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RESEARCH ARTICLE

# Drift dives and prolonged surfacing periods in Baikal seals: resting strategies in open waters?

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## ABSTRACT

Many pinnipeds frequently rest on land or ice, but some species remain in open waters for weeks or months, raising the question of how they rest. A unique type of dive, called drift dives, has been reported for several pinnipeds with suggested functions of rest, food processing and predator avoidance. Prolonged surfacing periods have also been observed in captive seals and are thought to aid food processing. However, information from other species in a different environment would be required to better understand the nature and function of this behavior. In this study, we attached multi-sensor tags to Baikal seals *Pusa sibirica*, a rare, freshwater species that has no aquatic predators and few resting grounds during the ice-free season. The seals exhibited repeated drift dives (mean depth, 116 m; duration, 10.1 min) in the daytime and prolonged periods at the surface (mean duration, 1.3 h) mainly around dawn. Drift dives and prolonged surfacing periods were temporally associated and observed between a series of foraging dives, suggesting a similar function, i.e. a combination of resting and food processing. The maximum durations of both drift and foraging dives were 15.4 min, close to the aerobic dive limit of this species; therefore, metabolic rates might not be significantly depressed during drift dives, further supporting the function of food processing rather than purely resting. Our results also show that drift diving can occur in a predator-free environment, and thus predator avoidance is not a general explanation of drift dives in pinnipeds.

**KEY WORDS: Diving behavior, Food processing, Predator avoidance, Accelerometer**

## INTRODUCTION

Pinnipeds (seals, sea lions and walruses) are morphologically, physiologically and behaviorally well adapted to a marine lifestyle, but still leave the water ('haul out') and spend considerable time on land or ice for giving birth, lactation and molting (Bonner, 1994). Even in periods of no such seasonal activities, many pinniped species stay close to land or ice and haul out frequently to rest (Bengtson and Cameron, 2004). However, some species during certain seasons remain in open waters for weeks or months without hauling out. For example, northern elephant seals, *Mirounga angustirostris*, perform 2- to 8-month-long trips from the colony twice a year (i.e. post-breeding and post-molting) in the northern Pacific, and they do not haul out during those trips (Le Boeuf et al., 1989, 2000). These observations have raised an intriguing question: how do they rest in the water?

Elephant seals exhibit an interesting type of dive, called drift dives, during which the seals sink (or 'drift') passively in the water column before actively swimming back to the surface (Crocker et al., 1997). Although many seal species perform foraging dives that include passive swimming periods (i.e. prolonged gliding while descending) (Williams et al., 2000; Watanabe et al., 2006), drift dives are distinct from those dives in that (i) the rates of depth changes during drift phases are constant, and hence the time-series depth data are characterized by a straight segment, and (ii) the swim speeds during drift phases are unusually low, often below the minimum detectable value of the speed sensor (Crocker et al., 1997). Many drift dives often occur sequentially, and the frequency of drift dives (computed on a weekly basis) are positively related to the frequency of foraging dives (Crocker et al., 1997). In addition, a recent study using accelerometers and magnetometers revealed that elephant seals are on their backs during drift phases, with the heading direction on the horizontal plane changing constantly over 360 deg (Mitani et al., 2010). Based on these observations, it is currently accepted that drift dives represent resting or food processing by the seals (Crocker et al., 1997; Mitani et al., 2010), although it is difficult to determine whether the seals sleep during drift dives. Drift dives have also been reported for hooded seals, *Cystophora cristata* (Andersen et al., 2014), and New Zealand fur seals, *Arctocephalus forsteri* (Page et al., 2005), and an additional function of predator avoidance was proposed. That is, repeating drift dives might be safer for seals than resting at the surface in the presence of predators such as white sharks, *Carcharodon carcharias* (Page et al., 2005). However, it is still unclear whether drift diving is a common behavior among pinnipeds, and, if so, whether predator avoidance is a general explanation of drift dives.

