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Adapted to change: Low energy requirements in a low and unpredictable productivity environment, the case of the Galapagos sea lion



Stella Villegas-Amtmann^{a,*}, Birgitte I. McDonald^b, Diego Páez-Rosas^{c,d},
David Aurióles-Gamboa^e, Daniel P. Costa^a

^a University of California Santa Cruz, Long Marine Lab, 100 Shaffer Rd., COH, CA 95060, USA

^b Moss Landing Marine Laboratories, 8272 Moss Landing Rd., Moss Landing, CA 95039, USA

^c Universidad San Francisco de Quito and Galápagos Science Center, San Cristóbal Island, Galápagos, Ecuador

^d Dirección Parque Nacional Galápagos, Unidad Técnica Operativa San Cristóbal, San Cristóbal Island, Galápagos, Ecuador

^e Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional, Ave IPN s/n Colonia Playa Palo de Santa Rita, La Paz Baja California Sur, Mexico

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ABSTRACT

The rate of energy expenditure and acquisition are fundamental components of an animals' life history. Within mammals, the otariids (sea lions and fur seals) exhibit energetically expensive life styles, which can be challenging in equatorial regions where resources are particularly limited and unpredictable. To better understand how this energetically expensive life history pattern functions in an energetically challenging equatorial system, we concurrently measured the field metabolic rate (FMR) and foraging behavior of lactating Galapagos sea lions (GSL) rearing pups and yearlings. Females with pups tended to forage to the north, diving deeper, epi and mesopelagically compared to females with yearlings, which foraged to the west and performed dives to the sea bed that were shallower. FMR did not differ between females with pups or yearlings but, increased significantly with % time spent at-sea. Females with yearlings had higher water influx, suggesting greater food intake, but had lower body condition. The FMR (4.08 ± 0.6 W/kg) of GSL is the lowest measured for any otariid, but is consistent with Galapagos fur seals which also exhibit low FMR. The observation that these two otariids have reduced energy requirements is consistent with an adaptation to the reduced prey availability of the Galapagos marine environment compared to other more productive marine systems.

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1. Introduction

Metabolic rate and thus, the amount of energy required by an organism, are influenced by environmental conditions and life history traits such as body mass, age, sex, reproductive stage and phylogeny. To accommodate a decrease in energy availability, some terrestrial animals are capable of reducing their energy demands (metabolic rate) by means such as hibernation or estivation. Alternatively, metabolic rates can increase as a consequence of heat production, in order to maintain a constant body temperature in colder environments. Many aquatic mammals, exhibit a suite of adaptations in order to lower their energetic costs, such as swimming at speeds where the cost of transport is minimum (Sumich, 1983), or by having greater and more effective insulation in colder environments (Young, 1976). Due to the higher

costs of thermoregulation and transport in water, some taxonomic groups of aquatic carnivores such as otariids (sea lions and fur seals), have higher field metabolic rates (FMR) than those of terrestrial mammals (Hudson et al., 2013) resulting in energetically expensive life styles (Costa, 1993, 2009; Maresch, 2014). Most otariids live in mid to high latitude upwelling systems that are highly productive environments that makes possible their energetically expensive life history pattern (Costa, 1993). However, 2 of the 15 species of otariid live in equatorial regions, the Galapagos fur seal (*Arctocephalus galapagoensis*) and Galapagos sea lion (GSL) (*Zalophus wollebaeki*). Both the Galapagos fur seal and sea lion are endangered (Trillmich, 2015a,b) and appropriate conservation measures need to consider the species specific energetic requirements (metabolic rate), which are currently unknown for GSL.

While the Galapagos Islands are considered an upwelling region (Palacios, 2002; Schaeffer et al., 2008) and have a higher productivity than most equatorial systems, it is still lower and more unpredictable than higher latitude upwelling systems (Martin et al., 1994; Sakamoto et al., 1998). The oceanic system of equatorial

* Corresponding author.

E-mail address: stella.villegas@gmail.com (S. Villegas-Amtmann).

regions exhibits a lower range of variation in oceanographic conditions, such as temperature and productivity, compared to higher latitude regions, where seasonal change is more pronounced and therefore predictable. Numerous reports suggest there is no clear seasonal cycle in phytoplankton biomass in the Galapagos despite a seasonal pattern in SST (Feldman, 1986; Houvenaghel, 1978). Therefore, otariids living here face an unpredictable oceanic system with lower productivity and lower range of seasonal variation than sea lions living at higher latitudes. As an example, around Granito Island, a California sea lion (*Zalophus californianus*) rookery in Baja California, Mexico, chlorophyll-a concentration (used as a proxy for productivity) ranges from 0.3 to 6.0 mg/m³ (<http://coastwatch.pfeg.noaa.gov/>), while around San Cristobal Island, Galapagos, chlorophyll-a ranges only from 0.25 to 1.0 mg/m³ during different seasons each year (Schaeffer et al., 2008).

Additionally, El Niño–Southern Oscillation (ENSO) events, which originate in the eastern tropical Pacific, are intensified along the equator in front of the Ecuador and Peru coasts, where the Galapagos Islands are situated. Variations in temperature, stratification, insolation, and productivity associated with ENSO have implications for phytoplankton productivity, fish, birds, and other organisms in the region (Wang and Fiedler, 2006). Chlorophyll concentrations around the Galapagos Islands of Pinta, Marchena, Genovesa, San Cristobal and Española experienced a reduction from 0.4 mg/m³ during non-El Niño conditions (Mar–Dec 2005 and June–Jul 2006) to 0.1 mg/m³ during El Niño of November 2006 (Schaeffer et al., 2008). In November 1997, close to the peak of El Niño event, chlorophyll concentrations were less than 0.05 mg/m³ in the central and eastern equatorial Pacific and mean primary productivity was 35–40 mmol of C/m²/day—about half the climatological mean (Chavez et al., 1996; Chavez et al., 1999). Furthermore, the strength, length and frequency of El Niño events are variable (Pennington et al., 2006) and appear to be increasing, perhaps because of global warming and/or larger oscillations over 25-year periods (Chavez et al., 2003).

These strong El Niño events that Galapagos otariids encounter, and that lead to significant reductions in this already low productive environment, result in population declines (Trillmich and Limberger, 1985). Compared to the congeneric California sea lion, the Galapagos environment constrains the ability of GSL to invest in their pups, resulting in lower pup survival, reduced population growth and greater sensitivity to disturbance; ultimately limiting GSL to smaller and currently endangered populations (Costa et al., 2006; Villegas-Amtmann et al., 2011).

Measurements of free ranging metabolism exist for otariids from a variety of habitats (Arnould et al., 1996; Costa et al., 1991; Costa and Gales, 2000, 2003; Fowler et al., 2007; McDonald et al., 2012; Trillmich and Kooyman, 2001). However, measurements from tropical otariids exist only for Galapagos fur seals (Costa and Trillmich, 1988; Trillmich and Kooyman, 2001). These studies found that Galapagos fur seal females have a particularly low FMR in relation to other species (Trillmich and Kooyman, 2001), possibly as an adaptation to lower resource availability. Therefore, we might expect a similar reduction in metabolic rate in GSL.

