Does optimal foraging theory predict the foraging performance of a large air-breathing marine predator?

R. B. Tyson ^{* a, b}, A. S. Friedlaender ^{a, c}, and D. P. Nowacek ^a

^a Duke University Marine Laboratory, 135 Duke Marine Lab Road, Beaufort, North Carolina, USA, 28209

^b Sarasota Dolphin Research Program, Chicago Zoological Society, c/o Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, Florida, USA, 34236

^c Marine Mammal Institute, Oregon State University, 2030 SE Marine Science Drive, Newport, Oregon, USA, 97365

^{*} Corresponding author – email: rtyson@mote.org, phone: +1 (352) 408-6018, fax: +1 (941) 388-4223

Word count: 6769

1 Optimal foraging theory (OFT) suggests that air-breathing diving animals should
2 minimize costs associated with feeding under water (e.g., travel time, oxygen loss) while
3 simultaneously maximizing benefits gained from doing so (e.g., foraging time, energy
4 gain). Humpback whales (*Megaptera novaeangliae*) foraging along the Western
5 Antarctic Peninsula (WAP) appear to forage according to OFT, but the direct costs and
6 benefits in terms of their behaviours (e.g., allocation of time) have not been examined.
7 The foraging behaviour of humpback whales in this region inferred from multi-sensor
8 high-resolution recording tags was compared to their behaviour predicted by OFT time-
9 allocation models assuming the following currencies were being maximized: a) the
10 proportion of time spent foraging, b) the net rate of energetic gain, and/or c) the ratio of
11 energy gained to energy expended (i.e., efficiency). Model predictions for all three
12 currencies were similar, suggesting any of these OFT models were suitable for
13 comparison with the observed data. However, agreement between observed and optimal
14 behaviours varied widely depending on the physiological and behaviour values used to
15 derive optimal predictions, highlighting the need for an improved understanding of
16 cetacean physiology. Despite this, many of the theoretical OFT predictions were
17 supported: shallow dives (i.e., < 100) were short, executed most frequently, and yielded
18 the highest proportions of foraging time, the greatest net rates of energy gain, and were
19 the most efficient. In addition, dive and foraging times increased in duration rapidly with
20 increasing maximum dive depths to approximately 100 m and then at lower rates with
21 deeper dives. Our findings offer a thorough examination of the applicability of time-
22 allocation OFT models to the behaviours of a large, air-breathing, diving predator and

23 provide insights into the foraging ecology and physiology of humpback whales in the
24 WAP.

25

26 **KEYWORDS:** Antarctica, bio-logging, foraging behaviour, humpback whale, optimal
27 foraging theory

28 Optimal foraging theory (OFT) suggests that animals are adapted to exploit resources as
29 efficiently as possible; natural selection should favour foraging strategies that are
30 efficient in minimizing foraging costs (e.g., travel time, oxygen loss) while
31 simultaneously maximizing benefits (e.g., energy gain) (Macarthur & Pianka, 1966).
32 Mathematical models to predict the foraging behaviours of air-breathing, diving animals,
33 such as birds and marine mammals, have been developed under the framework of central-
34 place foraging (Orians, Pearson, Horn, Mitchell, & Stairs, 1979), where the surface acts
35 as the central place to and from which an animal returns between dives (Houston &
36 McNamara, 1985). Time-allocation OFT models theorized by Kramer (1988) and derived
37 by Houston and Carbone (1992) are commonly used for this purpose because they predict
38 the optimal foraging and surfacing durations of divers in response to changes in travel
39 time and dive depth assuming that either the proportion of foraging time, the net rates of
40 energetic gain, and/or the energy gained versus energy expended (i.e., efficiency) is being
41 maximized. These models are based on the assumption that the time spent traveling to
42 and from a prey patch will increase with increasing prey patch depth (Houston &
43 Carbone, 1992). Consequently, the amount of oxygen used during a dive and the time
44 needed to replenish it between dives will increase with increasing prey patch depth
45 (Kooyman & Ponganis, 1998) and the time available for foraging will decrease (Houston
46 & Carbone, 1992). Because prey acquisition is assumed to increase linearly with foraging
47 duration, air-breathing diving animals should maximize these currencies (i.e., foraging
48 time, energy gain, efficiency) by optimizing surface time and thus overall oxygen stores
49 (Houston & Carbone, 1992).
50

51 Initial tests of the Houston and Carbone (1992) OFT models (hereafter referred to as the
52 OFT models) were limited to experiments with captive animals (e.g., *Aythya ferina*;
53 Carbone & Houston 1994; *Aythya fuligula*, Halsey, Woakes & Butler 2003; *Uria lomvia*,
54 Elliott, Davoren & Gaston 2008), but the advancement of bio-logging tools (e.g., time-
55 depth recorders, accelerometers) has enabled further testing with free-ranging diving
56 animals including common eider ducks (*Somateria mollissima sedentaria*; Heath,
57 Gilchrist & Ydenberg 2007, Guillemette *et al.* 2004), harbor seals (*Phoca vitulina*
58 *concolor*; Healsip, Bowen & Iverson 2014), fin whales (*Balaenoptera physalus*;
59 Acevedo-Gutierrez, Croll & Tershy 2002), and blue whales (*Balaenoptera musculus*;
60 Acevedo-Gutierrez, Croll & Tershy 2002, Doniol-Valcroze *et al.* 2011). Such
61 applications allow for an examination into the extent that an animal's behaviour can be
62 explained in terms of its physiology and/or ecology (Houston, 2011). For example,
63 Acevedo-Gutiérrez *et al.* (2002) compared observed dive times of foraging blue and fin
64 whales to those predicted by an OFT model. Their results suggest that the foraging
65 strategies of blue and fin whales are energetically expensive and limit the dive time of
66 these large predators.

67

68 Blue and fin whales, like other Balaenopterids (e.g., humpback whales, *Megaptera*
69 *novaeangliae*; minke whales, *Balaenoptera bonaerensis*), feed via a process known as
70 lunge feeding, which involves accelerating with a burst of energetic fluking towards and
71 engulfing a mass of prey-laden water that may be greater than the whale's body mass
72 (Goldbogen, Potvin, & Shadwick, 2010), filtering the prey through keratinized plates of
73 baleen, and swallowing the captured prey. Simulations based on hydrodynamic models

74 that coupled balaenopterid structure and function, fluid dynamics, and krill evasion
75 behaviours have revealed that this process can be up to 3.7 times the active metabolic rate
76 for a 27 m blue whale, but varies widely with whale size (Potvin, Goldbogen, &
77 Shadwick, 2012). This high energetic cost associated with lunging (i.e., the amount of
78 oxygen consumed) may contribute to the dive durations of these large marine predators
79 being shorter than predicted for their body size (Acevedo-Gutiérrez et al., 2002;
80 Goldbogen et al., 2008; Goldbogen et al., 2006; Goldbogen, Pyenson, & Shadwick,
81 2007).

82
83 While the energetic cost of lunging may contribute to foraging dives being shorter than
84 expected in Balaenopterids, foraging dives may also be short because it is optimal for
85 them to be so (Doniol-Valcroze et al., 2011; Houston & Carbone, 1992; Kramer, 1988).
86 Because oxygen is acquired at the surface with diminishing returns, the lengthening of
87 dives increases the amount of time required on the surface for replenishing oxygen stores
88 (Kooyman & Ponganis, 1998), decreasing the time available for foraging under water
89 (Kramer, 1988). Thus, while air-breathing diving animals could theoretically perform
90 long dives at shallow depths, short dives allow for shorter recovery times and more time
91 spent underwater foraging (Kramer, 1988). In support of this prediction, Doniol-Valcroze
92 et al. (2011) found that shallow dives of blue whales (i.e., < 150 m) were short and had
93 the highest feeding rates. Similarly, Ware, Friedlaender, and Nowacek (2011) reported
94 that humpback whales executed only one or two lunges during shallow dives (i.e., < 25
95 m). While Ware et al. (2011) do not discuss the duration of these shallow dives, these

96 whales were physiologically capable of executing several lunges per dive but only did so
97 at greater depths (Friedlaender, Tyson, Stimpert, Read, & Nowacek, 2013).
98
99 There is evidence that humpbacks along the Western Antarctic Peninsula (WAP) feed
100 according to the general principles of OFT (Macarthur & Pianka, 1966). For example,
101 humpbacks in this region adjust their foraging behaviours according to the depth and
102 density of their primary prey, Antarctic krill (*Euphausia superba*) (Friedlaender,
103 Johnston, Tyson, Kaltenberg, et al., In Review). These whales forage almost exclusively
104 at night when krill are near the surface and rest or travel near the surface during the day
105 when krill are at depth (Friedlaender et al., 2013). In addition, these whales modulate
106 their feeding depth with respect to their prey, targeting denser prey patches on deeper
107 dives (Friedlaender et al., In Review). These behavioural choices suggest that whales are
108 altering their behaviours to maximize their benefits while foraging.
109
110 In this study, the diving and foraging behaviours of humpbacks along the WAP inferred
111 from multi-sensor high-resolution recording tags was compared to behaviours predicted
112 by OFT models. We hypothesized that humpbacks would allocate their time during
113 foraging dives to maximize at least one of the following currencies: a) the proportion of
114 time available for foraging, b) the net rate of energetic gain, and/or c) the ratio of energy
115 gained to energy expended (i.e., energetic efficiency). This hypothesis was addressed by
116 assessing agreement between observed and predicted behaviours and examining variation
117 in model fit and adherence to model assumptions. Our findings provide insights into the

118 foraging ecology and physiology of humpback whales and offer a thorough examination
119 of the OFT model's applicability to free-ranging, large, air-breathing diving predators.

120

121 **MATERIALS AND METHODS**

122 *Observed Whale Behaviour*

123 Multi-sensor archival digital acoustic recording tags (DTAGs, Johnson & Tyack, 2003)
124 were used to infer the diving and foraging behaviours of humpback whales ($N = 13$
125 adults) in the near-shore waters of the WAP during 2009 and 2010 (Table 1). DTAGs
126 (hereafter referred to as tags) are small data-loggers commonly used with marine
127 mammals that incorporate tri-axial accelerometers and magnetometers to record animal
128 orientation (50 Hz), a pressure sensor to record depth, and a hydrophone (96 KHz).
129 Whales were approached for tagging from oblique angles at idle or low speeds with a
130 Zodiac Mark V rigid-hulled inflatable boat with a 4-stroke outboard to minimize both
131 behavioural disturbance to the whale and to maximize personal safety. Tags were
132 deployed on whales using a 6 m hand-held carbon-fibre pole via four silicon suction
133 cups. Whale behaviour was not visibly affected by tagging (other than immediate startle
134 responses by some) and preliminary examinations of the tag data suggested a return to
135 pre-tagging behaviour within a few dives, consistent with other tagging studies (e.g.,
136 Hazen et al., 2009; Nowacek, Johnson, & Tyack, 2004). A corrodible active release was
137 programmed to release the tag's suction cups from the whales after ~24 hours, after
138 which tags were recovered and data downloaded for analysis. These research activities
139 were permissible under NMFS Permit 808-1735 ACA Permit 2009-014 and Duke
140 University IACUC A049-112-02.

