Seasonal variation in blood and muscle oxygen stores attributed to diving behavior, environmental temperature and pregnancy in a marine predator, the California sea lion

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A B S T R A C T

Survival depends on an animal's ability to find and acquire prey. In diving vertebrates, this ability is directly related to their physiological capability (e.g. oxygen stores). We studied the seasonal variation in oxygen stores, body temperature and body condition in California sea lions (Zalophus californianus) (CSL) as a function of seasonal variation in temperature, primary productivity, diving behavior and reproductive stage. During summer, blood oxygen stores were significantly greater and muscle oxygen stores were significantly lower than in winter. Total oxygen stores, body condition and body temperature did not change between seasons but variations in body temperature were greater during summer. Changes in oxygen stores are partly attributed to diving behavior, temperature and pregnancy that could increase oxygen consumption. Blood and muscle oxygen stores appear to be influenced by reproductive state. Blood oxygen stores are more likely influenced by diving behavior and temperature than muscle oxygen stores.

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1. Introduction

The physical environment changes at different temporal scales; over centuries, decades, years and seasonally within a year. Two of the most important features of seasonal change are temperature and light, which directly affect abundance, distribution, physiology and behavior of prey and their predators. Many taxa deal with an unsuitable seasonal change by migrating to a more suitable environment, such as butterflies, whales and birds (Urquhart and Urquhart, 1978; Mate et al., 1999; Tremblay et al., 2006) or by means of hibernation and aestivation as seen in bears, badgers and frogs (Schooley et al., 1994; Tanaka, 2006; Tracy et al., 2007). Colony breeding species are central place foragers and for some species like the California sea lion, Zalophus californianus (CSL) (Lesson, 1828) females are constrained by the need to remain with their pup throughout the year and thus are not able to migrate to a more suitable habitat.

Survival of a population is influenced by its foraging success. In diving vertebrates such as sea lions, foraging success is directly related to the distribution, quality and availability of prey coupled with their physiological capability to dive and acquire that prey. Important determinants of the physiological capability to dive and thus the time an animal can forage are its oxygen stores, its diving metabolic rate and the extent to which the oxygen stores can be depleted (Costa et al., 2001; Meir et al., 2009). In sea lions and fur seals oxygen to support aerobic metabolism during diving is stored in the lungs (10–21%), blood (41–70%) and muscle (20–43%) (Kooyman, 1989; Ponganis, 2011).

Oxygen stores have been measured in a variety of diving vertebrates, including penguins, seals, dolphins, moles, shags, turtles (Kooyman and Ponganis, 1990; Lutcavage et al., 1992; Ponganis et al., 1993; McIntyre et al., 2002; Noren et al., 2002; Burns et al., 2005; Cook et al., 2008; Hassrick et al., 2010), sea lion and fur seals (Lenfant et al., 1970; Horning and Trillmich, 1997; Costa et al., 1998, 2001; Richmond et al., 2006; Fowler et al., 2007; Weise and Costa, 2007; Villegas-Amtmann and Costa, 2010). However, only one study has examined the seasonal changes in oxygen stores concurrently with changes in diving behavior (Villegas-Amtmann and Costa, 2010). In this study individual Galapagos sea lions (ZSL) (Zalophus wollebaeki) exhibited three different diving patterns and each was associated with a different amount of stored oxygen. The longest diving individuals had the highest oxygen stores, while the shortest duration divers had the lowest oxygen stores. Further, while the diving behavior didn’t change between seasons, the blood and muscle oxygen stores did (Villegas-Amtmann and Costa, 2010).

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California sea lions are widely distributed from the western coast of North America, from the Gulf of Alaska to the south of Mexico, including the Gulf of California (Maniscalco et al., 2004; Aurioles and Trillmich, 2008). The population in the Gulf of California has been estimated at around 30,000 individuals (Szeret et al., 2006) of the 355,000 global population (Aurioles and Trillmich, 2008). In the Gulf of California, sea lions encounter a wide range of environmental temperatures within a year that influence primary productivity and prey availability. Sea surface temperature (SST) in the Gulf of California ranges annually from 15 to 31 °C and chlorophyll-a ranges from 0.3 to 6.0 mg/m³ (http://coastwatch.pfeg.noaa.gov/) between the coldest (winter) and warmest (summer) seasons of the year.

