Swimming and foraging behaviour of northern elephant seals during oceanic migrations

（回遊中のキタゾウアザラシにおける遊泳及び採餌行動に関する研究）

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CHAPTER 1. GENERAL INTRODUCTION

1.1. SWIMMING AND FORAGING BEHAVIOUR OF BREATH-HOLD DIVERS

Efficient foraging is invaluable for an animal striving to maintain the positive energy balance that is required for survival and reproduction (Stephens et al., 2007). The energy balance of foraging animals is determined by the difference between energy intake from prey ingestion and energy expenditure associated with foraging activities. As animals often search for or transit to aggregations of prey over long distances, locomotor cost (i.e. energy costs expended in propulsive activities) are a major component of the energy expended while foraging (Wilson et al., 2012). This is especially the case for breath-hold divers, as they repeatedly dive to search for and forage on prey by the way of energetically expensive swimming (Boyd, 1997; Dingle, 1996).

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, however, divers have the option to change swimming behaviour and hence how much oxygen they allocate to each phase of a dive. For example, a frequency of locomotor movements to achieve a swim speed that minimizes the cost of transport (U_{COTmin}) could allow divers to prolong time spent foraging at depth by saving oxygen to transit to and from foraging depths (Miller et al., 2012) (here, note that COT is a cost of transport, defined as the amount of mass-specific energy expended by an animal moving a unit distance (Tucker,

1975)). However, swimming at U_{COTmin} would not always be the best option, because a higher swim speed that deviates from U_{COTmin} may allow divers to reach foraging depth faster and hence increase the proportion of time spent foraging at depth by saving time to transit (Thompson et al., 1993). It is important to understand how breath-hold divers change swimming behaviour to exploit their environment most efficiently under natural conditions, where they simultaneously experience significant changes in biomechanical (buoyancy) and ecological (foraging depth) factors, which are major factors affecting divers' swimming behaviour and energetic costs of swimming.

1.2. Factors affecting swimming behaviour of breath-hold divers: Biomechanical and ecological factors

Buoyancy is one of the major biomechanical factors and primary external forces acting on moving breath-hold divers, together with hydrodynamic drag and lift. Buoyancy affects swimming behaviour as well as energetic costs of swimming in breath-hold divers (Alexander, 2003). The force is given by the difference of density of surrounding water and total density of the diver's body;

$$B = (\rho_{\mathrm{water}} - \rho_{\mathrm{animal}})Vg, \tag{1.1}$$

where B is buoyancy force (in N), ρ_{water} and ρ_{animal} are the density (in kg m^{-3}) of the surrounding water (e.g. 1027 kg m^{3} for seawater density (Aoki et al., 2011) and the animal, respectively, V is the volume of the animal (in m^{3}) and g is the acceleration of gravity (= 9.8 m s^{-2}). Here, ρ_{animal} is roughly determined by the proportion of amounts of two types of tissues with different densities: lean (e.g. muscle) and adipose (e.g. fat stores) tissues with higher and lower density

than water density, respectively (Webb et al., 1998) (e.g. 1340 and 901 kg m^3 for the densities of lean and adipose tissues in humans, respectively (Moore et al., 1963), which were often used in marine mammal studies (Aoki et al., 2011; Biuw et al., 2003; Gallon et al., 2007)). For example, the buoyancy is negative ($B < 0$) if the divers have more lean tissue relative to adipose tissue, resulting in higher density of diver's entire body than that of surrounding water ($\rho_{water} < \rho_{animal}$). The buoyancy is positive ($B > 0$), on the other hand, if the divers have less lean tissue relative to adipose tissue, resulting in lower density of diver's entire body than that of surrounding water ($\rho_{water} > \rho_{animal}$). Consequently, divers with negative or positive buoyancy are expected to expend extra energy (e.g. by increasing propulsive activity) when they move in the opposite direction of the buoyancy force, while they could save energy (e.g. by reducing propulsive activity) when moving in the same direction as this force (Sato et al., 2003; Watanabe et al., 2006; Williams et al., 2004). Thus, breath-hold divers are expected to change swimming behaviour in nature, where they experience significant changes in body density and hence buoyancy (e.g. the transition from negative to positive buoyancy; Biuw et al., 2003) by storing fat contents (adipose tissue) while foraging at sea.

Foraging depth is one of the major ecological factors that would reflect depth distribution of prey and could have significant effect on swimming behaviour in breath-hold divers (Thompson et al., 1993). This is because foraging depth affects energetic costs of swimming via changes in transit distance. Thus, breath-hold divers are expected to change swimming behaviour in response to foraging depth, which should vary spatiotemporally in nature (Guinet et al., 2014; Naito et al., 2013; Thums et al., 2011; Watanabe et al., 2014).

Accordingly, breath-hold divers are expected to adjust their swimming behaviour in response to both biomechanical (buoyancy) and ecological (foraging depth) factors simultaneously in nature, suggesting close relationships among buoyancy, swimming costs and

foraging behaviour. However, these relationships are poorly examined due to the technological limitations of recording the swimming behaviour and energetic costs of swimming in free-ranging breath-hold divers in relation to significant changes in their buoyancy, which occurs as fat stores increase while foraging at sea for months (e.g. Beck et al., 2000; Biuw et al., 2003).

1.3. Methods of recording swimming behaviour and measuring energetic costs of swimming: Long-term accelerometry as a potential tool to overcome the limitations of previous methods

Measuring the energetic cost of swimming has been a major focus of bioenergetics studies on marine animals (Costa and Williams, 1999). Previous studies estimated the energetic costs of swimming using measurements of heart rates or isotope dilution rates (Butler et al., 2004; Costa and Williams, 1999), but these approaches have some limitations in time resolution or in the requirement of surgical skills to implant loggers. An alternative approach is to quantify the behaviour of animals to estimate swimming costs. A key behavioural parameter is flipper stroking frequency 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). Accelerometry is an effective method to measure propulsive strokes, which are recorded as oscillating acceleration signals at high sampling rates (usually > 10 Hz). However, recording at high sampling rates limits the recording period due to limitations in logger memory or battery power (Halsey et al., 2009). Only one study, which used accelerometry, showed a change in

stroking effort of southern elephant seals over their post-breeding foraging migrations (< 80 days), but the study mainly focused on the validation of estimating seal density using stroking effort and swim speed (Richard et al., 2014). The paucity of long-term acceleration data have hindered further understanding of the relationships among buoyancy, swimming costs (as well as swimming behaviour) and foraging behaviour in long distance migrants such as highly pelagic marine animals.

To overcome these limitations, in this study, a novel instrument called 'Stroke Logger' was developed, that summarizes the predetermined acceleration signals (i.e. flipper strokes) from high frequency raw data to allow long recording durations (150 days at maximum). Also, this instrument was designed to record depth and pitch angles, which allowed me to calculate swimming speed with trigonometric function (Watanuki et al., 2006) (see the section of *Instrument*s in Chapter 2 for the detail about Stroke Logger).

1.4. ELEPHANT SEALS

I applied this newly-developed accelerometer to highly pelagic marine animals, elephant seals. Elephant seal is the ideal species to investigate the swimming strategy associated with the changes in both biomechanical (buoyancy) and ecological (foraging depth) factors, because they simultaneously experience the significant changes in both factors during their months-long oceanic foraging migrations.

There are two elephant seal species in the genus *Mirounga*: northern elephant seals *M. angustirostris* and southern elephant seals *M. leonina*. Both species inhabit different part of the world, and are major marine top predators in north Pacific Ocean and Southern Ocean (Le Boeuf and Laws, 1994). Both species are capital breeding species, and hence females need to store fat prior to the breeding season and then use them during the breeding season (Bowen et

al., 2002). Females of both species exhibit similar life cycles. They have two months-long oceanic foraging migrations, which are separated by breeding and moulting on land for about one month each other. During the breeding and moulting season on land, they lose fat contents by fasting. Consequently, females experience significant changes in buoyancy over their annual life cycles, especially during post-breeding (for two months) and post-moulting (for seven months) foraging migrations, where they increase buoyancy (fat stores) by foraging at mesopelagic zone of oceans.

Mesopelagic zone is a part of the pelagic zones that extends from a depth of 200 to 1000 metre below the ocean surface. Females of both elephant seal species are known to feed primarily on mesopelagic prey, such as myctophid fish, which represents diel vertical migration: stay at shallower and deeper depths during nighttime and daytime, respectively (Guinet et al., 2014; Naito et al., 2013). Consequently, female elephant seals dive shallower and deeper during nighttime and daytime, respectively, facing the changes in transit distance and hence swimming costs for round-trip to foraging depths within a day (Guinet et al., 2014; Naito et al., 2013).

1.5. OBJECTIVES OF THIS STUDY

In this thesis, I studied female northern elephant seals (Figure 1.1) to investigate how seals change their swimming behaviour in response to the changes in both biomechanical (buoyancy) and ecological (foraging depth) factors, during oceanic migrations that covers over the north Pacific Ocean (Figure 1.2). Using the newly-developed accelerometers ‘Stroke Loggers’, in Chapter 2, I investigate how buoyancy changes (biomechanical factor) affect swimming costs and hence time spent foraging at depth. Then, in chapter 3, I address how seals change swimming behaviour in response to the changes in foraging depth (ecological factor), together with buoyancy changes (biomechanical factor). Finally, in Chapter 4, I discuss how long-term

accelerometry technique would contribute to study the swimming and foraging strategies of a variety of free-ranging marine animals. Moreover, I extend the discussion to broad importance of this study and future perspectives.