141 Table 1: DTAG deployment information.

Whale ID	Tag on date	Local tag start time (GMT – 5 hr)	Tagging location	Total tag on time (hr)	Number of lunges (n)	Number of feeding dives (N)
122b	2009-May-02	14:28:44	Wilhelmina Bay	18.4	620	419
127a	2009-May-07	08:42:03	Wilhelmina Bay	24.6	383	89
136a	2009-May-16	09:09:54	Anvord Bay	23.0	456	82
140a	2009-May-20	10:58:03	Anvord Bay	22.5	40	7
148a	2009-May-28	09:48:17	Wilhelmina Bay	25.2	578	225
152a	2009-June-01	10:39:24	Wilhelmina Bay	22.3	826	462
132a	2010-May-12	09:58:38	Wilhelmina Bay	23.1	317	97
133a	2010-May-13	12:03:50	Wilhelmina Bay	22.2	392	102
139a	2010-May-19	11:02:58	Wilhelmina Bay	20.6	847	292
144a	2010-May-24	14:05:18	Wilhelmina Bay	21.1	943	307
146a	2010-May-26	15:17:42	Flandres Bay	20.0	498	64
151a	2010-May-31	10:23:51	Wilhelmina Bay	24.6	573	160
155a	2010-June-04	09:42:03	Flandres Bay	22.2	390	59
Totals					6863	2365

142 An automatic lunge detector in the software program TrackPlot (Ware, Arsenault, &
143 Plumlee, 2006) was used to identify putative feeding lunges executed by the whales from
144 the tag data (see Friedlaender et al., 2013; Tyson, Friedlaender, Stimpert, Ware, &
145 Nowacek, 2012; Ware et al., 2011). The detector locates distinct fluctuations in the flow
146 noise (speed) recorded by the tag's hydrophone that are characteristic of the rapid
147 accelerations and decelerations associated with lunging (Goldbogen et al., 2006; Ware et
148 al., 2011). Detections were identified as feeding lunges if they occurred along with: (1)
149 an isolated bout of fluking associated with a distinct speed maximum, followed by a rapid
150 reduction in speed, followed in turn by a period of gliding; and (2) continued swimming
151 and fluking throughout the lunge, particularly during the deceleration phase (Goldbogen
152 et al., 2006; Simon, Johnson, & Madsen, 2012; Ware et al., 2011). Lunges shallower than
153 3 m were excluded from analyses due to detection capabilities being diminished because
154 of surface interactions (i.e., abrupt changes in flow noise when the whale surfaced). Each
155 time series was scanned for missed lunge detections.

156

157 The surface times (s), dive times, and maximum dive depths of feeding dives (defined as
158 any submergence greater than 3 m with at least one lunge; Friedlaender et al., 2013) were
159 calculated for each whale in MATLAB[®]. In addition, each dive was divided into its
160 respective foraging time (t) and travel time (τ) for comparison with the OFT model
161 predictions. For the purposes of this study, t was defined as the number of lunges
162 executed per dive multiplied by the lunge duration for an average sized humpback whale
163 (i.e., 25 s for a 14 m whale, which includes prey approach time (8 s), engulfment time
164 (4.2), and filter/recovery time (13 s); Potvin et al. 2012) . Time spent approaching,

165 engulfing, filtering or recovering on the surface was subtracted from t because it was
 166 included in s . Observed values of travel time (τ) were calculated as dive durations $- t$.

167

168 *Optimal Models Based on Time Allocation*

169 Following Houston and Carbone (1992), a whale that spends time s on the surface before
 170 a dive gains oxygen as:

$$x(s) = K(1 - e^{-\alpha s}), \quad (1)$$

171 where K is the amount of oxygen that can be obtained and α is the initial proportional
 172 exchange rate of oxygen at the surface. While diving, a whale uses oxygen at a rate of m_τ
 173 when traveling and m_t when foraging and all of its feeding dives are balanced (Houston &
 174 Carbone, 1992); i.e., all of the oxygen stored prior to each dive is used during the present
 175 dive (in contrast to all of the oxygen they can store; Houston, 2011):

$$x(s) - m_\tau \tau - m_t t = 0 \quad (2)$$

176 (the dives are aerobic).

177

178 Assuming these constraints (and following some substitutions), the proportion of time
 179 spent foraging during a dive cycle (π):

$$\pi = \frac{t}{t + \tau + s}, \quad (3)$$

180 is maximized when:

$$\pi(s) = \frac{x(s) - m_\tau \tau}{m_t(\tau + s)} \quad (4)$$

181 (see Houston & Carbone, 1992). Because the optimality condition states that $\pi'(s) = 0$,

182 the optimal surface time (s^*) for a diver maximizing π can be found by solving

$$x'(s^*) = \frac{x(s^*) - m_\tau \tau}{\tau + s^*}. \quad (5)$$

numerically for s^* given τ , m_τ , K , and α .

Following similar logic, s^* can be solved numerically for divers maximizing

the net rate of energetic gain ($\hat{N}$):

$$\hat{N}(t, s) = \frac{g(t) - y(m_\tau \tau + m_t t + m_s s)}{t + \tau + s}, \quad (6)$$

and energetic efficiency ($\hat{Q}$):

$$\hat{Q}(t, s) = \frac{g(t)}{y(m_\tau \tau + m_t t + m_s s)}, \quad (7)$$

where $g(t)$ is the cumulative gross gain while foraging, y converts units of oxygen to

appropriate units of energy and ym_s is the rate of energy expenditure at the surface

(Houston & Carbone, 1992). Optimal foraging times (t^*) can be found for all currencies

using values of s^* , m_t and equation 2:

$$t^* = \frac{x(s^*) - m_\tau \tau}{m_t}. \quad (8)$$

Values of s^* and t^* were predicted for an average sized humpback whale (14.0 m; Potvin

et al., 2012) independently for each currency; K , α , m_τ , m_t , m_s , and $g(t)$ were estimated

assuming their best known approximations (Table 2). Because ascent and descent rates

(and thus τ) can vary in humpback whales (e.g., Dolphin, 1988; Goldbogen et al., 2008),

reported descent and ascent rates (mean = 1.6 m s⁻¹ and 1.45 m s⁻¹, respectively;

Goldbogen et al. 2008) were used to predict τ (hereafter denoted as τ') for humpbacks

diving to 0 – 400 m (depths are representative of the observed whales diving behavior;

200 Friedlaender et al., 2013). Optimal dive durations were then predicted to be $t^* + \tau'$
201 (Houston & Carbone, 1992). Finally, The diving lactate threshold (DLT), the dive
202 duration at which post-dive lactate concentration increases (Butler, 2006; Butler & Jones,
203 1997; Kooyman & Ponganis, 1998), was calculated to compare with $t^* + \tau'$:

$$\text{DLT}(\tau') = \tau' + \left(\frac{K - m_{\tau} \tau'}{m_{\tau}} \right) \quad (9)$$

204 (Doniol-Valcroze et al., 2011). Custom written code in R (R Core Team, 2013) was used
205 to derive all model predictions and compare them to observed data.

206 Table 2: Descriptions, equations, and values of parameters used in the OFT models. $*m_\tau$ was converted from W to L O₂ s⁻¹ and
207 $**$ factors in an estimated energetic savings attributed to gliding behaviours (Williams, 2001).

Parameter	Description (units)	Equation	Value	Reference
L	Length (m)		14	Potvin et al. (2012)
M	Body Mass (kg)	$16.473 \times L^{2.95}$	39614.16	Lockyer (1976)
K	Total oxygen storage capacity (L O ₂)	$0.03 \times M^{1.05}$	2017.74	Stephens et al. (2008)
α	Initial rate of oxygen replenishment (s ⁻¹)	$0.09 \times M^{-0.33}$	0.003	Stephens et al. (2008), Doniol-Valcroze et al. (2011)
m_τ	*Metabolic rate while traveling (L O ₂ s ⁻¹)	$6 \times 4 \times M^{0.75}$	3.21	Potvin et al. (2012)
m_τ	**Metabolic rate while traveling (L O ₂ s ⁻¹)	$m_\tau - (m_\tau \times 0.28)$	2.32	Williams (2001)
m_t	Metabolic rate while foraging (L O ₂ s ⁻¹)	$1.78 \times m_\tau$	4.14	Doniol-Valcroze et al. (2011), Goldbogen et al. (2010), Potvin, Goldbogen, and Shadwick (2009)
m_s	Metabolic rate while surfacing (L O ₂ s ⁻¹)	m_t	4.14	Houston & Carbone (1992)
$g(t)$	Cumulative gross gain while foraging	$b \times t$	---	Houston & Carbone (1992)
b	Rate of energy gain (1 lunge s ⁻¹)	---	41	Potvin et al. (2009)

209 Model validity was assessed (Mayer & Butler, 1993) by comparing the fit of the observed
 210 data to the model predictions in several ways, including examinations of the residuals of
 211 observed (y_i) versus predicted ($\hat{y}_i$) values ($y_i - \hat{y}_i$), the standard deviations of the model
 212 prediction errors (i.e., root mean squared error; RMSE), the Pearson's product moment
 213 correlations of y_i and $\hat{y}_i$ (Guisan & Zimmerman, 2000), and the modelling efficiencies
 214 (ME ; Loague & Green, 1991; Mayer & Butler, 1993):

$$ME = 1 - \frac{\sum(y_i - \hat{y}_i)^2}{\sum(y_i - \bar{y}_i)^2}, \quad (11)$$

215 where $\bar{y}_i$ is the mean of y_i . ME values equal to 1 indicated a perfect match of y_i and $\hat{y}_i$,
 216 ME values equal to 0 indicated that the fit of y_i and $\hat{y}_i$ was equal to the fit of y_i and $\bar{y}_i$,
 217 and ME values less than 0 indicated the $\bar{y}_i$ was a better predictor of the data than $\hat{y}_i$.
 218 Linear regressions of y_i and $\hat{y}_i$ were also computed to see if they deviated significantly
 219 from 1 and 0, respectively (Smith & Rose, 1995). All samples were tested for normality,
 220 linearity, homoscedasticity, and outliers and determined appropriate statistical tests based
 221 on the outcome of the sample's adherence to these assumptions. Individual variability
 222 was assessed by examining dive variables for each tagged whale separately. A principal
 223 component analysis (Pearson, 1901) was also conducted to determine the influence that
 224 individual variations may have had on the model agreement. A significance level of 0.05
 225 was used for all statistical analyses.

