed by diurnal transects located perpendicular to the coast (east–west), separated by 10 nmi (Fig. 2a,b). Coastal areas (<5 nmi) were surveyed in a special way, with north–south sailings repeated on at least 2 occasions. A scientific echosounder SIMRAD EK 60 with split beam transducer 38 kHz calibrated according to standard methods was used. Mid-water trawl surveys were conducted to confirm species identification.

Using the acoustic information, we produced Hovmöller diagrams to illustrate the

changes in fish density ($t \text{ nmi}^{-2}$) according to latitudes (by degree) and time (by year). Fish density was interpolated by triangulation to produce a colored grid of nodes representing the relative abundance of fish using Surfer software (Golden Software). We assumed that spatial and temporal variations in prey biomass are associated with differences in prey availability to lactating females.

RESULTS

Body condition and capture date

The distribution of sampled pups was spread over the capture periods in both colonies. In PP/PN, most of the captures were registered during the first 2 wk of February, whereas in Cobquecura they were recorded during the last week of January and the first week of February (Fig. 3). Body length of both males and females from PP/PN was significantly longer than those from Cobquecura (Males: $F_{1,196} = 23.46$, $p < 0.0001$; Females: $F_{1,140} = 9.09$, $p = 0.003$) (Table 1). On the contrary, male and female pups from Cobquecura showed a significantly greater weight than those from PP/PN (Males: $F_{1,196} = 76.02$, $p < 0.0001$; Females: $F_{1,140} = 57.03$, $p < 0.0001$) (Table 1).

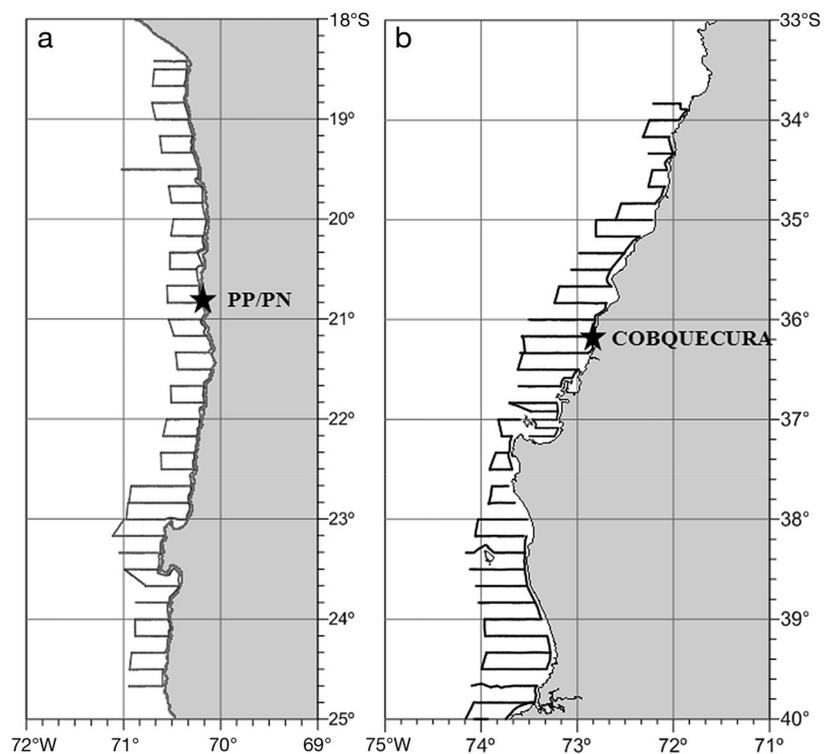


Fig. 2. Study zone and acoustic surveys in (a) north and (b) central-south zones of Chile during austral summer months (December and January)

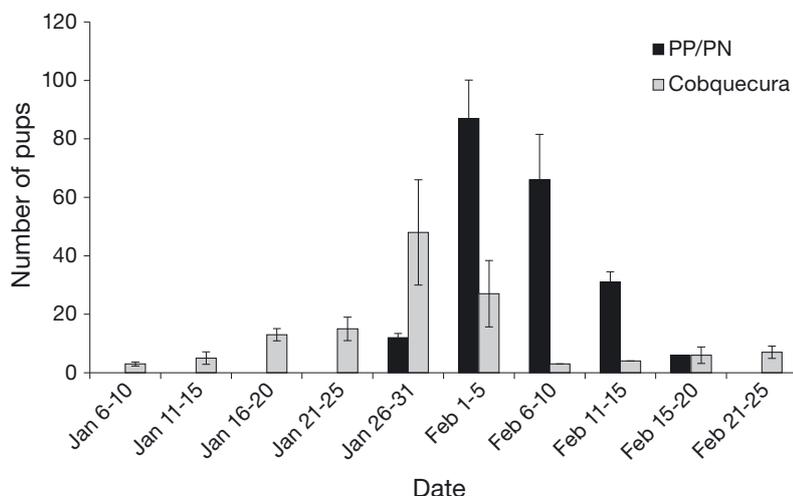


Fig. 3. Distribution of South American sea lions pups captured in the PP/PN and Cobquecura colonies. Data are combined all for years for each colony (2011 to 2013 in PP/PN and 2009 to 2012 in Cobquecura)