Lactation is the most energetically demanding period in the life of female mammals (Gittleman and Thompson, 1988; Hammond and Diamond, 1997; Williams et al., 2007). Otariid females, as central place foragers, alternate between foraging at sea and returning to land to nurse their pups. Therefore, otariid female energy acquisition is limited in space and time at sea by the physiological demands of the pup fasting on land. Characteristic of otariids living in lower latitudes, Galapagos sea lions and fur seals are among the otariids with longest lactation periods (~2–3 yrs) (Heath, 2002; Trillmich, 1986a, 1986b, 1990). GSL one- and two-year-old pups often continue to suckle and pups are weaned at a time when they are independently foraging—usually around two to three years old (Jeglinski et al., 2012; Trillmich, 1986a). We determined for the first time, the FMR and foraging effort of

lactating GSLs rearing young pups (~1 month old) and yearlings, in addition to simultaneously measuring their at sea behavior. Considering the GSL weaning age, and what is expected of maternal energy expenditure—increasing concurrently with pup mass/age; we hypothesized females with yearlings would exhibit greater energy expenditure and foraging effort than females with younger pups.

2. Methods

2.1. Field site and tagging procedures

Research was carried out at San Cristobal Island during October–November 2009 (0.90287°S, 89.61306°W) in the Galapagos Islands. We captured 10 lactating female GSL and their pups/yearlings, 6 of which were suckling young pups, ~1 month old and 4 were suckling yearlings (~1 year old). Sea lions were captured with hoop nets and administered with ~0.8–1.3 ml (0.06–0.1 mg/kg) of midazolam intra-muscularly (5 mg/ml, Hospira, Inc.). Once the females were calm, they were manually restrained while we collected blood samples, doubly labeled water (²H₂¹⁸O) was injected and instruments glued to their fur. Movement patterns and diving behavior were measured by instrumenting nine animals with Mk10-AF (Wildlife Computers, Richmond, WA, USA) and one with a Sirtrack GPS (Sirtrack, Havelock, North, New Zealand) and a MK9 TDR (time-depth recorder) (Wildlife Computers, Richmond, WA, USA). Additionally, animals were instrumented with radio transmitters (VHF; Sirtrack, Havelock, North, New Zealand) to aid in their recapture. The total weight of the instruments attached was ~293 g (0.4% of the animal's mass). Instruments were mounted on mesh netting and then glued with 5 min epoxy (Loctite) to the dorsal pelage of the lower back, between their shoulders. Animals were weighed using a tripod and a 250 kg (±0.1 kg) digital scale. Females were recaptured within 4–12 days, and manually restrained to collect a final blood sample and to remove the instruments. The residual epoxy mounts falls off within a few months during the animals' annual molt.

2.2. Tracking and diving behavior analyses

To determine the animals' habitat utilization and foraging range, GPS positions were decoded using the DAP processor (Wildlife Computers, Richmond, WA, USA) and GPS location data filtered using a custom software package written in Matlab (MathWorks Inc., USA) (IKNOS toolbox). The algorithm uses several criteria to remove unlikely locations: (1) realistic travel speeds of a subject between two fixes ($\leq 6 \text{ km h}^{-1}$) (2) change in azimuth between successive fixes (angle tolerance 180°), (3) on land locations and (4) time lapse between two consecutive fixes (10 min). There is no way to verify the accuracy of a given filtering process. The output from the filtering process is always considered satisfactory, on a more or less arbitrary basis (generally by visual inspection). The algorithm used here renders satisfactory results and has been extensively used (Kuhn et al., 2009; Tremblay et al., 2006; Villegas-Amtmann et al., 2008). Filtered GPS data were plotted using ArcGIS 10.1. Dive data were analyzed in Matlab using a dive analysis program (IKNOS, Tremblay, unpublished), which allows for a zero-offset correction at the surface and the identification of dives based on a minimum depth and duration. All MK9 and MK10-AF recorders had a 0.5 m depth resolution and sampled every 2 s. The minimum depth considered to be a dive was 5 m and the minimum duration was 12 s.

In order to provide a more accurate description of the diving behavior, dives were analyzed and classified based on their bimodal distribution (Fig. 1), as shallow dives ($\leq 100 \text{ m}$) and deep dives

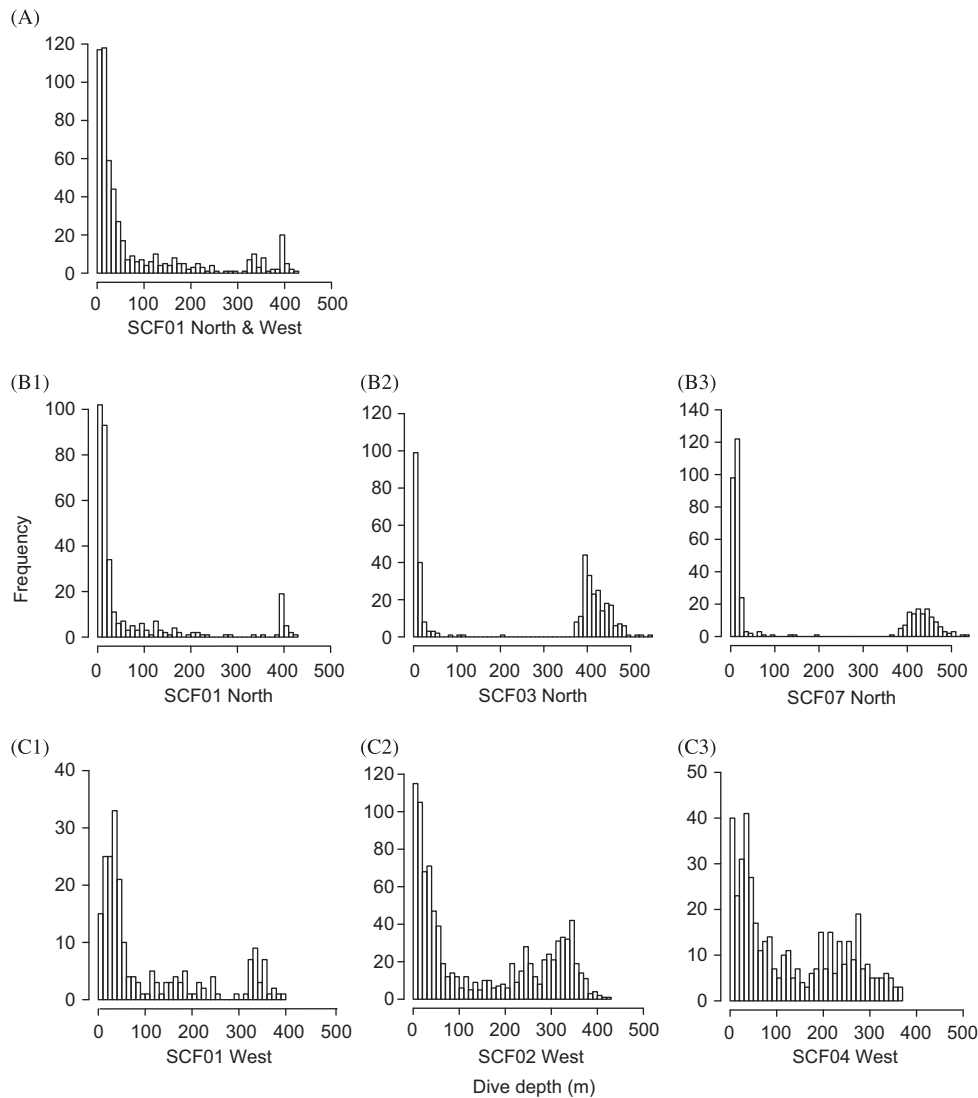


Fig. 1. Galapagos sea lion females dive depth histograms. A. SCF01 female that foraged north and west; B1. SCF01 female fraction of diving record when foraging north; B2–B3 females that foraged north; C1. SCF01 female fraction of diving record when foraging west; and C2–C3 females that foraged west of the breeding colony.