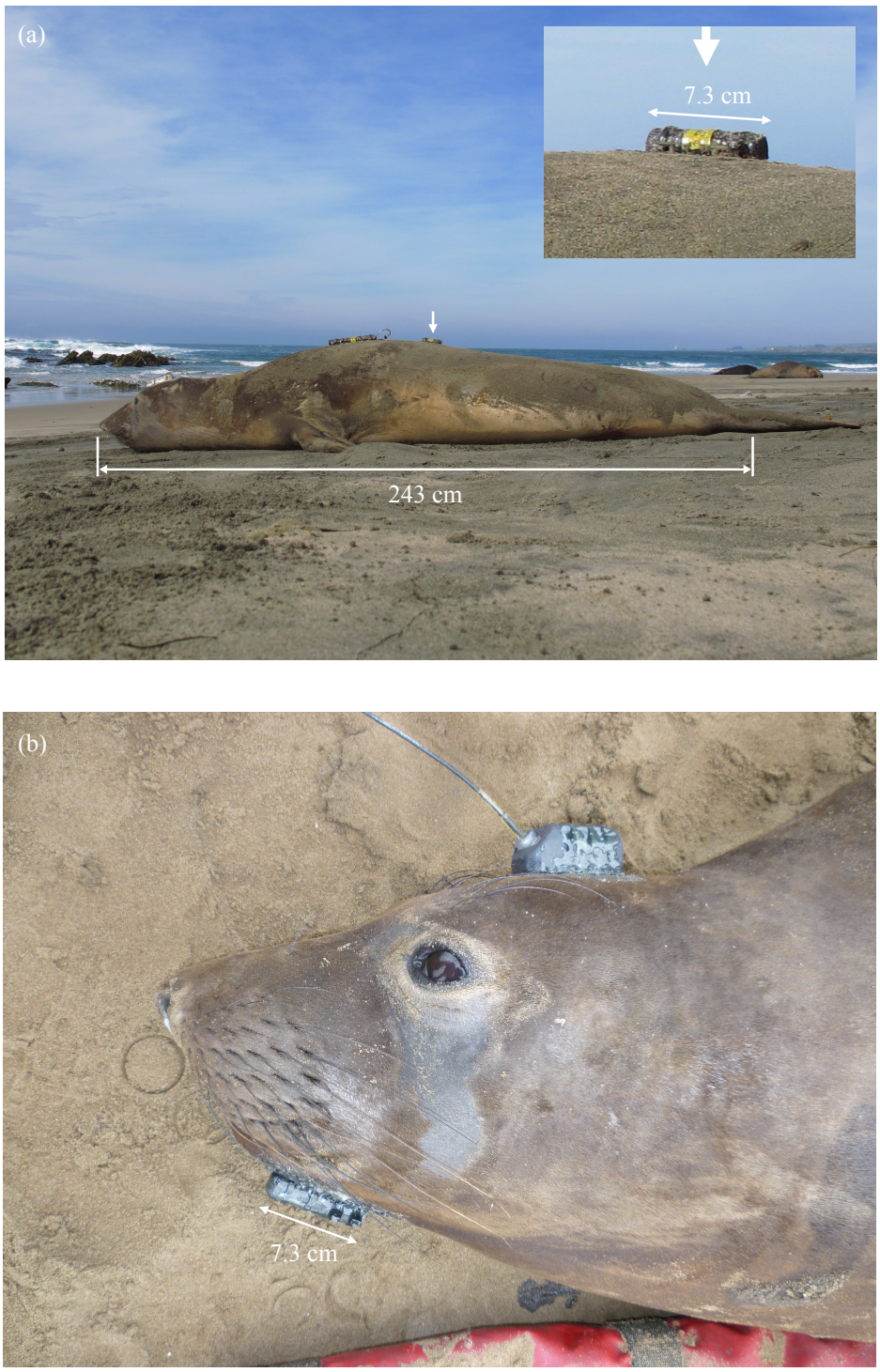


Figure 1.1 Female northern elephant seals, with (a) Stroke Logger on the back (see the section *Instruments* in Chapter 2 for the detail) and Kami Kami Logger on the mandible (see the section of *Instruments* in Chapter 3 for the detail). Photos by taken at Año Nuevo State Reserve, CA, USA, a colony of northern elephant seals.

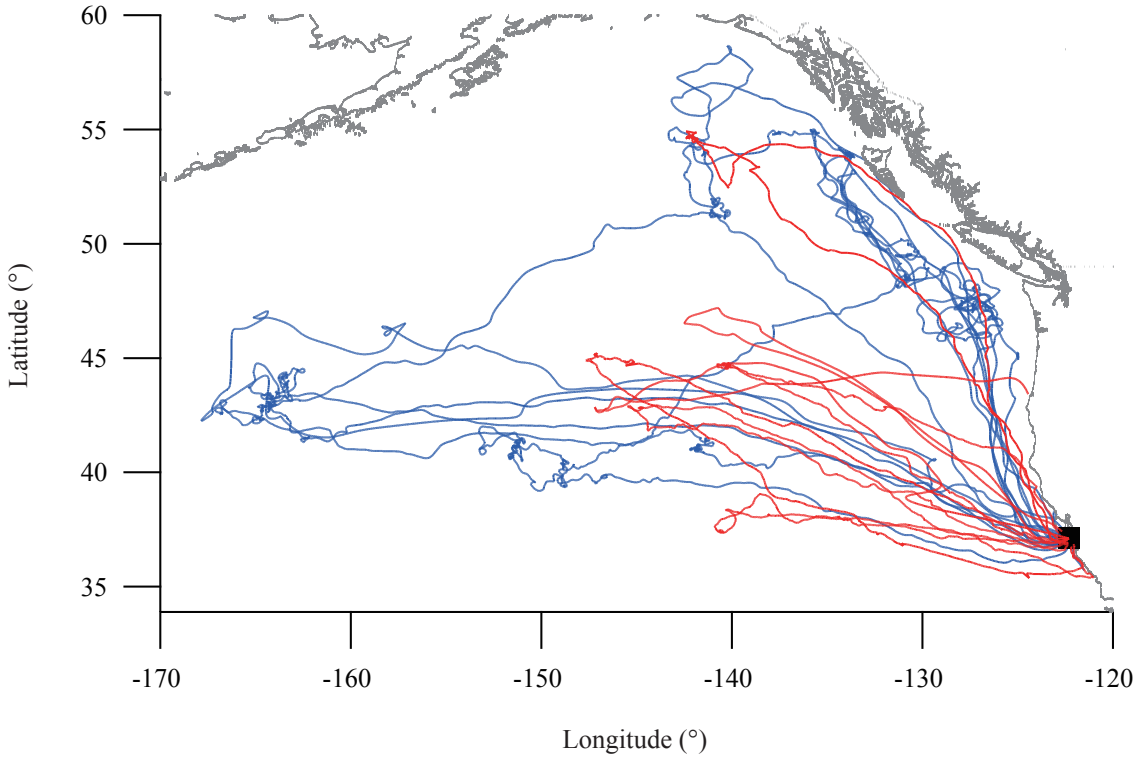


Figure 1.2 Satellite tracks of 14 female northern elephant seals during two-month post-breeding foraging migration (red lines, n = 7 seals) and seven-month post-moulting foraging migration (blue lines, n = 7 seals) in 2011 and 2012. A filled black square represents the position of Año Nuevo State Reserve, CA, USA, a colony of northern elephant seals.

CHAPTER 2. THE EFFECT OF BUOYANCY ON SWIMMING AND FORAGING BEHAVIOUR

2.1. INTRODUCTION

Foraging theory predicts that breath-hold divers adjust time spent foraging at depth depending on food abundance as well as the energetic cost of swimming (Houston and Carbone, 1992; Mori et al., 2002; Thompson and Fedak, 2001; Thompson et al., 1993). Changes in swimming costs are likely to have strong influences on time spent foraging at depth, and thus foraging efficiency (Thompson et al., 1993). For example, a reduction in swimming costs may allow for longer foraging durations at depth by saving oxygen that would have been used for transit to and from foraging depths (Costa, 1991; Costa and Gales, 2003). However, previous empirical studies have mostly focused on the effects of food abundance rather than the effect of changes in swimming costs on foraging strategies, except for a few studies (Carbone et al., 1996; Cornick et al., 2006).

Buoyancy is one of the primary external forces acting on moving breath-hold divers, together with hydrodynamic drag and lift. Buoyancy affects the swimming costs of aquatic animals via effects on swimming behaviour, such as stroking frequency, glide duration or pitch angle. The relationship between buoyancy and swimming strategy may apply across a range of aquatic animals, from fish to whales (e.g. fish (Watanabe et al., 2008; Weihs, 1974), diving mammals (Sato et al., 2003; Watanabe et al., 2006; Williams et al., 2000), birds (Lovvorn, 2001; van Dam et al., 2002; Watanuki et al., 2005) and sea turtles (Hays et al., 2007)), representing transitions from continuous stroking, to stroking-and-gliding, to prolonged gliding as buoyancy aids in generating thrust force along the swimming path. Previous studies suggest that marine

mammals may reduce swimming costs by employing prolonged gliding aided by negative buoyancy during the descent phase of dives (Costa and Gales, 2000; Sato et al., 2003; Williams et al., 2000). This was confirmed by experimental modification of buoyancy in seals (Aoki et al., 2011; Watanabe et al., 2006). However, the apparent benefits of negative buoyancy to swimming costs are less clear when the round-trip cost to and from foraging depths is considered, because divers that are aided by negative buoyancy during descent need to increase swimming effort to overcome negative buoyancy during ascent (Aoki et al., 2011; Sato et al., 2003; Sato et al., 2013; Watanabe et al., 2006). A modelling study suggested that the round-trip cost of transit to the foraging depth should be minimal when divers are neutrally buoyant (Miller et al., 2012). This prediction has not been fully tested under natural conditions due to the technological difficulties of measuring the swimming costs of free-ranging animals in relation to significant changes in their buoyancy that can occur as fat stores increase while foraging at sea for months (e.g. Beck et al., 2000; Biuw et al., 2003).

To overcome these difficulties and test if round-trip swimming costs of breath-hold divers is minimum at neutral buoyancy, a novel accelerometer called ‘Stroke Logger’ was developed, that summarizes the predetermined acceleration signals (i.e. flipper strokes) from high frequency raw data to allow long recording durations (150 days at maximum). In this chapter, I used this new long-term accelerometry technique to (1) continuously track the swimming costs of female northern elephant seals during their months-long oceanic foraging migrations, where seal buoyancy shifted from highly negative to neutral, (2) evaluate how natural changes in seal buoyancy affect swimming costs, and (3) test if changes in swimming costs affect time spent at foraging depth.

2.2. MATERIAL AND METHODS

2.2.1. Device design and attachment

2.2.1.1. Field experiments

I investigated the at-sea swimming behaviour of 14 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 = 7, addressing the two-month post-breeding foraging migration (Feb – Apr), hereafter referred to as the short foraging migration) and moulting season (n = 7, addressing the seven-month post-moulting foraging migration (Jun – Dec), hereafter referred to as the long foraging migration), 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 for the recovery of the data loggers and collection of post-deployment measurements.

Each seal was equipped with a Stroke Logger (see the next section *Instruments* for more detail), 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) and head (ARGOS transmitter) using five-minute epoxy with high-tension mesh netting and cable ties.