Using the values of the morphological measures on male and female pups for the 2 study areas, we estimated the CI_m for each sex and zone (Table 1). Three of the 4 regressions of CI_m on capture date showed no relationship; for the males and females from PP/PN ($r^2 = 0.0001$, $p = 0.791$; $r^2 = 0.030$, $p = 0.185$, respectively) and for the females from Cobquecura ($r^2 = 0.001$, $p = 0.854$). The only exception was found in males from Cobquecura ($r^2 = 0.056$, $p = 0.032$). Although significant, this result explained a very low proportion of the variance (3%), suggesting that date of capture did not produce a relevant effect on CI_m and thus was not considered.

Body condition and prey availability

When comparing CI_m between localities, both male and female pups from Cobquecura showed a significantly greater CI_m compared to those from PP/PN (Males: $F_{1,138} = 189.15$, $p < 0.0001$; Females: $F_{1,91} =$

52.468, $p < 0.0001$) (Table 1). Female pups from both colonies were in significantly better condition in 2011 than in 2012 ($F_{1,91} = 5.11$, $p = 0.026$). However, no differences between years were found in males ($F_{1,138} = 2.35$, $p = 0.128$), and there was no interaction between year and locality for males and females ($F_{1,138} = 1.93$, $p = 0.167$; $F_{1,91} = 0.54$, $p = 0.466$, respectively).

Relatively higher acoustic densities and biomass of anchovy and sardine were recorded in 2011 for both north and central-south zones (Fig. 4, Table 2). Although food availability for both areas was higher in 2011 compared to other years, a more remarkable higher acoustic density of anchovy and sardine was found in

the central-south area, especially for sardine as shown in Fig. 4. These spatial and temporal variations in prey biomass overlap with hotspots of foraging behavior by South American sea lions from the studied colonies. The foraging behavior of satellite-tracked South American sea lions from PP/PN was associated with shallow-coastal locations, mainly concentrated from $20^{\circ}43'$ to $21^{\circ}54'S$ (Hevia 2013). Foraging hotspots of sea lions from Cobquecura were also in shallow-coastal waters from 35° to $37^{\circ}S$ (Hückstädt et al. 2014).

A significant positive relationship between $\log_{10}(CI_m)$ and $\log_{10}(\text{fish biomass})$, both for male ($r^2 = 0.447$, $p < 0.00001$) and female ($r^2 = 0.452$, $p < 0.00001$) pups was found (Table 2). When analyzed separately, each locality maintained this tendency, both for males ($r^2 = 0.030$, $p = 0.036$) and females ($r^2 = 0.103$, $p = 0.002$) in PP/PN, and for males alone in Cobquecura ($r^2 = 0.092$, $p = 0.003$). Only females from Cobquecura did not show a relationship between CI_m and fish biomass ($r^2 = 0.018$, $p = 0.330$) (Table 2).

Table 1. Means, ranges and sample size of morphological variables recorded in males and females South American sea lion pups in the localities of PP/PN (north zone) and Cobquecura (central-south zone). CI_m = body condition index

	Males				Females			
	PP/PN		Cobquecura		PP/PN		Cobquecura	
	Mean (range)	n	Mean (range)	n	Mean (range)	n	Mean (range)	n
Standard length (cm)	83.6 (72–101)	116	79.6 (71–89)	82	80.1 (63–100)	86	77.5 (69–89)	56
Body mass (kg)	11.0 (7.0–18)	116	13.4 (10.6–17.8)	82	10.1 (7.0–18.6)	86	12.3 (9.8–15)	56
CI_m	0.92 (0.6–1.3)	116	1.16 (0.9–1.4)	82	0.92 (0.6–1.4)	86	1.17 (0.9–1.4)	56