226

227 **RESULTS**

228 *Observed Behaviours*

229 This study used tag data from 13 adult humpback whales (Table 1). Maximum foraging
230 dive depths ranged from 3.29 - 388.16 m (mean [median] $\pm$ SD = 66.06 [37.70] $\pm$ 75.06
231 m, $N = 2365$), but varied by individual (ANOVA: $F_{12,2352} = 374.18$, $P < 0.001$).
232 Despite the variation, 81.27% of foraging dives ($N = 1922$) were shallower than 100 m
233 and were distributed primarily between 5 - 40 m ($N = 1098$, 46.43%) and between 60 - 90
234 m ($N = 529$, 22.37%). Maximum dive depths were positively correlated to observed s (rs
235 = 0.68, $N = 2365$, $P < 0.001$), τ ($rs = 0.94$, $N = 2365$, $P < 0.001$), $t + \tau$ ($rs = 0.95$, $N =$
236 2365, $P < 0.001$), and t ($rs = 0.79$, $N = 2365$, $P < 0.001$).

238 *Model Agreement*

239 Values of s^* , $t^* + \tau'$, and t^* , and were derived from OFT models that maximized the
240 proportion of time spent foraging (π), the net rate of energetic gain ($\bar{N}$) and the energetic
241 efficiency ($\bar{Q}$) assuming τ' (Fig. 1). In all scenarios the optimal solutions derived for $\bar{Q}$
242 most closely matched the observed data (i.e., they had the highest correlation coefficients
243 and ME values and the lowest RMSE values; Table 3) and thus will be used below for all
244 comparisons between observed and predicted values. It should be noted; however, that all
245 derivations for each model were positively correlated to each other (e.g., s_{π}^* , $s_{\bar{N}}^*$; $rs =$
246 1.00, $P < 0.001$ for all comparisons).

247
248 Table 3. Pearson's product moment correlation coefficients (rs), model efficiencies (ME),
249 and root mean squared error ($RMSE$) values for comparisons between observed surface

(s), dive ($t + \tau$), and forage (t) times with predicted optimal times (s^* , $t^* + \tau'$, and t^*) given the following currencies are maximized: the proportion of time spent foraging (π), the net rate of energetic gain ($\bar{N}$) and the efficiency ($\bar{Q}$). Strongly positively correlated coefficients ($r > 0.9$; Cohen, 1988) are indicated with § . Model efficiencies greater than 0 are indicated with † . All Pearson's product-moment correlations were significant ($P < 0.001$).

	rs	ME	$RMSE$
s_{π}^*, s	0.65	-1.58	240.49
$s_{\bar{N}}^*, s$	0.65	-1.37	230.33
$s_{\bar{Q}}^*, s$	0.66	-0.94	208.82
$t_{\pi}^* + \tau', t + \tau$	0.95 §	0.44 †	124.02
$t_{\bar{N}}^* + \tau', t + \tau$	0.95 §	0.48 †	119.87
$t_{\bar{Q}}^* + \tau', t + \tau$	0.95 §	0.60 †	105.51
t_{π}^*, t	0.71	-3.05	124.64
$t_{\bar{N}}^*, t$	0.71	-2.76	120.10
$t_{\bar{Q}}^*, t$	0.74	-1.87	104.88

The OFT model predicted that s^* would increase with increasing maximum dive depth (Fig. 1 A). While s did increase with depth ($y = -16.94 + 1.36 \times \text{depth}$, $R^2 = 0.47$, $P < 0.001$), the models did not describe the data (Fig. 1 A, Table 3) and most foraging dives had shorter s than $s_{\bar{Q}}^*$ ($N = 2340$, 98.94%). The slope of the linear regression of s versus $s_{\bar{Q}}^*$ ($y = 189.45 + 0.68 \times s$, $R^2 = 0.43$, $P < 0.001$) as well as the RMSE values suggest that prediction accuracy of s varied by depth (AOV of RMSE values: $F_{38,2326} = 86.06$, $P < 0.001$): increasing depths generally resulted in s that were increasingly shorter than $s_{\bar{Q}}^*$ and had increasingly larger mean RMSE values; although RMSE values for dives between 120 - 250 m were equivalent (Tukey multiple comparisons for all n by n comparisons, $P > 0.05$). The mean maximum depths of foraging dives with shorter or

268 longer s than s_Q^* were significantly different (mean [median] $\pm$ SD = 65.08 [37.47] $\pm$
269 73.58 m, $N = 2340$ and 157.04 [189.35] $\pm$ 136.79 m, $N = 25$, respectively; $W = 36201$, P
270 = 0.04).
271

272

273 **Figure 1: Observed and predicted values of surfacing time (A), dive time (B), and**

274 **foraging time (C) of humpbacks as a function of maximum dive depth when the**

275 **following currencies are maximized: the proportion of time, the net rate of energetic**

276 **gain, and efficiency. The diving lactate threshold (DLT) is included (B) for**

277 **comparison.**

278

279 Dive times ($t + \tau$) were predicted well by the OFT models (Fig. 1 B; Table 3). The slope

280 of the linear regression between $t_{\hat{Q}}^* + \tau'$ and observed $t + \tau$ was not similar to 1,

281 suggesting however that prediction accuracy varied with maximum dive depth ($y =$

282 $128.40 + 0.76 \times (t + \tau)$, $R^2 = 0.91$, $P < 0.001$). Maximum dive depths of dives with

283 shorter or longer observed dive times than $t_{\hat{Q}}^* + \tau'$ were significantly different: mean

284 [median] $\pm$ SD = 51.69 [28.97] $\pm$ 56.93 m, $N = 2145$ and 206.07 [220.22] $\pm$ 85.90 m, $N =$

285 220, respectively; $W = 437966$, $P < 0.001$). In addition, dives with maximum depths

286 between 150 and 380 m ($N = 262$) had smaller median residuals (< 60 s) and lower

287 RMSE values (< 81 s) than shallower or deeper dives. Regardless of model agreement, t

288 $+ \tau$ increased with increasing maximum dive depth ($y = 24.59 + 2.11 \times \text{depth}$, $R^2 = 0.91$,

289 $P < 0.001$) and was positively correlated with this parameter ($rs = 0.95$, $N = 2365$, $P <$

290 0.001).

291

292 The DLT was predicted to increase with increasing maximum dive depth (Fig. 1 B).

293 While $t + \tau$ and DLT were positively correlated ($rs = 0.95$, $N = 2365$, $P < 0.001$), the ME

294 value was negative ($ME = -4.33$) suggesting that the whales were generally not diving

295 close to their DLT. The slope of $t + \tau$ and DLT ($y = 485.00 + 0.25 \times (t + \tau)$, $R^2 = 0.91$, P

296 < 0.001) and the RMSE values, however, suggest that the prediction accuracy of DLT

297 varied with depth (AOV of RMSE values: $F_{38,2326} = 718.90$, $P < 0.001$). Indeed, almost

298 all $t + \tau$ for dives greater than 200 m were equally similar to DLT (Tukey multiple

299 comparisons of RMSEs for n by n comparisons for dives greater than 200 m were

300 equivalent, $P > 0.05$; except for dives between 210 - 220 m and 230 - 240 m with 290 -

301 300 m, $P < 0.05$). In addition, the mean maximum depths of foraging dives that were
302 shorter or longer than the DLT predictions were significantly different (mean [median] $\pm$
303 SD = 63.56 [36.03] $\pm$ 71.47 m, $N = 26$ and 290.33 [295.78] $\pm$ 46.75 m, $N = 2339$,
304 respectively; $W = 59239$, $P < 0.001$).

305

306 Foraging time (t) was positively correlated to the OFT model predictions (Fig. 1 C; Table
307 3); however, the ME values were negative, suggesting the models cannot be
308 recommended for the observed data. In general, dives had shorter t than predicted:
309 96.62% ($N = 2285$) of observed t were shorter than t_Q^* . Dives with longer t than t_Q^*
310 (3.38%, $N = 80$) had significantly different maximum depths than dives with shorter t
311 than t_Q^* (mean [median] $\pm$ SD = 268.73 [276.23] $\pm$ 68.55 m and 58.96 [34.14] $\pm$ 64.66 m,
312 respectively; Wilcoxon Rank Sum Test: $W = 176788$, $P < 0.001$). Despite this, t did first
313 increase with increasing dive depth as predicted (Fig 1. C). In addition, while t did not
314 decrease at greater depths, t was equivalent for all dives deeper than 220 m (Tukey
315 multiple comparisons for all n by n comparisons, $P > 0.05$).

316

317 *Individual Variation*

318 Individuals whales had significantly different s ($F_{12,2352} = 113.53$, $P < 0.001$), $t + \tau$
319 ($F_{12,2352} = 278.29$, $P < 0.001$), and t (ANVOA; $F_{12,2352} = 117.21$, $P < 0.001$). These
320 differences resulted in varied agreement between their observed and predicted optimal
321 behaviours (Table 4). Despite this, a principal component analysis revealed that whale ID
322 was not a large source of variation in the data (Table 5). The first component explained
323 58.96 % of the variation, and Whale ID as well as time of day were not correlated to this

324 component ($rs = 0.01$ and $rs = 0.01$, respectively). Instead these variables were most
325 correlated to the second component ($rs = -0.71$ and $rs = -0.69$, respectively), which
326 accounted for 14.17 % of the data's variance.

Table 4. Pearson's product moment correlation coefficients (rs), model efficiencies (ME), and root mean squared errors (RMSE) for each individual whale for observed surface times (s), dive times ($t + \tau$), and foraging times (t) against predicted optimal surface times (s_Q^*), dive times ($t_Q^* + \tau'$), dive-lactate threshold times (DLT), and foraging times (t_Q^*) assuming that energetic efficiency is being maximized. Strongly positively correlated coefficients ($r > 0.9$; Cohen, 1988) are indicated with § . Model efficiencies greater than 0 are indicated with † .

