

## CHAPTER 3. THE EFFECT OF FORAGING DEPTH ON SWIMMING AND FORAGING BEHAVIOUR

### 3.1. INTRODUCTION

Breath-hold divers experience the dilemma of not being able to breathe and feed on prey at the same time; they forage underwater and return to the water surface to breathe (Carbone and Houston, 1994). This means that diving and foraging time is physiologically constrained by the amount of oxygen stores, as well as the rate of oxygen consumption, which is largely determined by the frequency of locomotor movements (Davis, 2014; Williams et al., 2004) or swim speed (Davis et al., 1985; Feldkamp, 1987), with a given basal metabolic rate. Within these physiological constraints, foraging theories predict that divers should maximize the proportion of time spent foraging at depth per dive cycle (the combination of transit time  $t_t$ , foraging time  $t_f$  and post-surface time  $t_s$ ) described as follows;

$$\frac{t_f}{t_t + t_f + t_s}, \quad (3.1)$$

where they make two assumptions: (1) the number of prey encounters is positively correlated with foraging time  $t_f$  and (2) post-surface time  $t_s$  is an increasing and accelerating function of the amount of oxygen consumed in the preceding dive (Kramer, 1988; Mori et al., 2002; Thompson et al., 1993). To maximize the output of equation (3.1), divers should reduce both their transit time  $t_t$  to the foraging depth and post-surface time  $t_s$  in relation to foraging time  $t_f$ . Therefore, divers are expected to change swimming behaviour and hence how much amount of oxygen they allocate to each phase of a dive, depending on the energetic cost of swimming, which varies with buoyancy (Chapter 2) as well as foraging depth (Houston and Carbone, 1992; Mori

et al., 2002; Thompson and Fedak, 2001; Thompson et al., 1993).

Foraging depth, in addition to buoyancy, is expected to affect swimming behaviour of breath-hold divers, via changes in transit distance and hence swimming costs. A modelling study by Thompson et al. (1993) predicted that the swim speed to maximize the proportion of time spent foraging at depth should decrease with depth and approach  $U_{\text{COTmin}}$  (i.e. a swim speed that minimizes cost of transport). This is because divers should reduce the rate of oxygen consumption in response to increased transit distance to and from a deeper foraging depth. On the other hand, a higher swim speed that deviates from  $U_{\text{COTmin}}$  would be preferred to forage at a shallower depth by decreasing the transit time  $t_t$  (as well as post-surface time  $t_s$ ) and hence increasing the proportion of time spent foraging at depth (Thompson et al., 1993). In accord with this prediction, a previous study reported decreased swim speed with distance to and from foraging area in captive grey seals using an experimental set-up, which was designed to remove the effect of buoyancy on their swimming behaviour (Gallon et al., 2007). However, this prediction has not been fully tested in free-ranging divers that experience significant changes in buoyancy (body density), because of the technological difficulties to distinguish between the effect of foraging depth and the effect of buoyancy on swimming behaviour under natural conditions (Gallon et al., 2007).

To overcome these difficulties and test if breath-hold divers decrease swim speed with foraging depth, I used two accelerometers called ‘Stroke Logger’ and ‘Kami Kami Logger’ that record swimming and foraging behaviour for long durations (150 days at maximum), respectively, allowing me to distinguish between the effect of foraging depth and the effect of buoyancy on swimming behaviour. In this chapter, I apply this long-term accelerometry technique to ocean-migrating northern elephant seals to investigate the changes in swimming behaviour in relation to the changes in buoyancy, as well as foraging depth. Also, prey patch

quality may affect swimming behaviour of breath-hold divers (Thompson and Fedak, 2001). Hence, I investigated number of feeding events (as an index of prey patch quality) as another potential factor that affects swimming behaviour of seals.

## 3.2. MATERIAL AND METHODS

### 3.2.1. Device design and attachment

#### 3.2.1.1. *Field experiments*

I investigated the at-sea swimming and foraging behaviour of 8 female northern elephant seals during their months-long oceanic foraging migrations. Fieldwork was conducted at the Año Nuevo State Reserve, CA, USA (37°5' N, 122°16' W) during the seals' breeding season (n = 4; seal ID: 1015, T35, R382 and U954, shown in Figure 2.1 & 2.2) and moulting season (n = 4, seal ID: U203, U458, U754 and WX444, shown in Figure 2.1 & 2.2), in 2011 and 2012. Each seal was immobilized with an intramuscular injection of Telazol (Tiletamine hydrochloride and Zolazepam hydrochloride, Fort Dodge Animal Health, Fort Dodge, IA, USA) to allow for the attachment of data loggers. Body mass and other morphometric measurements were obtained using standard protocols (Le Boeuf et al., 1988; Le Boeuf et al., 2000). Upon return from their foraging migration, seals were immobilized to allow for recovery of the data loggers and post-deployment measurements.

Each seal was equipped with a 'Stroke Logger' (see Chapter 2), a 'Kami Kami Logger' (see the next section), a 0.5 W ARGOS transmitter (Wildlife Computers, Redmond, WA, USA) and a VHF transmitter (ATS, Isanti, MN, USA). The data loggers were wrapped in rubber splicing tape and glued to the animal's back (Stroke Logger and VHF transmitter), mandible (Kami Kami Logger) and head (ARGOS transmitter) using five-minute epoxy with high-tension mesh netting and cable ties.

### *3.2.1.2. Instruments*

Stroke Loggers (Little Leonardo Co., Tokyo, Japan) were designed and set as described in Chapter 2.

Kami Kami Loggers (Figure 1.1(b); Little Leonardo Co., Tokyo, Japan; diameter 20.2 and 20.2 mm, length 73 and 96.8 mm, mass 48 and 68 g, for post-breeding and post-moulting deployments, respectively; same as Stroke Logger as described in Chapter 2) are designed to detect jaw motion events, which are identified by high-frequency surge (i.e. longitudinal) acceleration (Naito et al., 2013). Kami Kami loggers have a depth sensor, a temperature sensor, and an one-axis acceleration sensor (along the longitudinal body axis). Depth and temperature data were recorded every five seconds. Kami Kami Loggers were programmed to process highly-sampling (32 Hz) acceleration data on-board, and the use of the on-board data-processing algorithm and storage of summary data every five seconds allowed for a long recording duration. I set an amplitude threshold for longitudinal acceleration of 0.3 G to detect each jaw motion event (Naito et al., 2013), which was separated from next one by employing an event duration threshold (0.5 s). I only used jaw motion events occurred at over 100 m depths for analysis to eliminate jaw-motion noise recording in shallow water close to colony site (Naito et al., 2013). Then, the resulting number of jaw motion events was counted and recorded every five seconds in Kami Kami Loggers (see Naito et al., 2013, for more detail of the usage of the on-board data processing algorithm). In this study, I treated the jaw motion event data as binary data (i.e. 1 or 0 for the 5-second time window with at least one or no jaw motion event, respectively; hereafter, I referred to as ‘feeding events occurred’ for the 5-second time window where the binary data = 1).

### 3.2.2. Data analysis

#### 3.2.2.1. *Estimating seal buoyancy*

To estimate seal buoyancy, I calculated drift rate of each drift dive by the method described in Chapter 2. Then, I fitted a cubic spline to the drift rate data using a built-in function (*interpolate2*) in IGOR Pro version 6.04 (WaveMetrics Inc., Lake Oswego, OR USA) to estimate the value of drift rate during each dive (i.e. not day by day as in Chapter 2, but dive by dive in this chapter). The frequency of interpolant nodes was determined by the method of Robinson et al. (2010).

#### 3.2.2.2. *Dive phase and dive type definition*

Dive phase was defined as described in Chapter 2.

I categorized all dives into two dive types: ‘foraging’ and ‘non-foraging’ dives. Foraging dives were defined as follows with two criteria: a foraging dive should (1) have at least one feeding event and (2) not be a drift dive. Any drift dive was categorized into non-foraging dives regardless of the occurrence of feeding events, because seals are expected to aim to have a rest rather than feed on prey during drift dives for digesting food (Crocker et al., 1997) or sleeping (Mitani et al., 2010). In fact, most of drift dives ( $81.5 \pm 13.6\%$ , for all 8 seals) had no feeding event, suggesting that seals were resting during the drift dives. Any other dives with no feeding events were categorized into non-foraging dives. I analyzed the swimming behaviour during foraging dives to investigate the effect of foraging depth (see the next section of the definition of foraging depth).

### *3.2.2.3. Assessing the effect of foraging depth, as well as buoyancy, on swimming behaviour*

I calculated foraging depth of each foraging dive as the mean of depths where all feeding events occurred during the dive. I also calculated the number of feeding events during foraging dives, because I expect that the number of feeding events may affect swimming behaviour during transit phases of the dives (Thompson and Fedak, 2001). Number of feeding events of each foraging dive was defined as the sum of all feeding events occurred during the dive.

I calculated stroke rate, swim speed and pitch angle during the transit phases (i.e. both descent and ascent phases) of each foraging dive. Stroke rate was defined as the number of strokes divided by the time spent transiting. Swim speed and pitch angle were calculated by averaging the values during the transit phases.

Both buoyancy and foraging depth were expected to affect swimming behaviour of seals (Gallon et al., 2007; Sato et al., 2003). To distinguish between these effects on swimming behaviour, I calculated the index of swimming parameters (i.e. index of stroke rate, swim speed and pitch angle) during the transit phases of each foraging dive by following two steps; (1) calculating moving averages of each value of swimming parameters with 1-day time windows, and then (2) deriving index of swimming parameters by subtracting the moving average from the value of swimming parameters (i.e. calculating the deviation within a day; see Figure 3.1 for more detail). These processes appeared to cancel the effect of the changes in buoyancy (body density) (see Figure 3.1(e)), allowing me to facilitate assessing the effect of foraging depth on swimming behaviour by using those indices.

The total buoyancy of breath-hold divers changes with depth owing to residual air in the lungs, but this effect is reduced at greater depths because air volume decreases with depth following Boyle's law (Biuw et al., 2003). However, to minimize the effect of gases on

buoyancy, I only used data from depths 100 m or more, as per Aoki et al. (2011; same as in Chapter 2). This is because in this study I focused not on the effect of residual air but on the effect of body density on swimming behaviour, although the effect of residual should be small in elephant seals because they exhale before diving (Williams et al., 2000) and also dive deep (usually over 400 m in foraging dives; see Figure 3.5).

#### 3.2.2.4. Statistical analysis

Statistical analysis was carried out with R (v. 2.15.3, Foundation for Statistical Computing, Vienna, Austria). The *lmer* function in the *lme4* package was used to fit generalized linear mixed models (GLMM). All GLMMs in this study included individual as a random effect. In GLMM with multiple explanatory variables, Akaike's information criterion corrected for small sample size ( $AIC_c$ ) was calculated to select the most parsimonious model having the lowest  $AIC_c$  value. Also, marginal  $R^2$  was calculated to evaluate the variance explained by fixed effects, providing goodness-of-fit of each model (Nakagawa and Schielzeth, 2013). Figures showing the local densities at each point (represented by color gradient) were made using the *densCols* function in the *grDevices* package in R. Data are presented as means  $\pm$  standard deviation (s.d.) unless otherwise stated.

I expect that seals change swimming behaviour in response to the foraging depth (and number of feeding events) during a foraging dive for ascent phase, but during a preceding foraging dive for descent phase (Gallon et al., 2007). Therefore, swimming parameters of each foraging dive were statistically analyzed with the foraging depth (and number of feeding events) during the dives for ascent and during the preceding dives for descent. For this analysis, I excluded 6.39% of foraging dives, because those foraging dives were (1) separated from the prior dive by extended post-surface time (defined as over 10 minutes post-surface time) (0.05%),

(2) preceded by a non-foraging dive (i.e. a drift dive or a dive with no feeding event) (6.30%), or (3) both (0.04%).

The optimal diving model by Thompson et al. (1993) assumed that (1) the number of prey encounters is linearly correlated with foraging time and (2) post-surface time is an increasing and accelerating function of the amount of oxygen consumed in the preceding dive. To test if my empirical data satisfy these assumptions, I investigated the relationship between number of feeding events and bottom duration (for the assumption (1)), and also the relationship between post-surface time and dive duration (for the assumption (2)) in foraging dives. To investigate the assumption (2), I selected each dive duration with the shortest post-surface time from all foraging dives of all 8 individuals, as per Mori et al. (2002). Then, I determined the most parsimonious model (GLMM with  $AIC_c$ ) between a linear [ $y \sim x$ ] and a quadratic [ $y \sim x + x^2$  or  $y \sim x^2$ ] model to characterize the relationship between post-surface time and dive duration.

### 3.3. RESULTS

#### 3.3.1. Data collection

Stroke Loggers and Kami Kami loggers tracked the swimming and foraging behaviour of female northern elephant seals for the entire short, post-breeding foraging migration ( $72.6 \pm 2.8$  days,  $n = 4$  seals) and for  $56.3 \pm 10.0\%$  of the long, post-moulting foraging migration ( $128.6 \pm 20.4$  days,  $n = 4$  seals) that lasted for  $228.8 \pm 4.6$  days on average. A total of 46091 dives were recorded with means of  $4109 \pm 405$  dives and  $7414 \pm 1147$  dives for short and long foraging migration, respectively. Foraging dives accounted for  $85.0 \pm 5.2\%$  of total dives for all 8 seals. Foraging depth was linearly correlated with dive depth of each foraging dive (Figure 3.2; GLMM with  $AIC_c$ ). Number of feeding events during each foraging dive was linearly correlated with time spent at bottom phase (Figure 3.3; GLMM with  $AIC_c$ ), where most feeding events

( $87.8 \pm 15.0\%$ , for all 8 seals) occurred. Post-surface time in each foraging dive increased and accelerated with dive duration, characterized by a quadratic function with a minimum value at  $x = 0$  and a positive second derivative (the most parsimonious model having the lowest  $AIC_c$  value:  $y = 0.0006x^2 + 1.0850$ ) (Figure 3.4). Dive depth of foraging dives was significantly deeper than non-foraging dives (i.e. drift dives and any other dives with no feeding events, accounted for  $6.7 \pm 1.9\%$  and  $8.3 \pm 3.8\%$  of total dives for all 8 seals, respectively) (Figure 3.5; GLMM with  $AIC_c$ ).

### 3.3.2. The change in seal buoyancy and its effect on swimming behaviour during foraging dives

While I calculated all parameters per dive (this chapter) rather than per day (Chapter 2), I found the similar results of changes in seal buoyancy and swimming parameters (stroking effort, swim speed and pitch angle; note that I calculated stroke rate in this chapter rather than strokes-per-metre in Chapter 2 for representing stroking effort of seals), as described in the following paragraphs.

Negatively buoyant seals gradually became more buoyant as they increased their fat stores while foraging over the course of the migration, as indicated by increased drift rates (Figure 3.6; also see Figure 2.1 & 2.2). All seals were still negatively buoyant at the end of the short foraging migration, but two of four seals became neutrally buoyant by the end of the recording period during the long foraging migration, as indicated by the drift rates being zero (i.e. seals neither sink nor float during the drift phase (Biuw et al., 2003)).

Stroke rates during both descent and ascent phases were affected by drift rate in opposite ways with different magnitudes according to the direction of the swimming path (Figure 3.6 & 3.7). Drift rate had a positive and negative relationship with descent and ascent stroke rate,

respectively (Figure 3.7; GLMM with AIC<sub>c</sub>).

Swim speed during the descent phase decreased largely from approximately 2.5 to 1.0 m s<sup>-1</sup> as seals became more buoyant, but swim speed during the ascent phase remained around 1.5 m s<sup>-1</sup> (Figure 3.6 & 3.7; GLMM with AIC<sub>c</sub>). Both descent and ascent swim speeds were affected by drift rates, but descent swim speed was much more sensitive to changes in drift rates (Figure 3.7).

Pitch angles during both descent and ascent phase were affected by drift rate with different magnitudes according to the direction of the swimming path (Figure 3.8; GLMM with AIC<sub>c</sub>). Both descent and ascent pitch angles were steeper as seals became more buoyant, although descent pitch angle was much more sensitive to changes in drift rates (Figure 3.8).

### 3.3.3. The change in swimming behaviour in relation to foraging depth and number of feeding events during foraging dives

The index of stroke rate during transit phases of each foraging dive was positively correlated with the index of swim speed (Figure 3.9; GLMM with AIC<sub>c</sub>). Both of the indices of stroke rate and swim speed during transit phases were affected by both foraging depth and number of feeding events, as indicated by the most parsimonious models, although those indices of swimming parameter were much more sensitive to foraging depth than number of feeding events (Table 3.1; Figure 3.10 & 3.11). The indices of stroke rate and swim speed during both descent and ascent phases decreased significantly as seals foraged at deeper depths (Figure 3.10). On the other hand, number of feeding events had a slightly positive relationship with only the index of stroke rate during ascent phase and slightly negative relationships with others (i.e. indices of stroke rate during descent phase and swim speed during both descent and ascent phases) (Figure 3.11). Also, GLMM with absolute values of stroke rate or swim speed (rather

than those indices) as the response variables showed that both foraging depth and number of feeding events, in addition to drift rate (buoyancy), affected stroke rate and swim speed during both descent and ascent phases (Table 3.2).

