

The influence of depth on a breath-hold diver: Predicting the diving metabolism of Steller sea lions (*Eumetopias jubatus*)

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Abstract

Diving animals must endeavor to increase their dive depths and prolong the time they spend exploiting resources at depth. Results from captive and wild studies suggest that many diving animals extend their foraging bouts by decreasing their metabolisms while submerged. We measured metabolic rates of Steller sea lions (*Eumetopias jubatus*) trained to dive to depth in the open ocean to investigate the relationships between diving behaviour and the energetic costs of diving. We also constructed a general linear model to predict the oxygen consumption of sea lions diving in the wild. The resultant model suggests that swimming distance and depth of dives significantly influence the oxygen consumption of diving Steller sea lions. The predictive power of the model was tested using a cross-validation approach, whereby models reconstructed using data from pairs of sea lions were found to accurately predict the oxygen consumption of the third diving animal. Predicted oxygen consumption during dives to depth ranged from 3.37 L min⁻¹ at 10 m, to 1.40 L min⁻¹ at 300 m over a standardized swimming distance of 600 m. This equated to an estimated metabolic rate of 97.54 and 40.52 MJ day⁻¹, and an estimated daily feeding requirement of 18.92 and 7.96 kg day⁻¹ for dives between 10 and 300 m, respectively. The model thereby provides information on the potential energetic consequences that alterations in foraging strategies due to changes in prey availability could have on wild populations of sea lions. © 2006 Elsevier B.V. All rights reserved.

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1. Introduction

Resources in aquatic environments are usually distributed in three-dimensional space. To optimally exploit these resources, diving animals must endeavor to increase the range of their dive depths and prolong

the time they can spend foraging below the surface. Evidence from studies of both captive and wild animals suggests that many diving animals extend their foraging durations by decreasing their metabolic rates while submerged (Castellini et al., 1992; Gallivan, 1981; Hill et al., 1987; Hurley and Costa, 2001; Jones et al., 1973; Kooyman and Campbell, 1972; Kooyman et al., 1983, 1973; Ponganis et al., 1997; Sparling and Fedak, 2004; Webb et al., 1998), and by employing behavioural strategies that minimize the use of energy during dives (e.g. Videler and Nolet, 1990; Williams, 1999, 2001).

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The range of the observed metabolic changes and behavioural mechanisms used by diving animals appears to be relatively dynamic, and varies both within and between individuals (e.g. Sato et al., 2003; Sparling and Fedak, 2004). Some of this observed variation is potentially a function of intrinsic factors, such as body condition (Rosen and Trites, 1999), maturity, or digestive state (Rosen and Trites, 1997). However, individual responses are also likely to be affected by extrinsic factors such as water temperature, or behavioural strategies including the depth and duration of dives (Gallivan, 1981; Kooyman and Campbell, 1972; Thompson and Fedak, 1993). An understanding of how energy consumption varies in relation to diving behaviour and environmental conditions is integral to understanding the energetic requirements (Winship et al., 2002) and physiological constraints animals experience during foraging (Green et al., 2005). Such information is also required for constructing predictive bioenergetic models for wild populations, and for assessing the potential impacts that changes in prey distributions or types on species can have on predators (Winship et al., 2002).

Since the 1970s, significant declines in the numbers of Steller sea lions (*Eumetopias jubatus*) have been observed across much of their range (Loughlin et al., 1992; Trites and Larkin, 1996; Winship and Trites, 2006). A predominant hypothesis explaining the declines is nutritional inadequacy due to changes in prey availability or quality (Alverson, 1992; Calkins et al., 1998; Merrick et al., 1997; Trites and Donnelly, 2003). Over the past decade, a wealth of information has been gained from telemetry studies about the behavioural and foraging ecology of Steller sea lions in the wild (Loughlin et al., 1998, 2003; Merrick and Loughlin, 1997; Merrick et al., 1994). These data suggest that, like most other otariids, Steller sea lions tend to be relatively shallow, short duration divers. However, accurate estimates of the energetic consequences of either natural variation in foraging strategies (Merrick and Loughlin, 1997) or alteration of foraging behaviour due to changes in prey availability are severely limited by the paucity of data quantifying the differential energetic costs associated with different dive characteristics. Limited information is only available on the total energetic costs of surface locomotion (Rosen and Trites, 2002) and diving (Hastie et al., in press) in Steller sea lions.

We investigated the relationships between the energetic costs of diving, and behavioural parameters and environmental conditions using Steller sea lions that were trained to dive to fixed depths in the open ocean.