Whale ID	s_Q^*, s				$t_Q^* + \tau', t + \tau$				DLT, $t + \tau$				t_Q^*, t			
	rs	P	ME	$RMSE$	rs	P	ME	$RMSE$	rs	P	ME	$RMSE$	rs	P	ME	$RMSE$
122b	0.56	< 0.001	-67.22	153.75	0.91 §	< 0.001	-0.92	113.44	0.94 §	< 0.001	-28.05	440.36	0.74	< 0.001	-12.16	110.83
127a	0.56	< 0.001	-0.42	326.86	0.94 §	< 0.001	0.77 †	112.10	0.95 §	< 0.001	-0.47	289.52	0.51	< 0.001	-0.91	100.42
136a	0.54	< 0.001	0.00	442.96	0.84	< 0.001	0.59 †	56.48	0.85	< 0.001	-0.72	116.26	-0.06	0.60	-1.85	92.779
140a	0.40	0.38	-28.21	378.02	-0.43	0.34	-4.02	87.91	-0.43	0.34	-0.67	50.89	0.00	0.99	-0.45	107.21
148a	0.71	< 0.001	-5.90	155.28	0.93 §	< 0.001	0.18 †	103.32	0.94 §	< 0.001	-11.33	400.33	0.84	< 0.001	-2.65	105.49
152a	0.44	< 0.001	-3.37	146.22	0.91 §	< 0.001	-0.05	96.97	0.94 §	< 0.001	-20.00	433.34	0.82	< 0.001	-3.44	98.62
132a	0.62	< 0.001	-7.41	200.26	0.94 §	< 0.001	0.47 †	102.42	0.93 §	< 0.001	-5.39	357.05	0.65	< 0.001	-1.97	113.91
133a	0.63	< 0.001	-5.81	189.49	0.80	< 0.001	0.03 †	96.39	0.78	< 0.001	-8.35	299.69	0.53	< 0.001	-5.11	118.71
139a	0.64	< 0.001	-27.16	200.83	0.91 §	< 0.001	-0.08	111.74	0.92 §	< 0.001	-11.83	386.02	0.84	< 0.001	-3.50	106.98
144a	0.67	< 0.001	-31.82	194.54	0.91 §	< 0.001	-1.37	116.85	0.93 §	< 0.001	-24.87	386.34	0.70	< 0.001	-5.14	110.91
146a	0.08	0.52	-4.89	274.97	0.69	< 0.001	0.32 †	41.38	0.69	< 0.001	-2.01	87.21	-0.30	0.02	-0.44	30.44
151a	0.69	< 0.001	-8.97	202.85	0.89	< 0.001	-0.29	119.42	0.91 §	< 0.001	-11.07	365.41	0.79	< 0.001	-2.95	107.34
155a	0.30	0.02	-1.06	389.45	0.91 §	< 0.001	0.59 †	97.13	0.92 §	< 0.001	-0.88	207.27	-0.76	< 0.001	-0.64	89.42

Table 5. Principle component analysis of tag data.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Whale ID	0.01	-0.71	0.03	-0.69	0.13	0.04	0.02	0.01	0.00
Time of day	0.01	-0.69	0.19	0.70	-0.03	-0.04	-0.01	-0.01	0.00
Maximum dive depth	0.42	0.02	-0.01	0.03	0.32	0.09	-0.85	-0.01	0.78
Forage time	0.38	-0.08	-0.41	0.01	-0.38	-0.04	0.04	0.67	-
									0.29
Number of lunges	0.38	-0.09	-0.42	-0.01	-0.40	-0.05	0.03	-0.72	0.00
Travel time	0.40	0.05	0.05	0.07	0.57	0.09	0.42	-0.13	-
									0.55
Dive time	0.42	0.01	-0.12	0.06	0.25	0.05	0.31	0.16	0.78
Pre-dive surface time	0.32	0.08	0.51	-0.12	-0.16	-0.76	0.02	0.00	0.00
Post-dive surface time	0.30	0.07	0.58	-0.08	-0.40	0.63	0.06	0.00	0.00
Standard deviation	2.30	1.13	1.01	0.89	0.60	0.49	0.24	0.05	0.00
Proportion of variance	0.59	0.14	0.11	0.08	0.04	0.03	0.01	0.00	0.00
Cumulative proportion	0.59	0.73	0.85	0.93	0.97	0.99	1.00	1.00	1.00

Adherence of Data to Model Assumptions

Violations to model assumptions may have affected the optimal solutions presented above. Values of τ' used to predict optimal solutions were calculated assuming that humpbacks descend and ascend to target depths at 1.6 m s^{-1} and 1.45 m s^{-1} , respectively (Goldbogen et al. 2008). Assumed τ' was positively correlated with observed τ ($rs = 0.94$, $N = 2365$, $P < 0.001$) and the ME value was positive ($ME = 0.81$), suggesting that the use of τ' was satisfactory. However, the observed descent and ascent rates were lower than the rates used to calculate τ' (mean [median] $\pm$ SD = $1.18 [1.14] \pm 0.50 \text{ m s}^{-1}$ and $1.04 [1.08] \pm 0.33 \text{ m s}^{-1}$, respectively) and varied with depth (Fig. 2; AOV: $F_{38,2325} = 126.2$, $P < 0.001$; $F_{38,2326} = 17.58$, $P < 0.001$; respectively), suggesting that τ' may have been underestimated. When τ (which additionally includes search time between lunges) was used to derive optimal solutions, prediction accuracy improved for $t_Q^* + \tau$ and t_Q^* , but not for s_Q^* (i.e., these comparisons had higher ME and lower $RMSE$ values than those derived

348 using τ' , Table 2; $s_{\hat{Q}}^*$, s : $rs = 0.65$, $P < 0.001$, $ME = -1.21$, $RMSE = 222.85$; $t_{\hat{Q}}^* + \tau$, $t + \tau$:
 349 $rs = 0.96$, $P < 0.001$, $ME = 0.63$, $RMSE = 100.54$; and $t_{\hat{Q}}^*$, t : $rs = 0.68$, $P < 0.001$, $ME = -$
 350 1.64 ; $RMSE = 100.55$).

351
 352 **Figure 2: Descent (A) and ascent rates (B) of humpbacks traveling to target depth (i.e.,**
 353 **the depth at the first and last depth inflection during a foraging dive). Note, outliers**
 354 **are not included and each box is drawn with widths proportional to the square root of**
 355 **the number of observations in each group (R Core Team, 2013).**

356 The parameters used to represent whale physiology (Table 2) in the calculation of
 357 optimal predictions are best known approximations (hereafter referred to as K_0 , α_0 , $m_{\tau 0}$,
 358 and m_{i0}), but inaccuracies may have hindered model agreement with observed data.
 359 Holding all but one physiological value constant, optimal predictions of $s_{\hat{Q}}^*$, $t_{\hat{Q}}^* + \tau'$, and
 360 $t_{\hat{Q}}^*$ were derived for a number of plausible physiological parameter values (Appendix 2).
 361 Model agreement varied widely with the observed data when optimal predictions were
 362 derived using these values, with some values generating greater agreement between

363 observed and predicted behaviours than K_0 , α_0 , $m_{\tau 0}$, and m_{t0} (Fig. 3, Appendix 3). For
 364 example, m_{τ} values that were equivalent to the estimated basal metabolic rates (BMRs) of
 365 humpback whales and the BMR minus gliding costs (e.g., $m_{\tau 2}$: 1.07 L O₂ s⁻¹ and $m_{\tau 3}$: 0.77
 366 L O₂ s⁻¹, respectively) generated better agreement between s_Q^* , $t_Q^* + \tau'$, and t_Q^* with s , $t +$
 367 τ' , and t than $m_{\tau 0}$ (2.32 L O₂ s⁻¹, which was equivalent to the active metabolic rate (AMR)
 368 minus gliding costs). In addition, $t + \tau'$ and t were better predicted by the optimal models
 369 when K was set equivalent to 50% of K_0 (K_2 : 1008.87 L O₂), when α was derived using a
 370 smaller coefficient than α_0 (0.09 versus 0.75; α_2 : 0.002 s⁻¹), and when m_t was set
 371 equivalent to 3.7 times a humpback's estimated AMR (m_{t3} : 9.63 L O₂ s⁻¹) (Fig. 3,
 372 Appendix 3). Furthermore, the prediction accuracy of s_Q^* , $t_Q^* + \tau'$, and t_Q^* with s , $t + \tau'$, and
 373 t was better when these optimal predictions were derived using K_2 , α_2 , $m_{\tau 3}$, and m_{t3} than
 374 when they were derived using K_0 , α_0 , $m_{\tau 0}$, and m_{t0} (Table 2) (i.e., they had higher ME and
 375 lower RMSE values: $rs = 0.65$, $P < 0.001$, $ME = -0.28$, $RMSE = 169.33$; $rs = 0.95$, $P <$
 376 0.001 , $ME = 0.70$, $RMSE = 89.69$; and $rs = 0.83$, $P < 0.001$, $ME = -0.36$, $RMSE = 72.11$;
 377 respectively).
 378

379
 380 **Figure 3. Observed and predicted values of surfacing time, dive time, and foraging**
 381 **times of humpbacks as a function of maximum dive depth when $\hat{Q}$ was being**
 382 **maximized for a range of possible K values (A, B, and C; respectively), α values (D,**
 383 **E, and F; respectively), m_τ values (G, H, and I; respectively), and m_t values (J, K,**
 384 **and L; respectively). For each prediction, one parameter (K , α , m_τ , or m_t) was**
 385 **adjusted (Appendix 2); all other parameters were held constant according to their**
 386 **best known approximation (represented as K_0 , α_0 , $m_{\tau 0}$, or $m_{t 0}$; Table 2).**

387 The calculations of optimal models up to this point in this study have been derived
 388 assuming a constant value of K . However, K of each dive should vary depending on the
 389 amount of oxygen used the previous dive. Predicted values of s_Q^* , $t_Q^* + \tau'$, and t_Q^* were
 390 derived assuming that K of each dive was equivalent to the oxygen used the previous dive
 391 (i.e., $K_i = m_{\tau}\tau_{i-1} - m_{\tau}t_{i-1}$; Houston & Carbone 1992), where α , m_{τ} , and m_t were set
 392 equivalent to α_0 , $m_{\tau 0}$, and $m_{t 0}$ and α_2 , $m_{\tau 3}$, and $m_{t 3}$, respectively (Fig. 4; Appendix 2).
 393 Agreement of s_Q^* with s was not improved when predictions were derived assuming
 394 updated values of K with either set of physiological values (α_0 , $m_{\tau 0}$, and $m_{t 0}$: $rs = 0.13$, P
 395 < 0.001 , $ME = -45.63$, $RMSE = 1022.63$; α_2 , $m_{\tau 3}$, and $m_{t 3}$: $rs = 0.14$, $P < 0.001$, $ME = -$
 396 25.93 , $RMSE = 777.09$). However, agreement of $t_Q^* + \tau'$ with $t + \tau'$ and t_Q^* with t
 397 improved slightly when derived with both sets of physiological values (i.e., they had
 398 higher ME and lower $RMSE$ values; α_0 , $m_{\tau 0}$, and $m_{t 0}$: $rs = 0.87$, $P < 0.001$, $ME = 0.67$,
 399 $RMSE = 95.52$ and $rs = 0.96$, $P < 0.001$, $ME = 0.80$, $RMSE = 74.25$; α_2 , $m_{\tau 3}$, and $m_{t 3}$: $rs =$
 400 0.15 , $P < 0.001$, $ME = -1.38$, $RMSE = 95.52$ and $rs = 0.53$, $P < 0.001$, $ME = -0.44$, $RMSE$
 401 $= 74.25$; respectively).