(> 100 m). For each sea lion we calculated the following variables to summarize diving behavior: % shallow dives (or % deep dives: 100 – % shallow dives), shallow and deep dives mean dive depth (m), duration (min) and bottom time (min), maximum distance traveled (km) from the rookery, mean bottom wiggles (number of up and down movements at the bottom of a dive, that can imply epipelagic or mesopelagic foraging), mean descent and ascent rate (m/s), mean dive rate (dives/hr), mean post-dive interval (min) (time spent at the surface between each consecutive dive), % of intra-depth zone dives (IDZ) (% of dives in which their maximum dive depth is within ± 10 m of the maximum depth of the previous dive, and can imply benthic diving (Tremblay and Cherel, 2003)), maximum dive depth (m), duration (min) and bottom time (min) and % time spent diving. Dive depth and duration are directly correlated with each other. Bottom time tends to be greater on benthic dives compared to epipelagic or mesopelagic dives. Descent and ascent rate tend to be greater with increasing dive depth. Dive rate is inversely correlated, while post-dive interval is directly correlated with dive duration. We performed ANOVAs with the mean values of the diving variables, to determine differences in the females' diving behavior grouped by their pup mass/age (females with young pups vs. yearlings) and by their foraging location (north vs. west).

2.3. Field metabolic rate determination

We used the doubly-labeled water (DLW) technique to measure the energy expenditure of lactating GSL (Costa, 1987; Lifson and McClintock, 1966; Nagy, 1975). In this technique an indirect measurement of energy consumption is obtained from isotopic determination of CO_2 production, measured by injecting known amounts of ^2H and ^{18}O labeled water into the animal (Costa, 1987). The difference between the rates of decline of these two isotopes is proportional to the animal's CO_2 production (Lifson and McClintock, 1966; Nagy, 1975). Energy expenditure was calculated from CO_2 production using energy equivalents based on the carbohydrate, protein, and lipid content of the prey (Gessaman and Nagy, 1988). A more complete discussion of this method can be found in Lifson and McClintock (1966), Nagy (1980), Nagy and Costa (1980), Schoeller and Vansanten (1982), Speakman (1997) and Sparling et al. (2008).

Before injecting the DLW ($^2\text{H}_2^{18}\text{O}$) into the animal, we collected 10 ml of blood from the caudal-gluteal vein to determine background isotope levels ("background" sample). This was followed by intraperitoneal injections of 18-oxygen sterile saline (~ 1.3 ml/kg 10% or ~ 0.6 ml/kg 24% ^{18}O ; Cambridge Isotope Laboratories, Inc., Andover,

MA) and deuterated water (0.06 ml/kg 99.9% ^2H ; Cambridge Isotope Laboratories Inc., Andover, MA). Syringes were weighed prior to and after delivery to determine isotope dose precisely. To ensure a complete equilibration of the isotopes, females were held in a ventilated holding pen (approximately $1\text{ m} \times 1\text{ m} \times 1.5\text{ m}$) until the final 10 ml blood sample (“equilibrium sample”) was collected 3 hours later to determine total body water (TBW) and initial ^{18}O and ^2H levels. Equilibration of isotope is 97% complete after 90 minutes; however, complete equilibration is assured after three hours in adult sea lions (Costa, 1987). The female and pup were released in quick succession after the final blood sample. The mother/pup pairs were left undisturbed until recapture after 1–2 foraging trips, 4–12 days later. Upon recapture, a 10 ml blood sample (“final” sample) was collected to calculate water and CO_2 production from the change in ^{18}O and ^2H concentrations since day one after the equilibration sample.

Blood samples were centrifuged shortly after collection, and serum samples frozen at -20°C for later analysis. Serum samples were distilled in duplicate according to the method of Ortiz et al. (1978). ^2H enrichment levels were determined in duplicate by the University of California, Davis, Stable Isotope Facility, using a liquid water isotope analyzer, model DLT-100 (Los Gatos Research, Mountain View, CA). ^{18}O enrichment of the serum samples was determined by Metabolic Solutions (Nashua, NH) using gas isotope ratio mass spectrometry.

Total water influx rates were calculated using Eqs. (5) and (6) in Nagy and Costa (1980). CO_2 production was calculated using a single pool equation (Nagy and Costa, 1980, Eq. (3)) and two-pool equation (Speakman, 1997). CO_2 production from the single-pool equation was used to calculate FMR. This equation allows for mass change, appropriate for our study, since some of our study animals lost more than 5% of their mass between DLW measurements (Speakman, 1997). FMR was calculated from CO_2 production, using a conversion factor determined for California sea lions of 23.6 kJ/L CO_2 . This assumes that all of the fat and protein contained in the diet is oxidized, and fat metabolism yields 26.81 kJ/L CO_2 produced and protein metabolism yields 22.97 kJ/L CO_2 (Costa, 1987). On average, the composition of the diet of California sea lions is 80.3%

water, 1.3% fat, 16.7% protein, and 3.75 kJ/g energy (Costa et al., 1990). Although there may be metabolic differences between California and Galapagos sea lions, the metabolism of an animal would have no effect on the conversion of the energy in their diet. To estimate at-sea metabolic rate, we normalized the data by plotting FMR data (containing both at-sea and onshore components) as a function of percent time at-sea (determined from the TDR data) (Costa and Gales, 2003). Least squares linear regression was calculated and the equation was used to predict FMR for each animal at their respective percentage time spent at-sea (Costa and Gales, 2003). The difference (residual) between predicted and actual FMR was added to the extrapolated FMR where the animal spent 100% time at-sea to determine metabolism at-sea. Onshore FMR was calculated from the equation:

$$\text{FMR} = \text{at-sea FMR (\% time at-sea)} \\ + \text{onshore FMR (\% time onshore)}$$

2.4. Statistical analyses

We tested data for normality and for homogeneity of variance using a Kolmogorov–Smirnov one sample test or a Bartlett test and log/squared root transformed data when necessary.