The index of pitch angle during transit phases of each foraging dive was affected by both foraging depth and number of feeding events (Table 3.1; Figure 3.12 & 3.13). The index of pitch angle during ascent phase was much more sensitive to both foraging depth and number of feeding events than those during descent phase, although pitch angles were steeper as foraging depth and number of feeding events increased during both descent and ascent phases (Figure 3.12 & 3.13). Also, GLMM with absolute values of pitch angle (rather than the index) as the response variable showed that both foraging depth and number of feeding events, in addition to drift rate (buoyancy), affected pitch angle during both descent and ascent phases (Table 3.2).

## 3.4. DISCUSSION

### 3.4.1. Both seal buoyancy and foraging depth affect swimming behaviour

Using long-term accelerometry technique, I demonstrated that stroke rate, swim speed and pitch angle during the transit phases of each foraging dive changed in response to the changes in not only seal buoyancy but also foraging depth.

#### *3.4.1.1. The effect of seal buoyancy on swimming behaviour*

While I calculated all parameters per dive (this chapter) rather than per day (Chapter 2), I found the similar relationship between stroking effort and swim speed in relation to significant changes in buoyancy (note that I calculated stroke rate in this chapter rather than strokes-per-metre in Chapter 2 for representing stroking effort of seals), as described in the

following paragraph.

Stroke rate changed with different magnitudes according to the direction of the swimming path as seals approached neutral buoyancy (Figure 3.7). During descent phase (i.e. buoyancy-aided direction), stroke rate increased slightly as seals became more buoyant, but stayed low (compared to ascent stroke rate) over a range of negative buoyancy values (Figure 3.7). This indicates that seals largely relied on negative buoyancy as the thrust force for gliding, which kept stroking effort low (Sato et al., 2003; Williams et al., 2004). Also, descent pitch angles were steeper when seals were more buoyant (Figure 3.8), which might allow seals to descend with less stroking activity because a steeper pitch angle would bring the vector of forward motion close to the force of gravity (Sato et al., 2003). These trends were reflected in decreased descent swim speed for more buoyant seals (Figure 3.7) because gliding speed decreases as seals approach neutral buoyancy (Miller et al., 2012; Watanabe et al., 2006). During ascent phase (i.e. buoyancy-hindered direction), on the other hand, stroke rate largely decreased as seals approached neutral buoyancy, but the swim speed did not change largely (Figure 3.7). This suggests that seals adjusted stroking effort depending on buoyancy change to maintain a narrow range of ascent swim speed (Figure 3.7), which might reflect a swim speed that minimizes cost of transport ( $U_{COTmin}$ ) in the buoyancy-hindered direction (Miller et al., 2012; Sato et al., 2010; Watanabe et al., 2011).

#### *3.4.1.2. The effects of foraging depth and number of feeding events on swimming behaviour*

Seals changed stroking activities to adjust swim speeds during both descent and ascent phases (Figure 3.9) in response to the changes in foraging depth: they swam faster by stroking more frequently when they foraged at shallower depths (Figure 3.6 & 3.10). This result agrees

with the optimal diving model by Thompson et al. (1993) that predicted breath-hold divers should swim faster in shallower dives to maximize the proportion of time spent foraging at depth, under two assumptions (1) the number of prey encounters is linearly correlated with foraging time (Figure 3.3) and (2) post-surface time is an increasing and accelerating function of the amount of oxygen consumed in the preceding dive (Figure 3.4). In shallower dives, a faster swim speed achieved by stroking more frequently (Figure 3.9 & 3.10) would benefit seals from reducing transit time, reaching at the foraging depth faster with the combination of reducing post-surface time and consequently maximizing the proportion of time spent foraging at the shallower depth (Thompson et al., 1993). In deeper dives, it is inevitable to increase transit distance and hence the total energy cost expended for transit to and from foraging depths. Therefore, seals would decrease swim speed by stroking less frequently (Figure 3.9 & 3.10) to reduce oxygen consumption during transit, which would allow seals to maximize the proportion of time spent foraging at the deeper depth (Thompson et al., 1993). Also, steeper pitch angles in deeper dives possibly contribute to the reduction in time spent transiting and hence oxygen consumption during transit, although ascent pitch angles were much more sensitive to foraging depth than descent pitch angle (Figure 3.12). Given that swimming is more costly in buoyancy-hindered direction (i.e. ascent phase) (Miller et al., 2012), the regulation of pitch angle on ascending could be more important than on descending to reduce oxygen consumption when the round-trip cost to and from foraging depths is considered.

In contrast to my results, otariid seals and diving birds increased descent swim speed in deeper dives (Crocker et al., 2001a; Lovvorn et al., 2004; Ponganis et al., 1992). The effect of air in the lung could explain the different swimming behaviour in relation to foraging depth. Unlike phocid seals (such as elephant seals) that exhale before diving, otariid seals and diving birds store air in their lungs before diving (McDonald and Ponganis, 2012; Sato et al., 2002;

Sato et al., 2011; Williams et al., 2000). Therefore, otariid seals and diving birds are expected to work hard against buoyancy in shallow depth at the start of descending (i.e. at the start of the dive). Buoyancy should decrease in deeper depth because of decreased air volume in the lung with depth (Biuw et al., 2003), which allows them descend more easily. Therefore, mean descent swim speed during descent phase could increase in deeper dives, where they have to work against buoyancy during lower proportion of descent phase compared to in shallower dives. These explanations were also provided by Gallon et al. (2007) that showed an agreement with the optimality model by Thompson et al. (1993) to report decreased swim speed with distance to foraging area in captive grey seals using experimental set-up, which was designed to remove the effect of buoyancy on their swimming behaviour.

Similarly to otariid seals and diving birds, northern elephant seals were reported to increase swim speed with dive depth during descent phase only (Hassrick et al., 2007). Also, southern elephant seals were reported to increase swim speed with dive depth during both descent and ascent phases (Hindell and Lea, 1998). These results are contrary to my results, but the contradiction could be explained by the significant effect of both dive types and seal buoyancy on swim speed. First, mean swim speeds during both descent and ascent phases in shallower dives could be slower if non-foraging dives were included in the analysis. This is because non-foraging dives were shallower than foraging dives, and both descent and ascent swim speeds were significantly slower in non-foraging dives than in foraging dives when dive depth was controlled (Figure 3.5 & 3.14; GLMM with AIC<sub>c</sub>), possibly leading to a positive relationship between swim speed and dive depth (Hindell and Lea, 1998) (please note that my swim speed data are comparable with those from other studies although the methods of calculating swim speed vary among studies; see *Appendix* for more detail). This is probably not the case for the study by Hassrick et al. (2007) that investigated the relationship between swim

speed and dive depth during only ‘foraging dives’, which were distinguished from other dive types (such as drift dives) by visual inspection of the dive shape. Second, seal buoyancy should have significant effects on swim speed, especially during descent phase (Figure 3.7), precluding us from adequate investigation for the relationship between swim speed and dive depth if we do not distinguish between the effect of dive depth and the effect of buoyancy on swimming behaviour (as per Hassrick et al., 2007; Hindell and Lea, 1998). Finally, there might be the effect of residual air in the lung on seal buoyancy in shallow depths in the same manner to otariid seals and diving birds (Biuw et al., 2003), although the effect of residual air on mean swim speed during transit phases should be smaller in elephant seals because they exhale before diving and also dive deeper than otariid seals and diving birds. Hence, the residual air in the lung of elephant seals might have a potential effect on mean swim speed during transit phases, when we include swim speeds at shallower depths (< 100 m) (as per Hassrick et al., 2007; Hindell and Lea, 1998), rather than exclude them as in this study (see the section of *Materials and methods* in this chapter). In fact, the relationship between swim speed during transit phases and dive depth significantly changed when I did not consider the effect of dive type and seal buoyancy on swim speed, in terms of goodness-of-fit (marginal  $R^2$ ) of GLMM and the slopes (Figure 3.10 & 3.14). These results suggest that it is important to distinguish between biomechanical factor (buoyancy) and ecological factor (foraging depth) to investigate swimming strategy of free-ranging breath-hold divers, especially in highly migratory divers, such as elephant seals, that experience significant changes in both those factors simultaneously while foraging at sea (Biuw et al., 2003; Guinet et al., 2014; Naito et al., 2013; Robinson et al., 2010).

Prey patch quality may also affect swimming behaviour during transit phases (Thompson and Fedak, 2001). However, my study seals did not appear to change stroke rate and swim speed

largely in response to number of feeding events (Figure 3.11), compared to foraging depth (Figure 3.10). Only ascent pitch angle increased largely with number of feeding events (Figure 3.13). Seals might expend more oxygen at foraging depth during foraging dive with higher number of feeding events, because number of feeding events was linearly correlated with time spent foraging at depth (Figure 3.3), implying less oxygen available for ascending in more successful foraging dives. Therefore, seals might be urged to employ steeper pitch angle to save time spent ascending and hence oxygen consumption when they return to the surface to breathe. Alternatively, shallower ascent pitch angles in less successful foraging dives (i.e. with lower number of feeding events; Figure 3.13) might benefit seals from increasing horizontal distance covered during a foraging dive, potentially contributing to the move into a more profitable area in the following foraging dives (Sato et al., 2004).

One weakness in detecting feeding events by our accelerometry technique is that these do not provide information on sizes and species of prey. In terms of maximizing energy intake for foraging animals, the size and species of prey is important to determine prey patch quality, together with number of prey captured (Stephens et al., 2007). The lack of the information on the size and species of prey precluded me from quantitatively investigating the relationship between swimming behaviour and prey patch quality (Figure 3.11). However, recent studies using animal-borne still camera or stable isotope analysis suggested that female elephant seals primarily feed on myctophid fish, the small-sized and most dominant fish species in mesopelagic zone (Cherel et al., 2008; Irigoien et al., 2014; Naito et al., 2013). If so, the number of feeding events can be useful as an index of prey patch quality in elephant seals.

If myctophid fish represent major prey items for elephant seals, this may explain why seals were more sensitive to foraging depth than number of feeding events in relation to stroke rate and swim speed during transit phases of the foraging dives (Figure 3.10 & 3.11). Myctophid

fish are known to conduct diel vertical migration: staying at shallower and deeper depth during nighttime and daytime, respectively, which is clearly reflected in the diel pattern of foraging behaviour of elephant seals (Figure 3.6; Guinet et al., 2014; Naito et al., 2013). Therefore, elephant seals might be able to respond to the predictable diel changes in depth distribution of prey. On the other hand, prey patch quality in mesopelagic zone could vary spatiotemporally (Guinet et al., 2014; Naito et al., 2013) and hence might be less predictable than the depth distribution of prey. Therefore, elephant seals would be more sensitive to more predictable factor (foraging depth) than less predictable factor (number of feeding events), because it should be more risky to change behaviour largely in response to less predictable factors. Nevertheless, quantitative investigations of prey patch quality are needed to fully understand how seals change their swimming and foraging behaviour in response to the changes in the number of feeding events.

### 3.5. SUMMARY OF CHAPTER 3

In summary, I successfully tracked changes in the swimming and foraging behaviour in ocean-migrating elephant seals using long-term accelerometry technique. As negatively buoyant seals increased their fat stores and buoyancy, swim speed significantly decreased in the buoyancy-aided direction, but did not change largely in the buoyancy-hindered direction, with associated changes in stroking frequency. Seals changed swimming behaviour in response to not only buoyancy changes, but also to changes in foraging depth. Specifically, seals swam faster by stroking more frequently when they foraged in shallower depths, reflecting the swimming strategy of maximizing the proportion of time spent foraging at depth, in agreement with an optimality model for breath-hold divers. On the other hand, the number of feeding events had relatively small effect on swimming behaviour. These results characterize the swimming

behaviour of elephant seals, in which both biomechanical (buoyancy) and ecological (foraging depth) factors influence stroking frequency and swim speed.

Table 3.1. The results of generalized linear mixed models (GLMM) with index of swimming parameters (index of stroke rate, swim speed and pitch angle during both descent and ascent phase of each foraging dive) as the response variables, and foraging depth and number of feeding events as the explanatory variables, including individual as a random effect. Akaike's information criterion corrected for small samples ( $AIC_c$ ),  $AIC_{weight}$  and rank are shown for each model. The models with the lowest  $AIC_c$  are shown in bold type.

Candidate models	$AIC_c$	$AIC_{weight}$	rank
<b>Index of descent stroke rate ~ Foraging depth + No. of feeding events</b>	<b>-88243.8</b>	<b>0.632</b>	<b>1</b>
Index of descent stroke rate ~ Foraging depth	-88242.7	0.368	2
Index of descent stroke rate ~ No. of feeding events	-85335.7	0.000	3
Index of descent stroke rate ~ 1	-85334.6	0.000	4
<b>Index of ascent stroke rate ~ Foraging depth + No. of feeding events</b>	<b>-110017.5</b>	<b>1.000</b>	<b>1</b>
Index of ascent stroke rate ~ Foraging depth	-109775.2	0.000	2
Index of ascent stroke rate ~ No. of feeding events	-106678.4	0.000	3
Index of ascent stroke rate ~ 1	-106383.6	0.000	4
<b>Index of descent swim speed ~ Foraging depth + No. of feeding events</b>	<b>-38303.4</b>	<b>1.000</b>	<b>1</b>
Index of descent swim speed ~ Foraging depth	-38286.8	0.000	2
Index of descent swim speed ~ No. of feeding events	-37566.8	0.000	3
Index of descent swim speed ~ 1	-37564.0	0.000	4
<b>Index of ascent swim speed ~ Foraging depth + No. of feeding events</b>	<b>-48037.6</b>	<b>1.000</b>	<b>1</b>
Index of ascent swim speed ~ Foraging depth	-47999.1	0.000	2
Index of ascent swim speed ~ No. of feeding events	-43526.7	0.000	3
Index of ascent swim speed ~ 1	-43521.5	0.000	4
<b>Index of descent pitch angle ~ Foraging depth + No. of feeding events</b>	<b>196055.8</b>	<b>1.000</b>	<b>1</b>
Index of descent pitch angle ~ Foraging depth	196108.6	0.000	2
Index of descent pitch angle ~ No. of feeding events	196307.2	0.000	3
Index of descent pitch angle ~ 1	196343.9	0.000	4
<b>Index of ascent pitch angle ~ Foraging depth + No. of feeding events</b>	<b>195271.2</b>	<b>1.000</b>	<b>1</b>
Index of ascent pitch angle ~ Foraging depth	196848.7	0.000	2
Index of ascent pitch angle ~ No. of feeding events	197538.2	0.000	3
Index of ascent pitch angle ~ 1	198829.3	0.000	4

Table 3.2. The results of generalized linear mixed models (GLMM) with swimming parameters (stroke rate, swim speed and pitch angle during both descent and ascent phases of each foraging dive) as the response variables, and drift rate, foraging depth and number of feeding events as the explanatory variables, including individual as a random effect. Akaike's information criterion corrected for small samples ( $AIC_c$ ),  $AIC_{weight}$  and rank are shown for each model. The models with the lowest  $AIC_c$  are shown in bold type.

Candidate models	$AIC_c$	$AIC_{weight}$	Rank
<b>Descent stroke rate ~ Drift rate + Foraging depth + No. of feeding events</b>	<b>-80953.1</b>	<b>1.000</b>	<b>1</b>
Descent stroke rate ~ Drift rate + Foraging depth	-80884.6	0.000	2
Descent stroke rate ~ Drift rate + No. of feeding events	-77852.9	0.000	3
Descent stroke rate ~ Foraging depth + No. of feeding events	-72261.3	0.000	5
Descent stroke rate ~ Drift rate	-77846.4	0.000	4
Descent stroke rate ~ Foraging depth	-72064.6	0.000	6
Descent stroke rate ~ No. of feeding events	-70809.6	0.000	7
Descent stroke rate ~ 1	-70548.7	0.000	8
<b>Ascent stroke rate ~ Drift rate + Foraging depth + No. of feeding events</b>	<b>-88772.0</b>	<b>1.000</b>	<b>1</b>
Ascent stroke rate ~ Drift rate + Foraging depth	-88664.3	0.000	2
Ascent stroke rate ~ Drift rate + No. of feeding events	-87056.5	0.000	3
Ascent stroke rate ~ Foraging depth + No. of feeding events	-33324.2	0.000	5
Ascent stroke rate ~ Drift rate	-86894.7	0.000	4
Ascent stroke rate ~ Foraging depth	-32085.1	0.000	7
Ascent stroke rate ~ No. of feeding events	-32089.5	0.000	6
Ascent stroke rate ~ 1	-30981.9	0.000	8
<b>Descent swim speed ~ Drift rate + Foraging depth + No. of feeding events</b>	<b>-22855.1</b>	<b>0.864</b>	<b>1</b>
Descent swim speed ~ Drift rate + Foraging depth	-22851.4	0.136	2
Descent swim speed ~ Drift rate + No. of feeding events	-22216.2	0.000	4
Descent swim speed ~ Foraging depth + No. of feeding events	10874.2	0.000	5
Descent swim speed ~ Drift rate	-22218.2	0.000	3
Descent swim speed ~ Foraging depth	12181.5	0.000	8
Descent swim speed ~ No. of feeding events	11912.4	0.000	7
Descent swim speed ~ 1	13040.6	0.000	6

Table 3.2. Continued.