402

403 **Figure 4: Observed and predicted values of surface time (A), dive time (B), and foraging**
 404 **time (C) of humpbacks as a function of maximum dive depth when efficiency is maximized**
 405 **and K for each dive was set equivalent to the oxygen used the previous dive (i.e.,**
 406 **$K_i = m_\tau \tau_{i-1} - m_t t_{i-1}$; Houston & Carbone 1992), where α , m_τ , and m_t were set to α_0 ,**
 407 **$m_{\tau 0}$, and $m_{t 0}$ and α_2 , $m_{\tau 3}$, and $m_{t 3}$.**

408 *Observed time proportions, net rate of energy gain, and efficiency*

409 The proportional amount of time whales spent surfacing, diving, traveling during a dive
410 cycle (i.e., surface time + dive time) as well observed π , $\hat{N}$, and $\hat{Q}$ were also examined as
411 a function of maximum dive depth as an additional assessment of humpback whale
412 foraging behaviour (Fig. 5). The proportion of time spent surfacing and diving during a
413 dive cycle varied by maximum dive depth (AOV: $F_{38,2326} = 9.63$, $P < 0.001$). These
414 variables generally increased and decreased, respectively with increasing depths (Fig. 5 A
415 and B), but were equivalent for dives with maximum depths deeper than 110 m (Tukey
416 multiple comparisons of means, $P > 0.05$). The proportion of time spent traveling was
417 equivalent for dives with maximum depths deeper than 10 m (mean [median] $\pm$ SD =
418 0.40 [0.40] $\pm$ 0.13, $N = 1984$; Tukey multiple comparisons of means, $P > 0.05$; Fig. 5 C).
419 The proportion of time spent traveling for dives shallower than 10 m was low (mean
420 [median] $\pm$ SD = 0.27 [0.28] $\pm$ 0.16, $N = 381$).

422 **Figure 5: The proportion of time spent diving (A), surfacing (B), traveling (C), and**
 423 **foraging (D), as well as the net rate of energetic gain (E) and energetic efficiency (F)**
 424 **for foraging dives of humpback whales against maximum dive depth. Note: outliers**
 425 **are not included and each box is drawn with widths proportional to the square root of**
 426 **the number of observations in each group (R Core Team, 2013).**

427 All three foraging currencies examined varied with maximum dive depths (Fig. 5 D - F;
 428 AOV: $F_{38,2326} = 21.51, P < 0.001$; $F_{38,2326} = 21.86 P < 0.001$; and $F_{38,2326} =$
 429 $24.32, P < 0.001$; respectively). The shallowest dives had the highest π , $\bar{N}$, and $\bar{Q}$,
 430 although these values generally decreased with increasing maximum dive depths up to
 431 120 m, 110 m, and 150 m, respectively; values for each of these currencies were the
 432 lowest and equivalent for dives deeper than these respective depths (Tukey multiple
 433 comparisons of means, $P > 0.05$). Finally, the observed values of π , $\bar{N}$, and $\bar{Q}$ were
 434 positively correlated with each other (e.g., $\pi, \bar{N}$; $rs > 98, P < 0.001$, for all comparisons).

435

436 **DISCUSSION**

437 The humpback whales observed in this study exhibited diving behaviours that were in
 438 agreement with many of the theoretical predictions of the OFT models. Shallow dives
 439 (i.e., < 100 m) were short, executed the most frequently (81.27%), and yielded the highest
 440 proportions of foraging time (π), the greatest net rates of energy gain ($\bar{N}$), and were the
 441 most energetically efficient ($\bar{Q}$) (Fig. 5. D, E, and F). In addition, dive ($t + \tau$) and foraging
 442 (t) times increased rapidly in duration with increasing maximum dive depths to
 443 approximately 100 m and then at lower rates with deeper dives (i.e., > 100 m; Fig. 1 B
 444 and C). Direct comparisons between optimal and observed behaviours, however, varied
 445 widely depending on the physiological (e.g., K) and behavioural (e.g., τ) values used to
 446 derived optimal predictions, highlighting the need for an improved understanding of
 447 cetacean physiology. This lack of knowledge hinders our ability to precisely assess
 448 whether these whales were foraging according to OFT models.

449

450 Our hypothesis that humpbacks would allocate their time during foraging dives to
 451 maximize the proportion of time spent foraging (π), the net rate of energy gain ($\bar{N}$),
 452 and/or energy efficiency ($\bar{Q}$) was difficult to assess because of the varied model
 453 agreement between observed and predicted values (Fig. 1, Table 3). This result, as well as
 454 our finding that the observed values calculated for these currencies were positively
 455 correlated to one another, supports the finding that the results of models are difficult to
 456 distinguish (Houston & Carbone, 1992), and suggests that any of the OFT models are
 457 suitable for comparison with the observed data. Here, we used optimal solutions derived
 458 for $\bar{Q}$ to compare with the observed data (Fig. 1, 3, and 4; Table 3, Appendix 3), but note
 459 that a more thorough analysis may be needed to determine which (if any) of these
 460 currencies are being maximized over others.

461

462 Surface times (s) were shorter than predicted by the OFT models derived using the best
 463 known approximations of humpback whale physiology (K_0 , α_0 , m_{t0} , and m_{i0}) for 98.94%
 464 of the foraging dives we observed and were increasingly shorter than their optimal
 465 solution (s_Q^*) with increasing maximum dive depths (Fig. 1 A). Doniol-Valcroze et al.
 466 (2011) also found that blue whales had shorter recovery times following long dives than
 467 predicted and suggested that this may be a consequence of the oxygen replenishment rate
 468 (α) used to derive the optimal solutions not being a realistic measure of oxygen exchange
 469 in large whales. Solutions for s_Q^* with these OFT models are known to be sensitive to α
 470 (Houston & Carbone, 1992; Stephens et al., 2008). Indeed, in this study the best
 471 agreement between s_Q^* and s was found when s_Q^* was derived using a value of α that was
 472 approximately 2.67 times larger than α_0 (i.e., $\alpha_4 = 0.008 \text{ s}^{-1}$: $rs = 0.65$, $ME = 0.31$, $RMSE$

473 = 134.01; Fig. 3, Appendix 3). Predictions of $s_{\tilde{Q}}^*$ also varied depending on K , with $s_{\tilde{Q}}^*$
 474 increasing with lower values of K . Interestingly, some of the extreme values of s (i.e., >
 475 750 s, $N = 13$) we observed matched well with $s_{\tilde{Q}}^*$ derived using K_1 and K_2 (25% of K_0
 476 and 50% of K_0 , respectively; $N = 2$ and $N = 8$ of these s were within 180 s of $s_{\tilde{Q}}^*$;
 477 respectively), suggesting that these long periods of surfacing may have been the result of
 478 diminished oxygen stores.
 479
 480 Dive times ($t + \tau$) were predicted well by the OFT models (Fig. 1 B; Fig. 3 B, E, H, and
 481 K; Fig. 4 B; Table 3; and Appendix 3): shallow dives were short while deeper dives were
 482 longer and closer to the DLT (Houston & Carbone, 1992). This finding supports the
 483 prediction that animals, while physiologically capable, should dive for much shorter
 484 durations than DLT at shallow depths (Kramer, 1988). Indeed, π , $\tilde{N}$, and $\tilde{Q}$ were highest
 485 for shallow dives (Fig. 5 D - F), suggesting that humpbacks were diving for short
 486 durations at these shallow depths because it was optimal to do so, consistent with
 487 observations of blue whales (Doniol-Valcroze et al., 2011). Ware et al. (2011) described
 488 short and shallow looping dives executed by some of the tagged humpbacks presumably
 489 exploiting krill patches near the surface. By incorporating breathing into the lunge cycle,
 490 whales almost eliminated the need for surface time and instead could feed at a high and
 491 consistent rate (Ware et al., 2011). In addition, many lunges on these shallow dives
 492 occurred shortly before the whale surfaced, presumably allowing these animals to
 493 combine the time required for breathing with prey handling time (i.e., processing time).
 494 Strategies like these further enable these animals to maximize their foraging effort during
 495 these foraging dives.