We performed one-way ANOVA tests to compare the following physiological variables between females with young pups and yearlings and between females foraging at the different locations (north or west of the breeding colony): water influx, body condition, CO_2 production (FMR), at-sea FMR and %TBW. One-way tests were performed given that the number of individuals in each of the groups (by pup age or foraging location) was different. To detect differences in dive behavior, we also performed ANOVA's and one-way tests comparing the means of all the diving variables previously mentioned, between both female groups (by pup age and foraging location). We used linear regressions to explore the following relationships between diving and physiological variables: CO_2 production as a function of, % time diving, dive duration, % time spent at sea and dive rate; water influx as a function of mean trip

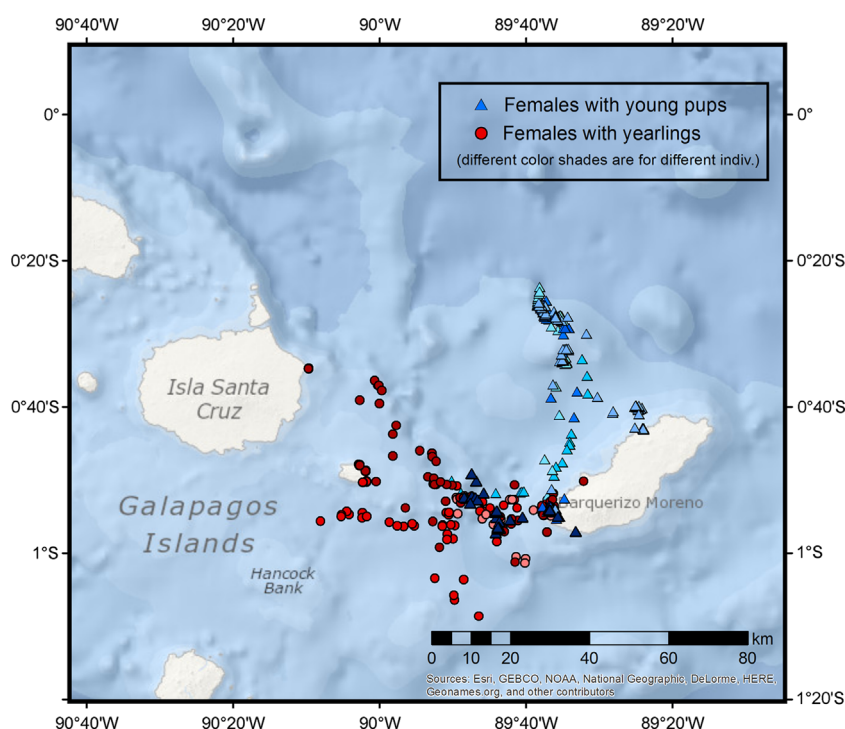


Fig. 2. Foraging locations of Galapagos sea lion females. Different color/shape indicates females with young pups or yearlings and different shades of the same color indicate different individuals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Galapagos sea lion females foraging location, mean of diving variables \pm SD and pup age category.

ID	Foraging location	% Shallow dives (≤ 100 m)	% Deep dives (> 100 m)	Mean dive depth (m) shallow dives	Mean dive depth (m) deep dives	Mean dive duration (min) shallow dives	Mean dive duration (min) deep dives	Mean dive depth (m)	Mean dive duration (min)	Mean bottom time (min)	Total # of dives	Mean dive rate dives/h	% Time spent diving at sea	Pup age category
SCF03	North	41.6	58.4	12.2 \pm 10.6	418.1 \pm 44.8	1.3 \pm 0.6	9 \pm 1.2	249.2 \pm 203.3	5.8 \pm 3.9	1.2 \pm 0.9	375	4.7 \pm 4.1	42.7	Pup
SCF06	North	72.9	27.1	15.1 \pm 14.1	401.4 \pm 82.0	1.4 \pm 0.6	8.6 \pm 1.8	119.8 \pm 177.5	3.3 \pm 3.4	0.8 \pm 0.6	476	8.0 \pm 7.4	42.0	Pup
SCF07	North	66.1	33.8	14.0 \pm 10.9	429.7 \pm 52.2	1.1 \pm 0.7	9.0 \pm 1.1	154.8 \pm 199.5	3.8 \pm 3.8	0.7 \pm 0.7	384	6.0 \pm 5.4	43.9	Pup
SCF08	North	61.2	38.8	21.8 \pm 20.4	406 \pm 58.8	1.9 \pm 1.0	8.9 \pm 1.1	170.9 \pm 191.6	4.6 \pm 3.6	1.1 \pm 0.9	652	5.7 \pm 4.9	40.4	Pup
SCF01	Northwest	75.3	24.7	24.5 \pm 20.7	261.3 \pm 107.3	2.0 \pm 1.0	6.2 \pm 2.0	83.0 \pm 116.7	3.1 \pm 2.2	0.9 \pm 0.8	546	10.5 \pm 6.0	58.7	Pup
SCF02	West	52.6	47.4	30.5 \pm 23.1	276.7 \pm 74	2.3 \pm 1.2	7.1 \pm 1.6	147.1 \pm 134.1	4.6 \pm 2.7	1.3 \pm 0.9	954	5.8 \pm 3.8	41.8	Yearling
SCF04	West	51.6	48.4	38.1 \pm 25.3	229.3 \pm 68.4	2.4 \pm 1.1	6.4 \pm 1.7	130.6 \pm 108.4	4.3 \pm 2.5	1.4 \pm 1.0	434	6.7 \pm 4.1	50.9	Yearling
SCF05	West	47.9	52.1	30.3 \pm 24.3	228.1 \pm 54.3	1.9 \pm 1.0	6.5 \pm 1.1	133.3 \pm 107.6	4.3 \pm 2.5	1.6 \pm 1.0	1043	5.2 \pm 4.3	34.9	Yearling
SCF09	West	47.4	52.6	36.5 \pm 22.8	206.9 \pm 52.6	2.6 \pm 1.0	5.8 \pm 1.1	126.1 \pm 94.6	4.3 \pm 1.9	1.4 \pm 0.9	523	7.4 \pm 3.2	52.8	Pup
SCF10	NA	63.4	36.6	22.2 \pm 22.1	359.2 \pm 67.9	1.9 \pm 1.1	8.6 \pm 1.6	145.6 \pm 168.6	4.4 \pm 3.4	1.2 \pm 1.0	527	5.8 \pm 3.4	44.8	Yearling
Mean		58.0	42.0	24.5	321.7	1.9	7.6	146.1	4.3	1.2	591.4	6.6	45.3	
SD		11.4	11.4	9.2	89.4	0.5	1.3	43.2	0.7	0.3	230.4	1.7	6.9	

duration; and TBW as a function of pup mass. Significance level was set at $P \leq 0.05$. All statistical analyses were performed in R and Sigma Plot 12.0.

3. Results

3.1. Tracking and diving behavior

Galapagos sea lion females exhibited segregation in their foraging areas, foraging either north or west of San Cristobal Island (Fig. 2). Females foraging at each of the two identified locations exhibited remarkable similarity in their diving behavior between them (Fig. 1, Appendix 1). All females foraging north showed a bimodal distribution of dive depths with a shallow peak at around 20–30 m and a deep peak around 400–430 m. These females exhibited very few to no dives between 100 and 380 m. Females foraging west dived shallower and showed a less pronounced bimodal distribution than females foraging north, with a shallow peak at 20–40 m and a deep peak between 240 and 350 m (Fig. 1, Table 1). A female (SCF01), that utilized both foraging locations (north and west), exhibited similar behavior to females foraging north, however, she exhibited more dives between 100 and 380 m.

When grouped by their pup age, most females with yearlings foraged in different areas than females with younger pups. All but one female with young pups foraged north (SCF09 foraged west), and all but possibly one female (SCF10 – no tracking data) with yearlings foraged west (Fig. 2). SCF10 might have foraged north, based on her dive behavior and dive depth frequency distribution (Fig. 1, Appendix 1). All females dove during the day and night.

Most of the differences in diving behavior between GSL females are explained by foraging location rather than pup mass. The only diving variables that were significantly different between females with young pups ($n=6$) vs. yearlings ($n=4$), were bottom time of deep dives, and number of bottom wiggles. Females with yearlings spent more time at the bottom of their deep dives (ANOVA, $P=0.04$, 1.6 ± 0.2 min, 2.0 ± 0.3 min respectively) and exhibited a greater amount of bottom wiggles (ANOVA, $P=0.02$, 4.5 ± 1.2 , 6.6 ± 1.1 respectively) compared to females with younger pups (Table 1). None of the other diving variables were significantly different between females with young pups or yearlings (Table 1).

