SCAR Fellowship Report 2013-2014

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Duration of Visit: 15 August 2014 – 22 December, 2014
Title: Estimating the physiology of Antarctic krill predators: a Bayesian Approach

Introduction

The physiology of free-living, diving marine predators can be difficult to measure due to the inherent difficulties associated with studying these animals. Thus, physiological studies of diving predators often use allometric relationships and equations to estimate parameters such as an individual's total oxygen storage capacity (K), their initial proportional rate of oxygen replenishment (α), and their metabolic rates during travelling and foraging (m_1 and m_2, respectively). Many of these relationships and equations, however, were developed using estimates of terrestrial or captured species' physiology (e.g., Kleiber 1975, Lockyer 1976, Halsey et al. 2006, Stephens et al. 2008) and few have been empirically tested. In fact, Leaper and Lavigne (2001) pointed out that many of the parameters used to model the energetics of cetaceans are often 'based on little more than guess work.' Despite this, these parameters have been used to model behaviors (e.g., foraging, energetics) of diving predators and to evaluate their response to current environmental conditions and/or to predict their response to future environmental changes. A large degree of error may be present in these subsequent models if the physiological parameters used to model their behavior were inaccurate.

Optimal foraging theory (OFT) suggests that organisms should favor foraging strategies that are efficient in minimizing costs (e.g., time, energy) while simultaneously maximizing benefits (e.g., energy, nutrients) (Macarthur & Pianka 1966). Tyson (2014) developed a model to estimate K, α, m_1 and m_2 of humpback whales (*Megaptera novaeangliae*) based on a time-allocation OFT model framework. The model uses Maximum Likelihood Estimation (MLE) techniques within a Bayesian framework and is built upon the assumption that recorded observations of humpback whale diving behavior (i.e., dive durations, foraging durations, travel durations, and post-dive surface durations) recorded with a high-resolution bio-logging tool were true and that the observed whales were allocating their time on foraging dives optimally (i.e., they were maximizing foraging durations while minimizing travel and post-dive surface durations; Kramer 1988, Houston & Carbone 1992). This method offered an alternative approach to allometric equations and scaling relationships for estimating these parameters and provides insights into both the accuracy of these relationships and the true values of these parameters.

Project Objectives

The current research involves adapting the physiological model developed by Tyson (2014) to estimate K, α, m_1 and m_2 of Antarctic fur seals (*Arctocephalus gazelle*, hereafter AFS) and Southern elephant seals (*Mirounaa leonine*, hereafter SES). These species are abundant krill predators in the Southern Ocean for which multiple bio-logging data sets exist.

Methods and Results to Date

Dive behaviors of AFS and SES were inferred from time-depth recording tags (TDRs) deployed on animals at Kerguelen Island (49° 02' S, 70° 45' E) between 1999 and 2014 during various research projects carried out by colleagues at the Institute for Marine and Antarctic Studies at the University of Tasmania. AFS were captured and fitted with MK7 TDRs (5 Hz; Wildlife Computers, Redmond WA, USA) at Cape Noir during their breeding season (December 1999 – February 2000). SES were fitted with Conductivity-Temperature-Depth Satellite Relay Data Loggers (4 Hz CTD-SRDL-9000; Sea mammal Research Unit, St. Andrews, UK) at the end of their annual breeding haul-out (prior to the post-breeding migration) or at the end of their annual molt haul-out (prior to the post-molt migration). AFS were weighed and measured during both the tag deployment and retrieval period. SES were weighed and measured during the tag deployment period (Field et al. 2002). TDR records from 47 AFS and 12 SES were used in this study.

TDR data for both species were corrected to account for drift in the pressure transducer accuracy and to identify individual dives using a Zero Offset Correction (ZOC) method (Heerah et al. 2014). Individual dives and their respective maximum depths, dive durations, bottom durations, and post-dive surface intervals were identified from the corrected TRD data (Hindell et al. 1991, Scheer & Testa 1996). Foraging dives were identified as any dive having a bottom duration of at least one sec and with at least one wiggle (i.e., a change in vertical direction during bottom time); non-foraging dives were not used in the analysis. Dive durations of foraging dives were split into their respective travel durations (i.e., time spent descending to or ascending from the bottom phase of a dive) and foraging durations (time spent during the bottom phase of a dive).