496

497 The OFT prediction that foraging durations (t) should first increase then decrease with
498 increasing dive depth (Houston & Carbone, 1992) was not fully supported by the
499 observed data (Fig. 1 A, Table 3). However, a more asymptotic response for t with
500 increasing dive depth was found for t_Q^* when it was derived using m_{t2} and m_{t3} (which are
501 estimated to be a humpback whales BMR; Appendix 2). This OFT result more closely
502 agreed with t (Fig.3, Appendix 3) and was supported by our finding that π , $\bar{N}$, and $\bar{Q}$
503 were equivalent for deep dives (i.e., > 120 m, 110 m and 150 m, respectively; Fig. 5 D-
504 F). Regardless of model agreement, long foraging durations at depth may be the result of
505 tagged humpback whales exploiting krill patches that increased in density with increasing
506 water depth in this region (Friedlaender et al. In Review). Blue whales have been found
507 to maximize energy intake over oxygen balance when prey density is high, and oxygen
508 balance over energy intake when prey density is low (Hazen et al. 2015). The humpbacks
509 tagged in this study may have been behaving similarly, as they were spatially and
510 temporally correlated with super-aggregations of Antarctic krill (Espinasse et al., 2012;
511 Nowacek et al., 2011). The finding that the tagged humpback whales were maximizing
512 energy intake over oxygen balance would support our finding that s was shorter than s_Q^*
513 for 98.94% of the foraging dives we observed (Fig. 1 C) and may contribute to the
514 finding that humpbacks in this region exhibit extreme diel behaviours (Friedlaender et al.
515 2013). Humpbacks foraging along the WAP feed at night when krill are near the surface
516 and rest during the day when krill are deep (Friedlaender et al. 2013). While the daily
517 resting behaviours observed in these whales may be related to processing ingested food
518 from the previous night (Friedlaender et al. 2013), they may also be related to the demand

519 associated with replenishing oxygen stores depleted during their nightly foraging bout. A
 520 more detailed analysis on the accuracy of humpback whale physiology as well as the
 521 density (and energetic quality) of exploited krill patches is needed to fully assess this
 522 hypothesis.
 523
 524 Prediction accuracy of the OFT models may have been affected by our prediction of
 525 travel time (τ'). We assumed that τ' would vary between the descending and ascending
 526 portions of a dive and derived it using previously reported estimates of humpback whale
 527 descent and ascent rates (Goldbogen et al., 2008). Interestingly, while the observed
 528 descent and ascent rates were lower than those used to derive τ' and varied by depth (Fig.
 529 2), prediction accuracy only improved for $t + \tau$ when observed tau (τ) was used to derive
 530 optimal solutions in place of τ' . This may be because τ also included time spent searching
 531 for prey between lunges at depth, which increased $t + \tau$; τ' did not consider search time at
 532 depth. Houston and Carbone (1992) discussed how searching complicates the OFT
 533 models and many studies use bottom time (e.g., time spent at target depth not including
 534 time spent vertically transiting) instead as a proxy for t (Doniol-Valcroze et al., 2011;
 535 Elliott et al., 2008; Heaslip et al., 2014; e.g., Heath et al., 2007). The use of τ' may be
 536 better suited for deriving optimal solutions to compare with bottom times than with more
 537 defined estimates of foraging time (e.g., lunge duration) because bottom time should
 538 include search time between feeding events. However, in our study, t more closely
 539 matched t_Q^* than bottom time whether τ' or τ were used to derive t^* (bottom time versus
 540 t_Q^* : $rs = 0.81$, $P < 0.001$, $ME = -3.05$, $RMSE = 190.97$; data not shown). This may be a
 541 result of bottom time not including time spent lunging while descending to or ascending

542 from maximum depth, a behaviour frequently observed by the tagged whales. The
543 proliferation of technology and methods for determining discrete feeding events, such as
544 those used in this study, will enable more studies to more accurately define t and may
545 warrant the development of OFT models that more explicitly consider the act of
546 searching during a dive cycle and its effect on the optimal solutions. In addition, models
547 that can incorporate changes in ascent and descent rates as well as their respective change
548 in metabolic rate may significantly enhance the predictive capacity and value of OFT
549 models (Houston & Carbone, 1992).

550

551 Our sensitivity analysis of physiological parameters reveals how dependent the OFT
552 model predictions are on the accuracy of K , α , m_r , and m_t (Fig. 3, Appendix 3; Houston &
553 Carbone 1992). Unfortunately, the physiology of humpbacks is poorly understood and is
554 estimated primarily from relationships based on crude estimates of body mass (Leaper &
555 Lavigne, 2001). The most significant advances have been made in regard to the energetic
556 cost of lunging (e.g., Goldbogen et al., 2010); however, m_t has not been directly
557 measured in Balaenopterids and has not been simulated for humpback whales (Potvin et
558 al. 2012). In addition, simulations for blue, fin, and minke whales reveal that m_t likely
559 varies over the duration of a lunge (Goldbogen et al., 2010; Potvin et al., 2009, 2012).

560 The OFT models used in this study assumed a constant m_t , which may be too simplistic to
561 accurately predict t^* . Further, the true size of the whales examined in this study was
562 unknown, which restricted the model predictions to be generalized to that of an average
563 sized adult humpback whale. Body size can influence metabolic rates (Goldbogen et al.,
564 2010; Potvin et al., 2009, 2012) and oxygen storage capabilities (Halsey, Butler, &

565 Blackburn, 2006; Stephens et al., 2008; Tenney & Remmers, 1964), and therefore may
 566 have influenced the agreement between predicted and observed behaviours reported in
 567 this study for individual whales (Table 4). We agree with Stephens et al. (2008) that
 568 future research should work towards obtaining more realistic measures of physiology in
 569 diving predators.
 570
 571 Typically OFT models have been computed assuming K for each dive is constant and
 572 equivalent to the total oxygen storage capacity (e.g., Doniol-Valcroze et al., 2011; Hazen
 573 et al., 2015; Heaslip et al., 2014). However, the amount of oxygen available for each dive
 574 will be dependent on the amount of oxygen stores used during the previous dive and
 575 gained prior to that dive (Kramer, 1988; Houston & Carbone, 1992). Oxygen
 576 replenishment rates (and s^*) will respectively vary with the available oxygen stores: α
 577 should be high when oxygen levels are very low (often a result of long dives) and slow
 578 when oxygen levels are closer to normal (often a result of short dives). When K was
 579 updated for each dive based on a more precise estimate of oxygen stores used on the
 580 previous dive and gained before that dive, greater agreement was found between $t_Q^* + \tau'$
 581 with $t + \tau'$ and t_Q^* with t regardless of the physiological parameters we used (Fig. 4). This
 582 suggests that OFT predictions may be improved if they incorporate fluctuations in K
 583 related to behavior (e.g., long or short duration dives). It is clear that these predictions,
 584 again, may be biased to an unknown degree if the physiological parameters used to
 585 generate them are inaccurate, but this analysis highlights the importance of considering
 586 more complex OFT models that incorporate fluctuations in physiology over time.
 587

588 The behaviours observed in this study did not conform to many of the OFT model
589 predictions, but they do support many of the theoretical predictions of OFT and suggest
590 that these animals were maximizing π , $\bar{N}$, and/or $\bar{Q}$ during foraging dives. We agree with
591 Halsey et al. (2006) and Heaslip et al. (2014) that current OFT models are too simplistic
592 to predict the foraging behaviours of large air-breathing marine predators diving animals
593 such as humpback whales, and we stress the importance of developing models capable of
594 incorporating more complex behaviour (e.g., searching) and multiple temporal scales
595 (e.g., Austin, Don Bowen, McMilan, & Iverson, 2006; Fortin, Fryxell, & Pilote, 2002;
596 McNamara & Houston, 2007). We further (and perhaps more strongly) suggest that
597 additional physiological studies are needed to verify the accuracy of physiological
598 parameters used to predict optimal behaviours in these and other animals and how they
599 may vary during the different behaviours exhibited during a dive cycle (e.g., travel
600 velocities, lunging), under different environmental conditions (e.g., depth, temperature),
601 and amongst animals with different life histories (e.g., animal size, age, sex) and feeding
602 strategies (e.g., bulk feeding, targeting individual prey). In addition, future work should
603 include an examination of how the maximization of π , $\bar{N}$, and/or $\bar{Q}$ varies with prey patch
604 structure and quality (e.g., Friedlaender et al., In Review). Humpbacks foraging along the
605 WAP during the tagging period were able to take advantage of a temporally and spatially
606 stable dense krill aggregation (Espinasse et al., 2012; Nowacek et al., 2011), but
607 humpbacks and other diving animals foraging in regions with more patchily distributed
608 prey may demonstrate different behaviours in an attempt to maximize these currencies.
609 Such a comparison would provide a more thorough understanding of foraging behaviours
610 in these and other large, air-breathing diving predators.

611 **REFERENCES**

- 612 Acevedo-Gutiérrez, A., Croll, D. A., & Tershy, B. R. (2002). High feeding costs limit
613 dive time in the largest whales. *Journal of Experimental Biology*, 205(12), 1747-
614 1753.
- 615 Austin, D., Don Bowen, W., McMilan, J. I., & Iverson, S. J. (2006). Linking movement,
616 diving, and habitat to foraging success in a large marine predator. *Ecology*, 87,
617 3095-3108.
- 618 Butler, P. J. (2006). Aerobic dive limit. What is it and is it always used appropriately?
619 *Comparative Biochemistry and Physiology a-Molecular & Integrative*
620 *Physiology*, 145(1), 1-6. doi: 10.1016/j.cbpa.2006.06.006
- 621 Butler, P. J., & Jones, D. R. (1997). Physiology of diving of birds and mammals.
622 *Physiological Reviews*, 77(3), 837-899.
- 623 Carbone, C., & Houston, A. I. (1994). Patterns in the diving behaviour of the pochard,
624 *Aythya ferina*: a test of an optimality model. *Animal Behaviour*, 48(457-465).
- 625 Carbone, C., & Houston, A. I. (1996). The optimal allocation of time over the dive cycle:
626 an approach based on aerobic and anaerobic respiration. *Animal Behaviour*, 51(6),
627 1247-1255.
- 628 Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd Edition ed.).
629 Hillsdale, NJ, USA: Lawrence Erlbaum Associates, Inc.
- 630 Dolphin, W. F. (1988). Foraging dive patterns of humpback whales, *Megaptera*
631 *novaeangliae*, in Southeast Alaska - a cost-benefit analysis. *Canadian Journal of*
632 *Zoology-Revue Canadienne De Zoologie*, 66(11), 2432-2441.