Females foraging at different locations exhibited significant differences in their foraging behavior. Only 8 out of the 10 females were considered in the foraging location comparative analysis of diving behavior because SCF01 utilized both foraging locations, and we were unable to obtain GPS data for SCF10 due to tag failure. The shallow dives of females foraging west ($n=4$) were significantly deeper, longer, and with longer bottom time (ANOVA, $P<0.00$, 33.9 ± 4.0 m; $P=0.006$, 2.3 ± 0.3 min; $P<0.00$, 0.9 ± 0.1 min respectively) compared to those of females foraging north ($n=4$) (15.8 ± 4.2 m, 1.4 ± 0.3 min and 0.5 ± 0.1 min, respectively). Overall, the dives of females foraging west exhibited significantly greater number of bottom wiggles than females foraging north (ANOVA, $P=0.01$, 6.7 ± 1.0 wiggles and 4.1 ± 0.9 wiggles). In contrast, the deep dives of females foraging north were significantly deeper (ANOVA, $P<0.000$, 413.8 ± 12.7 m) and longer (ANOVA, $P<0.000$, 8.9 ± 0.2 min) and overall, exhibited significantly deeper and longer maximum depth (ANOVA, $P=0.002$, 542.9 ± 21.7 m,) and duration (ANOVA, $P=0.05$, 11.9 ± 0.6 min) compared to females foraging west (235.2 ± 29.5 m, 6.5 ± 0.5 min and 394.0 ± 54.6 m, 10.1 ± 1.3 min respectively) (Tables 1 and 2). Female SCF01, who foraged at both sites (not incorporated into the diving behavior analysis per foraging location), had a pup with a mass intermediate to young pups and yearlings (16 kg), but it was closer to young pups' mass, therefore, we placed her in that group (Table 3).

Table 2Galapagos sea lion females foraging location, maximum dive variables, mean foraging trip variables \pm SD and pup age category.

ID	Foraging location	Max. dive depth (m)	Max. dive duration (min)	Max. bottom time (min)	# Foraging trips	Mean dive trip duration from rookery (h)	Mean trip duration (h)	Mean haul out duration (h)	Total # days recorded	Max. dist. traveled from rookery (km)	Pup age category
SCF03	North	548	12.4	4.6	1	84.3 \pm 0	84.3 \pm 0	NA	5.4	55.1	Pup
SCF06	North	520	11.5	3.4	1	63.1 \pm 0	63.1 \pm 0	NA	4.4	50.9	Pup
SCF07	North	533	11.2	3.8	1	55.4 \pm 0	55.4 \pm 0	NA	4.2	49.6	Pup
SCF08	North	571	12.4	4.6	4	145.2 \pm 27.5	30.9 \pm 27.5	7.2 \pm 3.6	7.6	51.1	Pup
SCF01	Northwest	422	10.7	5.2	2	23.8 \pm 5.2	23.8 \pm 5.2	24.6 \pm 0	3.7	38.7	Pup
SCF02	West	430	11.1	4.8	4	63.8 \pm 5.3	43.4 \pm 5.3	13.1 \pm 7.7	9.6	57.3	Yearling
SCF04	West	369	11.2	5.3	2	30.8 \pm 12.1	30.8 \pm 12.1	48.3 \pm 0	5.4	23.4	Yearling
SCF05	West	448	9.8	4.6	7	59.9 \pm 19.1	30.6 \pm 19.1	12.3 \pm 6.5	12.8	70.1	Yearling
SCF09	West	330	8.4	4.2	2	35.7 \pm 0.7	35.7 \pm 0.7	11.0 \pm 0	4.4	20.3	Pup
SCF10	NA	517	12.2	4.2	2	42.9 \pm 18.0	42.9 \pm 18.0	45.6 \pm 0	6.9	NA	Yearling
Mean		469	11.1	4.5	3.7	49.3	36.9	29.8	8.7	50.3	
SD		81	1.2	0.6	1.9	34.9	18.6	17.1	2.9	16.1	

3.2. Field metabolic rate

All females, with the exception of SCF05, were recaptured after approximately 5–10 days. SCF05 was recaptured after 12.8 days resulting in low ^{18}O levels in the final blood sample. However, her CO_2 values were comparable to the rest of the females. We therefore kept her in the analysis (Table 3).

GSL females exhibited an average CO_2 production of 0.62 ± 0.10 ml/g/h and mass specific FMR of 4.08 ± 0.64 W/kg (Table 3). There was no significant difference in FMR or at-sea FMR between females with young pups or yearlings, or females foraging north or west of the breeding colony. Water influx, body condition and % TBW were not significantly different between females foraging at the different locations. However, water influx, used as a proxy for food intake was greater for females with yearlings compared to females with young pups (93.0 ± 21.4 and 71.1 ± 10.3 L/kg/d respectively). Percent TBW (higher values indicate lower fat content and thus an index of body condition), increased significantly with increasing pup mass ($P=0.004$, $R^2=0.66$) and was significantly greater in females with yearlings than females with young pups (66.5 ± 2.6 and $58.6 \pm 5.2\%$ respectively, ANOVA, $P=0.02$) (Table 3, Fig. 3A). Correspondingly, body condition measured as mass/standard length was significantly greater in females with young pups compared to females with yearlings (0.52 ± 0.06 and 0.44 ± 0.02 respectively, ANOVA, $P=0.03$) (Table 3). Mean mass specific onshore FMR was 1.28 ± 0.48 W/kg and at-sea FMR was 5.84 ± 0.48 W/kg (Table 3).

There was no significant relationship between CO_2 production, FMR or at-sea FMR and dive rate, % time diving and dive duration. However CO_2 production and FMR increased significantly with % time at-sea ($P=0.04$, $R^2=0.43$ for both) (Fig. 3B–D). Water influx declined as the mean trip duration increased ($R^2=0.12$), but this relationship was not statistically significant (Fig. 3E). In contrast, water influx increased significantly with FMR ($P=0.05$, $R^2=0.4$) (Fig. 3F).

4. Discussion and conclusions

4.1. Diving behavior

Regardless of their foraging location, GSL showed remarkable diving abilities, exceeding the mean diving depths previously reported for New Zealand sea lions (*Phocartos hookeri*), considered to be the deepest diving sea lion (range of mean and mean maximum dive depth: 124–136 m and: 379–445 m respectively) (Chilvers et al., 2006; Costa and Gales, 2000; Leung et al., 2014). This is particularly interesting, given that GSL are the smallest sea lion

species (76.7 ± 8.3 kg, females in this study), with a considerably smaller mass than New Zealand sea lions (122.3 ± 5.7 kg (Leung et al., 2014)). GSL in this study exhibited mean dive depths of 146 ± 43 m and mean maximum dive depths of 469 ± 81 . Furthermore, when considering the GSL dive depths bimodal distribution, females exhibited a mean dive depth of 322 ± 89 m on $42 \pm 11\%$ of their dives (deep dives > 100 m). Their mean and mean maximum dive durations (4.2 ± 0.7 min, 11.1 ± 1.2 min respectively) also exceeded those reported for New Zealand sea lions (3.9 ± 1.0 min, 10.3 ± 0.5 min, respectively) (Chilvers et al., 2006)). GSL, the smallest in its group, might be the deepest diver of all sea lion species.