<b>Ascent swim speed ~ Drift rate + Foraging depth + No. of feeding events</b>	<b>-35192.1</b>	<b>1.000</b>	<b>1</b>
Ascent swim speed ~ Drift rate + Foraging depth	-35132.2	0.000	2
Ascent swim speed ~ Drift rate + No. of feeding events	-32036.4	0.000	5
Ascent swim speed ~ Foraging depth + No. of feeding events	-33263.8	0.000	3
Ascent swim speed ~ Drift rate	-32022.7	0.000	6
Ascent swim speed ~ Foraging depth	-32915.6	0.000	4
Ascent swim speed ~ No. of feeding events	-29705.7	0.000	2
Ascent swim speed ~ 1	-29465.8	0.000	8
 <b>Descent pitch angle ~ Drift rate + Foraging depth + No. of feeding events</b>	 <b>218180.6</b>	 <b>1.000</b>	 <b>1</b>
Descent pitch angle ~ Drift rate + Foraging depth	219158.4	0.000	2
Descent pitch angle ~ Drift rate + No. of feeding events	219424.2	0.000	3
Descent pitch angle ~ Foraging depth + No. of feeding events	225351.2	0.000	5
Descent pitch angle ~ Drift rate	220183.3	0.000	4
Descent pitch angle ~ Foraging depth	227622.8	0.000	7
Descent pitch angle ~ No. of feeding events	227064.4	0.000	6
Descent pitch angle ~ 1	228992.2	0.000	8
 <b>Ascent pitch angle ~ Drift rate + Foraging depth + No. of feeding events</b>	 <b>215252.1</b>	 <b>1.000</b>	 <b>1</b>
Ascent pitch angle ~ Drift rate + Foraging depth	218632.7	0.000	5
Ascent pitch angle ~ Drift rate + No. of feeding events	218115.7	0.000	3
Ascent pitch angle ~ Foraging depth + No. of feeding events	215272.8	0.000	2
Ascent pitch angle ~ Drift rate	220804.5	0.000	7
Ascent pitch angle ~ Foraging depth	218726.1	0.000	6
Ascent pitch angle ~ No. of feeding events	218121.1	0.000	4
Ascent pitch angle ~ 1	221031.7	0.000	8

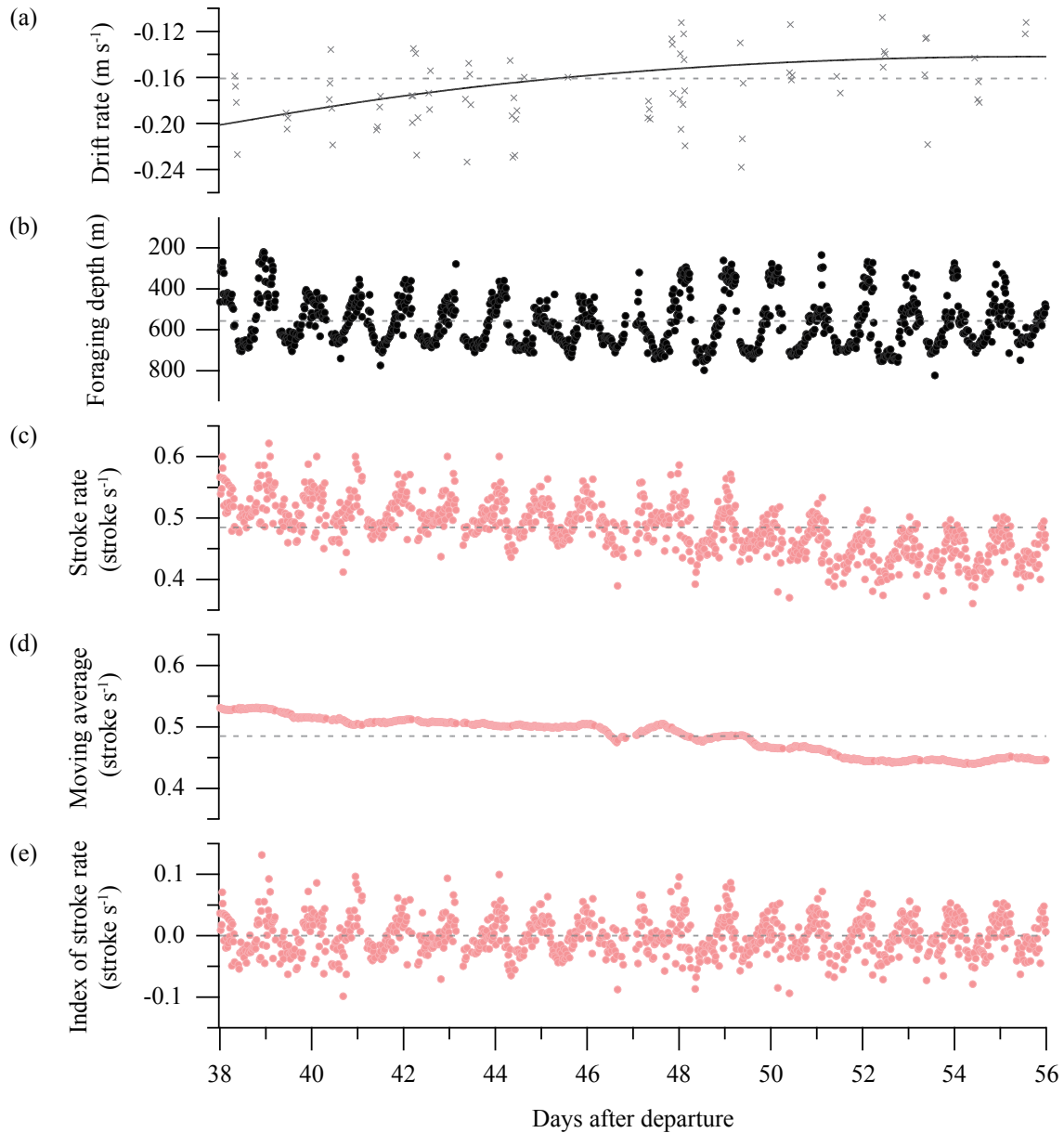


Figure 3.1 The detail of calculating index of swimming parameters during transit phases of each foraging dive: an example for ascent stroke rate during the period when seal buoyancy (drift rate) increased (seal ID: U954, shown in Figure 3.6). (a) Drift rates calculated from each drift dive (grey cross marks) and the interpolated values (black line). (b) Foraging depths of foraging dives. (c) Stroke rates during ascent phase in each foraging dive. (d) Moving averages of ascent stroke rate with 1-day time windows. (e) Index of ascent stroke rate (i.e. deviation within a day), which was calculated by subtracting moving average (panel (d)) from each value of ascent stroke rate (panel (c)).

Here, note that drift rates (buoyancy) had a negative relationship with ascent stroke rates and moving averages (i.e. drift rate increased, and ascent stroke rate and moving average decreased). However, note that the effect of buoyancy appeared to be cancelled out in index of ascent stroke.

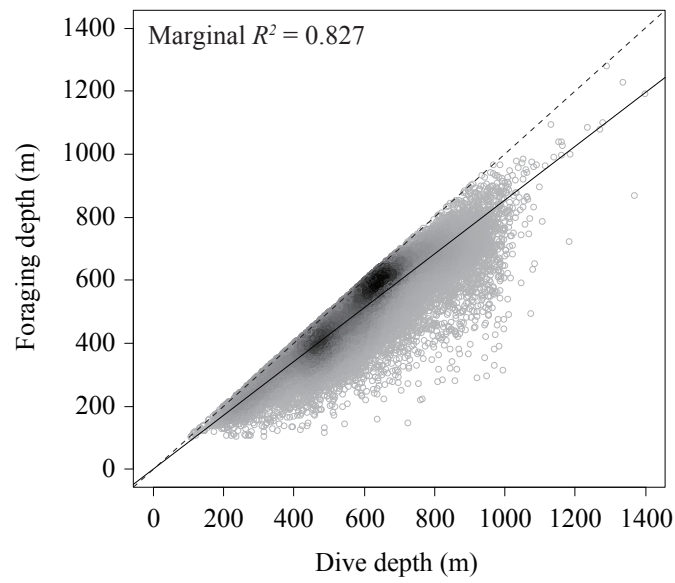


Figure 3.2. The relationship between foraging depth and dive depth of foraging dives for all 8 individuals. Color gradient indicates the local densities at each point. A dotted black line represents  $y = x$ . A solid black line shows the most parsimonious model (generalized linear mixed model: GLMM) having the lowest  $AIC_c$  value. Marginal  $R^2$  of the model was shown at the top of the figure.

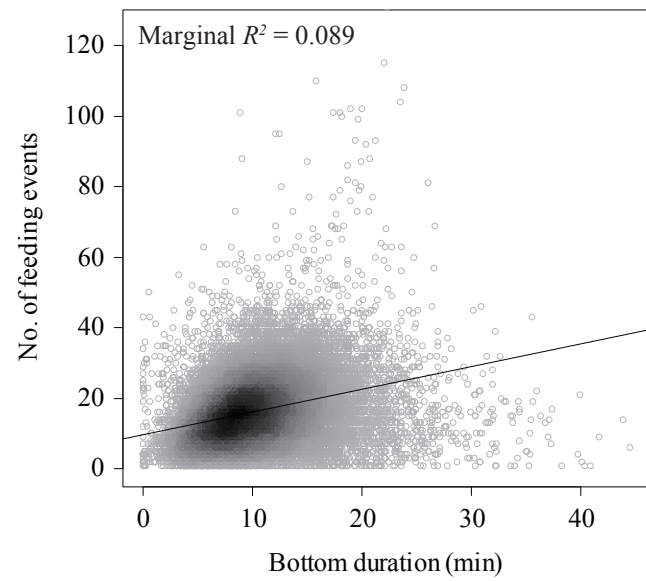


Figure 3.3. The relationship between number of feeding events and bottom duration during foraging dives for all 8 individuals. Color gradient indicates the local densities at each point. A black line shows the most parsimonious model (generalized linear mixed model: GLMM) having the lowest  $AIC_c$  value. Marginal  $R^2$  of the model was shown at the top of the figure.

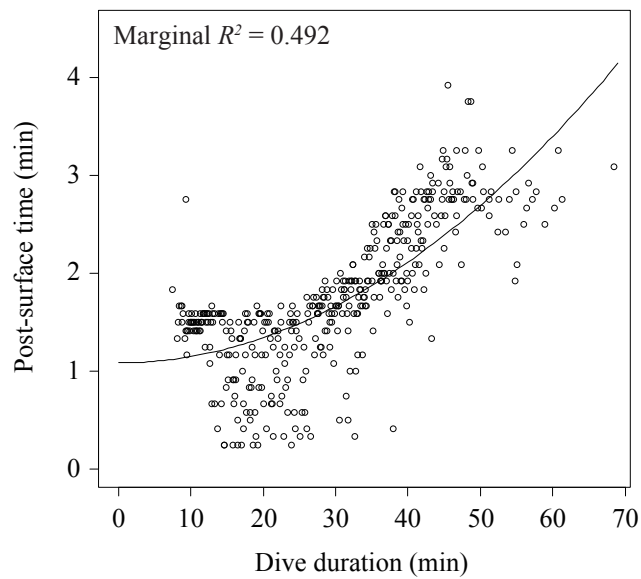


Figure 3.4. The relationship between post-surface time and dive duration of foraging dives. To determine the relationship, all foraging dives for all 8 individuals were pooled, and each dive duration with the shortest post-surface time ( $n = 415$  dives) were selected to determine the most parsimonious model (generalized linear mixed model: GLMM) having the lowest  $AIC_c$  (the quadratic function, shown by a black line). Marginal  $R^2$  of the model was shown at the top of the figure.

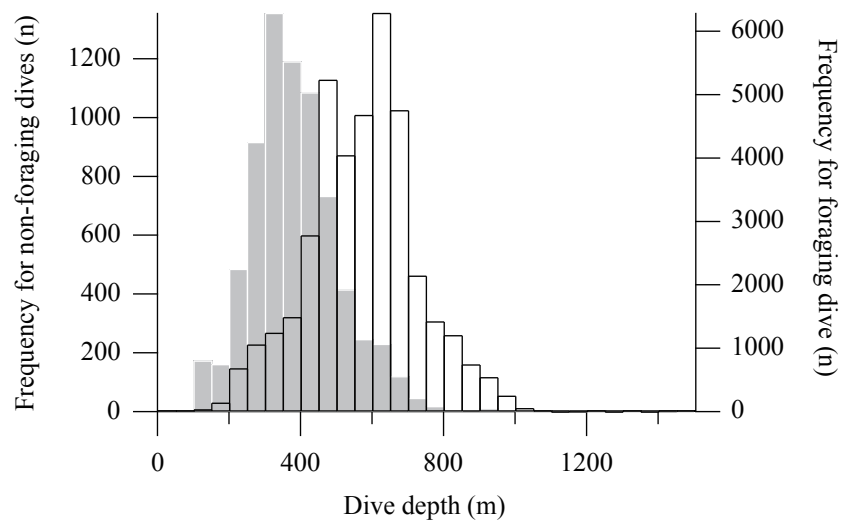


Figure 3.5. The frequency distribution of dive depth for all 8 individuals. Open black and filled grey bars represent the frequency of dive depth in foraging (right vertical axis) and non-foraging dives (i.e. drift dives and any other dives that had no feeding events; left vertical axis), respectively.

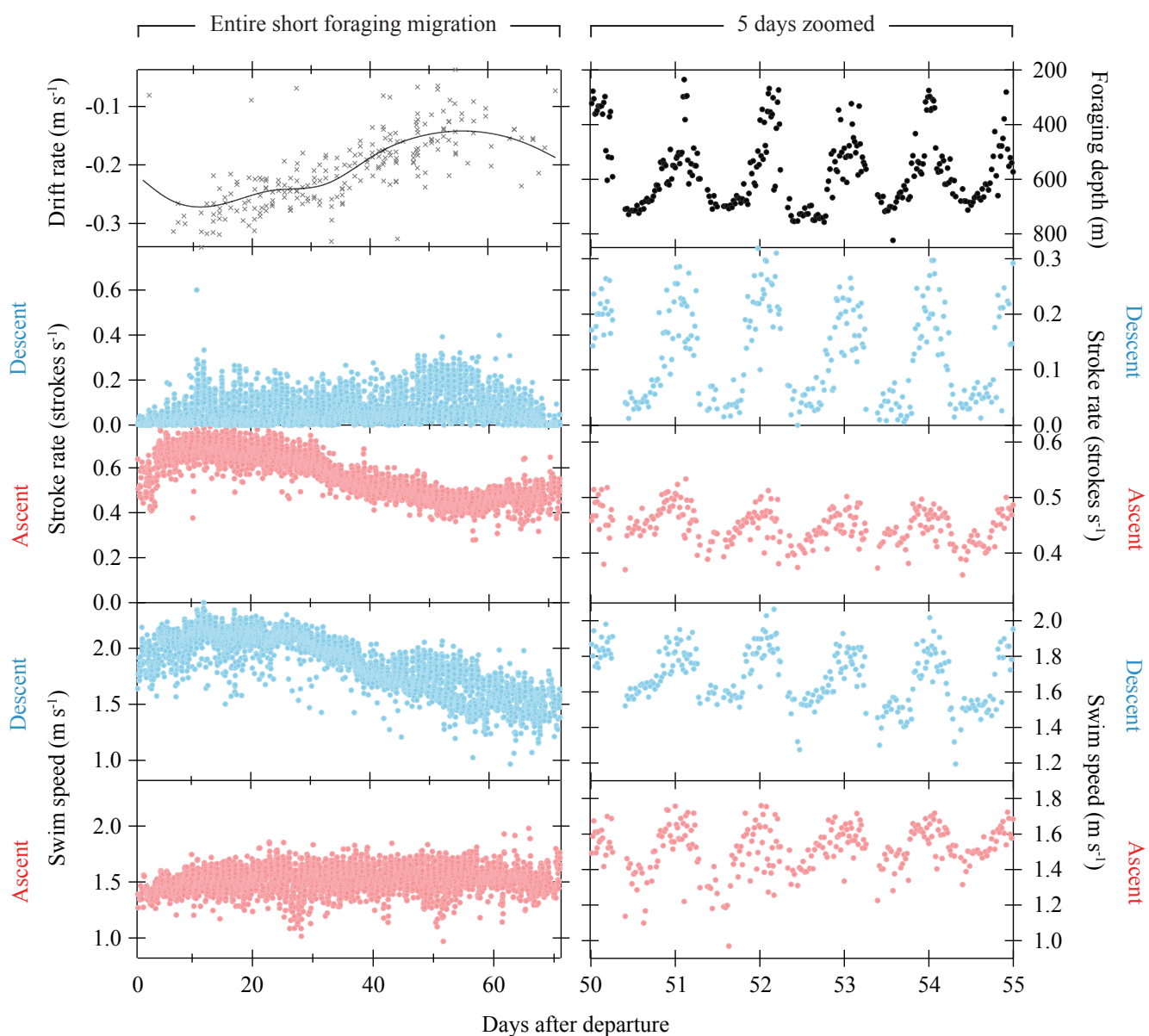


Figure 3.6. An example of the time series data from one seal (seal ID: U954) during short foraging migration. Left panels show the time series data of drift rate, stroke rate and swim speed during entire short foraging migration. Right panels show the time series data of foraging depth, stroke rate and swim speed for 5 days zoomed. In the left top panel, grey cross marks represent drift rates calculated from each drift dive. A thick black line represents interpolated values of drift rate. In the right top panels, open black circles represent averaged foraging depths of each foraging dive. In the second and third row panels for both left and right panels, filled blue and red circles represent values of descent and ascent stroke rates of each foraging dive, respectively. In the fourth row and bottom panels for both left and right panels, filled blue and red circles represent values of descent and ascent swim speed of each foraging dive, respectively. Also, in the right panels, scale bars along the horizontal axis indicate midnight.