When animals are resting, their metabolic rates are not necessarily reduced as a result of the reduced cost for locomotion, but can be increased as a consequence of an energy-demanding physiological process, i.e. food processing (Secor, 2009). The increased metabolic rate due to food processing represents a unique challenge for air-breathing diving animals, because increased metabolic rate is expected to reduce aerobic dive durations and thus time for foraging (Crocker et al., 1997). Some pinnipeds appear to circumvent this problem by temporarily separating food processing from foraging, although food processing and foraging can be compatible (Williams et al., 2004). For example, gray seals, *Halichoerus grypus*, in captivity process food while they are motionless at the surface, many hours after the end of foraging dives (Sparling et al., 2007). Northern elephant seals appear to process food during a series of drift dives after foraging dives (Crocker et al., 1997). However, information from other species is lacking, precluding us from better understanding the nature of the temporal separation of food processing and foraging in pinnipeds.

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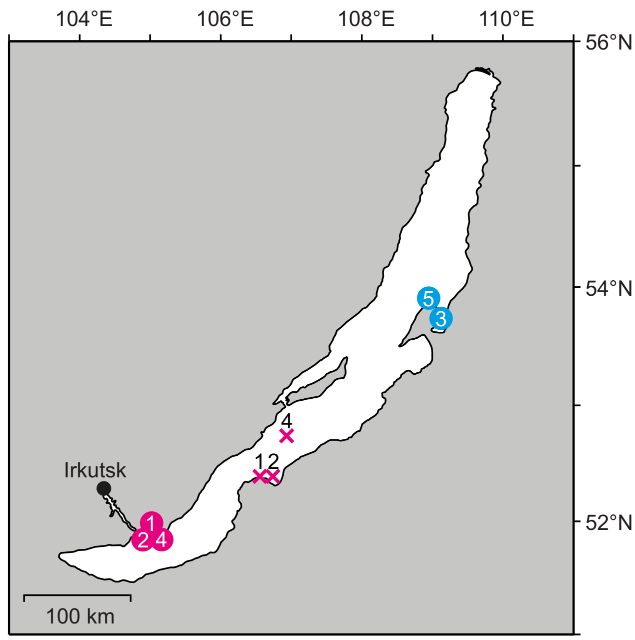


**Fig. 1. Map of Lake Baikal.** Individuals 1, 2 and 4 were captured at the sites denoted by pink crosses, and released on the shore in Listvyanka (pink circles) after a period of captivity. Individuals 3 and 5 were released following capture at the sites denoted by light blue circles.

Baikal seals, *Pusa sibirica* Gmelin, in Lake Baikal, Russia, represent a unique subject for studying how pinnipeds rest and process food in the water. When the lake is covered by ice from November to June, this endemic species frequently hauls out on the ice to rest, breed and molt. In contrast, during the ice-free period from June to November, Baikal seals rarely haul out on the shore of the lake, where they may encounter humans or brown bears, *Ursus arctos*. They do haul out on some islands in the lake (e.g. the Uschkani Islands); however, there are only a few haul-out grounds over the lake, which appear to have a total capacity of several hundred individual seals. The estimated total population of Baikal seals is 80,000–100,000 individuals (Burkanov, 2008), which means that most individuals must remain in the water during the ice-free period. Therefore, Baikal seals are expected to rest and process food in the water during drift dives (as in elephant seals) or during prolonged periods at the surface (as in captive gray seals), or both. Importantly, unlike many other pinnipeds, Baikal seals have no predators in the water, and the possible predator-avoidance function of drift dives (Page et al., 2005) can be excluded. Studying this species could thus provide deeper insights into how pinnipeds rest and process food in the water.

In this study, we attached multi-sensor tags to Baikal seals, for which diving behavior has rarely been recorded because of the difficulty in accessing the animals (Stewart et al., 1996; Watanabe et al., 2004, 2006). Our objectives were to determine whether Baikal seals exhibit drift dives and prolonged surfacing periods as a means of resting and food processing in the unique environment of Lake Baikal.