GSL females exhibited great similarities in their diving behavior within a foraging area utilized (north or west). Although SCF01 utilized both foraging areas, her overall foraging behavior was more similar to that of females foraging west. Interestingly, when her diving behavior is subdivided based on the foraging location, the behavior exhibited at each location, although diving somewhat shallower; corresponds to that of the other females exploiting the same area. This shows how the diving behavior of GSL can change and be adapted to fit the environment in which they forage. Furthermore, the pup of this female was the only one whose mass value differed the most from that of young pups or yearlings, but because it was closer to pups, it was considered in this group. However, her foraging behavior was more similar to females foraging west, most of which had yearlings. This suggests that females may switch foraging locations based on her metabolic needs at different stages of pup rearing.

Females foraging north or west were mostly segregated by their pup age (young pups or yearlings). All females with young pups foraged north with the exception of SCF09 who foraged west and all females with yearlings foraged west. We did not obtain GPS data from SCF10 who had a yearling, but her diving behavior suggests that she was foraging in the north.

Based on their diving behavior and the bathymetry of the exploited areas, females foraging north (mostly with young pups) were likely diving epi and mesopelagically. These females exhibited deeper and longer duration “deep dives”. The mean depth of these dives was 414 m while diving over 500–600 m water depth. Alternatively, females foraging west (with yearlings) were likely diving benthically as the mean depth of their “deep dives” was 235 m while diving over 200–300 m water depth. Furthermore, these females exhibited longer bottom times during their deep dives, implying benthic diving (when searching for food on the benthos, sea lions might spend longer time at the bottom phase of a dive compared to the time spent in the descent and ascent phase. Conversely, if searching for food in the water column, the time spent in the descent/ascent phase would be greater than the time spent at the bottom of a dive), compared to females foraging north,

Table 3

Galapagos sea lion females' mass, pup sex and mass, CO₂ production based on a single pool equation (Nagy) and a two-pool equation (Speakman), % time at sea and on land, FMR, at-sea FMR and on-shore FMR (based on the single pool equation (Nagy)), % total body water (%TBW), water influx, % body mass change and body condition index (BCI).

Female ID	Mean mass (kg)	Initial mass (kg)	Final mass (kg)	Pup sex	Pup mass (kg)	CO ₂ prod. (ml/g/h) (1 pool Nagy)	CO ₂ prod. (ml/g/h) (2 pool Speakman)	% Time at sea	% Time on land	FMR (W/kg)	At sea FMR (ml CO ₂ /g/h)	At sea FMR (W/kg)	On shore FMR (ml CO ₂ /g/h)	On shore FMR (W/kg)	TBW% (O-18)	Water influx (ml/kg/d)	%Body mass change/day	BCI (mass/std length)
w/pups																		
SCF01	75.6	76.2	75	F	16	0.72	0.55	53.0	47.0	4.70	1.04	6.84	0.35	2.28	65.42	73.61	−0.40	0.48
SCF03	94.8	94.8	94.8	F	7.5	0.55	0.41	64.7	35.3	3.59	0.79	5.20	0.10	0.63	49.45	71.87	0.00	0.63
SCF06	70.1	73.8	66.4	M	7.5	0.57	0.45	60.3	39.7	3.71	0.84	5.52	0.15	0.96	59.64	71.58	−2.23	0.51
SCF07	73.2	76.8	69.6	M	8	0.61	0.51	55.3	44.7	4.00	0.92	6.04	0.23	1.48	57.95	51.58	−2.08	0.47
SCF08	82.2	82.6	81.8	M	11.5	0.66	0.54	67.7	32.2	4.31	0.88	5.78	0.19	1.22	60.95	83.66	−0.12	0.52
SCF09	75.1	79.6	70.6	M	8	0.62	0.52	67.9	32.1	4.06	0.84	5.52	0.15	0.96	58.15	76.51	−2.47	0.52
Mean	78.5	80.6	76.4		9.8	0.62	0.50	61.5	38.5	4.06	0.89	5.82	0.19	1.26	58.59	71.47	−1.22	0.52
SD	8.93	7.57	10.5		3.4	0.06	0.05	6.4	6.4	0.41	0.09	0.58	0.09	0.58	5.24	10.72	1.16	0.06
w/yearlings																		
SCF02	75.7	76.4	75	M	24	0.77	0.38	75.5	24.5	5.07	0.94	6.19	0.25	1.63	67.84	107.90	−0.19	0.45
SCF04	65	69	61	M	27	0.45	0.42	47.2	52.7	2.96	0.82	5.36	0.12	0.80	69.50	70.89	−2.07	0.45
SCF05	63.2	63.2	63.2	F	26	0.72	0.48	70.0	30.0	4.73	0.93	6.10	0.24	1.54	64.85	114.47	0.00	0.42
SCF10	74.8	74.8	74.8	M	26	0.56	0.28	51.7	48.3	3.64	0.89	5.85	0.20	1.29	63.77	79.88	0.00	0.45
Mean	69.7	70.9	68.5		25.8	0.63	0.39	61.1	38.9	4.10	0.90	5.88	0.20	1.31	66.49	93.29	−0.57	0.44
SD	6.5	6.0	7.4		1.3	0.15	0.08	13.7	13.7	0.98	0.06	0.37	0.06	0.37	2.64	21.16	1.01	0.02
Overall mean	75.0	76.7	73.2		16.2	0.62	0.45	61.3	38.7	4.08	0.89	5.84	0.20	1.28	61.75	80.20	−0.96	0.49
SD	8.9	8.3	9.8		8.7	0.10	0.09	9.3	9.2	0.64	0.07	0.48	0.07	0.48	5.85	18.44	1.09	0.06

Using the two-pool model of [Speakman \(1997\)](#), females SCF02 and SCF10 CO₂ production values might not be accurate given this methodology, but we present the data for comparative purposes.