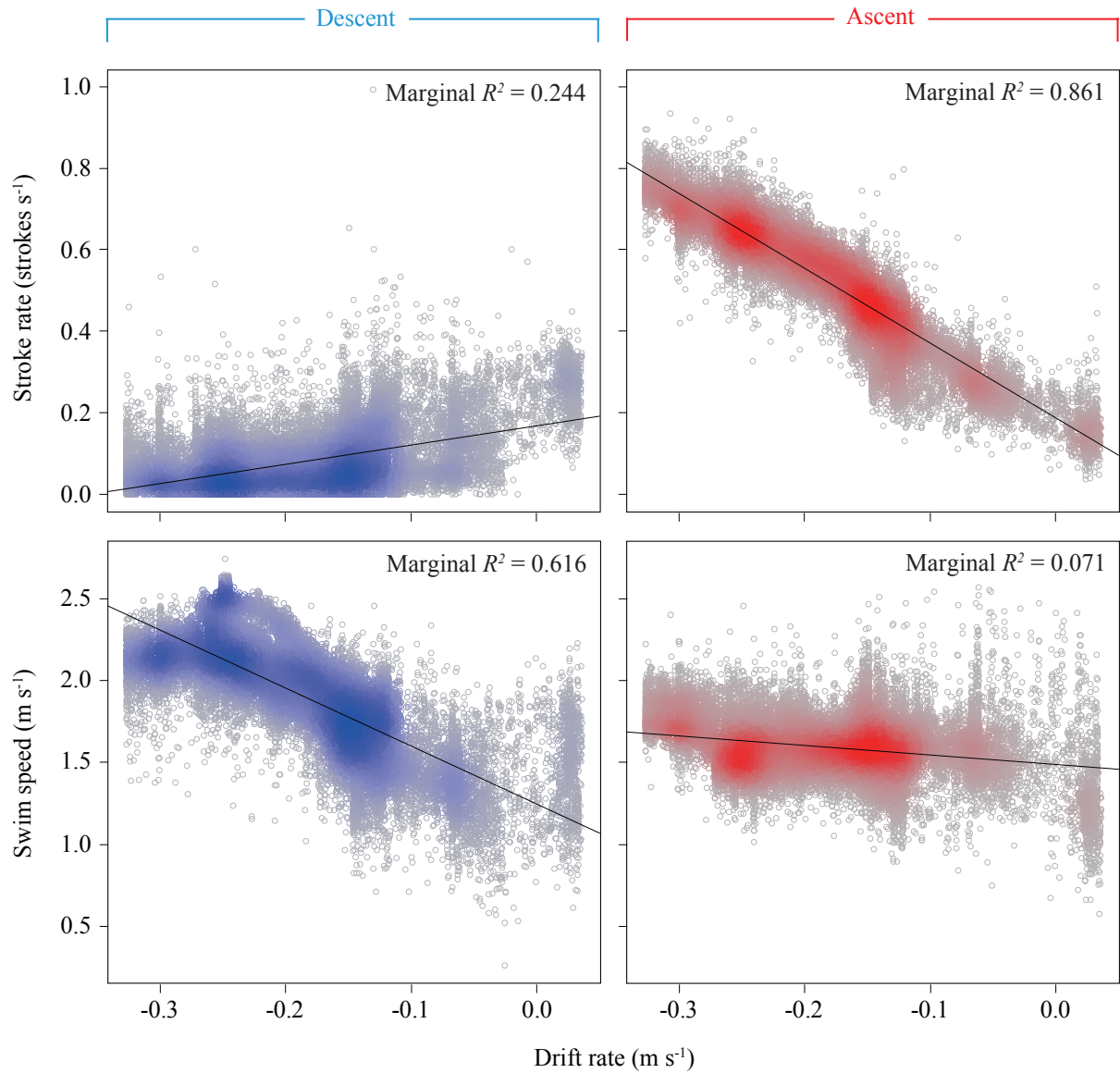


Figure 3.7. Stroke rate and swim speed, plotted against drift rates for all 8 individuals. Left and right panels show values during descent and ascent phases of each foraging dive, respectively. In all panels color gradients (blue or red for descent or ascent phase, respectively), indicate the local densities at each point. Black lines show the most parsimonious models (generalized linear mixed model: GLMM) having the lowest AIC<sub>c</sub> values. Marginal  $R^2$  of the model was shown at the top of each panel.

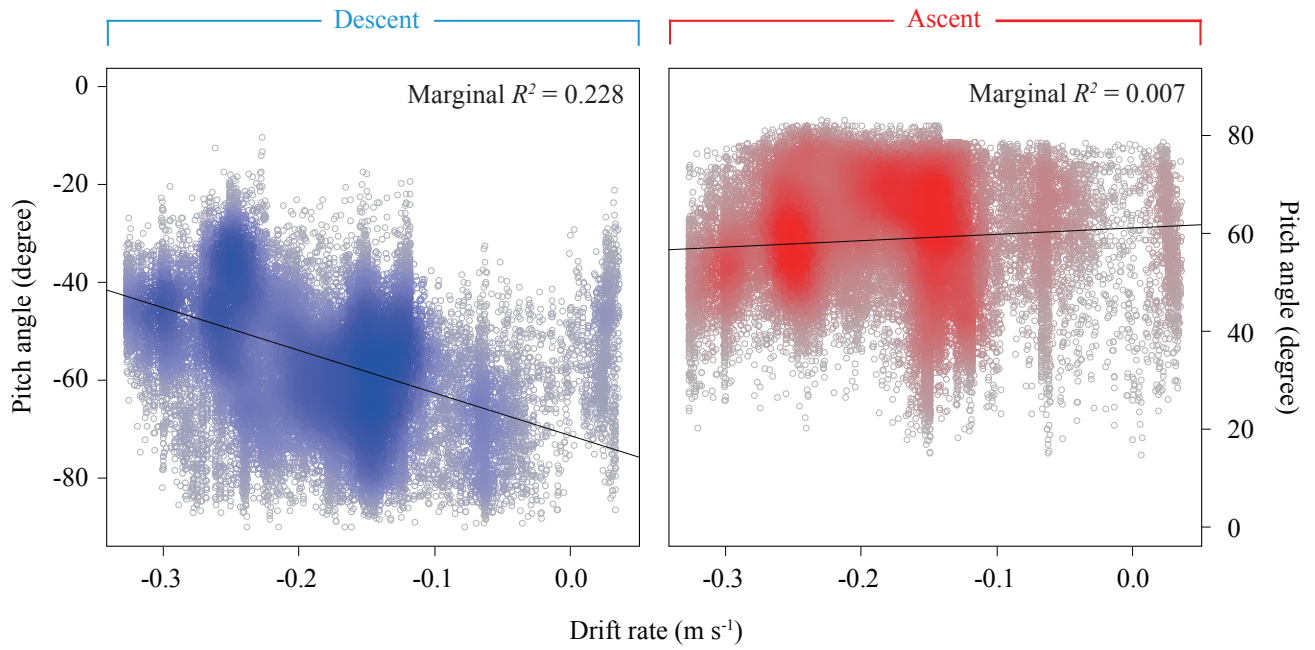


Figure 3.8. Pitch angle, plotted against drift rates for all 8 individuals. Left and right panels show values during descent and ascent phases of each foraging dive, respectively. In both panels, color gradients (blue or red for descent or ascent phase, respectively), indicate the local densities at each point. Black lines show the most parsimonious models (generalized linear mixed model: GLMM) having the lowest  $AIC_c$  values. Marginal  $R^2$  of the model was shown at the top of each panel.

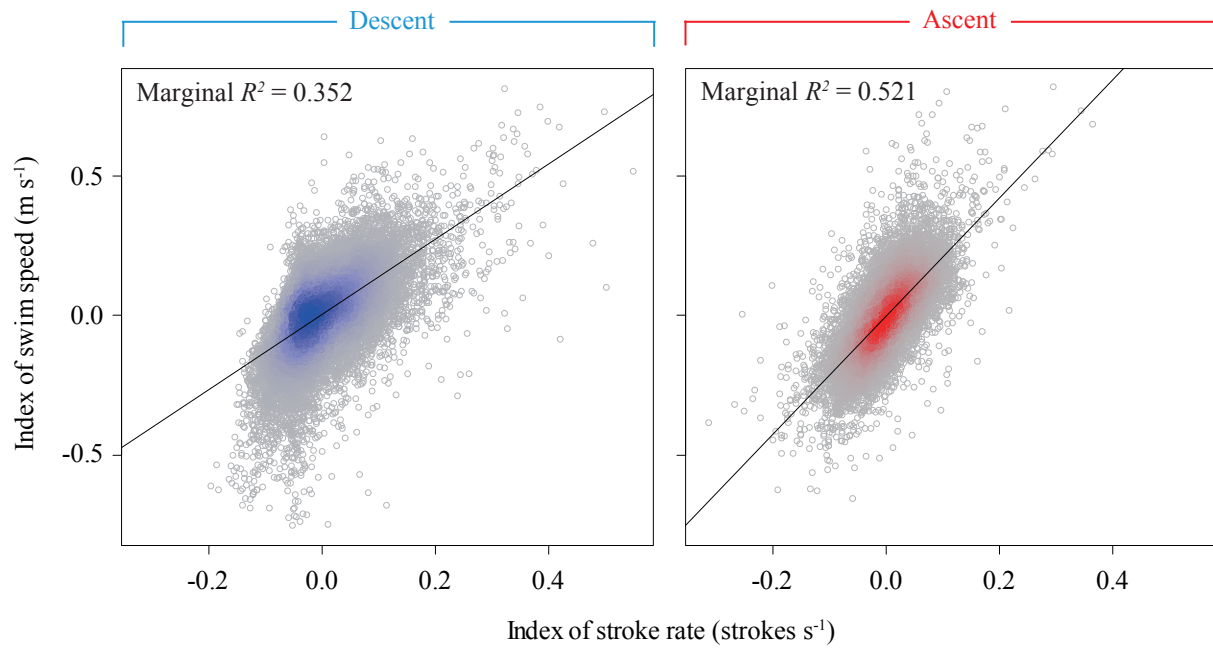


Figure 3.9. The relationship between index of swim speed and stroke rate for all 8 individuals. Left and right panels show values during descent and ascent phases of each foraging dive, respectively. In both panels, color gradients (blue or red for descent or ascent phase, respectively) indicate the local densities at each point. Black lines show the most parsimonious models (generalized linear mixed model: GLMM) having the lowest AIC<sub>c</sub> values. Marginal  $R^2$  of the model was shown at the top of each panel.

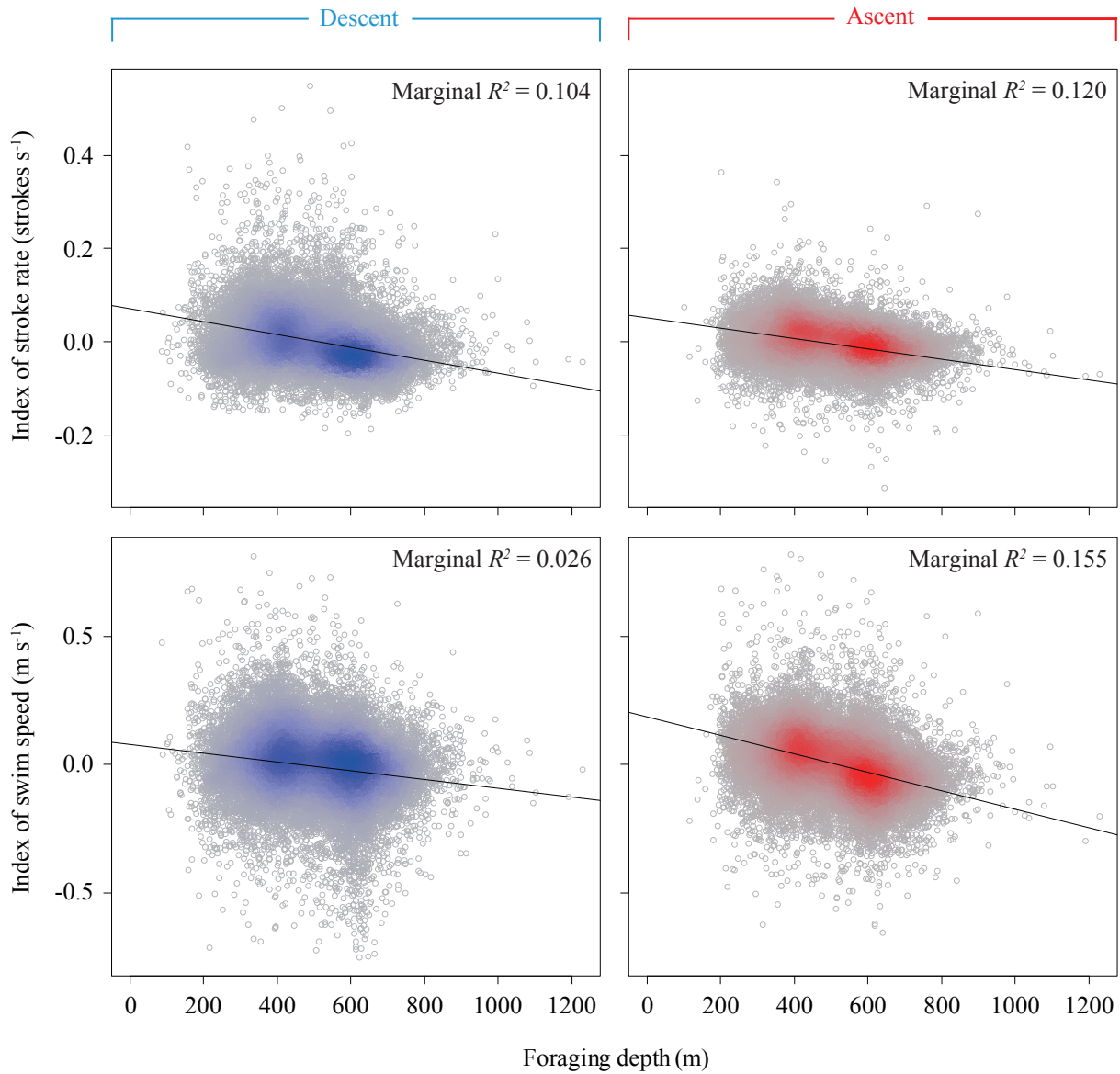


Figure 3.10. Index of stroke rate and swim speed, plotted against foraging depth for all 8 individuals. Left and right panels show values during descent and ascent phases of each foraging dive, respectively. In all panels, color gradients (blue or red for descent or ascent phase, respectively) indicate the local densities at each point. Black lines show the most parsimonious models (generalized linear mixed model: GLMM) having the lowest  $AIC_c$  values. Marginal  $R^2$  of the model was shown at the top of each panel.