A total of 49,408 AFS foraging dives and 125,040 SES foraging dives were isolated for use in this research. Dive durations, foraging durations, and post-dive surface durations generally increased with increasing maximum dive depth for both species (Figure 1). However, mean maximum dive depths, dive durations, foraging durations, and post-dive surface durations were significantly different for AFS and SES (Table 1; Welch Two Sample t-tests: t = -637.51, df = 137863.6, $p < 0.001$; t = -805.81, df = 128376.3, $p < 0.001$; t = -688.78, df = 126838.8, $p < 0.001$; and t = -4.63, df = 152791.6, $p < 0.001$; respectively).

Table 1. Dive parameters for Antarctic fur seals (AFS) and Southern Elephant Seals (SES). Values are listed as means (± SD).

Species	Maximum depth (m)	Dive duration (s)	Forage duration (s)	Post-dive surface duration (s)
AFS	47.23 (± 31.75)	103.47 (± 49.82)	58.39 (± 30.44)	64.59 (± 850.15)
SES	449.97 (± 217.61)	1668.97 (± 682.39)	1171.11 (± 569.19)	117.07 (± 3777.85)
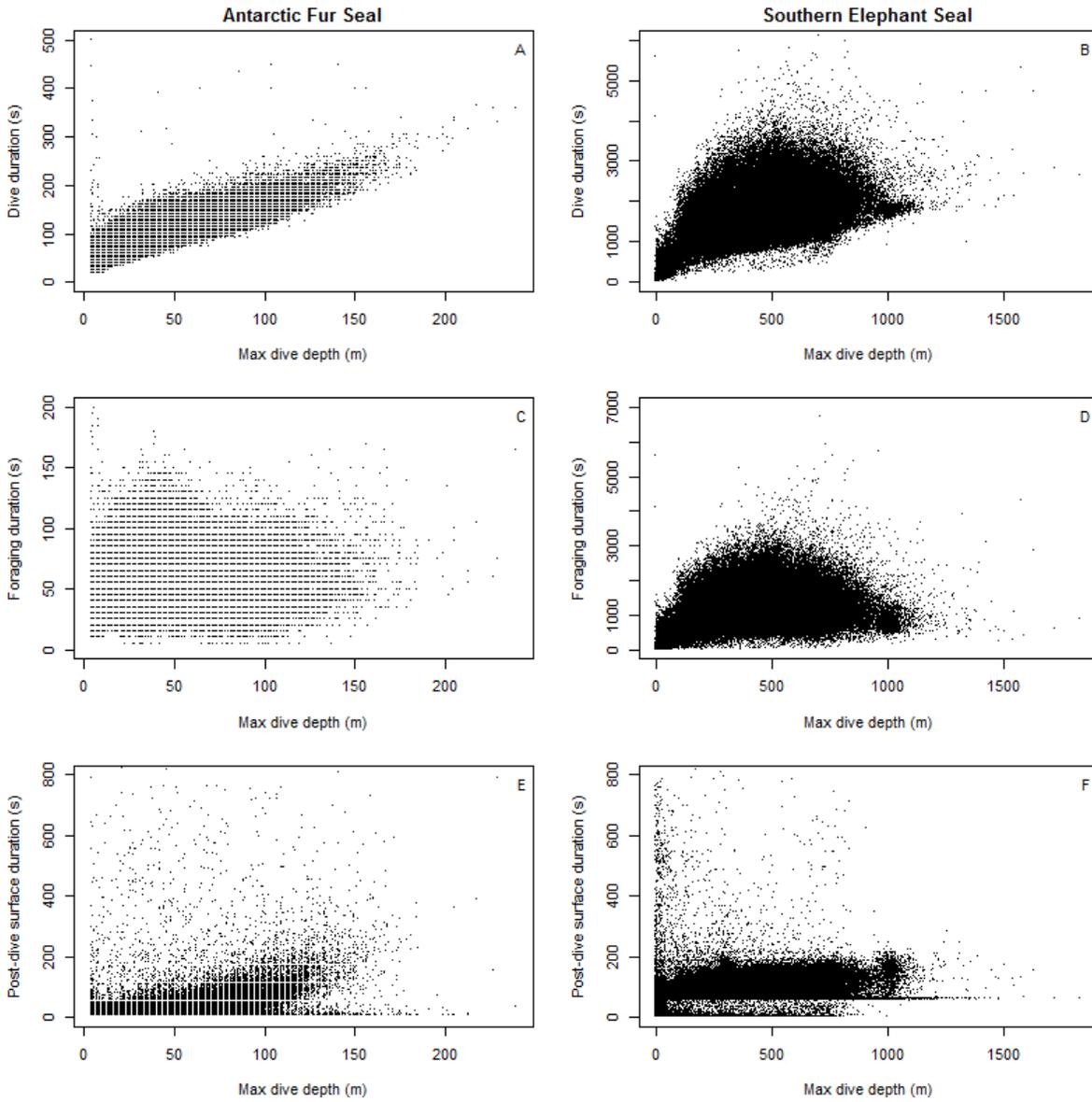
Figure 1. Dive durations (A, B), foraging durations (C, D), and post-dive surface durations (E, F) for Antarctic fur seals and Southern elephant seals, respectively.