We previously found that CSLs change their diving behavior between these contrasting seasons, exhibiting greater variability during the warm and less productive season (Villegas-Amtmann et al., 2011). In addition to these seasonal changes in diving behavior, SST and primary productivity, the reproductive pattern of CSLs varies with females giving birth followed by copulation and delayed implantation during the warm season (summer) with the active growth of the fetus occurring during the cold season (winter) (Odell, 1975).

Here we examine the seasonal variation of oxygen stores, core body temperature and body condition in California sea lions from Granito Island, Gulf of California, Mexico during the two most contrasting seasons of the year, summer and winter. We hypothesized that CSLs would exhibit higher oxygen stores, core body temperature and lower body condition during the warm season and that these differences would be associated with the changes in diving behavior (deeper and longer dives), warmer ambient and SST, lower primary productivity and reproductive stage (~1 month after giving birth).

2. Materials and methods

2.1. Field site and capture procedures

Measurements were carried out during a warm season, the end of July 2005, and a cold one, the end of February 2007 at Granito Island (29.55° N, 113.54° W) in the Gulf of California, Mexico. During the warm season we captured 10 lactating female CSLs, which were suckling small pups, 1 to 2 months after the peak pupping season. During the cold season we captured 11 lactating female CSLs, with older pups (8 to 9 months after peak pupping season). Due to the timing of the field effort the lactating females in each season were not the same individuals.

Sea lions were captured with hoop nets and anesthetized with isoflurane administered using a portable anesthesia machine (10 L/min with a 3 L rebreathing bag). Anesthesia was induced while the animal was inside the net by placing a plastic mask (modified highway road cone) on the sea lions’ snout with isoflurane delivered at 4 to 5% in 100% oxygen. Induction time varied from 5 to 25 min depending on the animal’s excitement and amount of apneas. Intravenous propofol at a dose of 1 mg/kg was used as an induction agent for some animals 5 min after the start of the isoflurane induction. Animals were intubated using a large laryngoscope blade (35 cm) and endotracheal tubes with an internal diameter of 14–18 mm. The anesthesia was maintained with 1.5 to 2% of isoflurane (Gales and Mattlin, 1997; Parás, 2008).

Samples were taken while the animal was anesthetized and the instruments were introduced and attached to measure core body temperature and locate the animals. The recovery of the instruments was facilitated by locating the animals using small VHF radio transmitters (Sirtrack; Havelock North, New Zealand) or ARGOS linked PTTs (Wildlife Computers, Redmond WA, USA). The radioimmunoassay was performed as per manufacturer
instructions and following the methods in Villegas-Amtmann et al. (2009) and Greig et al. (2007).

We tested data for normality using a Kolmogorov–Smirnov one sample test and for homogeneity of variance. Comparisons between seasons were performed using t-tests or when data were not normally distributed using Kruskal–Wallis tests (K–W).

3. Results

California sea lions exhibited changes in their oxygen stores between seasons. Blood oxygen store components measured: [Hb] (t-test, t = -2.49, df = 18, P = 0.03), Bv (t-test, t = -2.49, df = 18, P = 0.02) and Pv (t-test, t = -2.49, df = 18, P < 0.00) were significantly greater during the warm season compared to the cold season. In contrast, muscle oxygen stores measured as [Mb] (t-test, t = -2.43, df = 18, P = 0.02) were significantly lower during the warm season compared to the cold season. Hct values, mass and body condition index were not significantly different between seasons (Table 1, Figs. 1 and 2).

Mass specific total oxygen stores were not significantly different between seasons, but the relative contribution of the different oxygen stores was significantly different. During the warm season 12.5%, 55.2% and 32.3% of the total oxygen was stored in the lung, blood and muscle, while during the cold season it was 13.7%, 44.3% and 42% respectively. Mean mass specific total muscle oxygen stores were significantly greater during the warm season (18.4±2.8 mL/kg) than during the cold season (15.5±2.3 mL/kg, t-test, t = -2.46, df = 17, P = 0.02). Mean mass specific lung oxygen stores were not significantly different between seasons (6.0±0.05 and 6.0±0.03 mL/kg for the warm and cold seasons respectively) (Fig. 2).