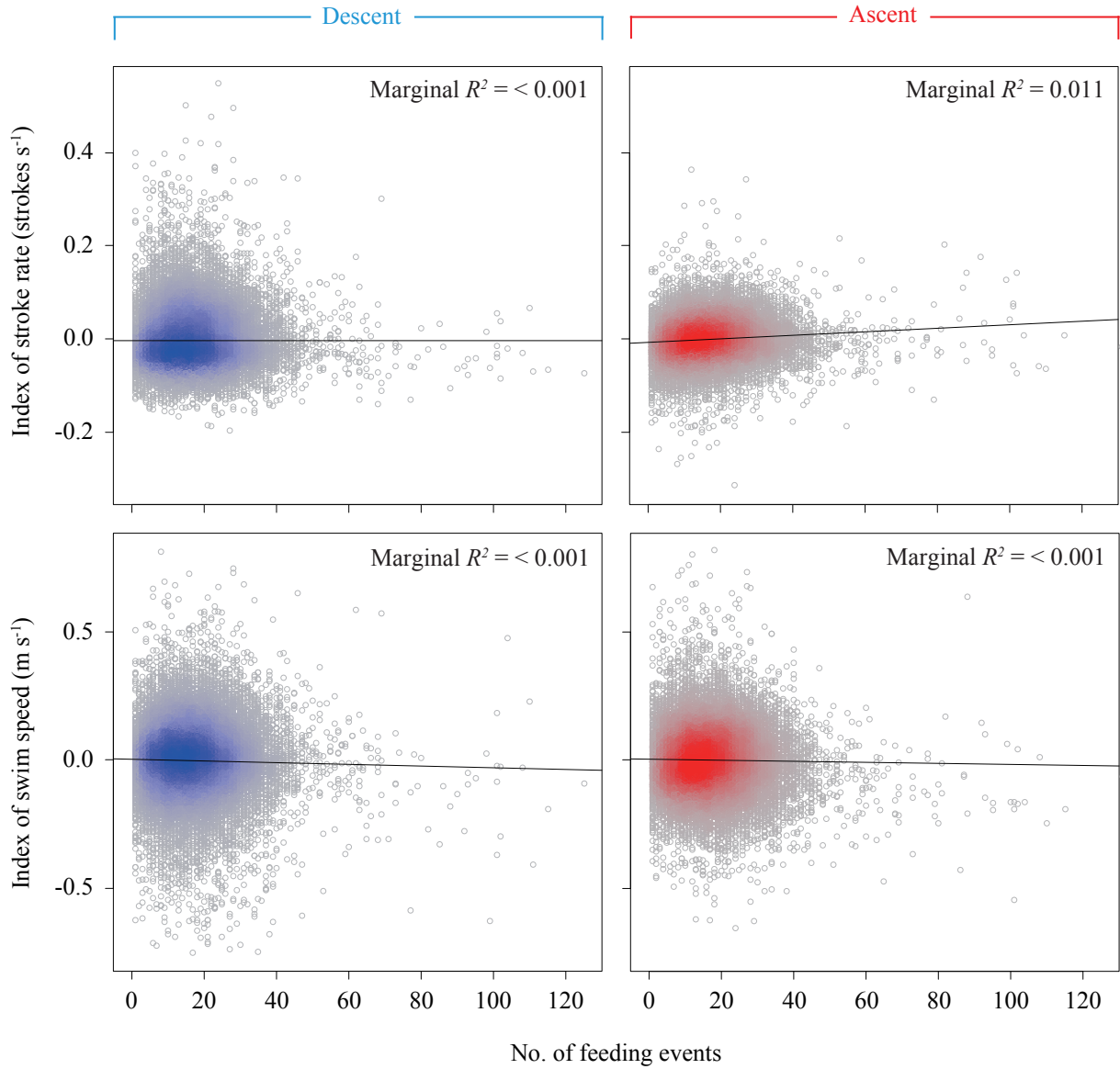


Figure 3.11. Index of stroke rate and swim speed, plotted against number of feeding events for all 8 individuals. Left and right panels show values during descent and ascent phases of each foraging dive, respectively. In all panels, color gradients (blue or red for descent or ascent phase, respectively) indicate the local densities at each point. Black lines show the most parsimonious models (generalized linear mixed model: GLMM) having the lowest  $AIC_c$  values. Marginal  $R^2$  of the model was shown at the top of each panel.

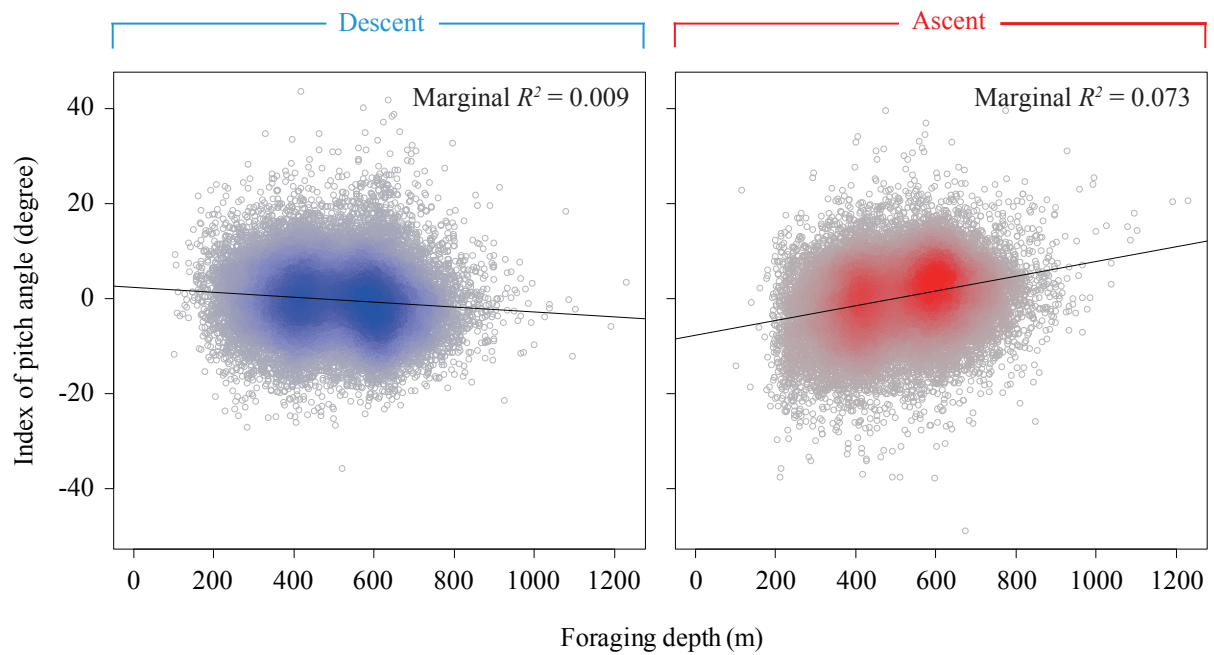


Figure 3.12. Index of pitch angle, plotted against foraging depth for all 8 individuals. Left and right panels show values during descent and ascent phases of each foraging dive, respectively. In both panels, color gradients (blue or red for descent or ascent phase, respectively) indicate the local densities at each point. Black lines show the most parsimonious models (generalized linear mixed model: GLMM) having the lowest  $AIC_c$  values. Marginal  $R^2$  of the model was shown at the top of each panel.

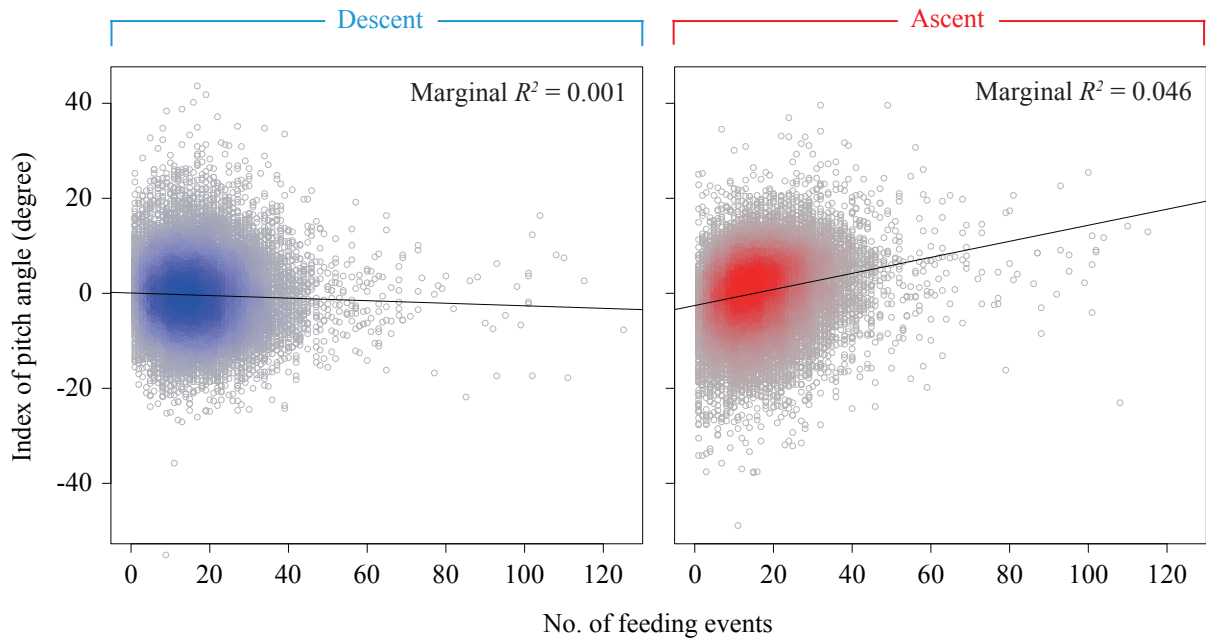


Figure 3.13. Index of pitch angle, plotted against number of feeding events for all 8 individuals. Left and right panels show values during descent and ascent phases of each foraging dive, respectively. In both panels, color gradients (blue or red for descent or ascent phase, respectively) indicate the local densities at each point. Black lines show the most parsimonious models (generalized linear mixed model: GLMM) having the lowest  $AIC_c$  values. Marginal  $R^2$  of the model was shown at the top of each panel.

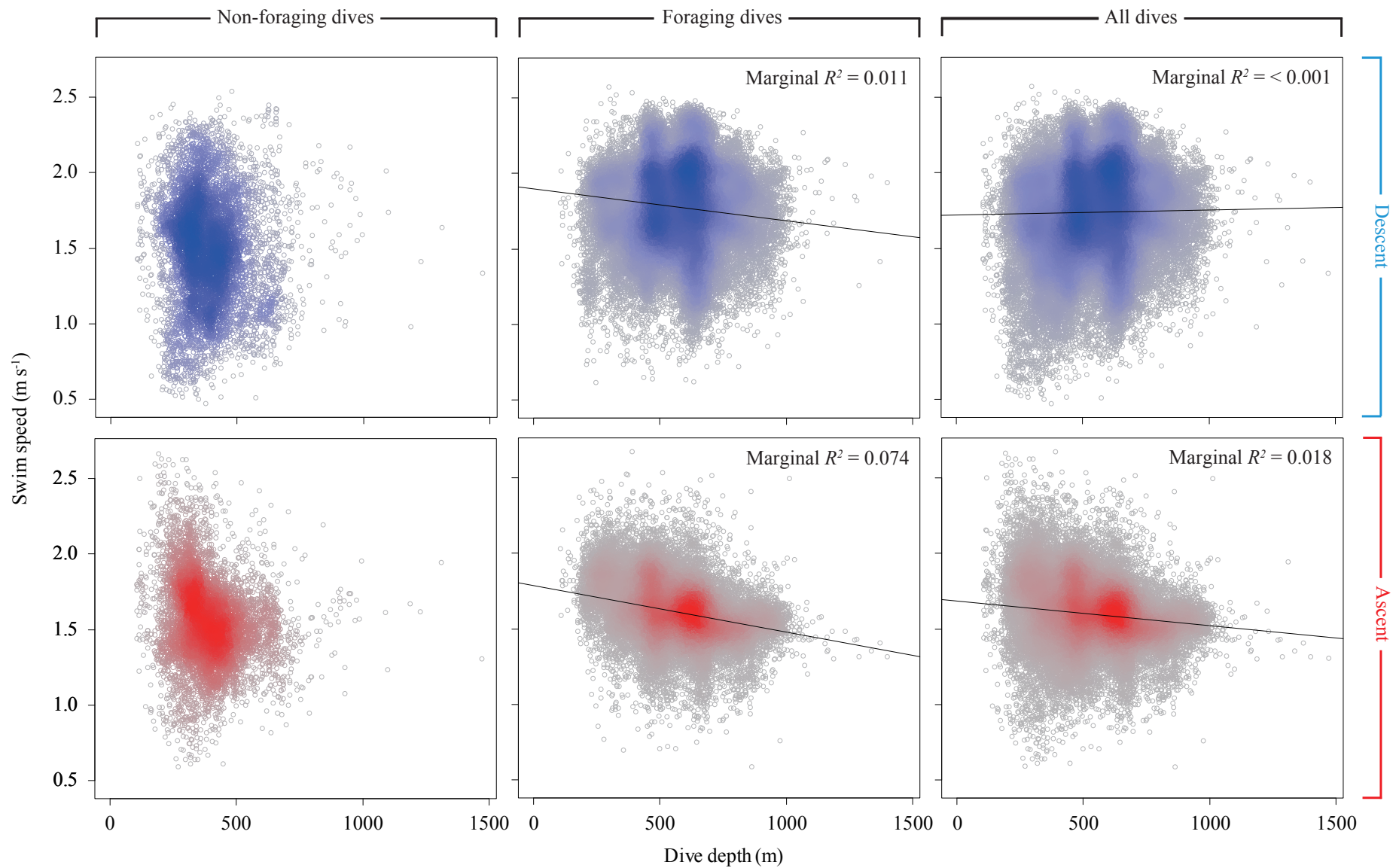


Figure 3.14. The relationship between swim speed and dive depth for all 8 individuals. Upper and lower panels show values during descent and ascent phases, respectively, during non-foraging dives (left panels), foraging dives (middle panels) and all dives (i.e. non-foraging dives + foraging dives; right panels). Color gradient (blue or red for descent or ascent phase, respectively) indicates the local densities at each point. In the panels for foraging and all dives, black lines show the most parsimonious models (generalized linear mixed model: GLMM) having the lowest  $AIC_c$  values. Marginal  $R^2$  of the model was shown at the top of each panel.

Each mean swim speed during both descent and ascent phases was calculated by including swim speeds at over 10 m depths (i.e. including shallower depths). Note that dive depth was linearly correlated with foraging depth (Figure 3.2). Also, note that swim speeds varied widely over the range of dive depths, especially during descent phase, where the relationship between descent swim speed and dive depth was overturned when I included only foraging dives (negative relationship) or included all dives (positive relationship).

## **CHAPTER 4. GENERAL DISCUSSION**

### **4.1. LONG-TERM ACCELEROMETRY: A POWERFUL TOOL TO STUDY SWIMMING AND FORAGING STRATEGIES OF A VARIETY OF FREE-RANGING MARINE ANIMALS**

In this thesis, I have presented the results of the close associations among seal buoyancy, swimming behaviour and foraging behaviour of female northern elephant seals during months-long oceanic foraging migrations, by long-term accelerometry technique that overcame technological limitations in previous methods of recording swimming behaviour and energetic costs of swimming under natural condition.

As I mentioned in Chapter 1, previous studies estimated the energetic costs of swimming using measurements of heart rates or isotope dilution rates, but these approaches have limitations in time resolution (Butler et al., 2004; Costa and Williams, 1999) and do not provide information on swimming behaviour. Alternatively, accelerometry with high sampling rates (usually  $> 10$  Hz) can estimate energetic costs of swimming along the behaviour (such as propulsive strokes, pitch angle and swim speed) in free-ranging marine animals at the fine scale (e.g. Sato et al., 2003; Watanuki et al., 2006), because the number of strokes and the dynamic acceleration caused by stroking correlate linearly with oxygen consumption in a variety of species (Elliott et al., 2013; Gleiss et al., 2010; Halsey et al., 2011; Williams et al., 2004; Wilson et al., 2006). However, accelerometry with high sampling rates limits the recording periods due to limitation in logger memory or battery power (Halsey et al., 2009), which had precluded us to investigate swimming behaviour in long distance migrants such as highly pelagic marine animals.

My long-term accelerometry technique overcame both the limitations in time resolution and recording period; the newly-developed accelerometer ‘Stroke Logger’ records number of strokes, together with depth and pitch angle that allow me to calculate swim speed ( $= \Delta \text{depth} / \sin \theta$ ), every 5 seconds for 150 days at maximum by using on-board data-processing algorithm. Consequently, I successfully tracked the changes in swimming behaviour and locomotor costs of swimming in relation to both the changes in biomechanical (Chapter 2: buoyancy) and ecological (Chapter 3: foraging depth) factors in elephant seals over the course of their months-long oceanic foraging migrations. These results suggest that long-term accelerometry technique is a powerful tool to study the swimming and foraging strategies of a variety of highly pelagic marine animals, although I should note that I could not obtain data for entire seven-month post-moulting foraging migrations even with Stroke Loggers (see Chapter 2 & 3). This implies that there is a room for improvement of recording devices to cover entire periods while they spent foraging at sea, probably allowing me to investigate their annual cycle strategies in the future.

## 4.2. THE LOCOMOTORY AND FORAGING BENEFITS OF BEING FAT: THE FUNCTIONS OF FAT STORES IN MARINE ANIMALS

In this thesis, I showed seal buoyancy affected both locomotor costs via reductions in propulsive activities and foraging gains via increased time spent foraging at depth, suggesting the locomotory and foraging benefits of achieving neutral buoyancy by being fat. These results suggest that fat stores have important functions in terms of not only thermoregulation and energy storage (Berta et al., 1999) but also locomotor and foraging activities in marine animals swimming with the effect of buoyancy. However, this is not the case for terrestrial animals, in

which generally getting fat increases the energetic cost of movement (Gosler et al., 1995), suggesting the opposite trend of marine animals to terrestrial animals in terms of reduced locomotor costs of movement by being fat.

While I examined the effect of buoyancy changes in elephant seals, my results are relevant to other marine animals whose body composition varies with the increase and decrease in fat stores over their long foraging migrations. For example, grey seals and New Zealand fur seals like elephant seals are aided by negative buoyancy during the descent phase (Beck et al., 2000; Page et al., 2005), suggesting that they passively glide on descent and stroke on ascent. However, right whales and deep-diving sperm whales are positively buoyant and stroke on descent and passively glide on ascent (Miller et al., 2004; Nowacek et al., 2001). Given that the parameters that govern the costs of locomotion are the same, I would expect that these species also have the foraging benefit of achieving neutral buoyancy by decreased locomotor costs of swimming and increased time spent foraging at depth.