## RESULTS

Five seals were instrumented and released at several sites in Lake Baikal from 2003 to 2006 (Fig. 1, Table 1). During a total of 160 h diving records obtained, 34 drift dives and nine prolonged (>15 min) surfacing periods were recorded (Fig. 2). Most (33 of 34) drift dives were recorded from individuals 3 and 5, which were released within a day of capture. In contrast, individuals 1, 2 and 4, which had been in captivity for 3–6 months before release, rarely exhibited drift dives, although some of them (individuals 1 and 4) did show prolonged surfacing periods (Fig. 3). Drift dives were observed mostly during the daytime, whereas prolonged surfacing periods tended to occur around dawn (Fig. 3). The mean (±s.d.) and maximum durations of prolonged surfacing periods were 1.3±1.3 h and 4.7 h ($N$=9 events), respectively. The seals were in an upright position (i.e. pitch angle – the angle between the long axis of the seal's body and the horizontal plane – was close to 90 deg) during the prolonged surfacing periods, except for individual 4, which alternated between upright and horizontal positions in the two prolonged surfacing events.

During each drift dive, the seals started descending with active flipper strokes and decreasing swim speed, and then stopped stroking and changed pitch angle to be closer to the horizontal at a mean depth of 26 m (i.e. the point of drift phase start) (Fig. 4). The point of drift phase start was deeper for individual 5 (48 m) than for individuals 3 and 4 (15–16 m) (Table 2). The following drift phase was characterized by a constant depth change, low swim speed, often below the stall speed of the sensor, no flipper strokes and relatively constant pitch angle and heading (i.e. the direction in which the animals are pointing on the horizontal plane). Roll angle (i.e. the angle between the dorso-ventral axis of the seal's body and the vertical plane) was relatively small (5–14 deg) during drift phases (Table 2). The vertical speed determined by the depth sensor during drift phases (mean, $0.25\ \mathrm{m\ s^{-1}}$) was higher than the stall speed of the propeller sensor ($0.04–0.10\ \mathrm{m\ s^{-1}}$), which meant that the seals were indeed drifting. That is, the seals were not moving forward and thus the propeller sensor, which was facing forward, could not measure their true speed in the water column. Following the drift phase, the seals ascended with active flipper strokes to the surface. Interestingly, the seals changed heading at the end of the drift phase (Fig. 4), and the difference in the heading between the

**Table 1. Summary for study animals and data collected**

| Animal ID | Sex | Body mass (kg) | Release month/ year | Wild animals? | Tag[a] | Data length (h) | No. of dives | No. of drift dives | No. of prolonged surfacing periods |
|---|---|---|---|---|---|---|---|---|---|
| Individual 1 | Female | 54.6 | 6/2003 | No[b] | PD2GT | 20 | 164 | 0 | 1 |
| Individual 2 | Female | 72.8 | 6/2003 | No[b] | PD2GT | 20 | 151 | 0 | 0 |
| Individual 3 | Male | 83.0 | 10/2004 | Yes | 3MPD3GT | 24 | 114 | 20 | 3 |
| Individual 4 | Female | 45.2 | 7/2005 | No[b] | 3MPD3GT | 72 | 311 | 1 | 5 |
| Individual 5 | Female | 30.5 | 8/2006 | Yes | 3MPD3GT | 24 | 114 | 13 | 0 |

[a]PD2GT records depth, swim speed, temperature and acceleration; 3MPD3GT records an additional parameter: geomagnetism.
[b]These individuals had been in captivity for 3–6 months before release.