We recovered data from 4 HTRs in 2005 that sampled body temperature from 4 h to 2 days and 4 HTRs in 2007 that sampled temperature from 4 h to 1 day. STTs were expelled by one sea lion in 2005 and all of them in 2007 before the initiation of diving and thus data are mostly from when animals were on land (less than 13% of temperature data are from when animals were at sea). In order to remove the effect of prey ingestion or diving activity on core body temperature, records were filtered to eliminate sudden changes in temperature that occurred over a period of no longer than 2 min. Mean core body temperature was determined for each individual and was not significantly different between seasons. However, the variance among individuals (calculated from the body temperature means of each individual) and the mean of the individual variances (± SD) (calculated from all body temperature data of each individual) was greater during the warm season (0.30 and 1.4±2.2 respectively) compared to the cold one (0.05 and 1.03±1.4 respectively) (Fig. 3).

Mean progesterone concentration (± SD) was higher during the cold season (February) (7.6±5.2 ng/mL, n = 10) than during the warm season (July) (4.8±2.9 ng/mL, n = 11). Seven out of 11 females were diagnosed as pregnant by veterinary physical examination and 6 females presented progesterone concentrations ≥7.4 ng/mL (Greig et al. 2007) found that progesterone concentrations of 7.44 ng/mL were indicative of California sea lions during mid-pregnancy. The mean progesterone concentration of our females was 11.8±2.8 ng/mL (n = 6) (Fig. 4). Only 2 out of 10 females presented progesterone concentrations ≥7.44 ng/mL during the warm season and none were diagnosed as pregnant by veterinary examination (Fig. 4).

The mean estrogen concentration was significantly greater during the cold season (11.0±7.0 ng/mL, n = 11) than during the warm one (0.3±0.2 ng/mL, n = 10, t-test, t = 2.09, df = 19, P = 0.00). The mean estrogen concentration of females that exhibited progesterone concentrations ≥7.44 ng/mL during the cold season was 1.3±0.8 ng/mL (n = 6) and the mean estrogen concentration of females that exhibited progesterone concentrations <7.44 ng/mL during the cold season was 0.7±0.3 ng/mL (n = 5) (Fig. 4).

4. Discussion

 CSL blood and muscle oxygen stores measured in this study are comparable to that of previous studies on the same species (Hedrick and Duffield, 1991; Ponganis et al., 1997; Weise and Costa, 2007). However, blood volumes for the warm season in this study are somewhat larger than those in previous studies possibly due to sampling periods and sex/mass differences. Hedrick and Duffield (1991) only sampled 2 sea lions and sex or mass was not specified. Sea lions in the Ponganis et al. (1997) study were immature animals and were smaller (34–42 kg) than the females in this study (65–109 kg). Smaller individuals have proportionally lower oxygen storage capacity (Costa et al., 2004; Weise and Costa, 2007). The Weise and Costa (2007) sampling period included 2 seasons (Sept.–Oct. and March) and their reported blood volumes are comparable to our values from the cold season (late February). The relative distribution of oxygen in the tissues of CSL is also consistent with that reported for other California sea lions (Kooyman and P.J., 1998; Weise and Costa, 2007).

Table 1

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<th>Mass (kg)</th>
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a Pregnant females based on [progesterone] > 7 ng/mL (Greig et al. 2007) and/or field examination.
4.1. Diving physiology and behavior

CSL blood and muscle oxygen stores changed between seasons; showing contrasting patterns. During the warm season blood oxygen stores were significantly greater and muscle oxygen stores significantly lower (assuming a constant muscle mass supported by morphometric measurements) than during the cold season when this pattern was reversed (Fig. 1). The diving behavior of these sea lions changed between seasons, with females diving deeper and longer during the warm season (Villegas-Amtmann et al., 2011). Such a change in diving behavior may be expected if there was a concurrent change in total oxygen stores, but total oxygen stores were not significantly different between seasons (Fig. 2). However, a change in diving behavior does not necessarily dictate a change in diving physiology as the animal may not have been operating at or near its aerobic dive limit. Thus, a change in diving behavior to longer/deeper dives does not necessarily require an increase in total oxygen stores. Nevertheless, the distribution of oxygen stores did vary significantly between seasons and blood oxygen stores were greater during the warm and less productive season concurring with sea lions diving deeper and longer (Villegas-Amtmann et al., 2011).

![Fig. 1. Mean oxygen stores of California sea lion females (Zalophus californianus) from Granito Island, Mexico: hematocrit (Hct), hemoglobin concentration ([Hb]), blood volume (Bv), myoglobin concentration ([Mb]), mass and body condition index (BCI – mass/std. length) ± SE during a warm (Jul–Aug 2005) and a cold (Feb–Mar 2007) season. * = statistical significance (two-sample Student’s t-test, P<0.05).]