A Markov Chain Monte Carlo (MCMC) simulation with a Gibbs sampler and a Metropolis sampling algorithm was used to obtain posterior densities of K, α, m_1 and m_2 for SES and AFS based on the likelihood that their observed dive behaviors were true and optimal according to the Houston and Carbone (1992) time-allocation OFT model:

$$u = \frac{K(1 - e^{-\alpha s}) - m_2 \tau}{m_1} + \tau$$

where u is the observed dive duration, s is the observed post-dive duration, and τ is the observed travel duration (Tyson 2014). Candidate values of each physiological parameter were randomly selected from a truncated normal density, having upper and lower bound values set wide around their values estimated from equations listed in Table 2 (i.e., the model used vague priors; see Tyson 2014 for more model details).

Table 2. Descriptions, equations, and values of parameters used as priors in the simulated model. Body masses are listed as the average value recorded for the tagged animals. Note: values of m_1, and m_2 were converted from Watts to L O2 s^{-1}.

Parameter	Description (units)	Equation	AFS Values	SES Values	Reference
M	Body Mass (kg)		31.78	362.36	
m_1	Metabolic rate while traveling (L O_2 s^{-1})	$6 \times 4 \times M^{0.75}$	0.02	0.09	Potvin et al. (2012)
m_2	Metabolic rate while foraging (L O_2 s^{-1})	$4 \times m_1$	0.06	0.38	Boyd and Croxall (1996)
K_afs	Total oxygen storage capacity (L O_2) for AFS	$0.03 \times M^{1.05}$	1.13	-------	Stephens et al. (2008)
K_ses	Total oxygen storage capacity (L O_2) for SES	$0.079 \times M$	-------	28.63	Kooyman (1989), Hindell et al. (1992)
α	Initial proportional rate of oxygen replenishment (s^{-1})	$0.075 \times M^{-0.33}$	0.02	0.01	Stephens et al. (2008)

Simulation runs were computationally expensive, therefore several simulations using a random sample of data (with approximately 50 - 2500 dives) for each species were run to obtain posterior densities of K, α, m_1 and m_2 (Table 3). Simulation runs included using SES and ASF behavioral parameters (u, s, and τ) from dives randomly selected from any day all seals were tagged (all days, all seals), from dives recorded any day one randomly selected seal was tagged (all days, one seal), and from one dive recorded from one randomly selected seal (one dive, one seal). In addition, simulations for SES were run using a subsample of their dive data based on their median dive durations and maximum foraging durations. One hundred simulations were run (86 for AFS, 11 for SES; Table 3) and each simulation was run for at least 100000 iterations in an attempt to allow the MCMC chains to reach convergence.

Table 3. How many times each type of simulation was run for AFS and SES. Note: all simulations used a random subset of AFS or SES data (10-2500 dives).

Species	All days	One day	One dive	All seals	One seal	Median sample	Max sample	Number of simulations
AFS	x			x				1
AFS	x				x			5
AFS		x			x			2
AFS			x		x			26
AFS			x		x			52
SES	x				x			4
SES		x			x			6
SES		x		x				1
SES				x		x		2
SES				x			x	1