#### 4.3. WHY DO NOT SEALS MAINTAIN NEUTRAL BUOYANCY WITH A CERTAIN AMOUNT OF FAT STORES?

Here, I suggested that neutral buoyancy is the best conditions in terms of locomotory costs and foraging time in elephant seals, but they were not always neutrally buoyant; in fact, they were negatively buoyant during most of the periods at sea (Figure 2.1 & 2.2). Why do not seals maintain neutral buoyancy with a certain amount of fat stores?

This question is closely related to their annual cycles. As I mentioned in Chapter 1, female elephant seals fast during one month on land twice a year: breeding and moulting seasons after long and short foraging migrations, respectively. During the fasting periods, they primarily rely

on fat stores as the source of energy supply to moult and breed, consequently losing large amount of fat stores, especially in the breeding season when they raise their pups in addition to maintain their own life activities (e.g. basal metabolism); female northern elephant seals lose approximately 28 and 58% of their fat stores over the entire moulting and breeding periods (Costa et al., 1986; Worthy et al., 1992). For these reasons, it should be inevitable to deviate from neutral buoyancy by losing fat stores on land, precluding them from maintaining neutral buoyancy over their annual cycles. However, the situation could be different in juvenile elephant seals that do not breed regardless of the sex (i.e. male or female), because they haul out for shorter periods and stay longer at sea for longer periods than adult seals (Le Boeuf and Laws, 1994). Juvenile seals are not constrained by reproduction in their annual cycles, and hence do not undergo the significant loss in body fat stores seen in adult females raising pups or adult males defending harems. This suggests the possibility to maintain neutral buoyancy over their annual cycles at young age, when growth and survivorship are crucial and would be aided by neutral buoyancy with increased foraging efficiency (Chapter 2) and maneuverability (to avoid predators without the effect of buoyancy), possibly related to their future reproductive success in a positive way.

#### 4.4. THE IMPLICATION OF THE TRADE-OFF BETWEEN REPRODUCTIVE BENEFITS ON LAND AND SWIMMING COSTS AT SEA

My results show that increasing fat stores by approaching neutral buoyancy have clear advantages in decreased locomotor cost of swimming at sea. Conversely, therefore, losing fat stores results in increased locomotor costs of swimming by deviating from neutral buoyancy. In contrast, on land, losing more fat stores by using more energy is beneficial for reproduction,

especially in capital breeding species such as elephant seals; pups grow faster and better when their mothers deliver more energy to them, demonstrating the clear fitness advantages of losing fat stores during reproduction on land (Crocker et al., 2001b; Le Boeuf and Laws, 1994). Therefore, I suggest that my results have an important implication of balancing the optimal amount of fat stores against reproduction on land and locomotor activities at sea. This raises the need for further investigations of annual and life cycle strategies of capital breeding species in the future, to examine the trade-off between reproductive benefits on land, where fat stores are reduced during lactation, and swimming costs at sea, where fat is stored while feeding on prey by way of energetically expensive swimming.

## **APPENDIX. VALIDATION OF MEASUREMENTS FROM STROKE LOGGER**

### **A.1. VALIDATION OF DETECTING STROKES**

I detected strokes by using Stroke Loggers that were programmed to process raw lateral accelerations and extract dynamic accelerations from raw lateral accelerations on board. Raw lateral accelerations often contain low frequency variations (i.e. static accelerations) that presumably relate to various turning and rolling movements (i.e., changes in posture) by seals (Sato et al., 2003). High-pass filtering has been applied to separate the static accelerations from raw lateral accelerations to obtain dynamic accelerations associated with propulsive activities (i.e. flipper strokes) of seals (e.g. Sato et al., 2003; Watanabe et al., 2006). In this study, I developed a simple on-board data-processing algorithm by using moving averages to obtain dynamic accelerations, instead of high-pass filtering algorithm, to reduce the battery consumption of loggers. Here, I describe the details of the algorithm and validate to detect strokes with the algorithm.

The details about the on-board data-processing algorithm are shown as Figure A.1. Static accelerations were separated from raw lateral accelerations (measured at 32 Hz: Figure A.1(b)) to obtain dynamic accelerations associated with propulsive activities (i.e. flipper strokes) of seals by following three steps below: (1) a moving average using 59 points from the raw lateral accelerations data was calculated to obtain static accelerations (associated with posture), (2) these static accelerations were subtracted from the raw lateral acceleration data to obtain dynamic accelerations (associated with propulsive activities) (Wilson et al., 2006), and (3) these dynamic accelerations were then filtered with a moving average window using three data points

to remove noise (e.g. Watanabe et al., 2006). These three steps gave me dynamic accelerations that closely matched those obtained by the high-pass filtering method (Figure A.1(c)), which has been applied to detect strokes in previous studies (e.g. Sato et al., 2003; Watanabe et al., 2006). Then, the dynamic accelerations obtained from the algorithm were used to detect each stroke (i.e. a cycle of swaying hind flippers), identified as an acceleration amplitude exceeding the threshold of 0.08 g within 2.5-second time windows (Figure A.1(c) & (d)). Finally, the resulting number of strokes were counted and recorded every five seconds in the Stroke Loggers.

Stroke Loggers were designed to record raw lateral accelerations (32 Hz) for 12 hours from the point where the seals firstly exceeded 900 m depth in their migrations. These raw lateral accelerations obtained from all 14 individuals (i.e. 168 hours including 424 dives in total, with a individual mean  $\pm$  s.d. of  $30.3 \pm 4.2$  dives) were used to show the variability of the algorithm to calculate number of strokes programmed in Stroke Loggers. The results are represented as Figure A.2 that shows the algorithm gave me number of strokes that closely matched those obtained by the high-pass filtering method (note that this algorithm is specific for elephant seals, and hence, another algorithm should be developed when this method will be applied for other species).

## A.2. VALIDATION OF CALCULATING SWIM SPEED

Swim speed was often calculated with the method of either the rotation of an external propeller (e.g. Sato et al., 2003) or the trigonometric function using the rate of depth change and pitch angle ( $\Delta\text{depth}/\sin\theta$ ) (e.g. Watanuki et al., 2003). In this study, I employed the trigonometric function to calculate swim speed with Stroke Logger. One weakness of the trigonometric function is that swim speed cannot be estimated when depth change rate ( $\Delta\text{depth}$ ) is small or pitch angle ( $\theta$ ) is shallow (Watanuki et al., 2003). To validate the use of the

trigonometric function in elephant seals, I attached a data logger with an external propeller (W1000L-3MPD3GT, Little Leonardo Co., Tokyo, Japan; diameter 26 mm, length 178 mm and 146 g) together with a Stroke Logger to one individual (seals ID: U954, during post-breeding migration). In calculating swim speed using the trigonometric function, anomalous swim speeds greater than  $3 \text{ m s}^{-1}$ , possibly resulted from errors because of small depth change rate ( $\Delta\text{depth}$ ) or shallow pitch angle ( $\theta$ ), were excluded from the further analysis (e.g. Watanuki et al., 2003), since the elephant seals rarely swim at over  $3 \text{ m s}^{-1}$  (Hassrick et al., 2007). This is also supported by my swim speed data obtained from W1000L-3MPD3GT with propeller rotations, which showed that there was no data point showing swim speed over  $3 \text{ m s}^{-1}$  during both descent and ascent phases of all dives ( $n = 476$  dives) during its recording durations (10.5 days). Then, I compared swim speeds obtained from two methods during both descent and ascent phases of three types of dives (i.e. foraging dives, drift dives and any other dives with no feeding events; see Chapter 3 for more detail about dive types) (Figure A.3 & A.4).

Results are represented as Figure A.4, showing the frequency distribution of values of swim speed calculated by propeller rotations divided by swim speed calculated using a trigonometric function (i.e. the value should be 1 if there is no deviation between swim speeds obtained from those two different methods). In all three dive types, the average values were around 1, showing the validity of calculating swim speed by using the trigonometric function with Stroke Loggers, although the values appears to be more variable in drift dives and any other dives with no feeding events than foraging dives (Figure A.4). Hence, my swim speed data are comparable with those from other studies that calculated swim speed using propeller rotations in elephant seals (Hassrick et al., 2007; Hindell and Lea, 1998) (please see the section of *Discussion* in Chapter 3).

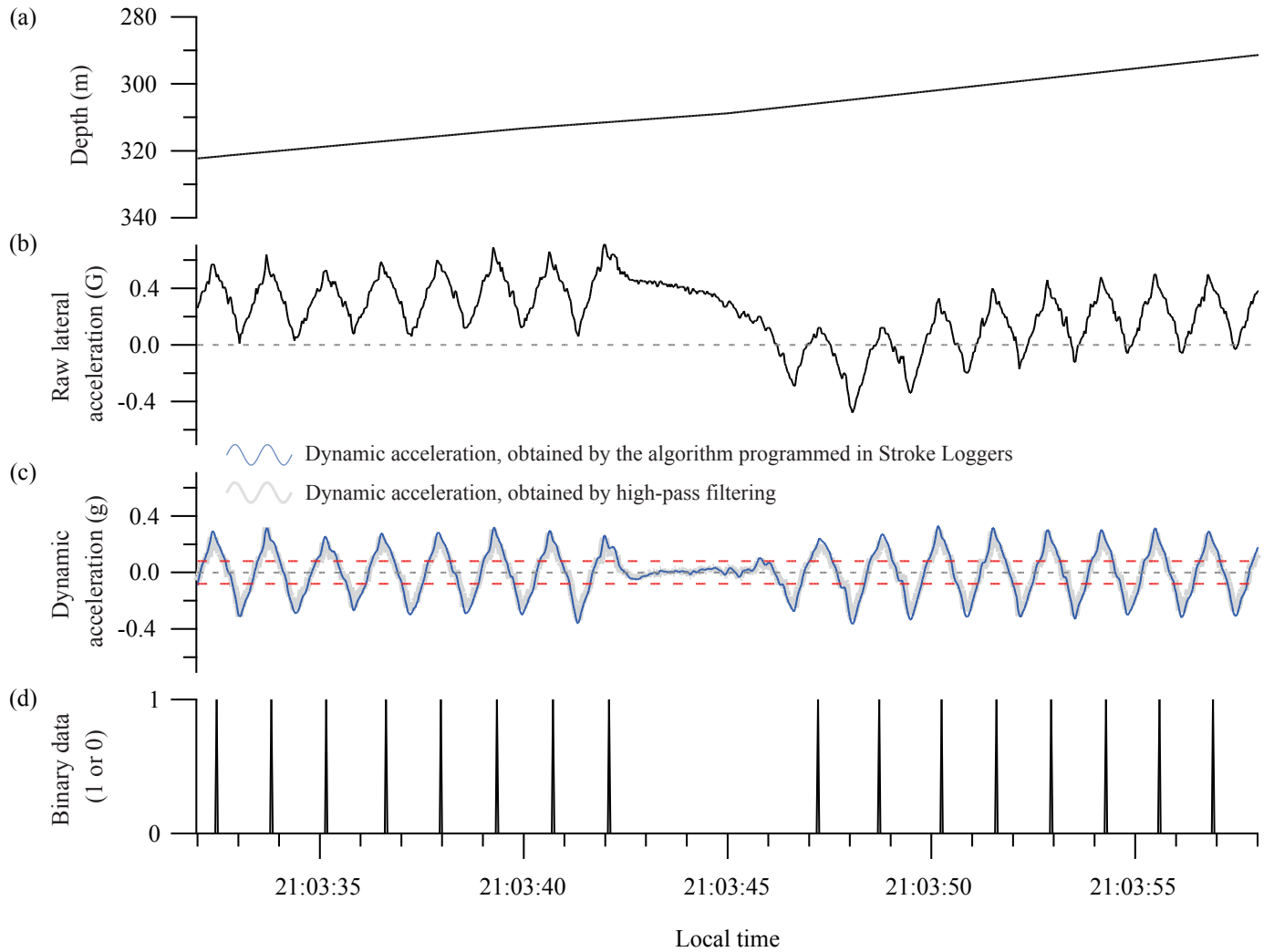


Figure A.1. The detail of the on-board data processing algorithm programmed in Stroke Loggers to detect strokes: an example during ascent phase. (a) Depth (black line). (b) Raw lateral accelerations measured at 32 Hz (black line). (c) Dynamic accelerations obtained by the algorithm programmed in Stroke Loggers (blue line) and high-pass filtering method (gray line). Each stroke was identified as cyclic oscillations in lateral acceleration signals with amplitude threshold of 0.08 G (red dotted lines) within 2.5-second time windows. (d) Binary data showing the occurrence of strokes.

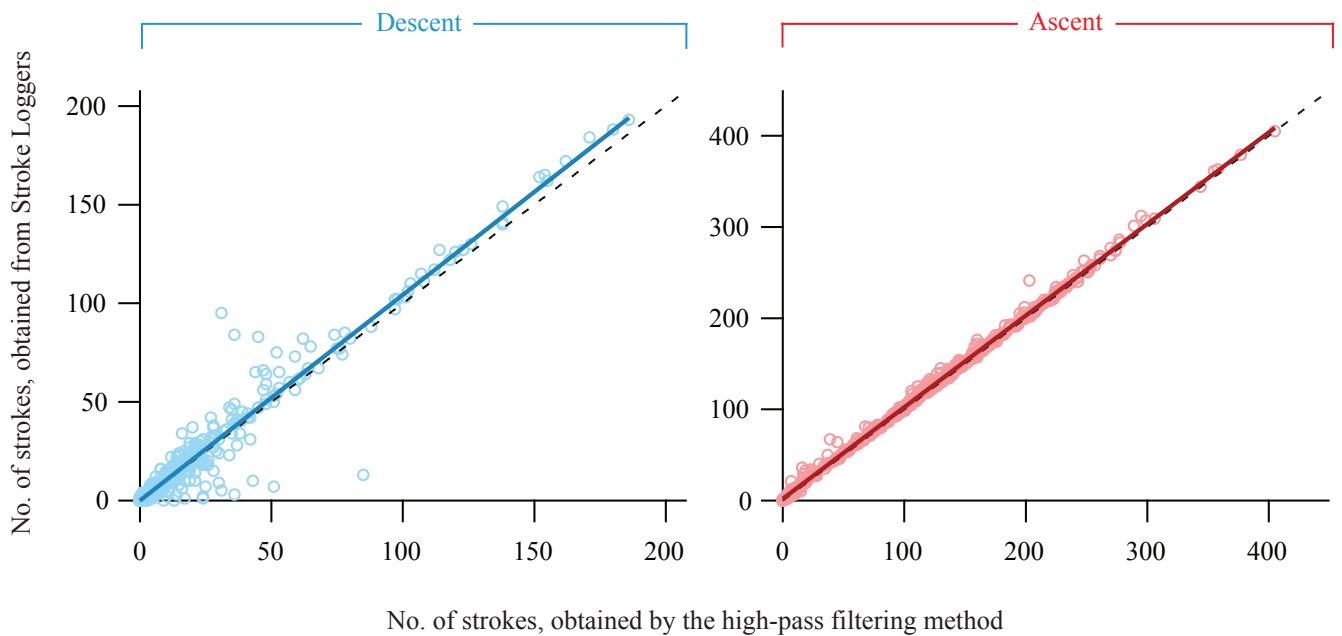


Figure A.2. The relationship between number of strokes obtained from Stroke Loggers and by the high-pass filtering method. Vertical axis indicates number of strokes obtained from Stroke Loggers with the on-board data processing algorithm (see Figure A.1). Horizontal axis indicates number of strokes obtained by high-pass filtering method (Sato et al. 2003; Watanabe et al. 2006) with the amplitude threshold of 0.08 G (the same value as Stroke Loggers: see Figure A.1) to detect each stroke for all 14 individuals. Open blue and red circles represent number of strokes during descent and ascent phase of each dive, respectively. Dotted black lines represent  $y = x$ . Blue and red lines represent regression lines obtained by the least-squares method for descent ( $y = 1.043x - 0.026$ , slope coefficient = 0.971) and ascent ( $y = 1.004x + 2.094$ , slope coefficient = 0.999) phase. Regression lines were fitted to all 14 individual data points pooled. Also, number of strokes was calculated when seals were over 100 m depth. Note that each stroke was detected as a cycle of swaying hind flippers.

