



# 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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## ABSTRACT

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 capacity 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 (GSL) (*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 (Szteren 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/m<sup>3</sup> (<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 animals' 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).

Core body temperature was obtained by equipping CSLs with heart rate-stomach temperature recorders (HTR) (set to sample only the stomach temperature) and stomach temperature transmitters (STT) (Wildlife Computers). We deployed 10 HTRs and STTs in 2005 and 8 in 2007, which were attached to the animal's back and placed in the

animal's stomach respectively. In the STT, 4 thermistors monitor the temperature, and the coldest measured temperature is relayed to the HTR. The STT "pings" a radio-pulse of 5 kHz. The ping-rate is temperature-dependent; the warmer the temperature, the faster the ping-rate. The STT is calibrated to measure 0 to 50 °C, with a resolution of 0.1 °C, and an accuracy of approximately ±1 °C (Wildlife Computers). The STT is eventually defecated or regurgitated (lost to the environment) and HTRs stop recording data at that time.

We mounted the instruments on mesh netting and glued them to the dorsal pelage of the lower back (HTR) and between the shoulders (PTT and VHF) of the animals using a 5 minute quick set Locktite epoxy (Locktite Quickset™, Henkel Corp., Dusseldorf, Germany).

The total weight of the instruments attached was approximately 230 g (~0.23% of the animal's mass). We weighed animals in a sling using a tripod and a 250 kg (±0.1 kg precision) capacity digital scale and took standard length measurements using a measuring tape.

The equipment was either removed by recapturing and physically restraining the animals without anesthesia or was recovered on the rookery around the rocks in the inter-tidal zone after falling off the animal during the molt (possibly at the beginning of August). Epoxy mounts fall off during the animals' annual molt.

This research was approved by the CARC (Chancellor's Animal Research Committee) at University of California, Santa Cruz, CA, USA (COST 00.05).

### 2.2. Physiological sample collection and analyses

We collected blood samples from CSLs from the caudal-gluteal vein for hematocrit (Hct) and hemoglobin concentration ([Hb]) determination in 2005 (n = 10) and 2007 (n = 11). Blood samples used to determine Hct were taken prior to induction of anesthesia because Hct values decline with time under anesthesia (Ponganis et al., 1992; Costa et al., 1998). Hct, [Hb], plasma volume (Pv) and blood volume (Bv) were determined following previously described methods (Swan and Nelson, 1971; Foldager and Blomqvist, 1991; El-Sayed et al., 1995; Costa et al., 1998; Villegas-Amtmann and Costa, 2010).

Muscle myoglobin concentration ([Mb]) was determined following the method of Reynafarje (1963) in muscle samples obtained using a 6 mm dermal biopsy punch (Miltex, Inc.) from the primary locomotion muscle, *supraspinatus* muscle, above the pectoral flipper. Muscle samples were stored at –80 °C until analysis.

We calculated the total body oxygen stores by adding blood, muscle and lung oxygen stores (Lenfant et al., 1970; Kooyman et al., 1983; Ponganis et al., 1997; Costa et al., 2001) following the methods of Fowler et al. (2007). Blood and muscle oxygen stores were obtained in this study and lung oxygen stores were derived by allometric estimates of lung volume for otariids (Kooyman, 1973; Kooyman and Sinnett, 1982; Costa et al., 2001). The body condition of CSL was calculated by dividing mass/standard length (Arnould, 1995; Kotiaho, 1999).

Core body temperatures (°C) were analyzed using a software provided by the manufacturer (HexDecode and 3M programs, Wildlife Computers) and seasonal means were compared using a two-sample Student's *t*-test.

The females sampled during the cold season were examined by a wildlife veterinarian (Paras-Garcia) in the field to determine if they were pregnant. Females were diagnosed as pregnant when they exhibited a considerably visible and palpable distended uterus and by palpation of the fetus, which can only be achieved at an advanced pregnancy state. Pregnancy was later confirmed by performing hormone analysis. We assayed serum samples in duplicate for progesterone using a commercial radioimmunoassay kit (Coat-A-Count Progesterone; Siemens, Los Angeles, CA, USA) and a double-antibody radioimmunoassay (MP Biomedicals, LLC, Orangeburg, NY, USA) for total estrogens. Radioactivity of the bound portion was determined using a gamma counter (Gamma C12; Diagnostic Products Corporation, Los Angeles, CA, USA). The radioimmunoassay was performed as per manufacturer

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