Our overall goal was to assess the influence of a range of behavioural parameters (dive characteristics) and water temperatures on diving oxygen consumption rates, and to construct a model that predicts the amount of oxygen Steller sea lions consume while diving in the wild. We also used the model to predict the potential energetic costs of foraging under different diving scenarios (i.e. dives of different depths or durations).

2. Materials and methods

2.1. Animals

Three female Steller sea lions were housed in a specially designed floating housing pen located in a coastal inlet in British Columbia, Canada. It allowed the sea lions access to seawater and provided a base for research in the surrounding waters. The sea lions freely chose to cooperate with all data collection and were never restrained or confined during any of the experimental trials. Two of the sea lions (F97HA and F97SI) were 8 years of age, with mean weights of 160.9 and 196.4 kg respectively. The third sea lion (F00BO) was 5 years of age, with a mean weight of 117.8 kg.

2.2. Measuring diving oxygen consumption

Sea lions were transported in a specially modified 22 ft boat from their holding pen to trial areas, where they dove from a floating respiratory dome to an underwater target light suspended at a predetermined depth.

All experimental trials were performed in the morning, at least 16 h postprandial. Prior to the daily trials, each sea lion was weighed (± 0.1 kg) and fitted with a discrete webbing body harness that held a VHF transmitter (used to locate the sea lion in the event of it swimming out of the trial area). A second 22 ft research boat carrying the respiratory equipment was anchored next to the respiratory dome and suspended the target light prior to the arrival of the sea lion. Details of the target light system and respiratory data collection procedures are described in Hastie et al. (in press). Essentially, the sea lions were trained stay in the respirometry dome until commanded to swim down to a light, stay at depth until the light was turned off, and then return to the respirometry dome for a set period. The sea lions initially remained in the dome for 6 min to measure pre-dive metabolism, and 10 min after the last dive until metabolism had returned to pre-dive levels.

Between one and five dives were carried out during each trial (one trial per day), with durations of individual

dives varying between 40 and 200 s. The sea lions were trained to swim down to a light on command, and stay at depth until it was turned off. We attempted to keep the duration of individual dives constant during a single daily experimental trial. Similarly, durations at the surface between dives varied between 7 and 25 s, but remained consistent during a single experimental trial. The depths of dives were set at 5 m, 10 m, 20 m, or 30 m, and were also held constant for each experimental trial. To ensure that sea lions were not naïve to the required dive parameters during a trial, we trained them at each depth and duration for around 7 to 10 days prior to collecting any data.

The water temperatures at the surface and at the target light system were monitored during each trial using remote temperature loggers (Onset Computer Corp., Pocasset, MA, USA). Temperatures at the surface ranged from 6.5 °C to 19 °C, while temperatures at depth ranged from 6.8 °C to 16.4 °C.

Diving oxygen consumption was estimated using the method described by Castellini et al. (1992), and adapted for at-sea conditions by Hurley and Costa (2001). Essentially, this was estimated from the oxygen consumption during the recovery period in excess of the pre-dive oxygen consumption measured during that trial divided by the duration of the dive. To estimate the oxygen consumption during a series of dives, the oxygen consumption between dives and the oxygen consumption during the recovery period were summed and divided by the total duration of all dives. Instantaneous rates of oxygen consumption were estimated using the computation described by Bartholomew et al. (1981).

2.3. Predicting diving oxygen consumption rates from behaviour

The influence of different dive parameters ('behaviour') on diving oxygen consumption rate was evaluated using a generalized linear modeling framework. This allowed us to construct models that could be used to predict rates of diving oxygen consumption based on a range of characteristics. Initial tests showed that potential differences in diving oxygen consumption due to slight differences in mass of the sea lions were not significant (one-way ANOVA: $F=3.3$, $df=1$, $P=0.08$). We therefore pooled data from all three sea lions to create the initial model, using diving oxygen consumption rate ($L \text{ min}^{-1}$) as the response variable, and temperatures and diving parameters as the independent variables. Selection and fitting of the models began by fitting each variable to the null model, with the term that

resulted in the greatest improvement in the model fit being selected for inclusion in the next step (based on minimizing the Akaike Information Criterion — AIC) (Akaike, 1974). At each successive step, all remaining variables were again tested individually for possible inclusion.