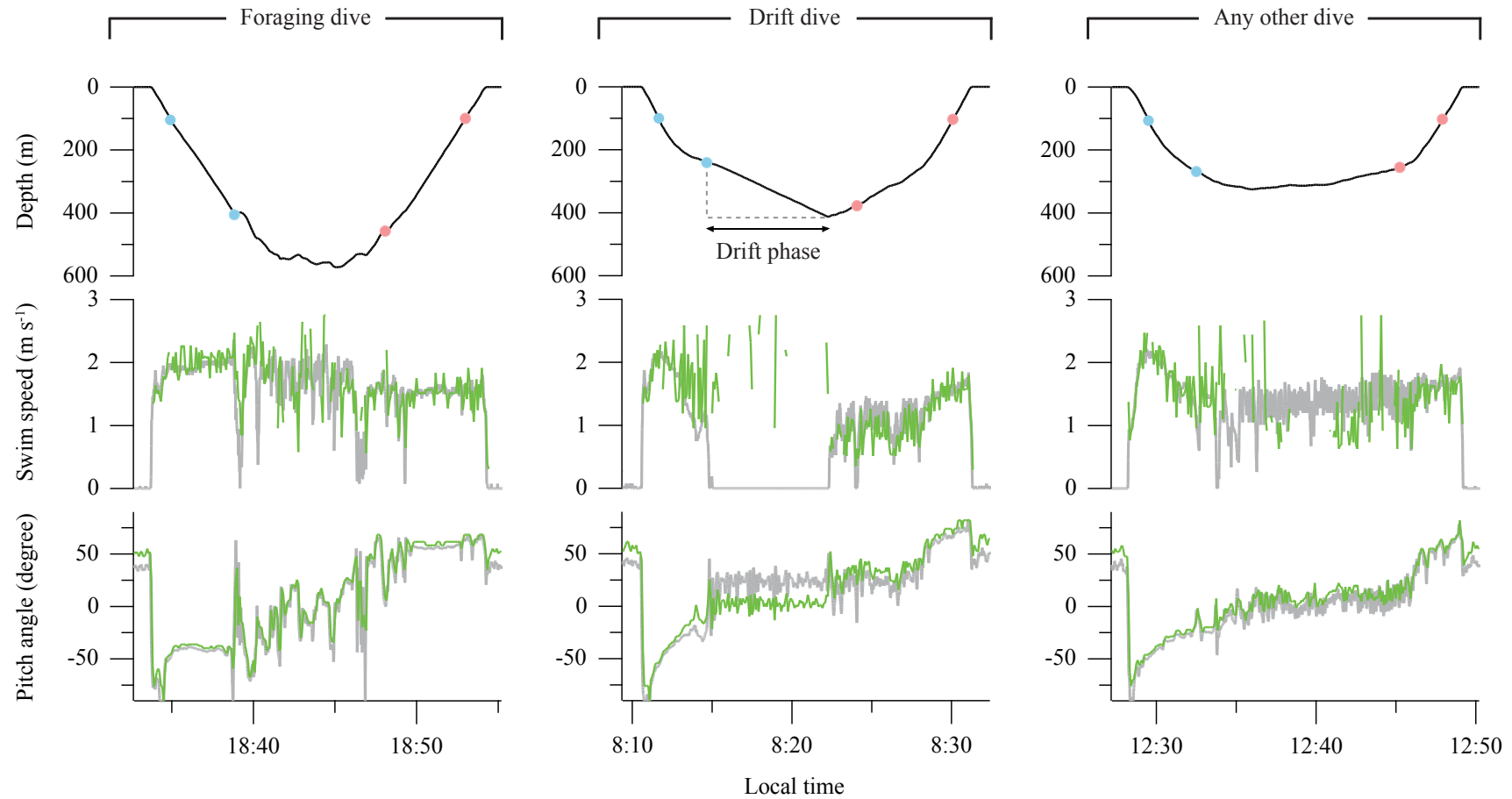


Figure A3. Examples of time series for depth (top panels), swim speed (middle row panels) and pitch angle (bottom panels) during a foraging dive (left panels), a drift dive (middle column panels) and any other dive with no feeding events (right panels) (see Chapter 3 for more detail about dive types). Data were obtained from an individual (seal ID: U954, during post-breeding migration). In the top panels, filled circles represent the points of start and end of descent (blue) and ascent (red) phases. Note that start of descent (end of ascent) was the first (last) point where depth was over 100 m. In the middle panels, grey and green lines show swim speeds calculated with the method of the rotation of an external propeller (with W1000L-3MPD3GT) and the trigonometric function ( $\angle \text{depth} / \sin \theta$ ; with Stroke Logger), respectively. In the bottom panel, gray and green lines represent pitch angles obtained from W1000L-3MPD3GT and Stroke Logger, respectively.

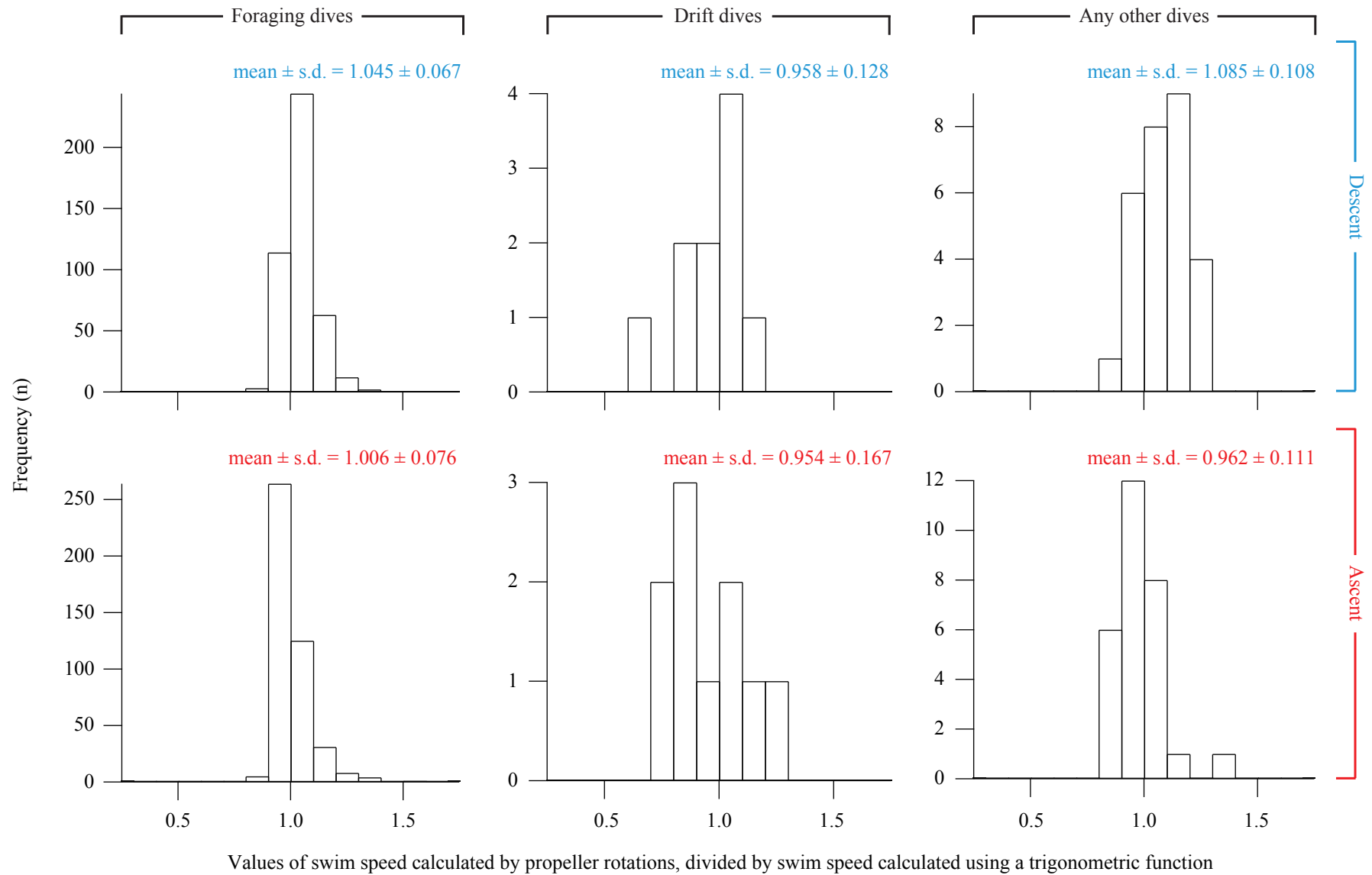


Figure A.4. The frequency distribution of swim speed calculated by propeller rotations, divided by swim speed calculated using a trigonometric function ( $\angle \text{depth} / \sin \theta$ ) for an individual (U954) that had two types of data loggers: W1000L-3MPD3GT (with propeller sensor) and Stroke Logger. Upper and lower panels show frequency distributions during descent and ascent phases, respectively, of foraging dives ( $n = 438$ ; left panels), drift dives ( $n = 10$ ; middle panels) and any other dives with no feeding events ( $n = 28$ ; right panels) during recording periods of W1000L-3MPD3GT (10.5 days). Mean  $\pm$  s.d. was shown at the top of each panel.

## ACKNOWLEDGEMENTS

Foremost, I would like to express my sincere gratitude to my supervisor Dr. Akinori Takahashi for the continuous support of my Ph.D study and research, for his patience, motivation and immense knowledge. I am also deeply grateful to my co-supervisor Dr. Yuuki Watanabe for his fruitful comments and suggestions on my research.

Besides my supervisors, I would like to thank the rest of my thesis committee: Dr. Katsufumi Sato, Dr. Yoshihisa Mori and Dr. Tsuneo Odate, for their encouragement, insightful comments, and thoughtful questions.

In addition, I would like to extend my gratitude to Dr. Yasuhiko Naito for his motivation, enthusiasm and kind words of encouragement. I also would like to show my appreciation to Dr. Daniel P. Costa at University of California Santa Cruz (UCSC) for his insightful comments on the manuscript, kindness and continuous support to give me great opportunities for staying at his laboratory to work with northern elephant seals under NMFS permit no. 1463 issued to him by the Institutional Animal Care and Use Committee (IACUC) at UCSC.

My sincere thanks also goes to all of my fellow colleagues in Japan and the members of Costa Lab in UCSC, for the stimulating discussions, for the kind help to babysit me at the field, and for all the fun we have had in the last five years.

Last but not the least, I wish to express special thanks to my future wife even if I am not sure if I have met already or have not met yet, for letting me dream a beautiful dream where *“We’re both traveling through time together every day of our lives, in which I love her everyday of the week and twice on Sundays; All I can do is do my best to relish this remarkable ride with her”* (Curtis, 2013; Eisner et al., 2002).

## REFERENCES

- Alexander, R. M.** (2003). *Principles of Animal Locomotion*. Princeton and Oxford: Princeton University Press.
- Aoki, K., Watanabe, Y. Y., Crocker, D. E., Robinson, P. W., Biuw, M., Costa, D. P., Miyazaki, N., Fedak, M. A. and Miller, P. J. O.** (2011). Northern elephant seals adjust gliding and stroking patterns with changes in buoyancy: validation of at-sea metrics of body density. *J. Exp. Biol.* **214**, 2973–2987.
- Beck, C. A., Bowen, W. D. and Iverson, S. J.** (2000). Seasonal changes in buoyancy and diving behaviour of adult grey seals. *J. Exp. Biol.* **203**, 2323–2330.
- Berta, A., Sumich, J. L. and Kovacs, K. M.** (1999). *Marine mammals: Evolutionary biology*. Academic Press.
- Biuw, M., McConnel, B., Bradshaw, C. J. A., Burton, H. and Fedak, M.** (2003). Blubber and buoyancy: monitoring the body condition of free-ranging seals using simple dive characteristics. *J. Exp. Biol.* **206**, 3405–3423.
- Bowen, W. D., Read, A. J. and Estes, J. A.** (2002). Feeding ecology. In *Marine Mammal Biology: An Evolutionary Approach* (ed. Hoelzel, A. R.), pp. 217–246. Wiley-Blackwell.
- Boyd, I. L.** (1997). The behavioural and physiological ecology of diving. *Trends Ecol. Evol.* **12**, 213–217.
- Butler, P. J., Green, J. A., Boyd, I. L. and Speakman, J. R.** (2004). Measuring metabolic rate in the field: the pros and cons of the doubly labelled water and heart rate methods. *Funct. Ecol.* **18**, 168–183.
- Carbone, C. and Houston, A. I.** (1994). Patterns in the diving behaviour of the pochard, *Aythya ferina*: a test of an optimality model. *Anim. Behav.* **48**, 457–465.
- Carbone, C., de Leeuw, J. J. and Houston, A. I.** (1996). Adjustments in the diving time budgets of tufted duck and pochard: is there evidence for a mix of metabolic pathways? *Anim. Behav.* **51**, 1257–1268.

- Charnov, E. L.** (1976). Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* **9**, 129–136.
- Cherel, Y., Ducatez, S., Fontaine, C., Richard, P. and Guinet, C.** (2008). Stable isotopes reveal the trophic position and mesopelagic fish diet of female southern elephant seals breeding on the Kerguelen Islands. *Mar. Ecol. Prog. Ser.* **370**, 239–247.
- Cornick, L. A., Inglis, S. D., Willis, K. and Horning, M.** (2006). Effects of increased swimming costs on foraging behavior and efficiency of captive Steller sea lions: Evidence for behavioral plasticity in the recovery phase of dives. *J. Exp. Mar. Biol. Ecol.* **333**, 306–314.
- Costa, D. P.** (1991). Reproductive and foraging energetics of pinnipeds: Implications for life history patterns. In *The Behavior of Pinnipeds* (ed. Renouf, D.), pp. 301–344. London: Chapman & Hall.
- Costa, D. P. and Gales, N. J.** (2000). Foraging energetics and diving behavior of lactating New Zealand sea lions, *Phocarctos hookeri*. *J. Exp. Biol.* **203**, 3655–3665.
- Costa, D. P. and Gales, N. J.** (2003). Energetics of a benthic diver: seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. *Ecol. Monogr.* **73**, 27–43.
- Costa, D. P. and Williams, T. M.** (1999). Marine mammal energetics. In *Biology of Marine Mammals* (ed. Reynolds, J. and Twiss, J.), pp. 176–217. Washington, DC.: Smithsonian Institution Press.
- Costa, D. P., Le Boeuf, B. J., Huntley, A. C. and Ortiz, C. L.** (1986). The energetics of lactation in the northern elephant seal, *Mirounga angustirostris*. *J. Zool.* **209**, 21–33.
- Crocker, D. E., Le Boeuf, B. J. and Costa, D. P.** (1997). Drift diving in female northern elephant seals: implications for food processing. *Can. J. Zool.* **75**, 27–39.
- Crocker, D. E., Gales, N. J. and Costa, D. P.** (2001a). Swimming speed and foraging strategies of New Zealand sea lions (*Phocarctos hookeri*). *J. Zool.* **254**, 267–277.
- Crocker, D. E., Williams, J. D., Costa, D. P. and Le Boeuf, B. J.** (2001b). Maternal traits and reproductive effort in northern elephant seals. *Ecology* **82**, 3541–3555.
- Curtis, R.** (2013). *About Time*. UK: Universal Pictures International (UPI).

- Davis, R. W.** (2014). A review of the multi-level adaptations for maximizing aerobic dive duration in marine mammals: from biochemistry to behavior. *J. Comp. Physiol. B* **184**, 23–53.
- Davis, R. W. and Weihs, D.** (2007). Locomotion in diving elephant seals: physical and physiological constraints. *Phil. Trans. R. Soc. B* **362**, 2141–50.
- Davis, R. W., Williams, T. M. and Kooyman, G. L.** (1985). Swimming metabolism of yearling and adult Harbor seals *Phoca vitulina*. *Physiol. Zool.* **58**, 590–596.
- Dingle, H.** (1996). *Migration: The Biology of Life on the Move*. New York: Oxford University Press.
- Eisner, B., Alcalá, F. E., Fawcett, J., Hooper, T., Kagan, J., Katleman, M., Mimica-Gezzan, S., Spicer, B., Woolnough, J. and Wright, T. J.** (2002). *Taken*. USA: DreamWorks Television.
- Elliott, K. H., Le Vaillant, M., Kato, A., Speakman, J. R. and Ropert-Coudert, Y.** (2013). Accelerometry predicts daily energy expenditure in a bird with high activity levels. *Biol. Lett.* **9**, 20120919.
- Fedak, M. A., Lovell, P. and Grant, S. M.** (2001). Two approaches to compressing and interpreting time-depth information as collected by time-depth recorders and satellite-linked data recorders. *Mar. Mammal Sci.* **17**, 94–110.
- Feldkamp, S. D.** (1987). Swimming in the California sea lion: morphometrics, drag and energetics. *J. Exp. Biol.* **131**, 117–135.
- Gallon, S. L., Sparling, C. E., Georges, J.-Y., Fedak, M. A., Biuw, M. and Thompson, D.** (2007). How fast does a seal swim? Variations in swimming behaviour under differing foraging conditions. *J. Exp. Biol.* **210**, 3285–3294.
- Gleiss, A. C., Dale, J. J., Holland, K. N. and Wilson, R. P.** (2010). Accelerating estimates of activity-specific metabolic rate in fishes: Testing the applicability of acceleration data-loggers. *J. Exp. Mar. Biol. Ecol.* **385**, 85–91.
- Gosler, A. G., Greenwood, J. J. D. and Perrins, C.** (1995). Predation risk and the cost of being fat. *Nature* **377**, 621–623.