![Fig. 2. Total oxygen stores showing their relative proportion in blood, muscle and lung for adult female California sea lions (Zalophus californianus) from Granito Island, Mexico during a warm (Jul–Aug. 2005, n=9) and a cold (Feb–Mar. 2007, n=10) season. * = statistical significance (two-sample Student’s t-test, P<0.05).]
During the warm season, warmer water temperatures and lower productivity might shift the distribution of sea lion prey deeper into the water column. The diet of CSLs at Granito Island varies seasonally. During the warm season they feed primarily on Pacific cutlassfish (Trichiurus lepturus), a benthopelagic fish (Riede, 2004), while during the cold season they feed mainly on sardine (Sardinops caeruleus) and sanddab (Citharichthys sp.), pelagic and demersal fish respectively (Lamb and Edgell, 1986; Garcia-Rodriguez and Aurioles-Gamboa, 2004; Riede, 2004). The seasonal variation in diet is consistent with the observed changes in diving behavior and the enhanced diving capability during the warm season. During the summer when the animals are feeding on deeper benthic prey they require greater blood oxygen stores to enable longer dives. Whereas during the winter they are feeding on deeper benthic prey they require greater blood oxygen stores to enable longer dives. Whereas during the warm season they feed primarily on Pacific sardine (Sardinops caeruleus) and sanddab (Citharichthys sp.), pelagic and demersal fish respectively (Lamb and Edgell, 1986; Garcia-Rodriguez and Aurioles-Gamboa, 2004; Riede, 2004). The seasonal variation in diet is consistent with the observed changes in diving behavior and the enhanced diving capability during the warm season. During the summer when the animals are feeding on deeper benthic prey they require greater blood oxygen stores to enable longer dives. Whereas during the winter they are feeding on deeper benthic prey they require greater blood oxygen stores to enable longer dives.

Environmental temperatures that exceed the upper critical temperature also result in an increase in metabolic rate as a consequence of the work required to dump excess heat (Matsuura and Whittow, 1973). An increase in total oxygen stores during the warm season could be partly attributable to an increase in metabolic rate and therefore oxygen consumption to thermoregulate. Although we did not find changes in total oxygen stores, blood oxygen stores ([Hb], Bv and Pv) were significantly higher during the warm season. Significantly elevated hemoglobin levels at warmer temperature regimes have been shown in fish (Houston and Gingrasbedard, 1994). Natural heat acclimatization often results in increases in the circulating blood volume in humans (Bass et al., 1955; Wyndham et al., 1968; Senay and Kok, 1976; et al., 1989; MacArthur et al., 2003). Therefore, changes in the distribution of blood oxygen stores observed in this study can be partly attributed to the diving behavior changes driven by prey distribution shifts due to seasonal change (water temperature).

4.2. Physiology and environmental temperature

CSLs encountered a broad range of sea surface temperatures (SST) (14–34.5 °C) (means of minimum and maximum SST) as measured by time–depth recorders deployed on these animals for a different study and air temperature (17–39 °C) between seasons (IBAJANOR1 weather station, wunderground.com). As expected, the mean SST was significantly greater during the warm season (28.8 ± 1.1 °C) than during the cold one (17.5 ± 0.9 °C) (Villegas-Amtmann et al., 2011).

Stomach temperature data was obtained almost exclusively on land due to the STTs being expelled before the diving activity began. CSL body temperature on land as approximated by stomach temperature measurements was not significantly different between seasons, but its variance was greater during the warm season (0.30) compared to the cold one (0.05) (Fig. 3). On land, the upper critical temperature in CSL beyond which its metabolic rate increases in order to thermoregulate has been defined as 21–22 °C (Matsuura and Whittow, 1973). In water, the upper critical temperature has not been defined yet; but in water temperatures of up to 30–32 °C, sea lions maintained a stable metabolic rate (Matsuura and Whittow, 1973; Liao, 1990). CSLs in this study encountered ambient and SST as high as 41 °C during the warm season (Villegas-Amtmann et al., 2011) that greatly exceeded their defined upper critical temperature on land. Matsuura and Whittow (1973) found that the CSL’s core body temperature increased when exposed to ambient temperatures of 32 °C. It may be more challenging for sea lions to thermoregulate under the temperature conditions encountered during the warm season, hence the greater fluctuation in their core body temperature (Fig. 3).