Model variables were grouped into two blocks (temperature and behaviour) to identify which variables might influence rates of diving oxygen consumption, and which might mask or complicate potential relationships. Variables in the temperature block (surface water temperature, water temperature at depth, and temperature difference between the surface and depth) were fitted to the null model using a stepwise procedure that retained terms that resulted in the greatest improvement in the model fit. Remaining variables in the temperature block were tested individually at each successive step for possible inclusion.

Variables from the behavioural block were added to the model after all significant variables from the temperature block had been identified. These behavioural variables included mean dive duration, maximum dive depth, mean duration at depth, mean swim speed, proportion of the dive cycle spent submerged, and the swimming distance during the trial (sum of all ascent and descent distances). Selecting variables from a block of variables using minimum AIC values meant that some of the temperature block variables might have had little explanatory value. We therefore further evaluated whether removal of any of the temperature variables improved the fit of the final model.

We tested the predictive power of the resultant model using a cross-validation approach. This was achieved by removing all of the experimental trial data for one sea lion, and refitting the model using the temperature and behaviour variables selected in the original model. We then used the resulting equation to predict the diving oxygen consumption rates of the excluded sea lion (Sparling and Fedak, 2004). These were based on the coefficients from the refitted model, and the temperature and behavioural information during each trial from the excluded sea lion. The predicted diving metabolic rates were then tested against the observed metabolic rates using paired *t*-tests. This was done by excluding each of the three sea lions in turn.

We used our generalized model of diving metabolism to make a series of predictions about how a range of simulated diving scenarios would affect oxygen consumption rates. We also used the model to estimate the daily fish requirements to maintain each level of activity. Data on the energetic content of fish for a mixed species diet was based on the energetic values and median

Table 1

The variables and coefficients of the generalized linear model that provided the best predictor of the rate of oxygen consumption rates for Steller sea lions while diving (AIC = -30.08)

Variable	Coefficient	S.E.	<i>t</i> value
Intercept	0.15	0.23	0.66
log(Maximum dive depth)	-0.58	0.13	-4.19
log(Swimming distance)	0.71	0.08	9.04

percentage biomass values detailed in Winship et al. (2002); the mixed species diet was assumed to consist of cephalopods (3.5%), flatfish (3.1%), forage fish (9.8%), gadids (34.2%), hexagrammids (23.2%), salmon (18.8%) and other (7.4%). All analyses were carried out using the software package SPLUS 2000 (Mathsoft Inc.).

3. Results

3.1. Behavioural parameters

Mean descent rates were 0.83 (S.D.±0.19), 1.15 (S.D.±0.33), and 0.80 (S.D.±0.28) m s⁻¹ for F00BO, F97HA, and F97SI respectively. Mean ascent rates were generally faster at 1.88 (S.D.±0.75), 1.12 (S.D.±0.74), and 1.79 (S.D.±0.62) m s⁻¹ for F00BO, F97HA, and F97SI. Mean swim speeds (mean rate for all descents and ascents) were 1.36 (S.D.±0.76), 1.64 (S.D.±0.75), and 1.30 (S.D.±0.69) m s⁻¹ for F00BO, F97HA, and F97SI respectively; and mean durations of individual dives were 107 (S.D.±37) for F00BO, 56 (S.D.±10) for F97HA, and 87 (S.D.±42) s for F97SI. Mean durations at depth were 75 (S.D.±35),

27 (S.D.±5), and 71 (S.D.±43) s for F00BO, F97HA, and F97SI. The swimming distance during the experimental trials ranged from 10 to 300 m; and the proportion of the dive cycle spent submerged ranged between 23% and 88%, with a mean of 75% (S.D. = 13%).

3.2. Predicting diving oxygen consumption rates from behaviour

The generalized linear modelling suggests that few explanatory variables significantly influenced oxygen consumption rates for diving Steller sea lions, particularly the depth of dives, and the swimming distance during dives (AIC = -30.08) (Table 1). None of the water temperature parameters – water temperature at depth, surface temperature and temperature difference between the surface and depth – significantly influenced diving oxygen consumption rate. There was a positive curvilinear relationship between diving oxygen consumption rate and the swimming distance during the dives (Fig. 1). The relationship between metabolism and maximum depth of dive was curvilinear with a peak in rate of oxygen consumption at dives to 5 m, and a minimum at dives to 30 m (Fig. 2).

The models created using data from each pair of sea lions were significant predictors of the diving oxygen consumption rates of the respective third sea lions (i.e. predicted diving oxygen consumption rates did not differ significantly from those observed: $t_{55}=1.11$, $P=0.27$).