2.2.1.2. Instruments

Stroke Loggers (Figure 1.1(a); 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) are designed to detect stroking behaviour and pitch angles using measurements of acceleration at a high sampling rate (32 Hz) with an on-board data-processing algorithm. The use of the algorithm and storage of summary data every five seconds allowed for a long recording duration. Stroke Loggers have a depth sensor and a two-axis acceleration sensor (along the longitudinal and lateral body axes). Depth data were recorded every five seconds. Raw longitudinal accelerations (measured at 32 Hz) were averaged every five seconds to extract the gravity vector (i.e. posture; see Sato et al., 2003), and the resulting values (-1 to +1 G) were converted into pitch angles by arcsin(longitudinal acceleration)*180/π (see Sato et al., 2003), assuming that the longitudinal axis of a seal matches that of the logger. Swim speed was calculated using a trigonometric function with depth and pitch angle data (i.e. ⊿depth/sinθ). Anomalous swim speeds greater than 3 m s^{-1}, possibly resulted from errors because of small depth change rate (⊿depth) or shallow pitch angle (θ), were excluded from the further analysis (e.g. Watanuki et al., 2003), since the elephant seals rarely swim at over 3 m s^{-1} (Hassrick et al., 2007). Lateral acceleration were often used to detect flipper strokes, because each flipper stroke is identified as cyclic oscillations in lateral acceleration signals (e.g. Sato et al., 2003). In this study, I developed a simple on-board data-processing algorithm to detect each stroke by using moving averages, which contributes to reduce the battery consumption. The resulting number of strokes (i.e. a cycle of swaying hind flippers) were counted and recorded every five seconds. More details about the on-board data processing algorithm and the validation of the measurements of Stroke Loggers are available in *Appendix*, in terms of (1) detecting strokes and (2) calculating swim speed.

2.2.2. Data analysis

2.2.2.1. Dive phase definition

Time at first dive was set as the start of the oceanic migration and each dive was defined using a minimum depth of 10 m. Descent, bottom and ascent phases of the dive were defined as follows (as per Aoki et al., 2011): (1) descent phase was the period from the start of a dive to the first time when the rate of depth change was negative, (2) bottom phase was the period between the end of the descent phase and the beginning of the ascent phase, and (3) ascent phase was the period from the last time when the rate of depth change was positive to the end of the dive. I considered the descent and ascent phases as transit phases, and the bottom phase as the time spent at foraging depth (Naito et al., 2013).

2.2.2.2. Calculating number of strokes per metre swam and time spent in prolonged gliding during the transit phases of each dive

I calculated locomotor costs of swimming as the number of flipper strokes divided by the distance travelled during the transit phases of each dive (i.e. number of strokes per metre swam, hereafter referred to as strokes-per-metre), based on the idea that the number of flipper strokes correlates linearly with oxygen consumption (Davis, 2014; Williams et al., 2004). The distance travelled was estimated with a trigonometric function using the rate of depth change and pitch angle (Δdepth/sinθ). Strokes-per-metre was calculated for the descent and ascent phase of each dive, and the round-trip strokes-per-metre was defined as the sum of descent and ascent strokes-per-metre. Note that I calculated strokes-per-metre during the transit phases of each dive, not including the bottom phase, because my aim of this chapter was to test if the locomotor cost during transit affects time spent at foraging depth. For statistical analysis, the strokes-per-metre values for each dive were averaged to obtain a daily mean strokes-per-metre.

I calculated the proportion of time spent in prolonged gliding during the transit phases of each dive, because prolonged gliding is a key strategy to reduce swimming costs (Williams et al., 2000). In this study, I defined prolonged gliding phases as any period during transit with no strokes for five seconds (the finest time resolution of the data from Stroke Loggers) or more. The total duration of prolonged gliding during the descent (or ascent) phase was calculated for each dive, and then divided by the descent (or ascent) duration to calculate the proportion of time spent in prolonged gliding during the transit phases of each dive. Then, those values were averaged daily for statistical analysis.

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). To minimize the effect of gases on buoyancy, I only used data from depths 100 m or more, as per Aoki et al. (2011), because in this study I focused not on the effect of residual air but on the effect of body density on swimming costs.

2.2.2.3. Estimating seal buoyancy

I calculated drift rate (the vertical rate of passive descent or ascent while drifting through the water column, represented in m s^{-1}) during so-called "drift dives" (Biuw et al., 2003) to estimate the buoyancy of the seal. The buoyancy of seals at depth is related to their relative amounts of adipose and lean tissue (Webb et al., 1998), making it possible to estimate changes in body density from their buoyancy, measured by drift rate (Biuw et al., 2003). Drift rate has strong positive correlations with body density obtained from isotope dilution analysis of body composition (Aoki et al., 2011). In this study, I constructed automated algorithms to select drift dives, detect drift phases and calculate drift rates by finding the inflection points in dive profiles. I modified the method described in Fedak et al. (2001) by adding four criteria as follows: a drift

phase should (1) have no depths less than 100 m (to minimize the effect of gases in the lungs on buoyancy as with calculating other swimming parameters), (2) have no strokes (i.e. the seal is passively drifting through the water column), (3) be longer than 20% of the total duration of the dive and (4) have little variance in depth change rate during the entire drift phase (i.e. mean squared residual should be less than 5 m^2 as per Biuw et al. (2003)). After running the automated algorithm, I excluded 5.3 ± 5.8% (mean ± s.d.) of drift rates as outliers by visual inspection of dive shape (Robinson et al., 2010). Then, 0.1 m s^{-1} was added to all drift values < -0.1 m s^{-1} and 0.1 m s^{-1} subtracted from all drift rates > +0.1 m s^{-1} to reduce the impact of abrupt transitions from -0.1 to +0.1 m s^{-1} (see Robinson et al., 2010, for detailed discussion). Finally, 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 daily drift rate (as per Robinson et al., 2010). Finally, the daily estimates of drift rates were used for comparisons with daily-averaged values of other parameters.

2.2.2.4. 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. The *mcmcsamp* function in the *coda* package was used to calculate 95% confidence intervals (95% CI) for slopes. In GLMMs 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. Data are presented as means ± standard error (s.e.) unless otherwise stated.

2.3. RESULTS

2.3.1. The change in seal buoyancy

Stroke Loggers tracked the swimming and diving behaviour of female northern elephant seals for the entire short, post-breeding foraging migration (78.1 ± 7.3 days, n = 7 seals) and for 61.4 ± 3.51% of the long, post-moulting foraging migration (139.9 ± 6.9 days, n = 7 seals) that lasted for 228.0 ± 5.9 days on average (mean ± s.d.). At the start of each migration, all 14 seals were negatively buoyant, as indicated by the negative drift rate values (Figure 2.1 & 2.2). Seals gradually became more buoyant as they increased their fat stores while foraging over the course of the migration. All seals were still negatively buoyant at the end of the short foraging migration, but five of seven 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)) (Figure 2.1 & 2.2).

2.3.2. The effect of buoyancy change on swimming behaviour and locomotor costs of swimming

The data from the Stroke Loggers allowed me to monitor the changes in the locomotor costs of swimming of the seals during their migrations. As the migration progressed, strokes-per-metre (number of strokes per metre swam) increased during the descent phase but decreased during the ascent phase (Figure 2.1 & 2.2). Round-trip strokes-per-metre, calculated as the sum of descent and ascent strokes-per-metre, gradually decreased, because ascent strokes-per-metre decreased more than descent strokes-per-metre increased (Figure 2.1, 2.2 & 2.3). Round-trip strokes-per-metre was lowest (approx. 0.25 strokes m^{-1}) when neutral buoyancy was achieved (Figure 2.4(a)), where strokes-per-metre during the descent and ascent phases of the dive was equivalent (Figure 2.3 & 2.5). Drift rates had a positive relationship with descent

strokes-per-metre (GLMM, slope mean = 0.386 with 95% CI of 0.370 to 0.402), but had a negative relationship with ascent strokes-per-metre (GLMM, slope mean = -1.009 with 95% CI of -1.027 to -0.989). Overall, drift rates had a negative relationship with round-trip strokes-per-metre (GLMM, slope mean = -0.622 with 95% CI of -0.641 to -0.604).

The proportion of time spent in prolonged gliding during the transit phases of each dive exhibited the opposite trend as did strokes-per-metre in response to changes in drift rates (Figure 2.1, 2.2 & 2.3). As the migrations progressed, the proportion of time spent in prolonged gliding gradually decreased during the descent phase, but gradually increased during the ascent phase (Figure 2.1 & 2.2). Then, those values were equivalent at approximately 0.4 when neutral buoyancy was achieved (i.e. drift rate was 0) (Figure 2.3). Drift rates had a negative relationship with the proportion of time spent in prolonged gliding during descent phase (GLMM, slope mean = -1.214 with 95% CI of -1.269 to -1.153), but had a positive relationship with that during ascent phase (GLMM, slope mean = 1.463 with 95% CI of 1.388 to 1.486).

Swim speed during the descent phase decreased largely from approximately 2.5 to 1.0 m s^{-1} as seals became more buoyant, but swim speed during the ascent phase remained around 1.5 m s^{-1} throughout the migrations (Figure 2.1, 2.2, 2.3 & 2.5). Both descent and ascent swim speeds were affected by drift rates, but descent swim speed was much more sensitive to changes in drift rates (GLMM, descent swim speed: slope mean = -3.27 with 95% CI of -3.36 to -3.19; ascent swim speed: slope mean = -0.55 with 95% CI of -0.62 to -0.47).

Pitch angle during the descent phase became steeper as drift rate increased (Figure 2.6; GLMM, slope mean = -74.2 with 95% CI of -80.2 to -68.1). However, pitch angle during the ascent phase was not significantly affected by drift rates (Figure 2.6; slope mean = -1.6 with 95% CI of -8.2 to 5.1), although pitch angles varied widely over the range of drift rates for both descent and ascent phases (Figure 2.6).

Transit duration during both descent and ascent phases slightly increased as seals became more buoyant (Figure 2.7; GLMM, descent transit duration: slope mean of drift rate = 5.29 with 95% CI of 4.79 to 5.79; ascent transit duration: slope mean of drift rate = 5.30 with 95% CI of 4.88 to 5.73). Transit duration also increased with dive depth (Figure 2.7; GLMM, descent transit duration: slope mean of dive depth = 0.003 with 95% CI of 0.002 to 0.003; ascent transit duration: slope mean of dive depth = 0.003 with 95% CI of 0.002 to 0.003).

2.3.3. The effect of changes in locomotor costs of swimming on foraging time

Seals spent more time at the bottom phases of dives (bottom duration) when seals approached neutral buoyancy (Figure 2.1, 2.2 & 2.8; GLMM, slope mean of drift rate = 35.9 with 95% CI of 34.5 to 37.3) and their round-trip strokes-per-metre decreased (Figure 2.4(b); GLMM, slope mean of round-trip strokes-per-metre = -48.9 with 95% CI of -50.9 to -46.8). Statistical analysis using AIC_c showed that the most parsimonious model explaining bottom duration included round-trip strokes-per-metre but not dive depth (Table 2.1(a)). Also, dive efficiency (i.e. bottom duration per dive cycle, which is composed of transit time, bottom time and post-surface time) increased as round-trip strokes-per-metre decreased (Figure 2.9), although dive depth also had a slight effect on dive efficiency (Table 2.1(b)).