633 Doniol-Valcroze, T., Lesage, V., Giard, J., & Michaud, R. (2011). Optimal foraging
 634 theory predicts diving and feeding strategies of the largest marine predator.
 635 *Behavioral Ecology*, 22(4), 880-888. doi: 10.1093/beheco/arr038
 636 Elliott, K. H., Davoren, G. K., & Gaston, A. J. (2008). Time allocation by a deep-diving
 637 bird reflects prey type and energy gain. *Animal Behaviour*, 75, 1301-1310.
 638 Espinasse, B., Zhou, M., Zhu, Y., Hazen, E. L., Friedlaender, A. S., Nowacek, D. P., . . .
 639 Carlotti, F. (2012). Austral fall-winter transition of mesozooplankton assemblages
 640 and krill aggregations in an embayment west of the Antarctic Peninsula. *Marine*
 641 *Ecology Progress Series*, 452, 63-80.
 642 Fortin, D., Fryxell, J. M., & Pilote, R. (2002). The temporal scale of foraging decisions in
 643 bison. *Ecology*, 83, 970-982.
 644 Friedlaender, A. S., Johnston, D., Tyson, R. B., Katlenberg, A., Goldbogen, J. A.,
 645 Stimpert, A. K., . . . Nowacek, D. P. (In Review). Two-step decisions in a central-
 646 place forager. *Royal Society Open Science*.
 647 Friedlaender, A. S., Tyson, R. B., Stimpert, A. K., Read, A. J., & Nowacek, D. P. (2013).
 648 Extreme diel variation in the feeding behavior of humpback whales along the
 649 western Antarctic Peninsula during autumn. *Marine Ecology Progress Series*,
 650 494, 281-289. doi: 10.3354/meps10541
 651 Goldbogen, J. A., Calambokidis, J., Croll, D. A., Harvey, J. T., Newton, K. M., Oleson,
 652 E. M., . . . Shadwick, R. E. (2008). Foraging behavior of humpback whales:
 653 kinematic and respiratory patterns suggest a high cost for a lunge. *Journal of*
 654 *Experimental Biology*, 211(23), 3712-3719. doi: Doi 10.1242/Jeb.023366

655 Goldbogen, J. A., Calambokidis, J., Shadwick, R. E., Oleson, E. M., McDonald, M. A., &
656 Hildebrand, J. A. (2006). Kinematics of foraging dives and lunge-feeding in fin
657 whales. *Journal of Experimental Biology*, 209(7), 1231-1244. doi:
658 10.1242/Jeb.02135

659 Goldbogen, J. A., Potvin, J., & Shadwick, R. E. (2010). Skull and buccal cavity allometry
660 increase mass-specific engulfment capacity in fin whales. *Proceedings of*
661 *Biological Science*, 277(1683), 861-868. doi: 10.1098/rspb.2009.1680

662 Goldbogen, J. A., Pyenson, N. D., & Shadwick, R. E. (2007). Big gulps require high drag
663 for fin whale lunge feeding. *Marine Ecology-Progress Series*, 349, 289-301. doi:
664 10.3354/Meps07066

665 Guillemette, M., Woakes, A. J., Henaux, V., Grandbois, J.-M., & Butler, P. J. (2004). The
666 effect of depth on the diving behaviour of common eiders. *Canadian Journal of*
667 *Zoology*, 82(11), 1818-1826.

668 Guisan, A., & Zimmerman, N. E. (2000). Predictive habitat distribution models in
669 ecology. *Ecological Modelling*, 135, 147-186.

670 Halsey, L. G., Butler, P. J., & Blackburn, T. M. (2006). A phylogenetic analysis of the
671 allometry of diving. *American Naturalist*, 167(2), 276-287.

672 Halsey, L. G., Woakes, A. J., & Butler, P. J. (2003). Testing optimal foraging models for
673 air-breathing divers. *Animal Behaviour*, 65, 641-653.

674 Hazen, E. L., Friedlaender, A. S., & Goldbogen, J. A. (2015). Optimal foraging strategies
675 minimize oxygen use and maximize energy gain across a prey density gradient in
676 the blue whale (*Balaenoptera musculus*). *Science Advances*.

677 Hazen, E. L., Friedlaender, A. S., Thompson, M. A., Ware, C. R., Weinrich, M. T.,
 678 Halpin, P. N., & Wiley, D. N. (2009). Fine-scale prey aggregations and foraging
 679 ecology of humpback whales *Megaptera novaeangliae*. *Marine Ecology-Progress*
 680 *Series*, 395, 75-89. doi: 10.3354/Meps08108

681 Heaslip, S. G., Bowen, D., & Iverson, S. J. (2014). Testing predictions of optimal diving
 682 theory using animal-borne video from harbour seals (*Phoca vitulina concolor*).
 683 *Canadian Journal of Zoology*, 92(4), 309-318. doi: 10.1139/cjz-2013-0137

684 Heath, J. P., Gilchrist, H. G., & Ydenberg, R. C. (2007). Can dive cycle models predict
 685 patterns of foraging behaviour? Diving by common eiders in an Arctic polynya.
 686 *Animal Behaviour*, 73, 877-884.

687 Houston, A. I. (2011). Assessing models of optimal diving. *Trends in Ecology &*
 688 *Evolution*, 26(6), 292-297.

689 Houston, A. I., & Carbone, C. (1992). The Optimal Allocation of Time during the Diving
 690 Cycle. *Behavioral Ecology*, 3(3), 255-265.

691 Houston, A. I., & McNamara, J. M. (1985). A General Theory of Central Place Foraging
 692 for Single-Prey Loaders. *Theoretical Population Biology*, 28(3), 233-262.

693 Johnson, M. P., & Tyack, P. L. (2003). A digital acoustic recording tag for measuring the
 694 response of wild marine mammals to sound. *IEEE Journal of Oceanic*
 695 *Engineering*, 28(1), 3-12. doi: 10.1109/Joe.2002.808212

696 Kooyman, G. L., & Ponganis, P. J. (1998). The physiological basis of diving to depth:
 697 birds and mammals. *Annual Review of Physiology*, 60, 19-32.

698 Kramer, D. L. (1988). The Behavioral Ecology of Air Breathing by Aquatic Animals.
 699 *Canadian Journal of Zoology*, 66(1), 89-94.

700 Leaper, R., & Lavigne, D. (2001). Scaling prey consumption to body mass in cetaceans.
 701 *Paper SC/J02/FW2 presented to the IWC Scientific Committee.*

702 Loague, K., & Green, J. A. (1991). Statistical and graphical methods for evaluating solute
 703 transport models: Overview and application. *Journal of Contaminant Hydrology*,
 704 7(1-2), 51-73.

705 Lockyer, C. (1976). Body Weights of Some Species of Large Whales. *Journal Du*
 706 *Conseil*, 36(3), 259-273.

707 Macarthur, R. H., & Pianka, E. R. (1966). On Optimal Use of a Patchy Environment.
 708 *American Naturalist*, 100(916), 603-609.

709 Mayer, D. G., & Butler, D. G. (1993). Statistical Validation. *Ecological Modelling*, 68(1-
 710 2), 21-32.

711 McNamara, J. M., & Houston, A. I. (2007). Optimal annual routines: behaviour in the
 712 context of physiology and ecology. *Philosophical Transactions of the Royal*
 713 *Society B*, 363, 301-319.

714 Nowacek, D. P., Friedlaender, A. S., Halpin, P. N., Hazen, E. L., Johnston, D. W., Read,
 715 A. J., . . . Zhu, Y. (2011). Super-aggregations of krill and humpback whales in
 716 Wilhelmina Bay, Antarctic Peninsula. *PLoS One*, 6(4), e19173. doi:
 717 10.1371/journal.pone.0019173

718 Nowacek, D. P., Johnson, M. P., & Tyack, P. L. (2004). North Atlantic right whales
 719 (*Eubalaena glacialis*) ignore ships but respond to alerting stimuli. *Proceedings of*
 720 *the Royal Society of London Series B-Biological Sciences*, 271(1536), 227-231.
 721 doi: 10.1098/rspb.2003.2570

722 Orians, G. H., Pearson, N. E., Horn, D. J., Mitchell, D. R., & Stairs, G. R. (1979). On the
 723 theory of central place foraging *Analysis of ecological systems* (pp. 155).
 724 Columbus, Ohio: Ohio State University Press.

725 Pearson, K. (1901). On Lines and Planes of Closest Fit to Systems of Points in Space.
 726 *Philosophical Magazine*, 11, 559-572.

727 Potvin, J., Goldbogen, J. A., & Shadwick, R. E. (2009). Passive versus active engulfment:
 728 verdict from trajectory simulations of lunge-feeding fin whales *Balaenoptera*
 729 *physalus*. *J R Soc Interface*, 6(40), 1005-1025. doi: 10.1098/rsif.2008.0492

730 Potvin, J., Goldbogen, J. A., & Shadwick, R. E. (2012). Metabolic expenditures of lunge
 731 feeding rorquals across scale: implications for the evolution of filter feeding and
 732 the limits to maximum body size. *PLoS One*, 7(9), e44854. doi:
 733 10.1371/journal.pone.0044854

734 R Core Team. (2013). R: a language and environment for statistical computing Vienna,
 735 Austria. Retrieved from <http://www.R-Project.Org>

736 Simon, M., Johnson, M., & Madsen, P. T. (2012). Keeping momentum with a mouthful
 737 of water: behavior and kinematics of humpback whale lunge feeding. *Journal of*
 738 *Experimental Biology*, 215, 3786-3798. doi: 10.1242/jeb.071092

739 Smith, E. P., & Rose, K. A. (1995). Model Goodness-of-Fit Analysis Using Regression
 740 and Related Techniques. *Ecological Modelling*, 77(1), 49-64.

741 Stephens, P. A., Carbone, C., Boyd, I. L., McNamara, J. M., Harding, K. C., & Houston,
 742 A. I. (2008). The scaling of diving time budgets: Insights from an optimality
 743 approach. *American Naturalist*, 171(3), 305-314. doi: 10.1086/527491

744 Tenney, S. M., & Remmers, J. E. (1964). Comparative quantitative morphology of the
 745 mammalian lung: diffusing area. *Nature*, 5(197), 54-56.

746 Tyson, R. B., Friedlaender, A. S., Stimpert, A. K., Ware, C., & Nowacek, D. P. (2012).
 747 Synchronous mother and calf foraging behaviour in humpback whales *Megaptera*
 748 *novaeangliae*: insights from multi-sensor suction cup tags. *Marine Ecology*
 749 *Progress Series*, 457, 209-220.

750 Ware, C., Arsenault, R., & Plumlee, M. (2006). Visualizing the underwater behavior of
 751 humpback whales. *IEEE Computer Graphics and Applications*, 26(4), 14-18.

752 Ware, C., Friedlaender, A. S., & Nowacek, D. P. (2011). Shallow and deep lunge feeding
 753 of humpback whales in fjords of the West Antarctic Peninsula. *Marine Mammal*
 754 *Science*, 27(3), 587-605. doi: 10.1111/j.1748-7692.2010.00427.x

755 Williams, T. M. (2001). Intermittent swimming by mammals: A strategy for increasing
 756 energetic efficiency during diving. *American Zoologist*, 41(2), 166-176.