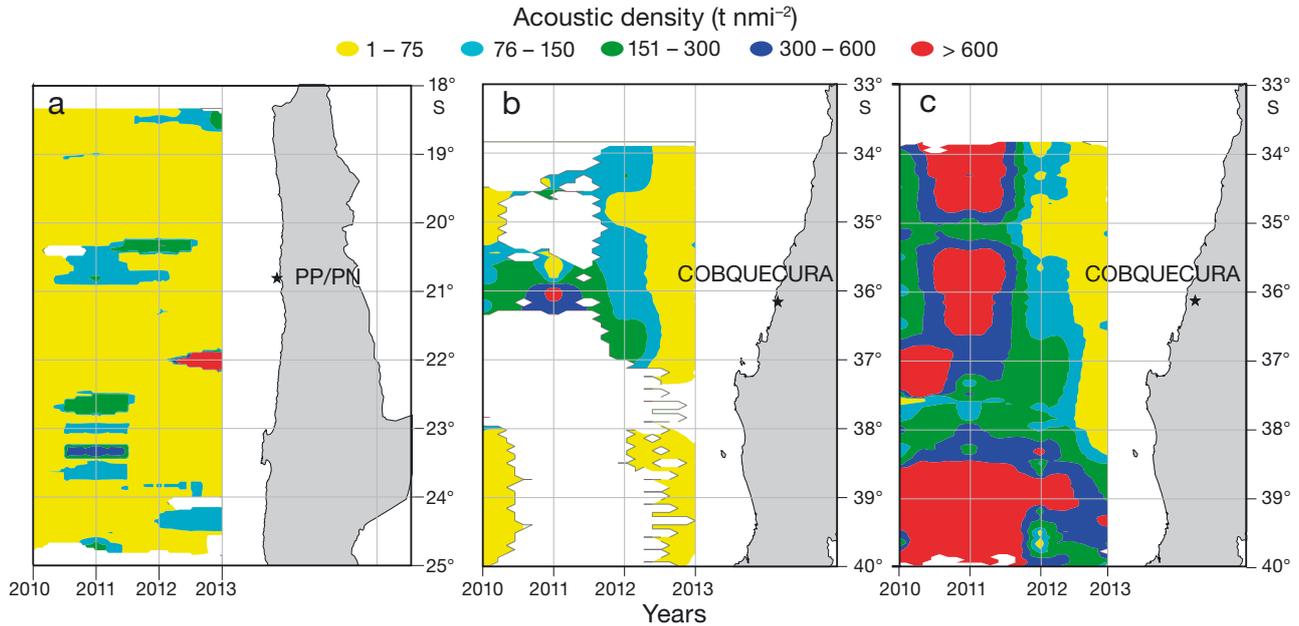


Fig. 4. Hovmöller diagrams of sardine and anchovy density by latitude during summer surveys from 2010 to 2013: (a) sardine in the north zone, (b) anchovy in central-south zone, (c) sardine in the central-south zone

Table 2. Body condition index (CI_m) for male and female South American sea lion pups in the localities of PP/PN (north zone) and Cobquecura (central-south zone), and estimates of fish biomass per zone from 2009 to 2013

Year	Mean (range) CI_m				Fish biomass ($t \times 10^3$)	
	PP/PN		Cobquecura		North	Central-south
	Male	Female	Male	Female		
2009			1.07 (0.9–1.2)	1.14 (1.0–1.2)		2032.5
2010			1.11 (1.0–1.4)	1.20 (1.0–1.4)		2632.3
2011	0.90 (0.7–1.1)	0.96 (0.8–1.2)	1.20 (1.0–1.4)	1.16 (1.0–1.3)	253.9	3620.4
2012	0.90 (0.7–1.1)	0.87 (0.6–1.2)	1.14 (1.0–1.4)	1.09 (0.9–1.2)	162.3	3943.9
2013	0.98 (0.6–1.3)	0.98 (0.6–1.4)			299.5	

DISCUSSION

Our results showed that body condition of the *Otaria flavescens* pups varied over time (variation between years), and between areas (north vs. central-south Chile). Also, a close relationship was found between prey availability and body condition of the pups. As previously indicated by other authors for different species of pinnipeds (e.g. Bradshaw et al. 2000), our results show that in spite of its simplicity, the relative pup condition index used here is useful for comparing body condition of pups among colonies (Bradshaw et al. 2000). However, because we sampled pups outside the colonies, our results should be taken with caution.

One major finding of this study is the spatial variation in the body condition of pups. The body

length of the pups measured in the north zone (PP/PN) was longer than that recorded in the central-south zone (Cobquecura), and higher than values reported by Cappozzo et al. (1991) (range: 79 to 82 cm) and Vaz-Ferreira (1982) (mean length: 81.7 and 75.0 cm for males and females, respectively) for *O. flavescens* pups on the Atlantic coast. In spite of this, body weight, and consequently body condition estimated by the morphometric index, suggest that body condition of the pups in the north was significantly lower than that of pups in the central-south zone. Because animals in better condition are predicted to maintain a more competent immune system and have higher potential survival (Boltnev et al. 1998, Green et al. 2010), differences in pup body condition between PP/PN and Cobquecura may have important consequences for

both overall health state and first year survival (Boltnev et al. 1998).