2.4. DISCUSSION

2.4.1. Buoyancy determines locomotor costs of swimming

Using long-term accelerometry, I demonstrated that the round-trip locomotor cost of swimming (round-trip strokes-per-metre) decreased as female northern elephant seals approached neutral buoyancy during their oceanic foraging migrations. The reduction of

round-trip locomotor costs (Figure 2.4(a)) was caused by the small increase in descent strokes-per-metre (buoyancy-aided direction) relative to the large decrease in ascent strokes-per-metre (buoyancy-hindered direction) (Figure 2.3), which means that buoyancy changes affect strokes-per-metre in opposite ways and with different magnitudes according to the vertical direction of the swimming path.

The different trends in descent and ascent strokes-per-metre could be explained by changes in stroking effort and time spent in prolonged gliding in relation to buoyancy changes. During descent, the proportion of time spent in prolonged gliding remained high when seals were negatively buoyant (range = 0.4 to 0.9; Figure 2.3). This indicates that seals largely relied on negative buoyancy as the thrust force for gliding, which kept their stroking effort low (Watanabe et al., 2006; Williams et al., 2000). Also, descent pitch angles were steeper when seals were more buoyant (Figure 2.6), which might allow seals to descend with less stroking activity because a steeper pitch angle would bring the vector of forward motion closer to that of the force of gravity (Sato et al., 2003). For these reasons, descent strokes-per-metre stayed low, compared to ascent strokes-per-metre, over a range of negative buoyancy values (Figure 2.3). During ascent, negatively buoyant seals employed prolonged gliding less than during descent (Figure 2.3). This is probably because seals had to generate thrust force by actively stroking to overcome negative buoyancy. In fact, strokes-per-metre at negative buoyancy was higher during ascent than during descent (Figure 2.3). As buoyancy increased, seals were able to ascend with less thrust force from active stroking. Hence, ascent strokes-per-metre decreased largely as seals approached neutral buoyancy (Figure 2.3). Overall, round-trip strokes-per-metre decreased as seals approached neutral buoyancy (Figure 2.4(a)).

The changes in strokes-per-metre and time spent in prolonged gliding were reflected in changes in swim speed. During descent, negatively buoyant seals largely relied on gliding

(Figure 2.3). Gliding speed is expected to decrease as seals approach neutral buoyancy (Miller et al., 2012; Watanabe et al., 2006). In accordance with this prediction, descent swim speed decreased as seals approached neutral buoyancy (Figure 2.3 & 2.5). In contrast, during ascent negatively buoyant seals employed active stroking (high ascent strokes-per-metre) more than prolonged gliding (Figure 2.3). Seals appeared to adjust stroking effort depending on buoyancy changes to maintain a narrow range of ascent swim speeds (Figure 2.3 & 2.5), which might reflect a swim speed that minimizes swimming cots in the buoyancy-hindered direction (Miller et al., 2012; Sato et al., 2010; Watanabe et al., 2011).

Here, I present the close relationships among locomotor costs of swimming (strokes-per-metre), time spent in prolonged gliding and swim speed (Figure 2.3). These results show a remarkable agreement with a biomechanical model by Miller et al. (2012) that predicted increased round-trip swimming costs as body density deviates from neutral buoyancy. Miller et al. (2012) also predicted that round-trip swimming costs would not change largely around neutral buoyancy, which is again supported by my results (Figure 2.4(a)). Seals around neutral buoyancy displayed similar swimming behaviours during descent and ascent, including similar values for proportion of time spent in prolonged gliding and swim speed (Figure 2.3), suggesting the effects of buoyancy changes on strokes-per-metre are similar for both descent and ascent swimming directions around neutral buoyancy.

2.4.2. Locomotor costs of swimming affect foraging time

Bottom duration increased significantly (from approx. 10 to 20 min) with decreasing round-trip locomotor costs of swimming during transit (from approx. 0.5 to 0.25 strokes m^{-1}), as seals' buoyancy changed from highly negative to neutral (Figure 2.4(b)). The results suggest that reduced oxygen consumption for locomotor movements during transit might contribute to

prolong bottom duration (Hays et al., 2000; Okuyama et al., 2012; Richard et al., 2014). Prolonged bottom duration (Figure 2.4(b)) will likely allow seals to increase the energy gained during foraging, as northern elephant seals forage primarily at the bottom of their dives (Naito et al., 2013). In addition, increased dive efficiency (i.e. increased bottom duration per dive cycle, shown in Figure 2.9) suggests that seals gained a foraging benefit from achieving neutral buoyancy by being fat. A similar foraging benefit has also been suggested in a study (Richard et al., 2014) that assessed the relationship among stroking effort and dive duration in southern elephant seals, a species that undergoes similarly significant changes in their body density (buoyancy) during oceanic migrations (Biuw et al., 2003).

Other, not mutually exclusive, factors may partly explain why bottom duration increased as seals approached neutral buoyancy and decreased round-trip strokes-per-metre. First, the quality of a prey patch at foraging depth may affect bottom duration. For example, seals may prolong bottom duration to increase foraging effort in richer feeding grounds, an idea supported by theoretical and empirical studies on the diving behaviour of some seal species (Sparling et al., 2007; Thompson and Fedak, 2001). Second, changes in body size may affect bottom duration, because large body mass increases oxygen carrying capacity while simultaneously reducing the rate of oxygen use, allowing seals to stay underwater longer (Hassrick et al., 2010; Hassrick et al., 2013). Third, seasonal hypometabolism (i.e. decreased field metabolic rate) may also contribute to increased time spent at foraging depth (Sparling et al., 2006). Fourth, using flipper-beat frequency alone may miss a substantial part of kinematic variation (i.e. stroke amplitude) and hence energy expenditure during transit (e.g. Aoki et al., 2011), possibly leading to the changes in bottom duration. Finally, bottom duration could increase due to decreasing locomotor costs of swimming during bottom phase. The bottom phase of dives contains a series of vertical excursions (i.e. swim up and down; e.g. Naito et al., 2013), and the swimming costs

during bottom phase may decrease as seals approach neutral buoyancy in the same manner to the transit phase. However, alternative hypotheses might explain the effect of prey patch quality or increased body size on bottom duration of dives. For example, higher prey patch quality may lead to decreased bottom duration depending on time-scales (Charnov, 1976; Watanabe et al., 2014), suggesting diving animals should stay longer at depth as the patch quality declines (Mori and Boyd, 2004; Thums et al., 2013). Also, increased body size may lead to decreased bottom duration by increasing swimming costs due to increased drag force (i.e. because of increased cross-sectional area) (Webb et al., 1998). Thus, these other factors may affect bottom duration of dives, but the magnitude of those effects is still unclear, raising the need for further investigations about the factors determining the increased bottom duration with decreased round-trip locomotor costs (Figure 2.4(b)).

One weakness in energetic estimates from accelerometry is that accelerometers do not provide information on changes in resting metabolic rates (i.e. maintenance cost) (Halsey et al., 2011). For a short-term study, one may be able to assume the same resting metabolic rates over the study period to estimate the total cost of transport (maintenance cost + locomotor cost) (e.g. Williams et al., 2004). However, for a long-term study such as mine, the resting metabolic rate of seals is likely to change largely due to changes in body mass, state of pregnancy, or seasonal hypometabolism (e.g. Hedd et al., 1997; Sparling et al., 2006), precluding me from quantitatively estimating the maintenance cost during dives. In this study, more buoyant seals increased transit (descent and ascent) duration slightly (Figure 2.7), indicating that seals expended more energy for maintenance costs during transit to a foraging depth, which should somewhat counteract the energetic benefits gained from prolonging bottom duration. But in fact, bottom duration increased disproportionally larger with drift rates compared to transit durations (Figure 2.7 & 2.8), suggesting a significant effect of decreased locomotor costs on bottom

duration (Figure 2.4(b)). Nevertheless, quantitative energetic estimates of maintenance costs are needed to understand fully how seals allocate available oxygen to locomotion and foraging activities.

2.5. SUMMARY OF CHAPTER 2

In summary, I successfully tracked changes in the locomotor cost of swimming in ocean-migrating seals by using long-term records of flipper strokes. 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. I also suggested that 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.

In this chapter, I focused to address the effect of buoyancy changes on swimming and foraging behaviour in female northern elephant seals by analyzing long-term records of their swimming behaviour at a daily scale. However, seals are expected to experience not only buoyancy changes, but also significant changes in foraging depth within a day because of diel vertical migration of mesopelagic prey, such as myctophid (Guinet et al., 2014; Naito et al., 2013). This indicates that seals may change swimming behaviour within a day in response to foraging depth. Therefore, in the next chapter, I investigate how seals change swimming behaviour in response to foraging depth, together with buoyancy change, by analyzing long-term records of their swimming behaviour at a dive scale.

Table 2.1. The results of generalized linear mixed models (GLMM) with (a) bottom duration and (b) dive efficiency (i.e., bottom duration per dive cycle, which is composed of transit time, bottom time and post-surface time) as the response variables, and round-trip strokes-per-metre (number of strokes per metre swam, represented in strokes m^{-1}) and dive depth as the explanatory variables, including individual as a random effect. Daily values are used for statistical analysis. Akaike's information criterion corrected for small samples (AIC_c), AIC_{weight}, intercept and slope coefficient are shown for each model. The mean as well as 95% confidence interval value of slope coefficient are also shown. The models with the lowest AIC_c are shown in bold type.