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Shapiro et al., 1981). Therefore we can partly attribute the observed changes in blood oxygen stores to environmental conditions (ambient and SST).

4.3. Hormone analyses

Taking into account progesterone concentration values reported in pregnant California sea lions (Greig et al., 2007) and physical examination of the sea lions performed in the field, we can confirm that at least 8 out of 11 females were pregnant during the cold season in February (Table 1, Fig. 4). High progesterone concentrations in 2 females during the warm season in July could have been caused by the increase in circulating progesterone concentration that follows a peak in estrogen concentration (estrus), as seen in Antarctic fur seals (Boyd, 1991a) and several species of seals (Atkinson, 1997). The California sea lion estrus and fertilization period occurs in July (Odell, 1975), thus the high progesterone concentrations were likely due to the normal luteal phase that follows ovulation (Atkinson, 1997).

We found significantly higher concentrations of estrogen during the cold season in February, when sea lions are in a mid to late gestational phase than during the warm season in July when females had given birth recently, ovulated, and entered the normal embryonic diapause (Fig. 4). Higher estrogen concentrations are expected in pregnant females as estrogen levels rise steadily during pregnancy (Reijnders, 1990). These results further confirm our detection of pregnant females during the cold season.

4.4. Diving physiology and pregnancy

We found significant changes in blood and muscle oxygen stores between seasons. Pregnancy can have important effects in the distribution of oxygen stores. Pregnant females face a higher oxygen demand to supply the fetus especially under hypoxic conditions when diving and blood volume typically increases in pregnant mammals. Maternal perfusion of the placenta continues during diving in Weddell seals (Elser et al., 1970; Liggings et al., 1980).

CSLs exhibited higher levels of Pv and Bv during the warm season (late July) when they have recently given birth (mid-late June, Luque and Aurioles-Gamboa, 2001) and are not pregnant compared to the cold season (late February) when they are in the active gestational phase of pregnancy (~5–6 months, assuming implantation in late Sept). This is contrary to previous studies in humans and other mammals where the plasma volume increases up to 50% during healthy pregnancies (Reynolds, 1953; Bond, 1958; Prince, 1982; Longo, 1983; Hytten, 1985; Letsky, 1995). However, in these studies pregnant and non-pregnant females were not lactating, differing to sea lions in this study. In several terrestrial mammals estrus and ovulation are usually suspended during lactation (lactational anestrus) (Hafez and Hafez, 2000) and therefore they are rarely pregnant while lactating. While we know that lactating female Steller sea lions often conceive during lactation (Atkinson, 1997; Maniscalco et al., 2002, 2006), we do not know the changes, if any, associated with Pv or Bv.

Otarids are unique in that most of the time they are simultaneously pregnant and lactating. Provisioning for the young represents the highest energetic demand during the annual cycle for female California sea lions (Williams et al., 2007). This cost added to pregnancy costs involve great physiological demands that are currently not well understood. After giving birth, there is only a short period when otarids are neither pregnant (2 weeks to 1 month for most otarids (Boyd, 1991b)) nor lactating (if weaning occurs some time before they give birth). Some otarids provision their young until the new pup is born (Trillmich, 1986) and therefore are always lactating (except in failed pregnancies).

High Bvs are maintained throughout lactation in cows, pigs, rabbits and rats (Reynolds, 1953; Bond, 1958; Anderson et al., 1970; Ota and Peaker, 1979) and return to control levels with the cessation of lactation (Reynolds, 1953). In women, Bv values are stabilized after 30 days postpartum (Caton et al., 1949; Landesman and Miller, 1963). Pv in pigs continues to rise during the first 14 days of lactation and then decreases steadily until weaning. This rise in Pv during the first days of lactation is either to maintain blood flow to the mammary glands or secondary to a general rise in body water (Anderson et al., 1970). These patterns can explain the higher Bv found in CSL females during the warm season when they have recently given birth (~1 month earlier). A rise in body water by means of a rise in Bv during lactation might also be necessary for sea lions to meet milk production requirements. Unlike terrestrial mammals, marine mammals do not have fresh water access and water is obtained mainly from their prey.