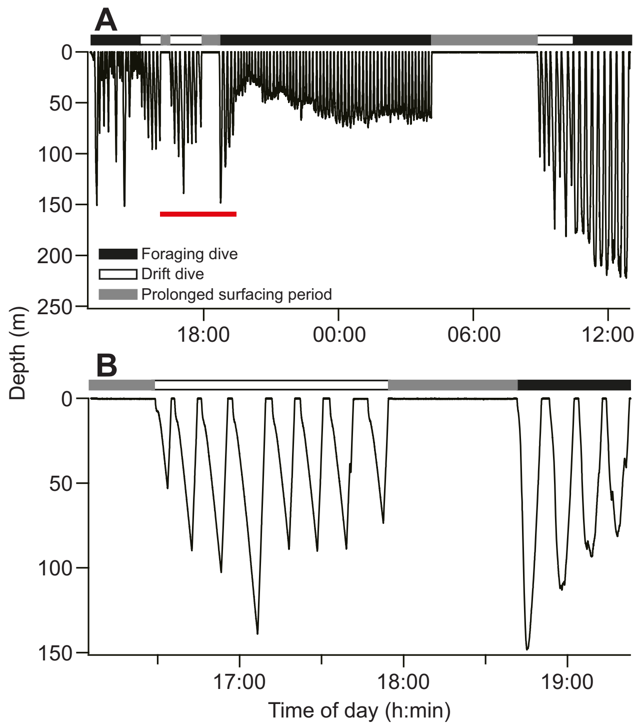


**Fig. 2. Depth record for individual 3.** (A) The whole 24 h record, showing foraging dives, drift dives and prolonged surfacing periods. (B) An enlarged view of the 3.5 h period denoted by the red horizontal bar in A.

drift phase and subsequent ascent phase was close to 180 deg, i.e. the opposite direction (Table 2).

All drift dives recorded in this study had similar behavioral patterns in general, but the maximum depth reached during the dives varied widely (53–182 m) (Fig. 2B). As a result, the relationship between dive depth and duration was highly linear for drift dives ($R^2$=0.89, $N$=34 dives), whereas the relationship showed considerable variation for foraging dives ($R^2$=0.49, $N$=793 dives) (Fig. 5). Least-squares regression lines in Fig. 5 indicate that dive durations are longer for drift dives than for foraging dives for a given dive depth. However, the maximum dive durations were 15.4 min for both drift and foraging dives, and this value was close to the aerobic dive limit (i.e. the dive duration beyond which post-dive lactate concentration increases above the resting level; Kooyman and Ponganis, 1998) of 15 min previously determined for this species in captivity (Ponganis et al., 1997).

## DISCUSSION

### Confirmation of drift dives

Among the 34 extant pinniped species, Baikal seals are now the fifth species that has been confirmed to perform drift dives, together with northern and southern elephant seals, hooded seals and New Zealand fur seals (Hindell et al., 1991; Crocker et al., 1997; Page et al., 2005; Andersen et al., 2014). A common feature of the five species showing drift dives is that they spend, during a certain time of the year, a considerable amount of time in open waters, without nearby land or ice that can be used for hauling out. In contrast, some species are associated with rocky coasts (e.g. harbor seals), fast sea ice (e.g. Weddell seal) or floating pack ice (e.g. crabeater seal) throughout the year, and no drift dives have been detected in the diving records of these species (Bengtson and Stewart, 1992; Lesage et al., 1999; Davis et al., 2003). Therefore, our finding, together with those of the previous studies (Hindell et al., 1991; Crocker et al., 1997; Page et al., 2005; Andersen et al., 2014), indicates that drift diving is an option for pinnipeds to rest or process food when there are no places to haul out.

Of the five individuals released in this study, two wild individuals performed many drift dives, whereas the other three individuals that had been in captivity rarely exhibited drift dives, although some of them did exhibit prolonged surfacing periods. This difference might not stem from the difference in motivation for resting or food processing, because the captive individuals foraged during diving, as confirmed by an animal-attached camera (Watanabe et al., 2004). The captive individuals may have lost some of their natural behavior at least for the first few days of release, and future work examining drift dives should use wild animals alone.

### Functional implications

Although some individual Baikal seals exhibited both drift dives and prolonged surfacing periods, others showed either drift dives or prolonged surfacing periods (Fig. 3). In addition, in the individual that exhibited drift dives most frequently, drift dives occurred immediately prior or subsequent to prolonged surfacing periods (Fig. 2). These observations suggest that the functions of drift dives and prolonged surfacing periods are similar, i.e. a combination of resting and food processing. A similar temporal association of drift dives and prolonged surfacing periods was reported for elephant seals (Crocker et al., 1997), although prolonged surfacing periods are rare in elephant seals, presumably because of the presence of predators such as white sharks.