(a)				Slope coefficient					
				Round-trip strokes-per-metre			Dive depth		
Candidate models	AIC_c	AIC_{weight}	Intercept	mean	2.5% CI	97.5% CI	mean	2.5% CI	97.5% CI
Bottom duration ~ Round-trip strokes-per-metre + Dive depth	6243.7	0.326	30.010	-49.130	-51.202	-46.643	-0.0006	-0.0019	0.0012
Bottom duration ~ Round-trip strokes-per-metre	**6242.2**	**0.674**	**29.610**	**-48.860**	**-50.911**	**-46.773**			
Bottom duration ~ Dive depth	7454.5	0.000	6.974				0.0094	0.0074	0.0117
Bottom duration ~ 1	7526.3	0.000	12.040						

(b)				Slope coefficient					
				Round-trip strokes-per-metre			Dive depth		
Candidate models	AIC_c	AIC_{weight}	Intercept	mean	2.5% CI	97.5% CI	mean	2.5% CI	97.5% CI
Dive efficiency ~ Round-trip strokes-per-metre + Dive depth	**-5010.4**	**1.000**	**0.917**	**-0.787**	**-0.830**	**-0.772**	**-0.0003**	**-0.0003**	**-0.0003**
Dive efficiency ~ Round-trip strokes-per-metre	-4745.6	0.000	0.720	-0.677	-0.721	-0.635			
Dive efficiency ~ Dive depth	-4089.4	0.000	0.536				-0.0001	-0.0001	-0.0001
Dive efficiency ~ 1	-4058.3	0.000	0.477						

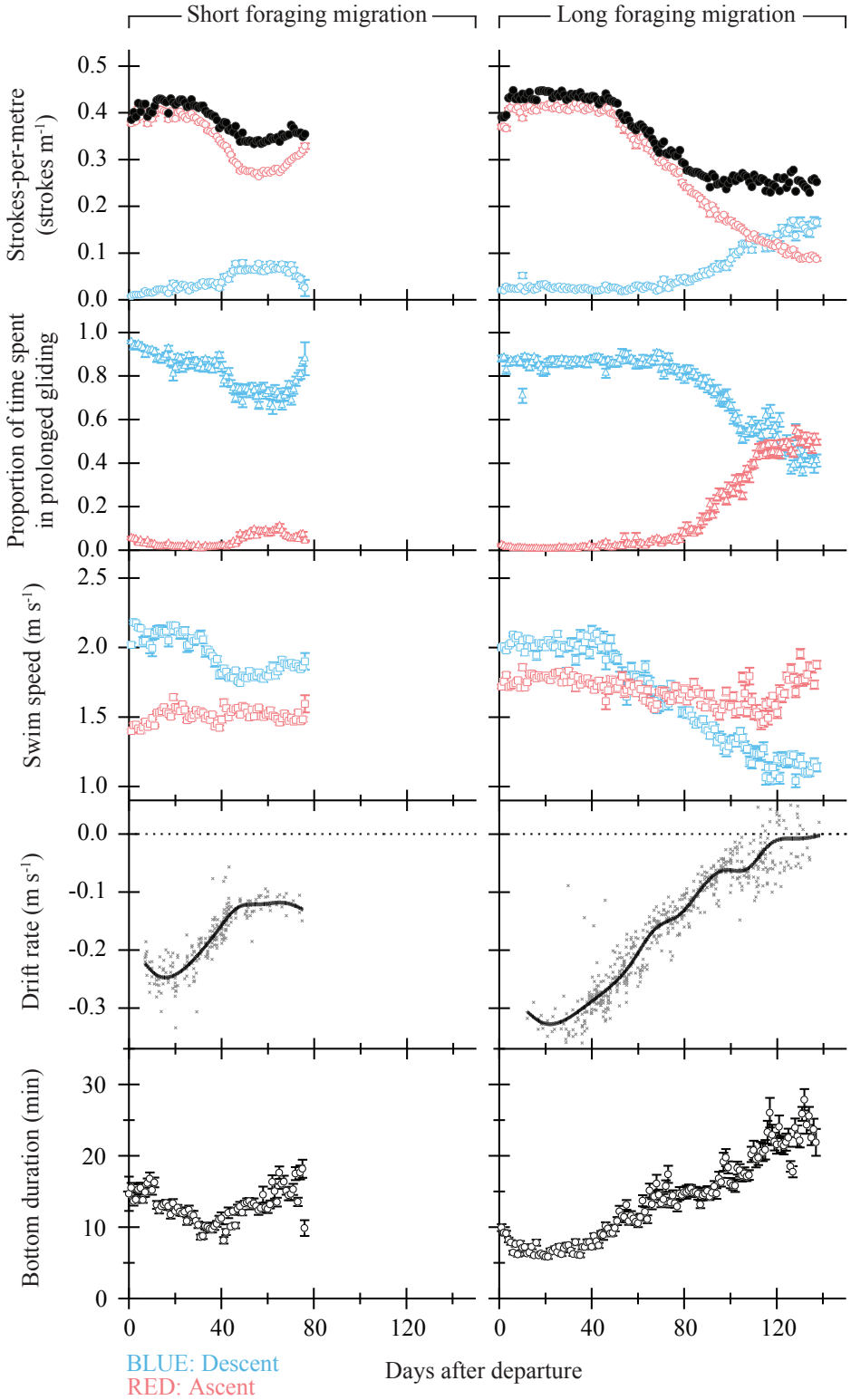


Figure 2.1. Examples of the time series for strokes-per-metre (number of strokes per metre swam, represented in strokes m^{-1}; top panels), the proportion of time spent in prolonged gliding (second row panels), swim speed (third row panels), drift rate (fourth row panels) and bottom duration (bottom panels). Left and right panels each show one seal during the short (seal ID: T35) and long (seal ID: U754) foraging migration, respectively (all other 12 seals are shown in Figure 2.2). In the top panels, open blue and red circles represent daily-averaged values of descent and ascent strokes-per-metre, respectively, with standard errors. Filled black circles represent round-trip strokes-per-metre, which is calculated as the sum of descent and ascent strokes-per-metre. In the second row panels, open blue and red triangles represent daily-averaged values of the proportion of time spent in prolonged gliding during the descent and ascent phases, respectively, with standard errors. In the third row panels, open blue and red squares represent daily-averaged values of descent and ascent swim speed, respectively, with standard errors. In the fourth panels, grey cross marks represent drift rates calculated from each drift dive. Thick black lines represent interpolated values of drift rate. Grey dotted lines indicate neutral buoyancy (i.e., drift rate = 0). In the bottom panels, open black circles represent daily-averaged values of bottom duration with standard errors.

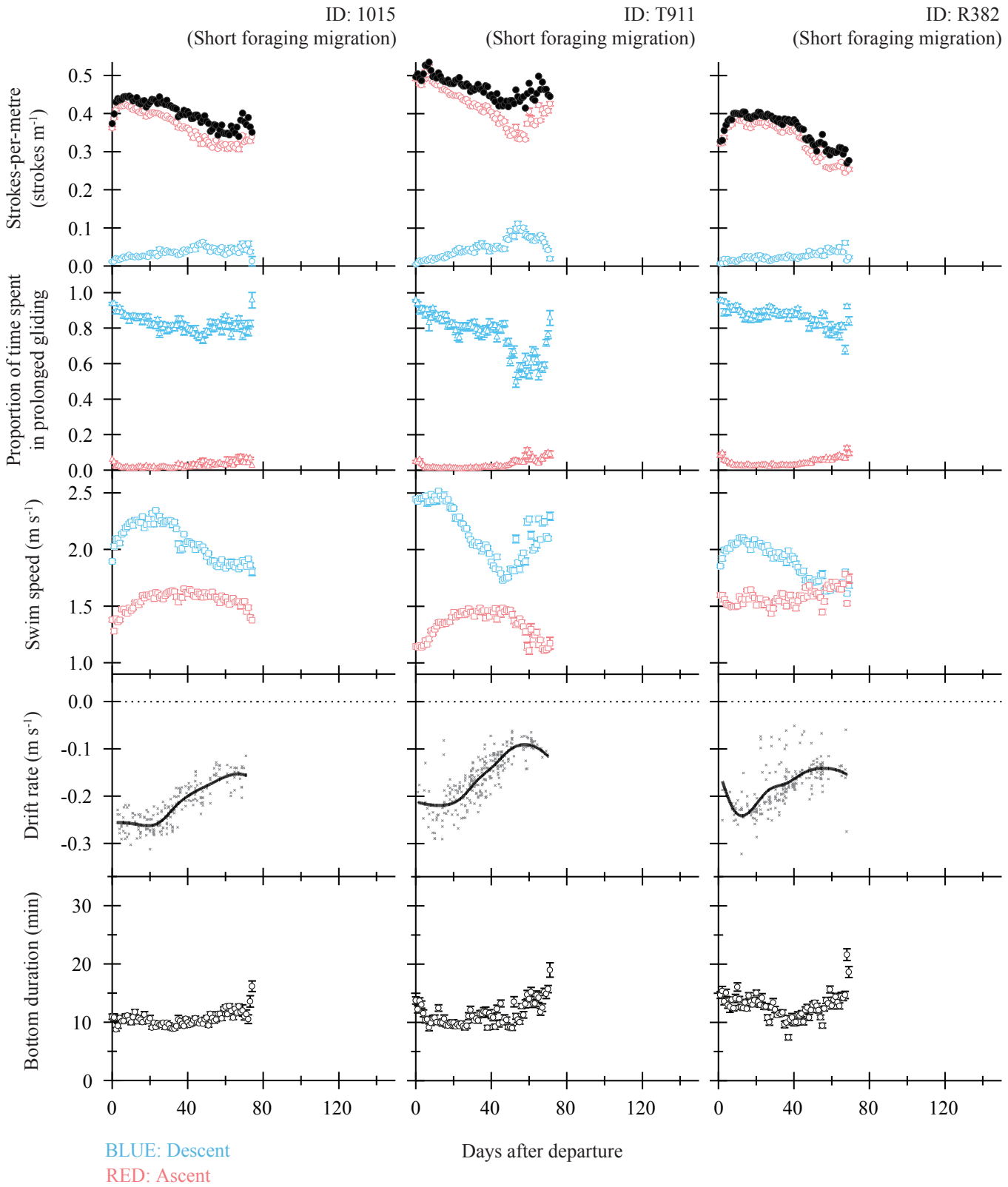


Figure 2.2. Time series data for strokes-per-metre (number of strokes per metre swam, represented in strokes m^{-1}; top panels), the proportion of time spent in prolonged gliding (second row panels), swim speed (third row panels), drift rate (fourth row panels) and bottom duration (bottom panels) for all other 12 seals during short and long foraging migration. In the top panels, open blue and red circles represent daily-averaged values of descent and ascent strokes-per-metre, respectively, with standard errors. Filled black circles represent round-trip strokes-per-metre, which is calculated as the sum of descent and ascent strokes-per-metre. In the second row panels, open blue and red triangles represent daily-averaged values of the proportion of time spent in prolonged gliding during descent and ascent phases, respectively, with standard errors. In the third row panels, open blue and red squares represent daily-averaged values of descent and ascent swim speed, respectively, with standard errors. In the fourth panels, grey cross marks represent drift rates calculated from each drift dive. Thick black lines represent interpolated values of drift rate. Grey dotted lines indicate neutral buoyancy (i.e., drift rate = 0). In the bottom panels, open black circles represent daily-averaged values of bottom duration with standar errors.