Bv in sea lions might start to decrease with the onset of weaning and lactation cessation (such as in the above studies), when sea lion pups are starting to feed on their own. This would explain the lower Bv values found in this study during the cold season (late Feb) when pups are approximately 8 months old. Pups might start to supplement their milk intake by feeding independently at 6 months of age (Melin et al., 2000; Williams et al., 2007). Bv possibly starts to rise again when full lactation resumes after giving birth, corresponding to what we found during the warm season (late July). Similar to results from this study, Galapagos sea lion Bv was also lower in the season when most females were pregnant (Villegas-Amtmann and Costa, 2010). Pregnant northern elephant seals did not show an increase in Bv (Hassrick et al., 2010).

Furthermore, the observed decrease in Bv could be an artifact because the Evan’s blue dye does not cross the placenta (Reynolds, 1953; Whipple et al., 1955). Therefore, our Bv measurements only represent the mother and do not include the Bv of the fetus. Since our Bv measurements were determined relative to the total mass of the mother, which includes the fetus, the total Bv for that mass (female and fetus) would be underestimated. In an attempt to correct for this we subtracted 5 kg (estimated fetal mass; J.B.W. Wolf, pers. comm.) from the females’ mass and Bv values remained significantly lower during the cold season. Moreover, females gain body weight during pregnancy in addition to fetal mass which would also affect mass specific Bv calculations, but female’s mass was not significantly different between seasons.

In contrast to Bv, [Mb] was significantly greater during the cold season, when most females were pregnant. For pregnant sea lions, diving likely results in greater muscular exertion and oxygen consumption than for non-pregnant ones. Noren et al. (2011) found an increase in drag forces, reduction in stroke amplitude and distance per stroke and reductions in swim speeds in pregnant dolphins compared to non-pregnant ones, providing a mechanism for diminished locomotor performance.

Additionally, a dive response (apnea, bradycardia and peripheral vasocostriction (Irving, 1934; Scholander, 1940; Elsner, 1965; Andersen, 1966)) is necessary to maximize and extend aerobic dive limit. This response should be less pronounced as the level of muscular exertion increases (Davis et al., 2004). Endogenous muscle oxygen stores can only be accessed by the muscle. Therefore, higher [Mb] observed during the cold season could be the result of an increased drag and diminished locomotor performance to be able to maintain the dive response by decreasing muscular exertion and maximizing the aerobic dive limit.

We attribute the observed seasonal changes in oxygen stores partly to differences in diving behavior, environmental temperature, and most importantly to reproductive state. The same seasonal pattern in oxygen stores was observed in Galapagos sea lions. They exhibited significantly greater blood oxygen stores and significantly lower muscle oxygen stores during a warm season, compared to a cold one when most females were in a late pregnancy status (Villegas-Amtmann et al., 2009; Villegas-Amtmann and Costa, 2010) further supporting our conclusions.

We found seasonal changes in muscle and blood oxygen stores, but no change in total oxygen stores. Therefore, we suggest that oxygen store studies, in particular those investigating changes or inter-species comparisons, should consider the different oxygen store components.
independently as well as consider the blood volume and reproductive state of the animals. By only looking at total oxygen stores one might draw misleading conclusions if the separate components are overlooked.

5. Conclusions

CSL oxygen stores changed between seasons; during the warm season blood oxygen stores were significantly greater and muscle oxygen stores were significantly lower compared to the cold season. Total oxygen stores were not significantly different between seasons. Although the total oxygen storage capacity remained constant between seasons, blood oxygen stores were greater during the warm and less productive season concurring with sea lions diving deeper and longer (Villegas-Amtmann et al., 2011). Therefore physiological changes in the distribution of oxygen stores can be partly attributed to diving behavior changes driven by prey distribution shifts due to seasonal change (water temperature).

Mean SST was significantly greater during the warm season than during the cold one.

CSL body temperature as approximated by stomach temperature measurements was not significantly different between seasons, but its variance was greater during the warm season.

An increase in oxygen stores during the warm season could be partly attributable to an increase in metabolic rate and therefore oxygen consumption to thermoregulate. Although we did not find changes in total oxygen stores, blood oxygen stores were significantly higher during the warm season. Therefore we partially attribute the observed changes in blood oxygen stores to environmental conditions (ambient and SST).

At least 8 out of 11 females were pregnant during the cold season in February. Pregnancy can have important effects in the distribution of oxygen stores. CSLs exhibited higher levels of Pv and Bv during the warm season, therefore we largely attribute the observed changes in oxygen stores, blood oxygen stores were significant during the warm season. Physiological changes in the distribution of oxygen stores can be partly attributed to diving behavior changes driven by prey distribution shifts due to seasonal change (water temperature).

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