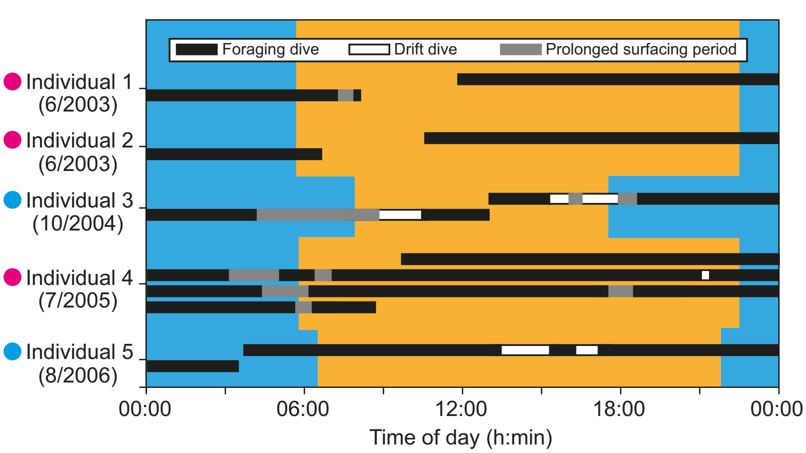


**Fig. 3. Time of the day when foraging dives, drift dives and prolonged surfacing periods were observed.** The orange and blue background denote daytime and night-time, respectively, based on the local sunset and sunrise time. Pink and light blue circles denote the individuals with and without a captivity period before release, respectively. Month/year of release is also shown in parentheses for each individual.

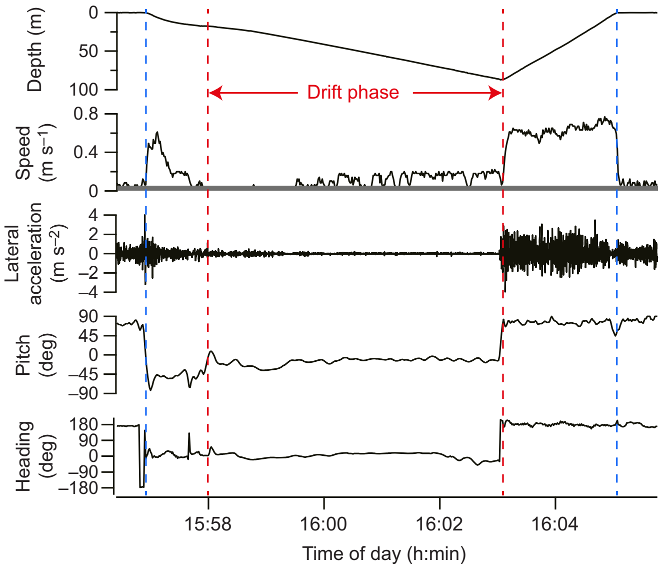


**Fig. 4. A typical drift dive recorded from individual 3.** The parameters shown are depth, swim speed, the high-frequency component of lateral acceleration (i.e. indicative of flipper stroking activity), pitch angle and heading. Pitch angle is the angle between the long axis of the seal's body and the horizontal plane, with positive values indicating ascents and negative values indicating descents. Heading is the direction in which the animal is pointing on the horizontal plane, with 0, +90, −90 and ±180 deg representing magnetic north, east, west and south, respectively. Blue vertical dashed lines denote the start and end of the dive. Red vertical dashed lines denote the start and end of the drift phase. Note that swim speed is often below the stall speed of the sensor (0.04 m s$^{-1}$; denoted by the gray horizontal bar) during the drift phase.

A combination of resting and food processing function for drift dives is also suggested by our analysis of dive duration. Although drift dives tended to be longer than foraging dives for a given dive depth, the maximum dive duration was the same (15.4 min) for the two types of dive (Fig. 5). If metabolic rates are reduced during drift dives, as expected if the single function of drift dives is resting, then the maximum dive duration of drift dives would be longer than that of foraging dives. Intriguingly, the maximum dive duration (15.4 min) agrees with the aerobic dive limit of this species, previously determined for voluntary submersions of captive animals in a tank (Ponganis et al., 1997). This observation suggests that metabolic rates of Baikal seals are not significantly depressed during drift dives, and that dive duration is limited by their aerobic dive limit regardless of dive type. Our suggestion is supported by the previous finding that blood oxygen stores are depleted to a similar level during diving in elephant seals, irrespective of dive type (i.e. foraging dives and drift dives; Meir et al., 2013).