- Guinet, C., Vacquié-Garcia, J., Picard, B., Bessigneul, G., Lebras, Y., Dragon, A. C., Viviant, M., Arnould, J. P. Y. and Bailleul, F.** (2014). Southern elephant seal foraging success in relation to temperature and light conditions: insight into prey distribution. *Mar. Ecol. Prog. Ser.* **499**, 285–301.
- Halsey, L. G., Green, J. A., Wilson, R. P. and Frappell, P. B.** (2009). Accelerometry to estimate energy expenditure during activity: best practice with data loggers. *Physiol. Biochem. Zool.* **82**, 396–404.
- Halsey, L. G., Shepard, E. L. C. and Wilson, R. P.** (2011). Assessing the development and application of the accelerometry technique for estimating energy expenditure. *Comp. Biochem. Physiol. A* **158**, 305–314.
- Hassrick, J., Crocker, D. E., Zeno, R., Blackwell, S., Costa, D. P. and Le Boeuf, B. J.** (2007). Swimming speed and foraging strategies of northern elephant seals. *Deep-Sea Res. II* **54**, 369–383.
- Hassrick, J. L., Crocker, D. E., Teutschel, N. M., McDonald, B. I., Robinson, P. W., Simmons, S. E. and Costa, D. P.** (2010). Condition and mass impact oxygen stores and dive duration in adult female northern elephant seals. *J. Exp. Biol.* **213**, 585–592.
- Hassrick, J. L., Crocker, D. E. and Costa, D. P.** (2013). Effects of maternal age and mass on foraging behaviour and foraging success in the northern elephant seal. *Funct. Ecol.* **27**, 1055–1063.
- Hays, G. C., Hochscheid, S., Broderick, A. C., Godley, B. J. and Metcalfe, J. D.** (2000). Diving behaviour of green turtles: dive depth, dive duration and activity levels. *Mar. Ecol. Prog. Ser.* **208**, 297–298.
- Hays, G. C., Marshall, G. J. and Seminoff, J. A.** (2007). Flipper beat frequency and amplitude changes in diving green turtles, *Chelonia mydas*. *Mar. Biol.* **150**, 1003–1009.
- Hedd, A., Gales, R. and Renouf, D.** (1997). Inter-annual consistency in the fluctuating energy requirements of captive harp seals *Phoca groenlandica*. *Polar Biol.* **18**, 311–318.
- Hindell, M. A. and Lea, M.** (1998). Heart rate, swimming speed, and estimated oxygen consumption of a free-ranging southern elephant seal. *Physiol. Zool.* **71**, 74–84.

- Houston, A. I. and Carbone, C.** (1992). The optimal allocation of time during the diving cycle. *Behav. Ecol.* **3**, 255–265.
- Irigoin, X., Klevjer, T. A., Røstad, A., Martinez, U., G.Boyra, Acuña, J. L., Bode, A., Echevarria, F., Gonzalez-Gordillo, J. I., Hernandez-Leon, S., et al.** (2014). Large mesopelagic fishes biomass and trophic efficiency in the open ocean. *Nat. Commun.* **5**, 3271.
- Kramer, D. L.** (1988). The behavioral ecology of air breathing by aquatic animals. *Can. J. Zool.* **66**, 89–94.
- Le Boeuf, B. J. and Laws, R. M.** (1994). *Elephant Seals: Population Ecology, Behavior, and Physiology*. University of California Press.
- Le Boeuf, B. J., Costa, D. P., Huntley, A. C. and Feldkamp, S. D.** (1988). Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. *Can. J. Zool.* **66**, 446–458.
- Le Boeuf, B. J., Crocker, D. E., Costa, D. P., Blackwell, S. B., Webb, P. M. and Houser, D. S.** (2000). Foraging ecology of northern elephant seals. *Ecol. Monogr.* **70**, 353–382.
- Lovvorn, J. R.** (2001). Upstroke thrust, drag effects, and stroke-glide cycles in wing-propelled swimming by birds. *Amer. Zool.* **41**, 154–165.
- Lovvorn, J. R., Watanuki, Y., Kato, A., Naito, Y. and Liggins, G. A.** (2004). Stroke patterns and regulation of swim speed and energy cost in free-ranging Brünnich's guillemots. *J. Exp. Biol.* **207**, 4679–4695.
- McDonald, B. I. and Ponganis, P. J.** (2012). Lung collapse in the diving sea lion: hold the nitrogen and save the oxygen. *Biol. Lett.*
- Miller, P. J. O., Johnson, M. P., Tyack, P. L. and Terray, E. A.** (2004). Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. *J. Exp. Biol.* **207**, 1953–1967.
- Miller, P. J. O., Biuw, M., Watanabe, Y. Y., Thompson, D. and Fedak, M. A.** (2012). Sink fast and swim harder! Round-trip cost-of-transport for buoyant divers. *J. Exp. Biol.* **215**, 3622–3630.

- Mitani, Y., Andrews, R. D., Sato, K., Kato, A., Naito, Y. and Costa, D. P.** (2010). Three-dimensional resting behaviour of northern elephant seals: drifting like a falling leaf. *Biol. Lett.* **6**, 163–6.
- Moore, F. D., Olsen, K. H., McMurray, J. D., Parker, H. V., Ball, M. R. and Boyden, M. C.** (1963). *The Body Cell Mass and its Supporting Environment: Body Composition in Health and Disease*. Philadelphia, PA: W. B. Saunders.
- Mori, Y. and Boyd, I. L.** (2004). The behavioral basis for nonlinear functional responses and optimal foraging in Antarctic fur seals. *Ecology* **85**, 398–410.
- Mori, Y., Takahashi, A., Mehlum, F. and Watanuki, Y.** (2002). An application of optimal diving models to diving behaviour of Brünnich’s guillemots. *Anim. Behav.* **64**, 739–745.
- Naito, Y., Costa, D. P., Adachi, T., Robinson, P. W., Fowler, M. and Takahashi, A.** (2013). Unravelling the mysteries of a mesopelagic diet: a large apex predator specializes on small prey. *Funct. Ecol.* **27**, 710–717.
- Nakagawa, S. and Schielzeth, H.** (2013). A general and simple method for obtaining  $R^2$  from generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**, 133–142.
- Nowacek, D. P., Johnson, M. P., Tyack, P. L., Shorter, K. A., McLellan, W. A. and Pabst, D. A.** (2001). Buoyant balaenids: the ups and downs of buoyancy in right whales. *Proc. R. Soc. B* **268**, 1811–1816.
- Okuyama, J., Kataoka, K., Kobayashi, M., Abe, O., Yoseda, K. and Arai, N.** (2012). The regularity of dive performance in sea turtles: a new perspective from precise activity data. *Anim. Behav.* **84**, 349–359.
- Page, B., McKenzie, J., Hindell, M. A. and Goldsworthy, S. D.** (2005). Drift dives by male New Zealand fur seals (*Arctocephalus forsteri*). *Can. J. Zool.* **83**, 293–300.
- Ponganis, P. J., Gentry, R. L., Ponganis, E. P. and Ponganis, K. V.** (1992). Analysis of swim velocities during deep and shallow dives of two northern fur seals, *Callorhinus ursinus*. *Mar. Mammal Sci.* **8**, 69–75.
- Richard, G., Vacqu  -Garcia, J., Jouma’a, J., Picard, B., G  nin, A., Arnould, J. P. Y., Bailleul, F. and Guinet, C.** (2014). Variation in body condition during the post-moult

- foraging trip of southern elephant seals and its consequences on diving behaviour. *J. Exp. Biol.* **217**, 2609–2619.
- Robinson, P. W., Simmons, S. E., Crocker, D. E. and Costa, D. P.** (2010). Measurements of foraging success in a highly pelagic marine predator, the northern elephant seal. *J. Anim. Ecol.* **79**, 1146–1156.
- Sato, K., Naito, Y., Kato, A., Niizuma, Y., Watanuki, Y., Charrassin, J. B., Bost, C., Handrich, Y. and Le Maho, Y.** (2002). Buoyancy and maximal diving depth in penguins: do they control inhaling air volume? *J. Exp. Biol.* **205**, 1189–1197.
- Sato, K., Mitani, Y., Cameron, M. F., Siniff, D. B. and Naito, Y.** (2003). Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *J. Exp. Biol.* **206**, 1461–1470.
- Sato, K., Charrassin, J.-B., Bost, C.-A. and Naito, Y.** (2004). Why do macaroni penguins choose shallow body angles that result in longer descent and ascent durations? *J. Exp. Biol.* **207**, 4057–4065.
- Sato, K., Shiomi, K., Watanabe, Y., Watanuki, Y., Takahashi, A. and Ponganis, P. J.** (2010). Scaling of swim speed and stroke frequency in geometrically similar penguins: they swim optimally to minimize cost of transport. *Proc. R. Soc. B* **277**, 707–714.
- Sato, K., Shiomi, K., Marshall, G., Kooyman, G. L. and Ponganis, P. J.** (2011). Stroke rates and diving air volumes of emperor penguins: implications for dive performance. *J. Exp. Biol.* **214**, 2854–2863.
- Sato, K., Aoki, K., Watanabe, Y. Y. and Miller, P. J. O.** (2013). Neutral buoyancy is optimal to minimize the cost of transport in horizontally swimming seals. *Sci. Rep.* **3**, 2205.
- Sparling, C. E., Speakman, J. R. and Fedak, M. A.** (2006). Seasonal variation in the metabolic rate and body composition of female grey seals: fat conservation prior to high-cost reproduction in a capital breeder? *J. Comp. Physiol. B* **176**, 505–512.
- Sparling, C. E., Georges, J.-Y., Gallon, S. L., Fedak, M. and Thompson, D.** (2007). How long does a dive last? Foraging decisions by breath-hold divers in a patchy environment: a test of a simple model. *Anim. Behav.* **74**, 207–218.

- Stephens, D. W., Brown, J. S. and Ydenberg, R. C.** (2007). *Foraging: Behavior and Ecology*. Chicago: University of Chicago Press.
- Thompson, D. and Fedak, M. A.** (2001). How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. *Anim. Behav.* **61**, 287–296.
- Thompson, D., Hiby, A. R. and Fedak, M. A.** (1993). How fast should I swim? Behavioural implications of diving physiology. *Symp. Zool. Soc. Lond.* **66**, 349–368.
- Thums, M., Bradshaw, C. and Hindell, M. A.** (2011). In situ measures of foraging success and prey encounter reveal marine habitat-dependent search strategies. *Ecology* **92**, 1258–1270.
- Thums, M., Bradshaw, C. J. A., Summer, M. D., Horsburgh, J. M. and Hindell, M. A.** (2013). Depletion of deep marine food patches forces divers to give up early. *J. Anim. Ecol.* **82**, 72–83.
- Tucker, V. A.** (1975). The energetic cost of moving about: Walking and running are extremely inefficient forms of locomotion. Much greater efficiency is achieved by birds, fish—and bicyclists. *Am. Sci.* **63**, 413–419.
- van Dam, R. P., Ponganis, P. J., Ponganis, K. V., Levenson, D. H. and Marshall, G.** (2002). Stroke frequencies of emperor penguins diving under sea ice. *J. Exp. Biol.* **205**, 3769–3774.
- Watanabe, Y., Baranov, E. A., Sato, K., Naito, Y. and Miyazaki, N.** (2006). Body density affects stroke patterns in Baikal seals. *J. Exp. Biol.* **209**, 3269–3280.
- Watanabe, Y., Wei, Q., Yang, D., Chen, X., Du, H., Yang, J., Sato, K., Naito, Y. and Miyazaki, N.** (2008). Swimming behavior in relation to buoyancy in an open swimbladder fish, the Chinese sturgeon. *J. Zool.* **275**, 381–390.
- Watanabe, Y. Y., Sato, K., Watanuki, Y., Takahashi, A., Mitani, Y., Amano, M., Aoki, K., Narazaki, T., Iwata, T., Minamikawa, S., et al.** (2011). Scaling of swim speed in breath-hold divers. *J. Anim. Ecol.* **80**, 57–68.

- Watanabe, Y. Y., Ito, M. and Takahashi, A.** (2014). Testing optimal foraging theory in a penguin-krill system. *Proc. R. Soc. B* **281**, 20132376.
- Watanuki, Y., Niizuma, Y., Gabrielsen, G. W., Sato, K. and Naito, Y.** (2003). Stroke and glide of wing-propelled divers: deep diving seabirds adjust surge frequency to buoyancy change with depth. *Proc. R. Soc. B* **270**, 483–488.
- Watanuki, Y., Takahashi, A., Daunt, F., Wanless, S., Harris, M., Sato, K. and Naito, Y.** (2005). Regulation of stroke and glide in a foot-propelled avian diver. *J. Exp. Biol.* **208**, 2207–2216.
- Watanuki, Y., Wanless, S., Harris, M., Lovvorn, J. R., Miyazaki, M., Tanaka, H. and Sato, K.** (2006). Swim speeds and stroke patterns in wing-propelled divers: a comparison among alcids and a penguin. *J. Exp. Biol.* **209**, 1217–1230.
- Webb, P. M., Crocker, D. E., Blackwell, S. B., Costa, D. P. and Le Boeuf, B. J.** (1998). Effects of buoyancy on the diving behavior of northern elephant seals. *J. Exp. Biol.* **201**, 2349–2358.
- Weihs, D.** (1974). Energetic advantages of burst swimming of fish. *J. Theor. Biol.* **48**, 215–229.
- Williams, T. M., Davis, R. W., Fuiman, L. A., Francis, J., Le Boeuf, B. J., Horning, M., Calambokidis, J. and Croll, D. A.** (2000). Sink or swim: strategies for cost-efficient diving by marine mammals. *Science* **288**, 133–136.
- Williams, T. M., Fuiman, L. A., Horning, M. and Davis, R. W.** (2004). The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddellii*: pricing by the stroke. *J. Exp. Biol.* **207**, 973–982.
- Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R. and Butler, P. J.** (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *J. Anim. Ecol.* **75**, 1081–1090.
- Wilson, R. P., Quintana, F. and Hobson, V. J.** (2012). Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proc. R. Soc. B* **279**, 975–980.

**Worthy, G. A. J., Morris, P. A., Costa, D. P. and Le Boeuf, B. J. .** (1992). Moulting energetics of the northern elephant seal (*Mirounga angustirostris*). *J. Zool., Lond.* **227**, 257–265.

## OVERALL SUMMARY OF THIS STUDY

Breath-hold diving represents a major behaviour in marine top predators, such as seabirds and marine mammals, in polar and temperate regions. Exploring the factors affecting the swimming and foraging behaviour of breath-hold divers is fundamental to a better understanding of the behavioural adaptations of marine top predators to their polar and temperate environments.

Breath-hold divers experience the dilemma of not being able to breathe and feed on prey at the same time; they forage underwater and return to the water surface to breathe. This means that diving and foraging time is physiologically constrained by the amount of oxygen stores, as well as the rate of oxygen consumption, which is largely determined by the frequency of locomotor movements or swim speed, with a given basal metabolic rate. Within these physiological constraints, foraging theories predict that divers have the option to change swimming behaviour and hence how much oxygen they allocate to each phase of a dive in response to (1) biomechanical factor (i.e. buoyancy; body density in other words) that affects swimming behaviour and the energetic costs of swimming, and (2) ecological factor (i.e. foraging depth) that also affects the energetic costs of swimming via changes in transit distance. However, little is known about the relationships among buoyancy, swimming costs and foraging behaviour in free-ranging divers, due to the technological limitations of previous methods: limitations in time resolution and recording periods. These technological limitations have precluded fine-scale, long-term measurements of swimming behaviour and their associated energetic costs in relation to the significant changes in buoyancy, which occurs as fat stores increase while foraging at sea for months.

To overcome these limitations, a novel accelerometer called ‘Stroke Logger’ was developed,

that records the number of strokes (together with depth and pitch angle, allowing me to calculate swim speed by  $\Delta\text{depth}/\sin\theta$ ) every 5 seconds for 150 days at maximum by an on-board data-processing algorithm. Using this long-term accelerometry technique, I successfully tracked changes in the locomotor cost of swimming (number of strokes per metre swam, hereafter referred to as strokes-per-metre) in female northern elephant seals during their months-long oceanic foraging migrations, where they experience significant changes in buoyancy (body density). As negatively buoyant seals increased their fat stores and buoyancy, the strokes-per-metre increased slightly in the buoyancy-aided direction (descending), but decreased significantly in the buoyancy-hindered direction (ascending), with associated changes in swim speed, gliding durations and pitch angles. Overall, the round-trip strokes-per-metre decreased and reached a minimum value when seals achieved neutral buoyancy. In addition, seal buoyancy appeared to affect not only locomotor costs via reductions in propulsive activities, but also foraging gains via increased time spent at foraging depth, suggesting a foraging benefit of achieving neutral buoyancy by being fat.

Seals changed swimming behaviour in response to not only buoyancy changes, but also to changes in foraging depth. Specifically, seals swam faster by stroking more frequently when they foraged in shallower depths, reflecting the swimming strategy of maximizing the proportion of time spent foraging at depth, in agreement with an optimality model for breath-hold divers. On the other hand, the number of feeding events had relatively small effect on swimming behaviour. These results characterize the swimming behaviour of elephant seals, in which both biomechanical (buoyancy) and ecological (foraging depth) factors influence stroking frequency and swim speed.

My results show that increasing fat stores by approaching neutral buoyancy have clear advantages in decreased locomotor cost of swimming at sea. Conversely, therefore, losing fat

stores results in increased locomotor costs of swimming by deviating from neutral buoyancy. In contrast, on land, losing more fat stores by using more energy is beneficial for reproduction, especially in capital breeding species such as elephant seals; pups grow faster and better when their mothers deliver more energy to them, demonstrating the clear fitness advantages of losing fat stores during reproduction on land. Therefore, I suggest that my results have an important implication of balancing the optimal amount of fat stores against reproduction on land and locomotor activities at sea. This raises the need for further investigations of annual and life cycle strategies of capital breeding species in the future, to examine the trade-off between reproductive benefits on land, where fat stores are reduced during lactation, and swimming costs at sea, where fat is stored while feeding on prey by way of energetically expensive swimming.