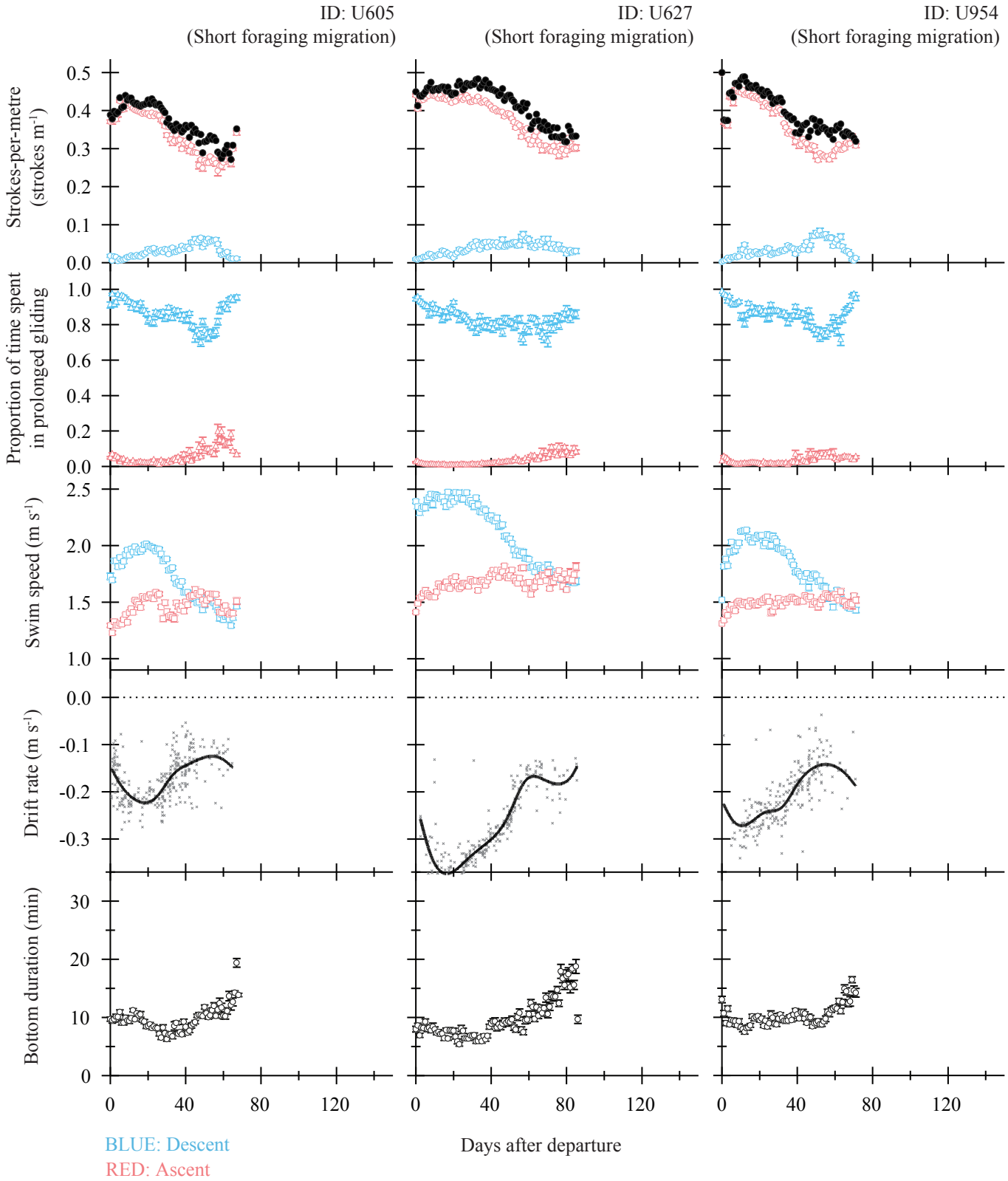
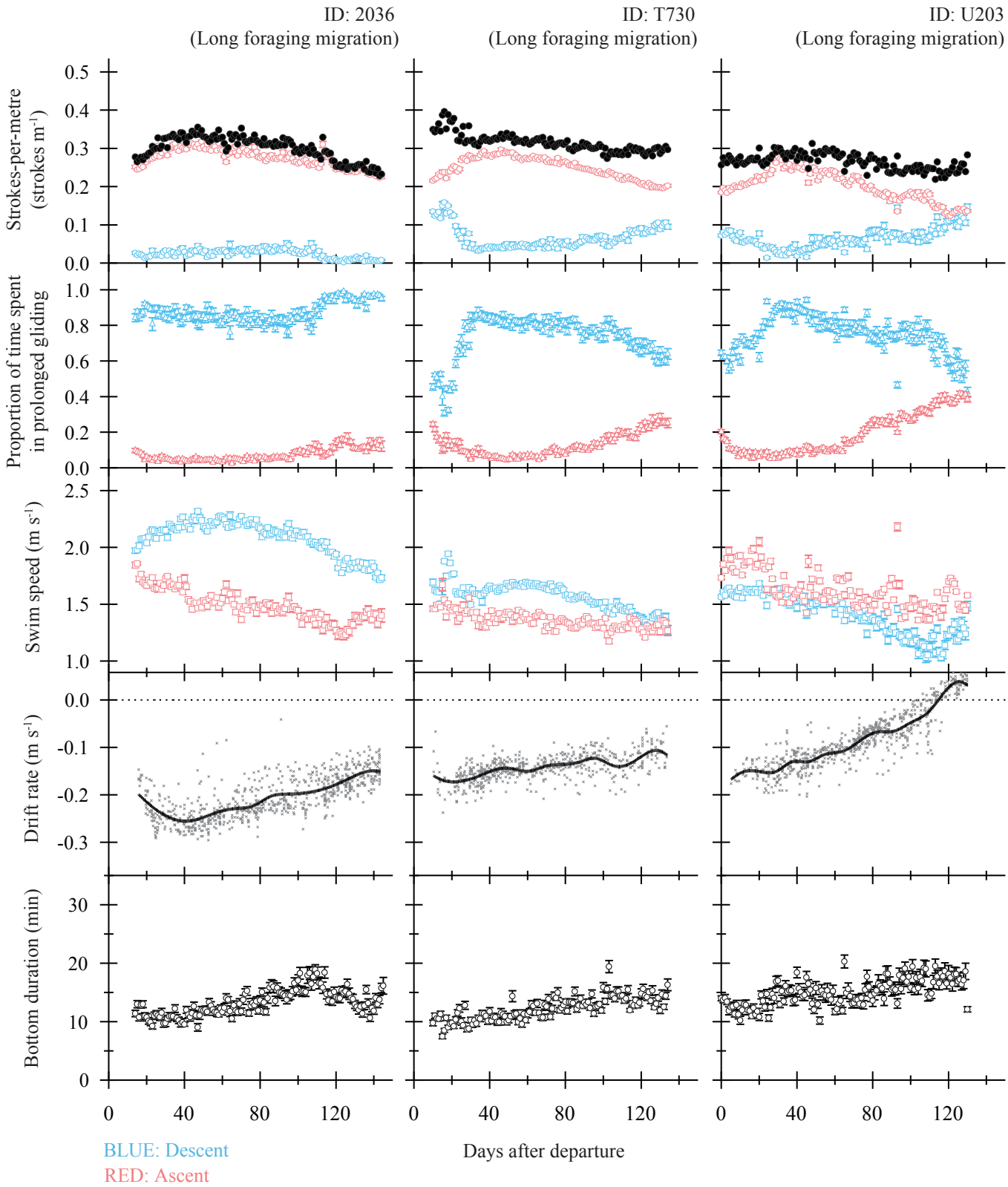


Figure 2.2. Continued.



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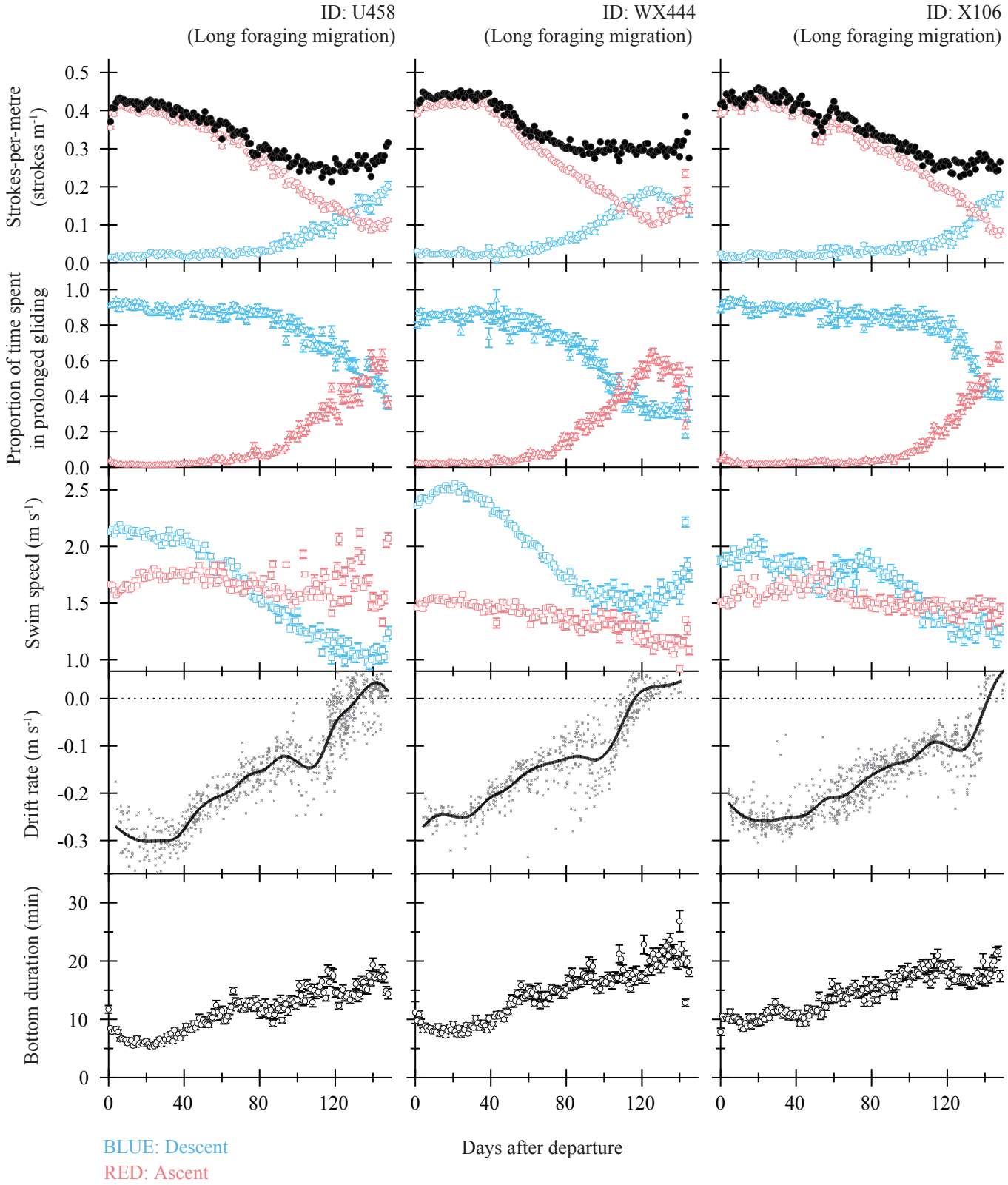