Convergence of the MCMCs for each physiological parameter varied by simulation but was generally weak for α, m_1 and m_2; convergence of the MCMCs for K was generally strong (e.g., Figure 2). Poor convergence of α, m_1 and m_2 occurred despite running multiple MCMCs within a single simulation and using a variety of prior and starting values. This could be the result of insufficient MCMC iterations (i.e., the simulations should run longer than 10000 iterations), the data being not suitable or too variable to allow for the MCMCs to converge, and/or the model not being appropriate for the proposed purpose. For example, it may be too simplistic to assume that α, m_1 and m_2 are fixed. In addition, it is possible that the resolution of the data was too poor and/or that the classification of behavioral states was not appropriate.
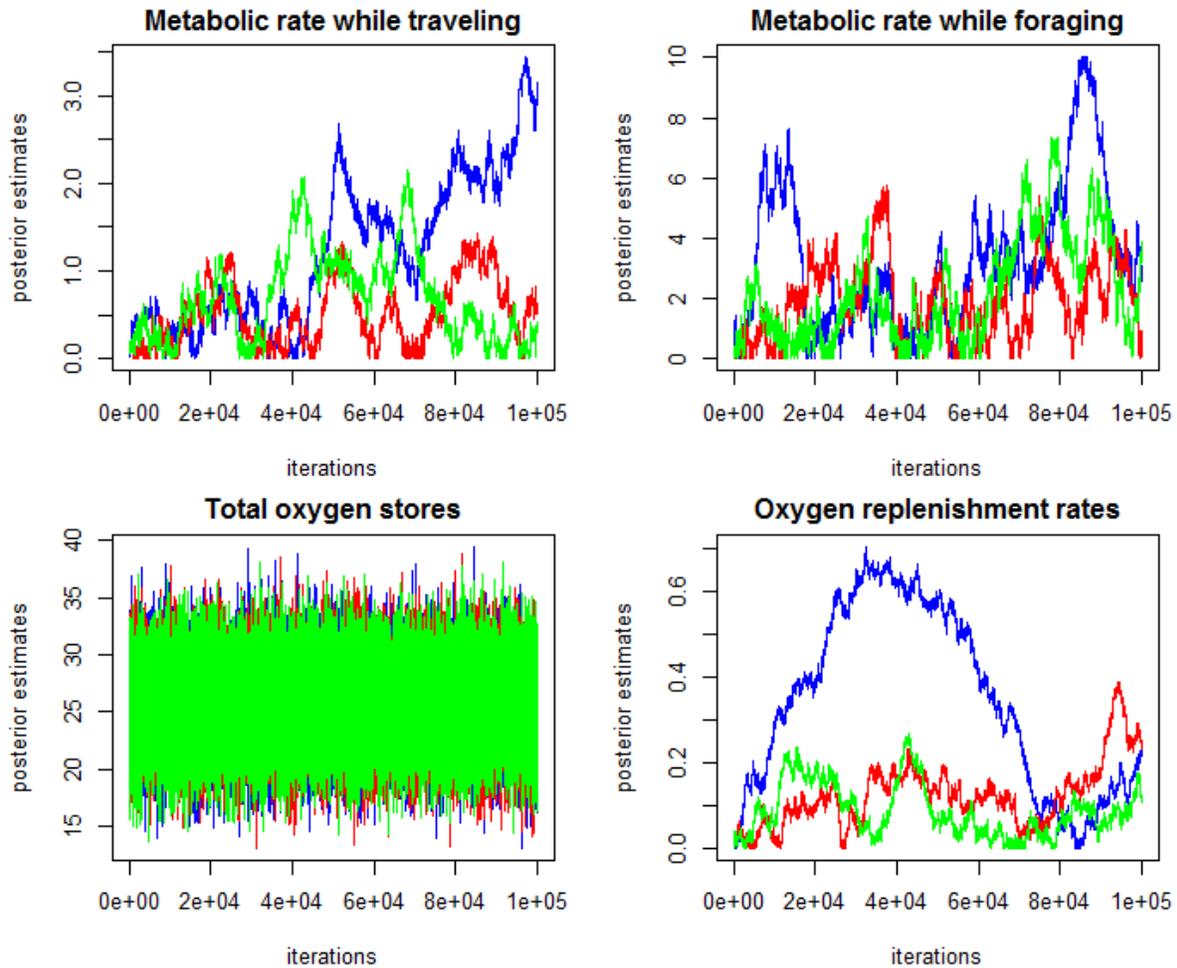
Figure 2. MCMC chains for a southern elephant seal's metabolic rate while traveling (m_1), metabolic rate while foraging (m_2), total oxygen stores (K) and rate of oxygen replenishment (a). These chains were produced using all foraging dive data collected for all days with one southern elephant seal.

Future Steps
The results thus far have suggested that they physiology of diving predators such as SES and ASF may be more complex than previously considered. Future steps in this research will include examining the influence of step size within the metropolis algorithm, using higher resolution data, and further examining how subsets of the data influence model results. In addition, the use of more complex OFT models as the basis of the framework for the simulation will be explored (e.g., Carbone & Houston 1996).

Presentations:
Tyson, R. B., Clark, J., Friedlaender, A. S., and Nowacek, D. P. (August 2014). Insights into the physiology of foraging humpback whales from an optimality approach. XXXII Scientific Committee of Antarctic Science 2014 Open Science Conference, Auckland, New Zealand. Poster Presentation.

Tyson, R. B. (November 2014). Examining the physiology of diving Antarctic predators. R Users Group & Australian Marine Mammal Centre at the Australian Antarctic Division.

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