Baikal seals are a rare pinniped species in that they have no aquatic predators. Although this species has long been hunted by humans, it is mainly targeted on the ice in the spring, and it is unlikely that the swimming or diving behavior of Baikal seals has been altered by human hunting activity. Therefore, the previous proposal that drift diving is a predator-avoidance strategy (i.e. it is safer for seals to repeat drift dives than to rest at the surface) (Page et al., 2005) is not applicable. Our finding cannot rule out the possibility that drift dives function as predator avoidance in some species; however, it does demonstrate that the presence of predators is not a prerequisite for pinnipeds to perform drift dives.

Baikal seals tended to exhibit prolonged surfacing periods around dawn after a series of foraging dives at night (Fig. 3). Given that the function of prolonged surfacing periods is similar to that of drift dives, our results agree with those for elephant seals, which exhibit drift dives most frequently in the morning after a long series of forging dives at night (Crocker et al., 1997). Drift dives of Baikal seals are observed during the daytime, which is inconsistent with findings for hooded seals (Andersen et al., 2014) and New Zealand fur seals (Page et al., 2005), which exhibit drift dives at night-time. Overall, it appears that some pinnipeds have a diel rhythm for the timing of drift dives and prolonged surfacing periods, presumably related to the timing of a series of foraging dives, and that the diel rhythm differs among species.

### Comparison with other species

Drift dives of Baikal seals differ from those of other species in several respects. First, the depths at which drift phases start (26 m) are shallower for Baikal seals than for northern and southern elephant seals (approx. 200 m; Hindell et al., 1991; Crocker et al., 1997) and New Zealand fur seals (87 m; Page et al., 2005). This difference could be explained by the fact that Baikal seals are freshwater seals. Most seals are positively buoyant at the surface, but as they descend in the water column, they become less and less buoyant as a result of the compression of air volume in the lungs by hydrostatic pressure (Falke et al., 1985; Williams et al., 2000). Consequently, seals can start sinking at a certain depth, which is determined by the animals' body density and the surrounding water density (Watanabe et al., 2006). Because freshwater is about 3% less dense than seawater, Baikal seals become negatively buoyant at shallower depths than marine seals, given that their body densities (primarily determined by lipid content in the body and air volume in the lungs) are similar. One of our seals (individual 5) started drifting at greater depth than the others (individuals 3 and 4), presumably reflecting a lower body

**Table 2. Summary for drift dives**

| | Dive | | | Drift | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Animal ID | No. | Depth (m) | Duration (min) | Start depth (m) | Duration (min) | Vertical speed (m s$^{-1}$)[a] | Pitch angle (deg)[b] | Roll angle (deg)[c] | Change in heading (deg)[d] |
| Individual 3 | 20 | 105±32 | 9.6±2.5 | 15±4 | 6.1±1.8 | 0.24±0.02 | −23±7 | 5±11 | 171±9 |
| Individual 4 | 1 | 119 | 10.6 | 16 | 7.0 | 0.25 | −11 | 14 | 174 |
| Individual 5 | 13 | 123±16 | 10.1±0.5 | 48±7 | 5.1±0.8 | 0.25±0.02 | −28±2 | 9±5 | 127±29 |
| Grand mean | | 116 | 10.1 | 26 | 6.1 | 0.25 | −21 | 9 | 157 |

Means±s.d. are presented for individuals 3 and 5.
[a]Vertical speed was determined by the depth sensor during the drift phase.
[b]Negative pitch angle represents a downward position of the animal.
[c]Positive roll angle represents a tilt to the right by the animal.
[d]Change in heading between drift phase and the following ascent phase, potentially ranging from 0 to 180 deg.