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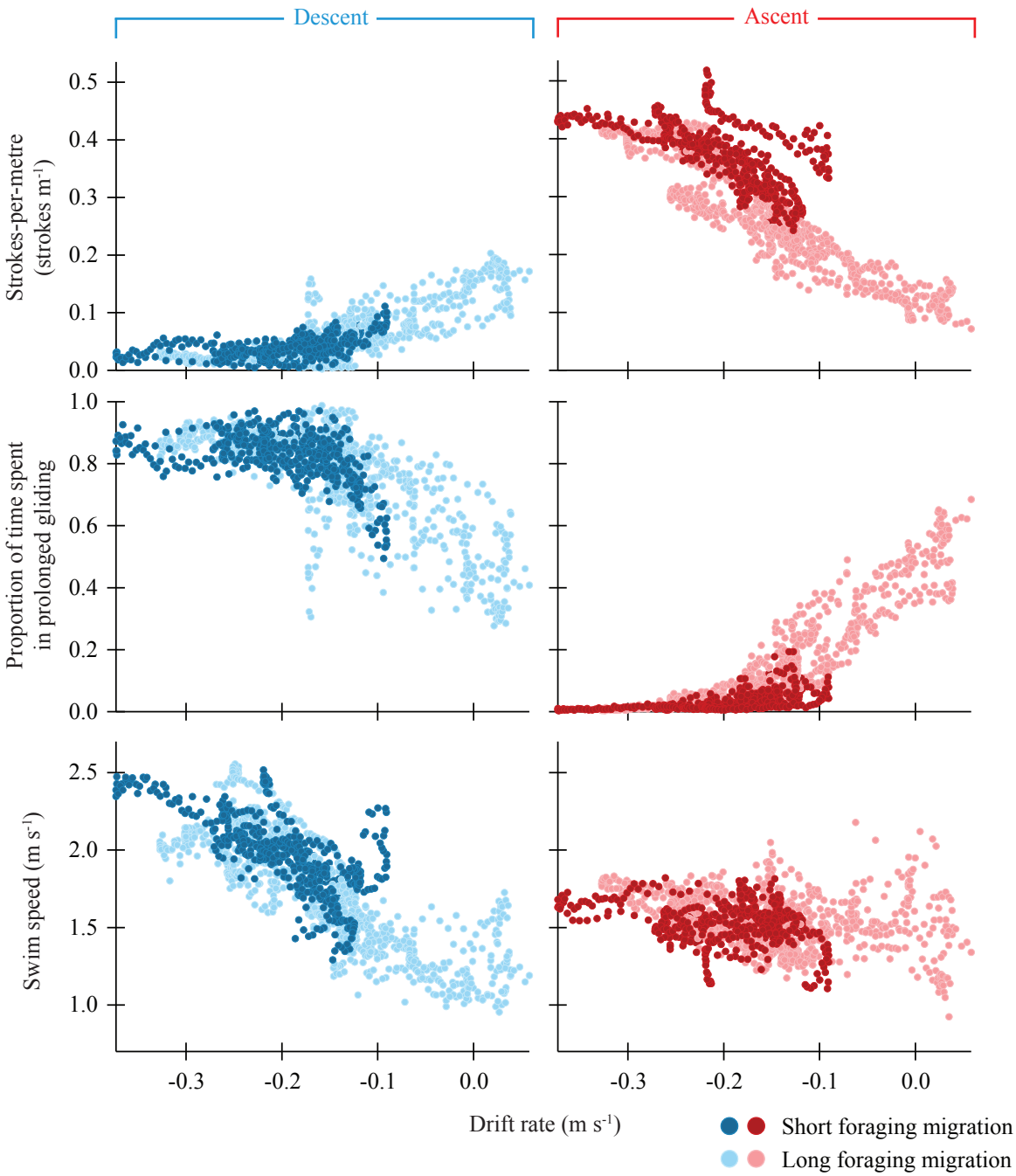

Figure 2.3. Strokes-per-metre (number of strokes per metre swam, represented in strokes m^{-1}; top panels), proportion of time spent in prolonged gliding (middle panels) and swim speed (bottom panels), plotted against drift rates for all 14 individuals. Left and right panels show daily values of each parameter during the descent (blue colors) and ascent (red colors) phases, respectively. Filled dark and light blue (or red) circles represent daily values for seals during short and long foraging migration, respectively.

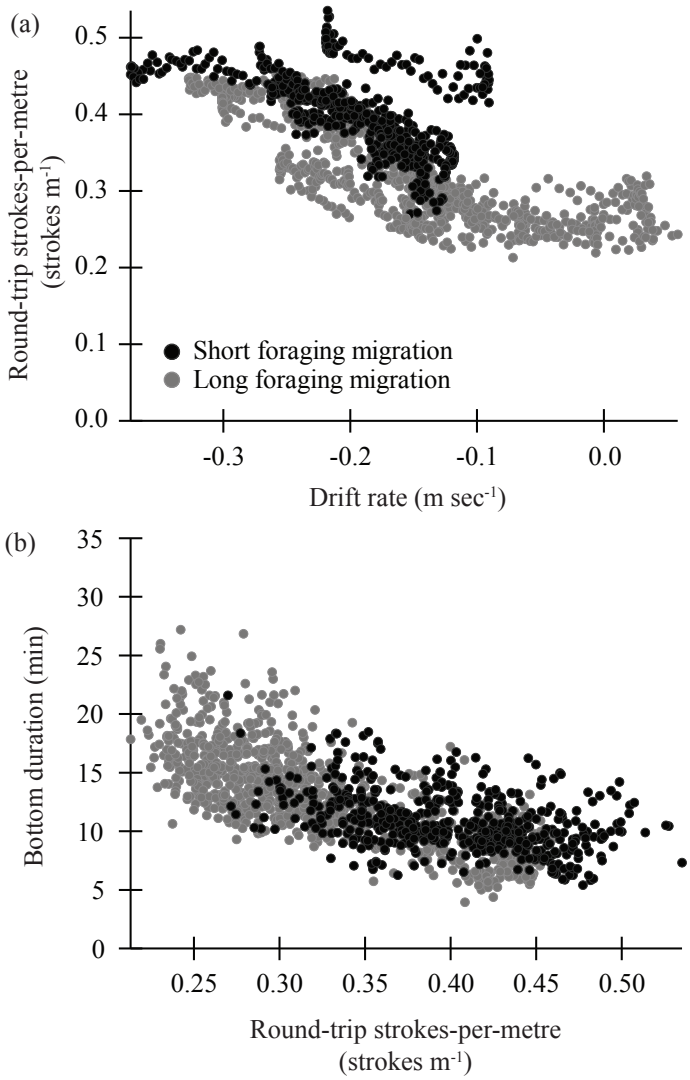

Figure 2.4. The relationships among drift rates, round-trip strokes-per-metre (number of strokes per metre swam, represented in strokes m^{-1}) and bottom duration for all 14 individuals. (a) Round-trip strokes-per-metre, plotted against drift rates. (b) Bottom duration, plotted against round-trip strokes-per-metre. In both panels, filled black and grey circles represent daily values for seals during short and long foraging migration, respectively.

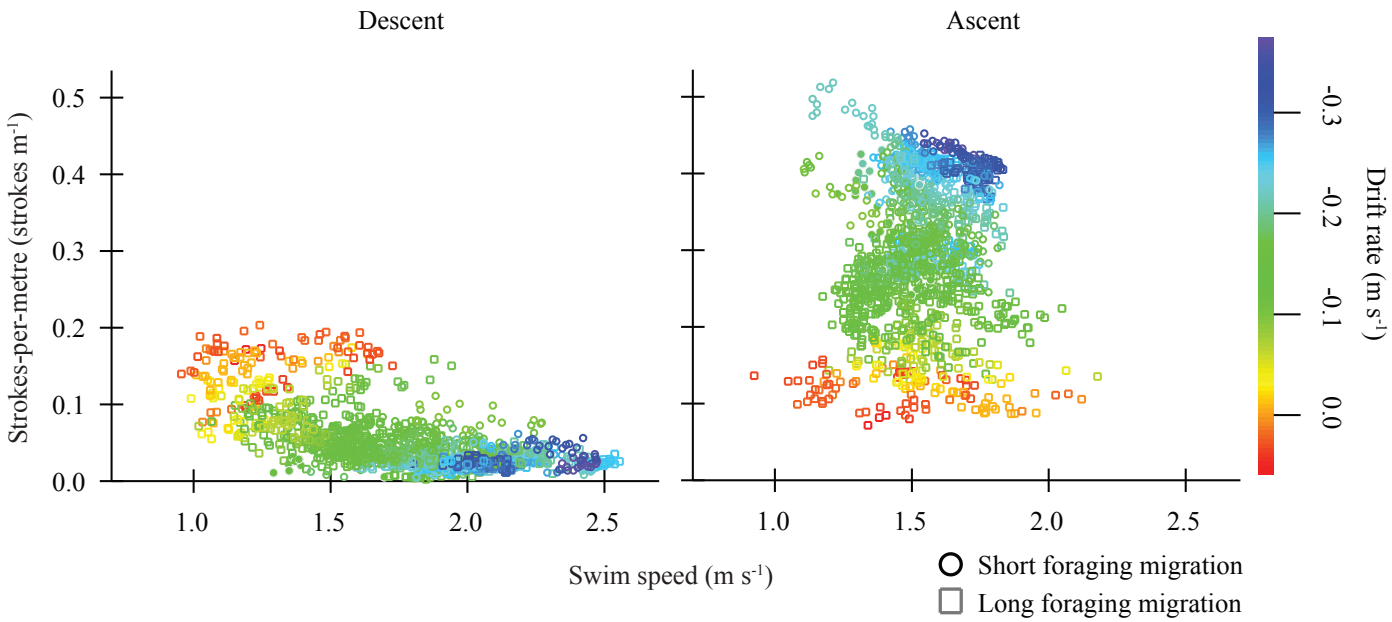

Figure 2.5. The relationship between strokes-per-metre (number of strokes per metre swam, represented in strokes m^{-1}) and swim speed during dives for all 14 individuals. Circles and squares represent daily values for seals during the short and long foraging migration, respectively. The color indicates values of drift rate. Left and right panels show descent and ascent phase, respectively.