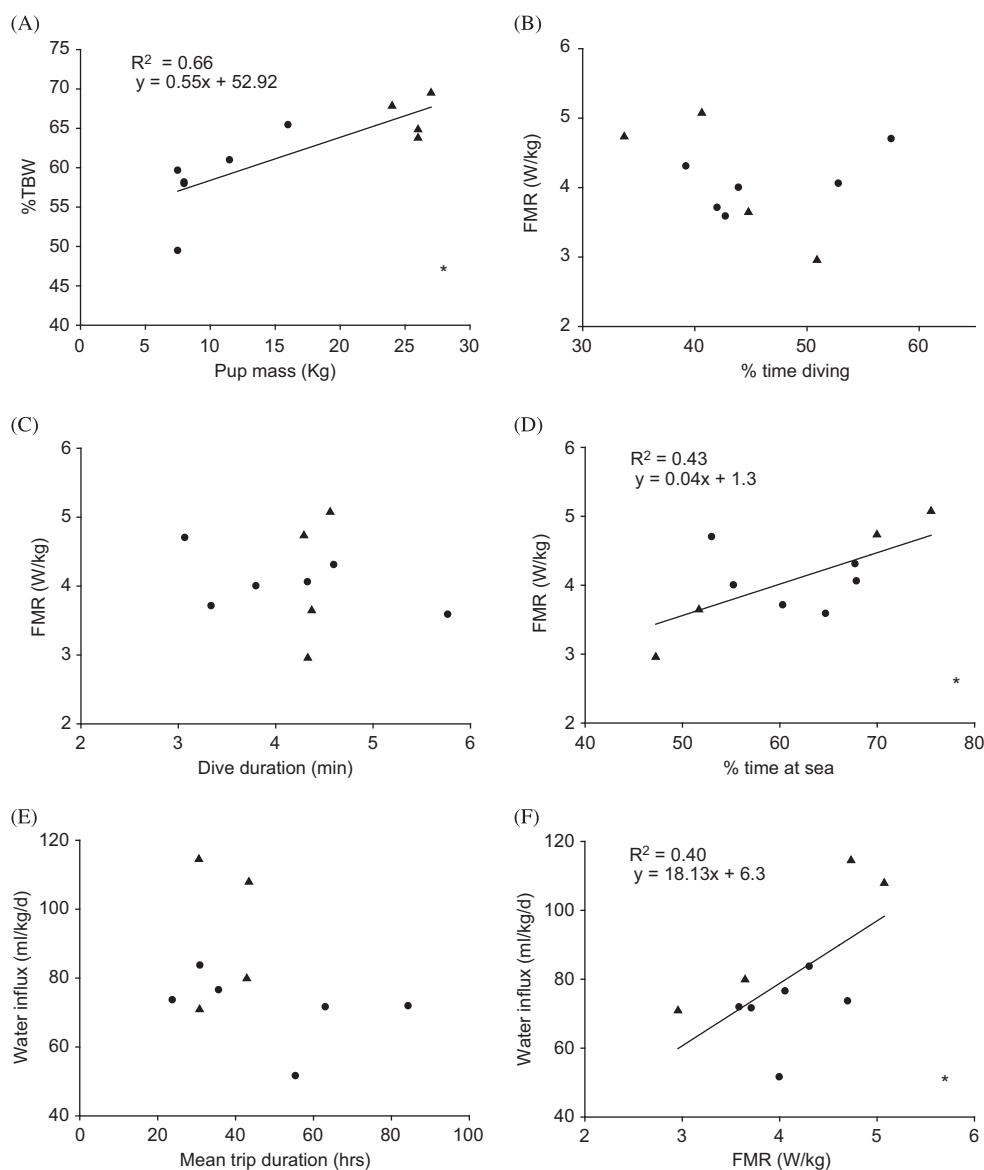


Fig. 3. Galapagos sea lion females (A) % TBW vs. pup mass (kg), $P=0.004$; (B) FMR (W/kg) vs. % time spent diving; (C) FMR (W/kg) vs. dive duration (min); (D) FMR (W/kg) vs. % time spent diving, $P=0.04$; (E) Water influx (ml/kg/d) vs. mean trip duration (days); and (F) Water influx (ml/kg/d) vs. FMR (W/kg), $P=0.05$. Circles are for females with pups and triangles females with yearlings, * denotes statistically significant relationship for which R^2 values and regression equations are given.

although this difference was not significantly different. Females with pups, foraging north, and probably mesopelagically, exhibited extremely deep dives, greater mean dive depth (413.8 m vs. 235.2 m) and duration (8.9 min vs. 6.5 min) of “deep dives”, and greater overall maximum dive depth (542.9 m vs. 394.0 m) and duration (11.9 min vs. 10.1 min), than females foraging west, mostly with yearlings. However, they dived significantly shallower on their “shallow dives” (16 m) compared to females foraging west (34 m).

4.2. Field metabolic rate

GSL exhibited the lowest CO_2 production and mass specific FMR yet reported for any other otariid species, considerably lower than California sea lions, its closest related species and lower than the other Galapagos pinniped, the Galapagos fur seal (Table 3, Fig. 4). Mass specific metabolic rates are expected to be lower with increasing body mass (Benedict, 1938; Brody and Procter, 1932; Kleiber, 1975), therefore sea lions are expected to have lower metabolic rates compared to fur seals due to body mass. However, the GSL is the smallest of the sea lion species and exhibited the

lowest mass-specific FMR. Compared to other otariids the GSL and Galapagos fur seal (Trillmich and Kooyman, 2001) exhibit the lowest FMR of this group (Fig. 4), which indicates that the environment plays a fundamental role in shaping the physiology of these animals. The Galapagos sea lion and fur seal are the only pinnipeds living in an equatorial region and are both endangered (Trillmich, 2015a, b). Low energy requirements in these otariids that live in a warm, low and unpredictable productivity environment may be an adaptation to lower resource availability.

While we might expect maternal energy expenditure to increase as the pup gets larger (Bowen et al., 2001; Thometz et al., 2014), we found no difference in CO_2 production, FMR or at-sea FMR between GSL females with young pups or yearlings or between females foraging north or west of the breeding colony. Similarly, the FMR of Galapagos fur seals did not vary among females with young pups, 6-month-old pups and yearlings (Trillmich and Kooyman, 2001). While older pups and yearlings may have higher energy requirements it is possible that they are supporting these larger energy requirements by foraging on their own (Jeglinski et al., 2012).

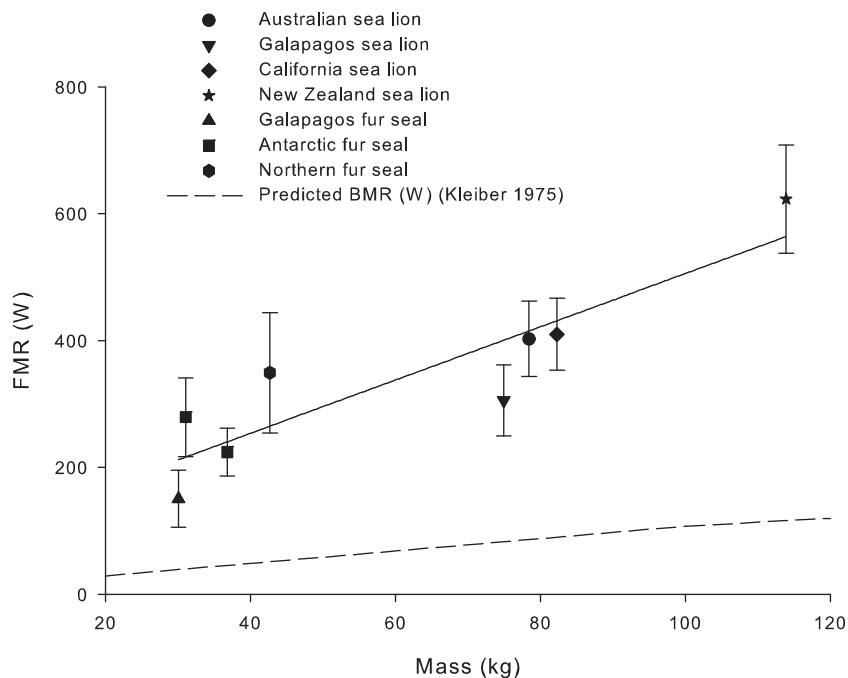


Fig. 4. Otariid FMR (W). FMR of Galapagos sea lions plotted relative to values available for other otariids as a function of their body mass (kg) \pm SD. Data for Australian sea lions are from Costa and Gales (2003), California sea lions: Costa et al. (1990), New Zealand sea lion: Costa and Gales (2000), Antarctic fur seal: Arnould et al. (1996) and Costa and Trillmich (1988), Galapagos fur seal: Trillmich and Kooyman (2001) and Northern fur seal: Costa and Gentry (1986). The linear regression for predicted standard metabolic rate (BMR) is for terrestrial mammals (Kleiber, 1975).