757

758 APPENDIX 1: Description of acronyms and symbols used throughout the paper (in order
759 of appearance).

Symbol	Description
OFT	Optimal foraging theory
WAP	Western Antarctic Peninsula
DTAG	Digital acoustic recording tag
s	Observed surface time
t	Observed foraging time
τ	Observed travel time
K	Oxygen stores that can be obtained
α	Initial proportional rate of oxygen replenishment
m_τ	Metabolic rate during traveling
m_t	Metabolic rate during foraging
π	Proportion of time spent foraging during a dive cycle
s^*	Optimal surface time
$\bar{N}$	Net rate of energetic gain
$\bar{Q}$	Ratio of energy gained to energy expended (i.e., Energetic efficiency)
$g(t)$	Cumulative gross gain while foraging
Y	Converts units of oxygen to appropriate units of energy
M_s	Metabolic rate during surfacing
t^*	Optimal forage time
τ'	Predicted travel time
$t^* + \tau'$	Optimal dive time
DLT	Dive lactate threshold
$X(s)$	Rate of change in oxygen stores
y_i	Observed data
$\hat{y}_i$	Predicted data
$RMSE$	Root mean squared error
ME	Model efficiency
$\bar{y}_i$	Mean of observed data
t_π^*	Optimal foraging time when the proportion of time foraging is maximized
$t_{\bar{N}}^*$	Optimal foraging time when the net rate of energetic gain is maximized
$t_{\bar{Q}}^*$	Optimal foraging time when efficiency is maximized
$t + \tau$	Observed dive time
$t_\pi^* + \tau'$	Optimal dive time when the proportion of time foraging is maximized

$t_N^* + \tau'$	Optimal dive time when the net rate of energetic gain is maximized
$t_Q^* + \tau'$	Optimal dive time when efficiency is maximized
s_π^*	Optimal surface time when the proportion of time foraging is maximized
s_N^*	Optimal surface time when the net rate of energetic gain is maximized
s_Q^*	Optimal surface time when the energetic efficiency is maximized

760

761

762 APPENDIX 2: Descriptions, equations, and values of parameters used in the sensitivity analysis of the OFT models (Figure 4). K_0 ,
763 α_0 , m_{t0} , or $m_{\tau0}$ are the best known approximations of each physiological variable (Table 2). M represents body mass, with values
764 calculated assuming the mass of a 14 m length humpback whale (39614.16 kg).

Parameter ID	Description (units)	Equation	Value	Reference
K_0	Total oxygen storage capacity (L O ₂)	$0.03 \times M^{1.05}$	2017.74	Stephens et al. (2008)
K_1	25% of K_0 (L O ₂)	$0.03 \times M^{1.05} \times 0.25$	504.43	
K_2	50% of K_0 (L O ₂)	$0.03 \times M^{1.05} \times 0.5$	1008.87	
K_3	75% of K_0 (L O ₂)	$0.03 \times M^{1.05} \times 0.75$	1513.30	
K_4	125% of K_0 (L O ₂)	$0.03 \times M^{1.05} \times 1.25$	2533.17	
K_5	200% of K_0 (L O ₂)	$0.03 \times M^{1.05} \times 2.00$	4035.47	
α_0	Rate of oxygen replenishment assuming oxygen uptake is limited by the surface area available for gaseous exchange (s ⁻¹)	$0.09 \times M^{0.33}$	0.003	Stephens et al. (2008), Doniol-Valcroze et al. (2011)
α_1	Rate of oxygen replenishment assuming oxygen uptake scales with the same exponent as metabolism (symmorphosis) (s ⁻¹)	$0.09 \times M^{0.25}$	0.006	Stephens et al. (2008); Weibel et. al.
α_2	Surface area argument of α_0 with plausible constant value (s ⁻¹)	$0.075 \times M^{0.33}$	0.002	Stephens et al. (2008)
α_3	Symmorphosis argument of α_1 with plausible constant value (s ⁻¹)	$0.075 \times M^{0.25}$	0.005	Stephens et al. (2008)
α_4	Surface area argument of α_0 with	$0.25 \times M^{0.33}$	0.008	

	extreme constant value (s^{-1})			
α_5	Symmorphosis argument of α_I with extreme constant value (s^{-1})	$0.25 \times M^{0.25}$	0.018	
m_{t0}	Active metabolic rate (AMR) minus the cost of gliding ($L O_2 s^{-1}$)	$6 \times 4 \times M^{0.75} - (6 \times 4 \times M^{0.75} \times 0.28)$	2.32	Potvin et al. (2012); Williams (2001)
m_{t1}	AMR ($L O_2 s^{-1}$)	$6 \times 4 \times M^{0.75}$	3.21	Costa & Williams (1999); Croll, Kudela, & Tershy (2006)
m_{t2}	Basal metabolic rate (BMR) ($L O_2 s^{-1}$)	$2 \times 4 \times M^{0.75}$	1.07	Klieber (1975); Klieber & Rogers (1975)
m_{t3}	BMR minus the cost of gliding ($L O_2 s^{-1}$)	$2 \times 4 \times M^{0.75} - (2 \times 4 \times M^{0.75} \times 0.28)$	0.77	
m_{t0}	Active metabolic rate (AMR) minus the cost of gliding x 1.78 ($L O_2 s^{-1}$)	$6 \times 4 \times M^{0.75} - (6 \times 4 \times M^{0.75} \times 0.28) \times 1.78$	4.14	Doniol-Valcroze et al. (2011), Goldbogen et al. (2010), Potvin et al. (2009)
m_{t1}	AMR ($L O_2 s^{-1}$)	$6 \times 4 \times M^{0.75}$	3.21	Potvin et al. (2012)
m_{t2}	AMR x 1.78 ($L O_2 s^{-1}$)	$6 \times 4 \times M^{0.75} \times 1.78$	5.71	Doniol-Valcroze et al. (2011)
m_{t3}	AMR x 3.7 ($L O_2 s^{-1}$)	$6 \times 4 \times M^{0.75} \times 3.7$	11.91	Potvin et al. (2012)
m_{t4}	AMR x 4 ($L O_2 s^{-1}$)	$6 \times 4 \times M^{0.75} \times 4$	12.84	Boyd & Croxall 1996, Croll et al. 2001

APPENDIX 3: Pearson's product moment correlation coefficients (r_s), model efficiencies (ME), and root mean squared errors (RMSE) for observed surface times (s), dive times ($t + \tau$), and foraging times (t) against predicted optimal surface times (s_Q^*), dive times ($t_Q^* + \tau'$), and foraging times (t_Q^*) assuming that energetic efficiency is being maximized for a range of possible physiological parameter values. For each prediction, one parameter (K , α , m_τ , or m_t) was adjusted (Appendix 1); all other parameters were held constant according to their best known approximation (represented as K_0 , α_0 , $m_{\tau 0}$, or $m_{t 0}$; Table 2). Strongly positively correlated coefficients ($r > 0.9$; Cohen, 1988) are indicated with § . Model efficiencies greater than 0 are indicated with ‡ . All Pearson's product moment correlations were significant ($P < 0.001$). Result derived using the best known approximations of humpback whale physiology are included in the first row for reference. Results that provided greater agreement with the observed values than those derived using best known approximations for at least two of the three statistical comparisons (r_s , ME , $RMSE$) are denoted in light grey; results with the best agreement for each parameter are denoted in dark grey.

Parameter IDs	s_Q^*, s			$t_Q^* + \tau', t + \tau$			t_Q^*, t		
	r_s	ME	$RMSE$	r_s	ME	$RMSE$	r_s	ME	$RMSE$
$K_0, \alpha_0, m_{\tau 0}, m_{t 0}$	0.66	-0.94	208.82	0.95 §	0.60 ‡	105.51	0.74	-1.87	104.88
$K_1, \alpha_0, m_{\tau 0}, m_{t 0}$	0.65	-20.49	694.14	0.96 §	0.54 ‡	112.35	-0.56	-1.34	95.66
$K_2, \alpha_0, m_{\tau 0}, m_{t 0}$	0.68	-5.65	386.09	0.96 §	0.77 ‡	80.06	0.08	-0.10	65.02
$K_3, \alpha_0, m_{\tau 0}, m_{t 0}$	0.67	-1.69	245.72	0.96 §	0.76 ‡	81.04	0.60	-0.42	73.75
$K_4, \alpha_0, m_{\tau 0}, m_{t 0}$	0.65	-0.62	190.73	0.95 §	0.29 ‡	140.24	0.83	-17.68	267.57
$K_5, \alpha_0, m_{\tau 0}, m_{t 0}$	0.64	-0.25	167.99	0.95 §	-1.46	260.61	0.74	-1.87	104.88
$K_0, \alpha_1, m_{\tau 0}, m_{t 0}$	0.65	0.28 ‡	127.17	0.95 §	0.34 ‡	134.71	0.70	-3.81	135.84
$K_0, \alpha_2, m_{\tau 0}, m_{t 0}$	0.66	-1.74	247.77	0.95 §	0.63 ‡	100.86	0.75	-1.60	99.82
$K_0, \alpha_3, m_{\tau 0}, m_{t 0}$	0.65	0.20 ‡	134.01	0.95 §	0.41 ‡	137.37	0.71	-3.29	128.16
$K_0, \alpha_4, m_{\tau 0}, m_{t 0}$	0.65	0.31 ‡	124.10	0.94 §	0.27 ‡	142.27	0.68	-4.39	143.69

$K_0, \alpha_5, m_{\tau 0}, m_{t0}$	0.64	$0.23^{\ddagger}$	131.47	$0.93^{\S}$	-0.24	184.65	0.59	-8.13	187.09
$K_0, \alpha_0, m_{\tau 1}, m_{t0}$	0.67	-2.18	267.10	$0.94^{\S}$	$0.50^{\ddagger}$	117.94	0.54	-2.54	116.56
$K_0, \alpha_0, m_{\tau 2}, m_{t0}$	0.64	$0.11^{\ddagger}$	141.10	$0.96^{\S}$	$0.78^{\ddagger}$	77.30	0.84	-0.48	75.36
$K_0, \alpha_0, m_{\tau 3}, m_{t0}$	0.64	$0.25^{\ddagger}$	129.86	$0.96^{\S}$	$0.83^{\ddagger}$	67.07	0.85	-0.04	63.22
$K_0, \alpha_0, m_{\tau 0}, m_{t1}$	0.66	-0.94	208.82	$0.94^{\S}$	$0.21^{\ddagger}$	147.23	0.74	-4.86	149.87
$K_0, \alpha_0, m_{\tau 0}, m_{t2}$	0.66	-0.94	208.82	$0.96^{\S}$	$0.80^{\ddagger}$	73.83	0.74	-0.16	66.54
$K_0, \alpha_0, m_{\tau 0}, m_{t3}$	0.66	-0.94	208.82	$0.96^{\S}$	$0.82^{\ddagger}$	70.56	0.74	$0.28^{\ddagger}$	52.48
$K_0, \alpha_0, m_{\tau 0}, m_{t4}$	0.66	-0.94	208.82	$0.96^{\S}$	$0.81^{\ddagger}$	72.48	0.74	$0.23^{\ddagger}$	54.27

781