Predicted oxygen consumption during dives to depth ranged from 3.37 L min⁻¹ at 10 m to 1.40 L min⁻¹ at 300 m (based on the resultant model standardized to a

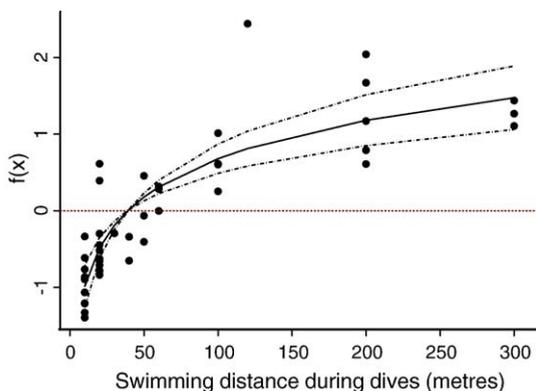


Fig. 1. Generalized linear model describing the relationship between swimming distance and the rate of oxygen consumption rates for Steller sea lions while diving. Functions are scaled to the model mean, and the dashed lines represent two standard error bands. The horizontal dashed line represents $f(x)=0$.

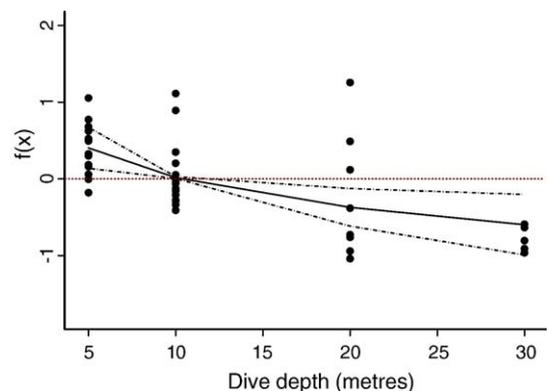


Fig. 2. Generalized linear model function describing the relationship between depth and the rate of oxygen consumption of Steller sea lion while diving. Functions are scaled to the model mean. The dashed lines represent two standard error bands, and the horizontal dashed line represents $f(x)=0$.

Table 2

Predicted rates of oxygen consumption, energy consumption rate, and food mass requirements for Steller sea lions diving to 10–300 m

Dive depth (m)	DO ₂ (L min ⁻¹)	DMR (MJ day ⁻¹)	Fish mass (kg day ⁻¹)
10	3.37 (0.23)	97.54 (6.66)	18.92 (1.29)
50	2.44 (0.16)	70.62 (4.63)	13.70 (0.90)
100	2.03 (0.22)	58.76 (6.37)	11.39 (1.23)
150	1.80 (0.26)	52.10 (7.53)	10.10 (1.46)
200	1.63 (0.29)	47.18 (8.39)	9.15 (1.63)
250	1.50 (0.32)	43.42 (9.23)	8.42 (1.79)
300	1.40 (0.34)	40.52 (9.84)	7.86 (1.91)

Values are based on dives to the depths listed with the swimming distance standardized to 600 m. Standard errors are shown in parentheses.

swimming distance of 600 m; Table 2). This equated to estimated metabolic rates of 97.54 and 40.52 MJ day⁻¹, and estimated daily biomass requirements of 18.92 and 7.96 kg day⁻¹, for dives to 10 m and 300 m, respectively (Table 2).

4. Discussion

Our study provides the first quantitative data on the diving oxygen consumption of Steller sea lions during a series of dives to depth, and shows that relatively simple measures of behaviour during the dives can be used to accurately predict diving oxygen consumption rates.

The dives carried out by our trained sea lions were similar to those made by wild sea lions. Although the depths of dives of our study animals were well below the maximums recorded for wild Steller sea lions, they did encompass a significant proportion of the wild dives (Loughlin et al., 2003; Merrick and Loughlin, 1997). Furthermore, the mean proportion of the dive cycle spent submerged that we measured (75%, S.D.=13%) was similar to the range of values measured in other species. For example, New Zealand fur seals (*Arctocephalus forsteri*) spend a mean of 72.2% of time submerged (Crocker et al., 2001), and Australian sea lions (*Neophoca cinerea*) spend a mean of 57.9% of their time at depths below 6 m (Costa and Gales, 2003). Mean swimming speeds measured during our study (between 1.3 and 1.64 m s⁻¹) were also similar to those measured in wild sea lions (e.g. Crocker et al., 2001), and were close to the minimum cost of transport of 1.53–1.60 m s⁻¹ predicted for Steller sea lions (Rosen and Trites, 2002). However, unlike most previous studies of wild animals (e.g. Crocker et al., 2001; Le Boeuf et al., 1992), descent rates were significantly lower than ascent rates in our study, but are consistent with other studies of

trained animals diving in the open sea where food-based training may have been an artifact (Shaffer et al., 1997; Williams et al., 1999), or where the animals' food resource is at the surface rather than at depth.