The direct benefit of higher survival during the lactation period may have positive effects that persist during the first several years of life (Baker & Fowler 1992), thus probably affecting population trends of sea lions. The abundance of sea lions (including pups) in the Cobquecura colony has remained relatively constant for the last 12 yr (Quiñones et al. 2011), while the abundance of sea lions (especially pups) in the PP/PN colonies (particularly in Punta Negra) has decreased in the last 15 yr (Sielfeld & Guzmán 2002). These differences in population trends between the areas cannot be explained by diet composition, because sea lions from the 2 colonies are both important consumers of common sardine and anchovy (Sielfeld 1999, Muñoz et al. 2013), showing a clear pattern of epipelagic and coastal foraging (Hevia 2013, Hückstädt et al. 2014). In addition, no effect of prey energetic content is expected on sea lion populations because these 2 prey species are of a similar size and have a similar diet composition, suggesting a similar utilization of resources and energetic content (Llanos et al. 1996). Further research should be focused on evaluating whether a relationship exists between body condition and abundance in these populations, or if other factors, such as the interactions with artisanal fisheries and/or latitudinal movements of individuals to other places may explain the decrease in the sea lion abundance in the PP/PN colonies.

Our results suggest that spatial variation in the pups' body condition may be associated with differences in biological productivity around the breeding colonies. Boyd (1998) indicated that the productivity of an area is of great relevance for pinnipeds, since these species have adapted to exploit locally abundant resources. In the South American sea lion, females tend to remain in the same place and show a high degree of philopatry (Feijoo et al. 2011). Females nurse their young on land for 8 to 10 mo (Cappozzo & Perrin 2009), and as evidenced from satellite data, they forage close to the breeding sites during their foraging trips (Rodríguez et al. 2013), thus local productivity is an important factor for them. Considering this species is a central forager that shows a strong dependence upon local prey availability, it can be expected that the greater productivity of the central-south zone compared to that of the north zone would allow female *O. flavescens* to obtain more food in less time, thus decreasing the time they spend away from their offspring and increasing the lactating period (Muñoz et al. 2011). The difference

in productivity may explain, at least partly, the lower body condition of the pups in the north zone compared to those of the central-south zone. According to Gerrodette & DeMaster (1990) the knowledge of trends in both abundance and condition indices could be used to deduct changes in carrying capacity. The lower body condition of pups together with a decline in the abundance trend of sea lions in the PP/PN colonies may suggest an overall lower carrying capacity for *O. flavescens* at those localities due to lower productivity.

It is important to consider that pup body condition not only may vary in relation to food availability, but also due to other factors, such as size, age, and experience level of the mothers, and also parturition date (Boltnev & York 2001). For instance, Boyd & McCann (1989) and Boltnev & York (2001) found a positive relationship between maternal size and pup size in some pinniped species. Similarly, a positive relationship between maternal age and pup size has been shown (e.g. Bowen et al. 1994). Because we did not consider maternal effects in this study, we cannot rule out if these factors may explain, at least in part, the spatial variation in the pups' body condition.

The variability of physical climate, such as El Niño or La Niña events (Barber & Chavez 1983) may also explain the spatial and temporal differences in body condition of the pups. These perturbations produce changes in primary productivity which lead to abrupt changes in the distribution and abundance of prey species (Barber & Chavez 1983, Daneri et al. 2000). Temporal fluctuations in prey abundance may affect the foraging behavior of lactating females and eventually the body condition of their pups in different years (Soto et al. 2006). The higher values of female pup body condition in 2011 may be explained by a cold La Niña phenomenon affecting the Chilean coast between July 2010 and March 2011, which was associated with greater productivity in the coastal area. According to hydroacoustic surveys, the fish biomass in central-south Chile was at its highest in 2011, suggesting greater food availability for sea lions in that year, and probably reflecting better body condition of pups born in 2011. This fact highlights the importance of multi-year sampling in order to detect the relationship between productivity variation and the potential responses of top predators such as the South American sea lion.

In conclusion, spatial and temporal variations in prey availability appear to strongly affect the body condition of South American sea lion pups. These results corroborate the findings in other pinniped species (e.g. Bradshaw et al. 2000). Future studies

should focus on the relationship of these spatial and temporal differences to sea lion population survival and reproductive aspects, and also evaluate if these differences represent a different strategy to confronting environment fluctuations (such as El Niño) that strongly affect the sea lion populations of north Chile. Additionally, due to the fact that other potential factors such as maternal influences seem to also affect the body condition of pups, their incorporation in further studies is crucial.

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