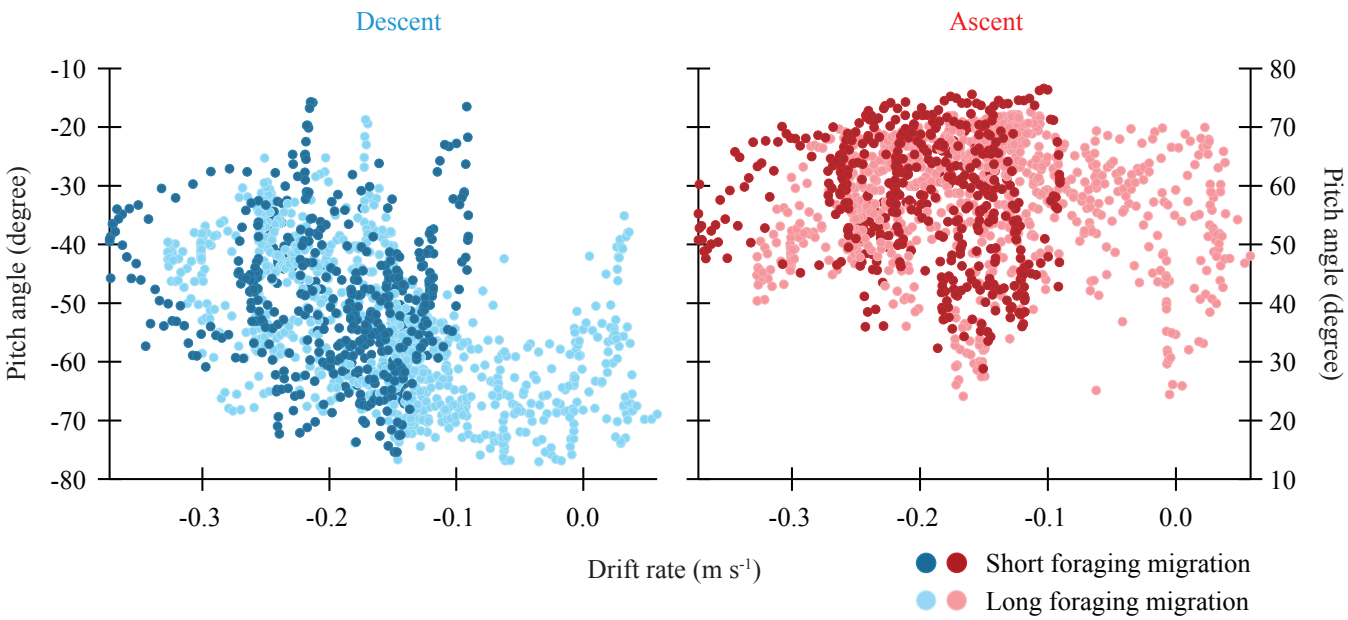

Figure 2.6. The relationship between dive pitch angle and drift rate for all 14 individuals. Left and right panels show daily values of descent (blue colors) and ascent (red colors) pitch angle, respectively. Filled dark and light blue (or red) circles represent daily values for seals during the short and long foraging migration, respectively.

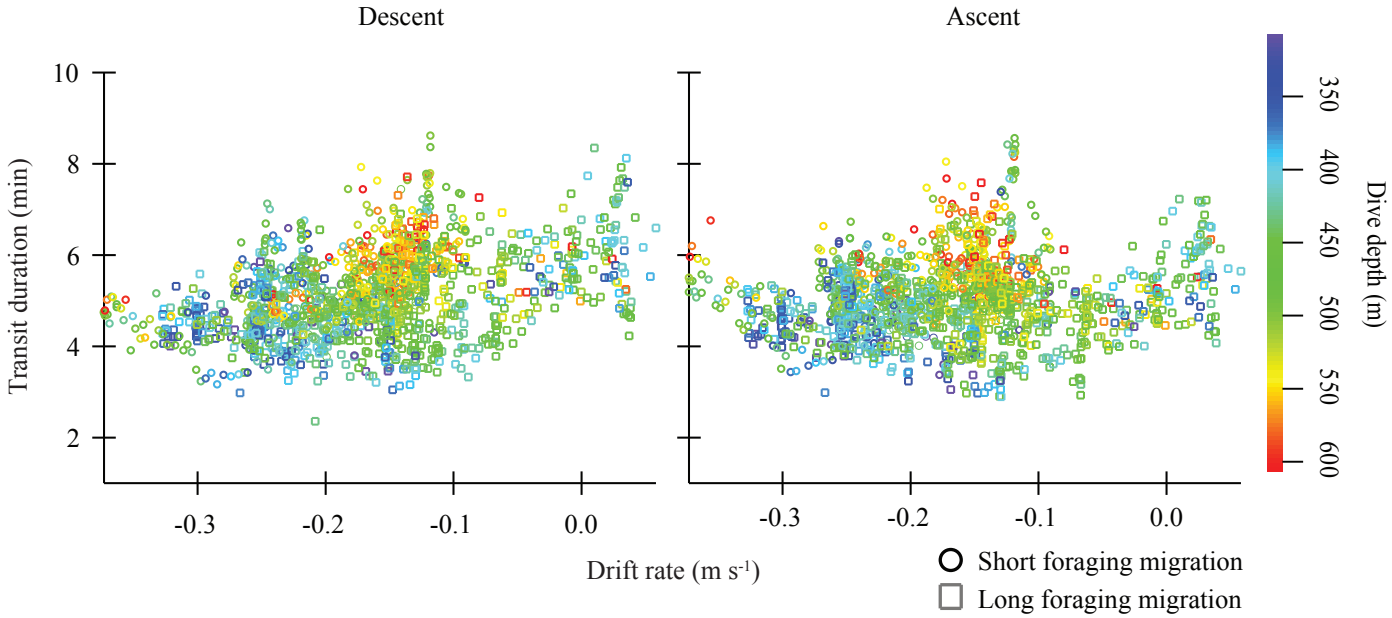

Figure 2.7. The relationship between transit duration and drift rate during dives for all 14 individuals. Circles and squares represent daily values for seals during the short and long foraging migration, respectively. The color indicates values of dive depth. Left and right panels show descent and ascent phase, respectively.

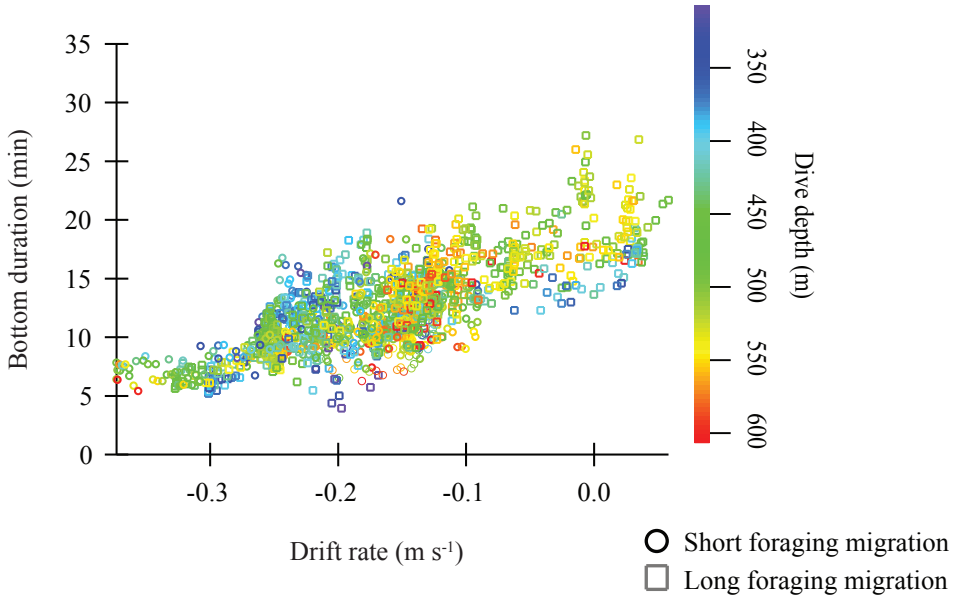

Figure 2.8. The relationship between bottom duration and drift rate during dives for all 14 individuals. Circles and squares represent daily values for seals during the short and long foraging migration, respectively. The color indicates values of dive depth. Left and right panels show descent and ascent phase, respectively.

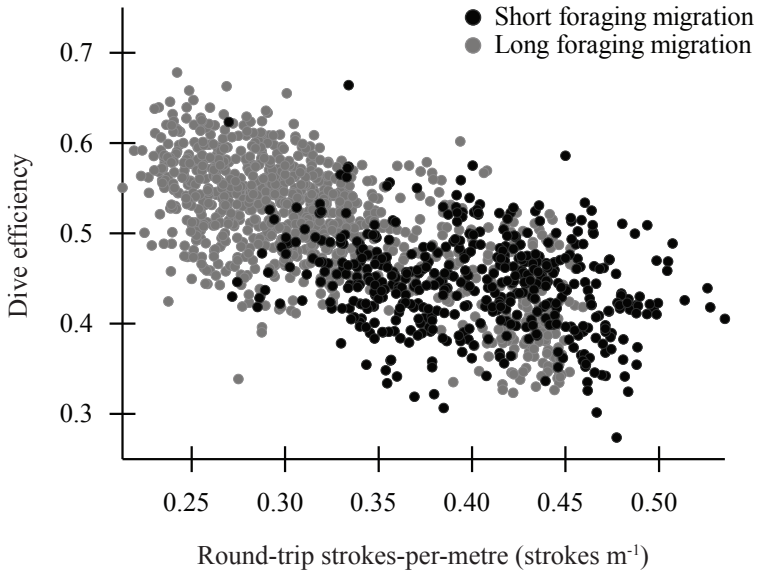

Figure 2.9. The relationship between dive efficiency (bottom duration per dive cycle, which is composed of transit time, bottom time and post-surface time) and round-trip strokes-per-metre (number of strokes per metre swam, represented in strokes m^{-1}) for all 14 individuals. Filled black and grey circles represent daily values for seals during short and long foraging migration, respectively.