GSL showed a slight decrease in CO_2 production and FMR with increasing % time diving and dive duration. A lower metabolic rate would increase the aerobic dive limit making possible a greater number of dives and/or an increase in their duration. Studies on captive California sea lions and gray seals (*Halichoerus grypus*) have shown that they can lower their metabolic rate as the duration of submergence increases (Hurley and Costa, 2001; Sparling and Fedak, 2004). However, CO_2 production increased significantly with % time spent at sea, implying that on longer foraging trips females traveled longer distances, resulting in greater energy expenditure. These results are consistent with what has been shown in Antarctic fur seals (Arnould et al., 1996; Costa et al., 2000). Traveling is energetically expensive for these animals (Fish, 1994), thus it might be more efficient to explore additional food patches on the vertical plane by diving deeper rather than on the horizontal plane, by swimming and traveling further. Moreover, the distance a female sea lion might travel to find food, is also constrained by her pup needs and the amount of time a pup is able to fast before nursing again. GSL females in this study did not travel extraordinarily long distances from the rookery (mean maximum distance traveled was 46.3 ± 16.1 km) but exhibited remarkably deep dives. Furthermore, depending on an animals' surface area to volume ratio and the type and amount of insulation, the longer an animal spends at sea, the greater the amount of body heat that will be lost to the environment. GSL increased their FMR (CO_2 production) when spent greater % time at sea, possibly due to the increased costs of thermoregulation. Although the lower critical temperature for California sea lions has been determined to be 6.4°C , measurements were taken for a period of only 30–120 min (Liwanag et al., 2009), while GSL spent from 20 to 84 h at sea on a single foraging trip. Furthermore some females in this study dived continuously to the bottom encountering average temperatures of 6.8°C (measured by temperature sensor on TDR tag). For example, an animal that dived to 393–407 m on 30 consecutive dives accumulated a total bottom time of 46 min at $\sim 6.8^\circ\text{C}$. GSL are smaller than California sea lions and live in significantly warmer climates year round, thus, their

thermoneutral zone might be narrower than that of California sea lions. This could be one of the reasons why female GSL have been observed to haul out at several places other than their breeding rookery, during a foraging trip, when lactating young pups (Villegas-Amtmann et al., 2008). Considering these animals are constantly diving to deep dives and spending a considerable amount of time at the bottom of benthic dives, they might be working outside the lower limits of their thermoneutral zones.

Food intake (water influx) was greater in females with yearlings (foraging west and most likely benthically) than females with younger pups. Females that are nursing younger pups are expected to require less energy than those nursing older pups (Arnould and Boyd, 1995; Fowler et al., 2014; Gales et al., 1996; Riet-Sapirza et al., 2012). This may also be explained by differences in their foraging strategies resulting from distinct foraging locations, at which they are possibly targeting different prey types. Females foraging in the north (mostly with young pups) dive deeper, longer and mesopelagically, given that the bathymetry of this area is deeper than that of the west foraging area. These females are possibly feeding on aggregated, and although smaller in mass, more abundant and energy dense prey. In contrast, females foraging west, diving at shallower depths may be diving benthically, where prey is less abundant and consuming bigger but lower quality prey. Consequently, they obtain less energy/prey mass (Anthony et al., 2000). Females are possibly foraging on diverse prey types, as a result of the differing available bathymetry, rather than hydrographic differences, given that sea surface temperature and chlorophyll-a concentration of the sea lions foraging areas, during our study period, did not vary (MODIS, NOAA NMFS SWFSC ERD). Although water influx was greater in females with yearlings than females with younger pups, their FMR did not vary. Therefore, regardless of pup age and foraging strategy, energy expenditure was the same for all females. Consistent with our results, a trend of increased food intake (water influx) with increasing pup age has also been observed in three groups of Galapagos fur seal females with differing pup age classes (Trillmich and Kooyman, 2001).

Trillmich and Kooyman (2001) also found that % TBW in Galapagos fur seal females varied significantly with pup age, being greater in mothers of yearlings than mothers of 6-month-old pups (Trillmich and Kooyman, 2001). Similarly, body condition of females with yearlings in our study, estimated by %TBW was significantly lower (greater %TBW) compared to females with younger pups. In addition, we estimated body condition as mass/standard length and the results showed the same trend. Despite females with yearlings exhibiting significantly lower body condition, their food intake was greater. This suggests that energy intake of females with yearlings, likely diving benthically, was higher; but demands by their older pups were greater than prey availability and were not compensated for by a greater energy intake. Although there was no difference in FMR between females with differing pup age or foraging location, overall, females that exhibited greater food intake might have been working harder, as their FMR were higher. This could also result from specific dynamic action-energy expenditure due to the cost of processing food.

Our data show that females with young pups are in better body condition than females with older pups or yearlings. This suggests that females are supplementing their energy intake by utilizing stored body reserves to ensure that their pups receive sufficient milk energy (Bowen et al., 2001; Thometz et al., 2014). This is supported by the fact that both Galapagos fur seals and sea lions have prolonged lactation periods, between 1 and 2+ years (Trillmich, 1986a,b), indicating that they may be constrained by available prey resources.

We observed a trend of decreasing food intake with increasing trip duration, suggesting that while some females might increase their foraging time to increase energy intake, resource availability might be limited. Therefore, the added energetic costs of foraging for longer might not be compensated by greater prey availability and energy intake.

4.3. Conclusion and future implications

GSL showed remarkable diving abilities, being the smallest in its group, it might be the deepest diver of all sea lion species, as it exceeded the mean diving depths reported for New Zealand sea lions (*Phocartos hookeri*, considered the deepest diving sea lion).

GSL females at San Cristobal mainly utilized two foraging areas, north and west of the breeding colony. Their individual diving behavior within each of these two foraging areas was strikingly similar. In addition, females may switch foraging locations based on her needs at different stages of pup rearing. This shows how the diving behavior of GSL can change and be adapted to fit the environment in which they forage.

GSL exhibited the lowest CO₂ production and mass specific FMR yet reported for any other otariid species. Low energy requirements in these otariids that live in a warm, low and unpredictable productivity environment may be an adaptation to lower resource availability.

The GSL has shown to be highly plastic in regards to their foraging behavior and exhibit multiple foraging strategies (Villegas-Amtmann et al., 2008). Additionally, they have adapted to a low productivity system by decreasing their metabolic needs. Given their plasticity, it is possible that this species could easily adapt to changes in the environment, such as prey distribution. However, compared to other higher latitude otariid species, such as California sea lions, the endangered GSL living in an equatorial and less productive environment exhibit greater foraging effort, lower foraging success and their pups face higher nutritional stress (Villegas-Amtmann et al., 2011). Furthermore, GSL are possibly at a greater risk of extinction compared to other temperate species (Ferguson and Higdon, 2006). Therefore, if oceans continue on a warming trend and productivity in this area becomes even

lower (Bopp et al., 2013), this species, that might already be working at its lower physiological limit (low metabolic rate and energy requirements), might not be capable of adapting to a further decrease in productivity and resource availability.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr2.2016.05.015>.

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