Using trained animals diving in the open sea under a range of diving conditions allowed us to investigate the influence of environmental determinants and behavioural parameters on diving metabolism. Our results suggest that the range of water temperature indices we measured (6.5–19 °C: temperature at the surface, temperature at depth, and the difference in temperature between the surface and depth) were poor predictors of oxygen consumption. Although no information exists on the thermoneutral zone (TNZ) for Steller sea lions, previous studies suggest that the lower critical temperature for California sea lions (*Zalophus californianus*) is 14 °C (Liao, 1990). It is therefore somewhat surprising that the variation we recorded in water temperatures (between 6.5 and 19 °C) was not an underlying determinant of the variation in rates of oxygen consumed while diving.

Diving behaviour significantly influenced the rate at which our sea lions consumed oxygen while diving. In particular, two relatively simple behavioural measures – maximum depth of dives and the swimming distance during dives – appear to reliably predict diving metabolism. There was a positive curvilinear relationship between swimming distance and oxygen consumption, and an inverse curvilinear relationship between dive depth and oxygen consumption. These results highlight the complex tradeoffs that breath-holding divers must balance between exercise and diving responses (i.e. they need to maximize the time spent foraging at depth while maximizing their foraging success).

Most previous studies that have attempted to link diving behaviour with changes in metabolism have been limited to measurements of cardiac output (e.g. Culik, 1992; Hicks et al., 2004; Hill et al., 1987; Hindell and Lea, 1998; Southwood et al., 1999; Thompson and Fedak, 1993; Williams et al., 1991) or total field metabolic rate (FMR) (e.g. Costa and Gales, 2000). Although many studies have described inverse relationships between dive duration and metabolism (e.g. Andrews et al., 1997; Hill et al., 1987; Hindell and Lea, 1998; Thompson and Fedak, 1993), a limited number have detailed relationships between dive depth and metabolism. For example, bottlenose dolphins (*Tursiops truncatus*) trained to dive to depth showed a greater degree of bradycardia on the bottom phase of 210 m dives compared to dives to 60 m (Williams et al., 1999). Similarly, diving leatherback turtles (*Dermochelys coriacea*) showed a significant negative rela-

tionship between dive depth and heart rate (Southwood et al., 1999). Furthermore, Costa and Gales (2000) showed a significant negative relationship between FMR and dive depth in wild New Zealand sea lions (*Phocarctos hookeri*), with FMR falling from approximately 7.1 W kg^{-1} during dives to 60 m, to 5.7 W kg^{-1} during dives to 180 m. Another study of the development of diving physiology in harbour seal (*Phoca vitulina*) pups also revealed a decrease in heart rate variability (generally lower heart rates) with increasing depth (Hicks et al., 2004).

It might be suggested that sea lions 'choose' to decrease metabolism upon deeper dives in order to facilitate longer times at depth. However, the stronger relationship between dive depth and metabolism compared to dive time suggests a more basic physical mechanism is at least partly responsible for the stronger 'dive response' at increasing depth. In general, Steller sea lions dive on inhalation, indicating that they dive with inflated lungs. The role of pressure therefore likely plays a significant role in the changes we observed in oxygen consumption rates with depth. Lung compression results in lower pulmonary reserves (Ridgway et al., 1969) and modifications in swimming mode resulting from changes in buoyant forces (Skrovan et al., 1999) may promote energetic savings on dives to deeper depths.

As the lungs account for approximately 21% of oxygen reserves in otariids (Ponganis et al., 1997), lung compression may significantly affect the amount of oxygen that a sea lion can store while diving to depth. Full alveolar collapse has been estimated to occur at depths of around 160 m in California sea lions (Kooyman and Sinnett, 1982), indicating that no gas exchange can occur at depths greater than this. Although increased partial pressures with depth may, to some extent, counteract pulmonary shunt caused by a reduction in alveolar surface area (Scholander, 1940), increased hypometabolism with increased dive depths would allow the sea lion to partially offset decreasing pulmonary reserves and increase the duration of their dives. Additionally, the drop in blood oxygen saturation due to pulmonary shunting may actually facilitate the utilization of oxy-myoglobin (Davis et al., 2004).

Changes in lung volume also produce changes in the buoyancy of diving animals. This has been shown to provide a mechanism for energy saving changes in locomotory gaits by many diving animals. As depth increase, relative buoyancy decreases and, as a result, the work the animal has to perform to dive further or maintain depth also decreases (Lovvorn and Jones, 1991). Although few studies have quantified the

energetic costs of swimming at depth, Williams et al. (2004) found that the oxygen consumption by Weddell seals (*Leptonychotes weddellii*) diving under ice increased linearly with the number of flipper strokes taken on the dive, with a net cost of $0.044 \text{ ml O}_2 \text{ kg}^{-1} \text{ stroke}^{-1}$. Intermittent swim stroke patterns, ranging from burst/coast locomotion to prolonged gliding, therefore represent a potential mechanism to conserve energy that could extend the duration of dives (van Dam et al., 2002). For example, in diving emperor penguins (*Aptenodytes forsteri*), highest stroke frequencies occurred during the initial descent phase with swimming effort being reduced significantly during other phases of the dive (while traveling below 12 m depth, during foraging ascents/descents, and during final ascents to the surface) (van Dam et al., 2002). Diving Weddell seals exhibited a similar behaviour strategy with stroke frequencies being significantly higher during descent than ascent, and the highest stroke frequencies occurring during the initial descent phases (Sato et al., 2003). Williams et al. (2000) showed that seals that incorporated such a behavioural strategy could reduce their rates of oxygen consumption by 9.2% to 59.6%, with greater savings occurring during deeper dives. These patterns also support Costa and Gale's (2000) hypothesis that an inverse relationship between metabolic rate and dive depth observed in New Zealand sea lions is consistent with an efficient burst and glide form of locomotion that results in deep-diving sea lions spending a greater proportion of their dive gliding. It therefore appears that the relationship we observed between dive depth and oxygen consumption rate is characteristic of the pressure-induced changes in locomotory gait that has been observed in many other diving animals (e.g. Sato et al., 2003; van Dam et al., 2002; Williams et al., 2000).

In an ecological context, our study results also have important implications for parameterizing bioenergetic models for wild populations. Previous models for Steller sea lions have relied on activity parameter estimates from other species to describe foraging energetics at sea (Winship et al., 2002). Metabolic predictions from our model suggest that the costs of diving to depth ranged from 40.52 to $97.54 \text{ MJ day}^{-1}$, which is similar to the maximum daily energy requirements of around 30 to 90 MJ day^{-1} estimated by Winship et al. (2002) for adult female Steller sea lions. However, the costs associated with activity estimated by Winship et al. were less, ranging from approximately 25 to 75 MJ day^{-1} . Estimated daily food requirements of between 7.68 and $18.92 \text{ kg day}^{-1}$ of fish and cephalopods in our study

were also similar to previous estimates of around 6 to 17 kg day⁻¹ (Winship et al., 2002).

A certain degree of caution should be applied to our energetic estimates. As with all predictive outputs that encompass parameter ranges outside those measured in any given study, we are limited by having no direct information about the physiological or behavioural changes that occur at depths greater than 30 m. Nevertheless, our study provides new insights into metabolic processes that occur in Steller sea lions when diving to depth, and suggests that changes in locomotory gait with depth may help reduce the energetic costs of diving to depth as in other species. Furthermore, the results of the modeling procedures provide an energetic basis for interpreting diving behaviour in wild animals, as well as insights into the potential energetic consequences for sea lions that change their foraging strategies or are faced with changing prey dynamics. Further studies should now be focused on understanding the predicted links between locomotory behaviour and metabolic rates at depth in Steller sea lions, and the physiological mechanisms underlying metabolic changes during dives to depth.

5. Conclusions

Our study used Steller sea lions trained to dive to depth in the open ocean to measure and relate diving oxygen consumption rates to diving behaviour. Two characteristics of the dive profile – swimming distance and dive depth – were found to be the most robust predictors of oxygen consumption. The generalized linear model we constructed to predict the energetic costs of diving to depth provides insights into the influence of behavioural changes on sea lion metabolism. It is also a valuable tool to help understand the potential energetic consequences that changes in prey availability or quality, and changes in foraging strategies could have on sea lions. Further studies should now be focused on understanding the physiological mechanisms underlying metabolic changes during dives to depth.

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