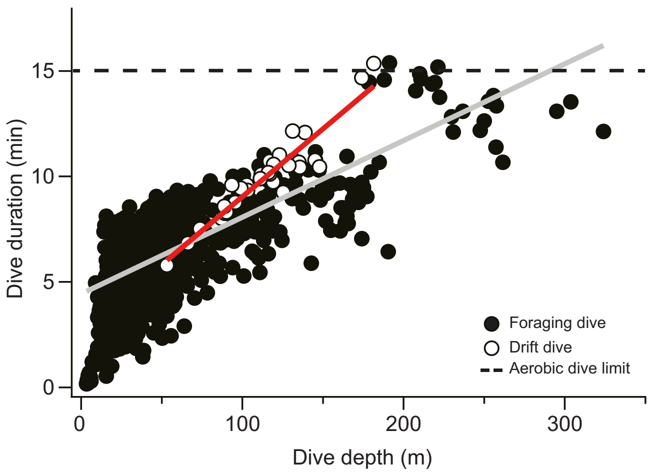


**Fig. 5. Relationship between dive depth and dive duration for foraging dives and drift dives.** Least-squares regression lines are as follows: duration=0.036×depth+4.4 for foraging dives; duration=0.064×depth+2.6 for drift dives. Data from the three seals that exhibited drift dives (individuals 3–5) are pooled in this figure. The dotted horizontal line denotes the aerobic dive limit (i.e. the dive duration beyond which post-dive lactate concentration increases above the resting level) of 15 min previously determined for this species in captivity (Ponganis et al., 1997).

density due to a higher lipid content or larger air volume in this individual.

Second, Baikal seals maintained small roll angles (5–14 deg) and relatively constant headings during drift phases. This result is in marked contrast with northern elephant seals, which sink on their back with their heading rotating over 360 deg without moving in a particular horizontal direction (Mitani et al., 2010). Interestingly, Baikal seals changed their heading at the end of the drift phase, and started ascending in almost the opposite direction. Although the patterns in the changes of heading are different between Baikal and elephant seals, both species are expected to be able to stay close to the original position at the end of each drift dive (i.e. Baikal seals turn around at the end of the drift phase, whereas elephant seals do not move in a particular direction during the drift phase). Such behavior may be beneficial in open waters for navigation purposes.

In conclusion, we found that Baikal seals exhibit both drift dives and prolonged surfacing periods in the ice-free period in Lake Baikal, presumably as means of resting and food processing. The maximum duration of drift dives suggests that metabolic rates of the seals are not significantly depressed during drift phases, further supporting the function of food processing rather than purely resting. Importantly, Baikal seals have no aquatic predators, and thus predator avoidance is not a general explanation for drift dives in pinnipeds.

## MATERIALS AND METHODS

Fieldwork was conducted at various sites in Lake Baikal from 2003 to 2006, and five seals were instrumented and released (Table 1, Fig. 1). Individuals 1 and 2, and individual 4 were captured using nets in the Selenga River Delta and offshore in the middle Baikal, respectively. These individuals were transported by car to the Limnological Institute Aquarium in Listvyanka, and kept in a tank for 3–6 months, before they were released from the shore in Listvyanka. Individuals 3 and 5 were captured using nets and released within a day in Chivirkuy Bay and Uschkani Island, respectively. The diving behavior of individuals 1 and 2 and 1–4 was previously reported (Watanabe et al., 2004, 2006) with the focus on their foraging behavior and the effect of buoyancy on their swimming patterns, respectively.

Two types of multi-sensor tags were used in this study depending on the individual (Table 1). A PD2GT (22 mm diameter, 124 mm length and 92 g; Little Leonardo Co., Tokyo, Japan) recorded depth, swim speed (measured by a propeller sensor), ambient temperature at 1 s intervals, and biaxial acceleration (along lateral and longitudinal axes) at 1/16 s intervals. A 3MPD3GT (26 mm diameter, 175 mm length and 135 g; Little Leonardo Co.) recorded tri-axial acceleration (along lateral, dorso-ventral and longitudinal axes) at 1/16 or 1/32 s intervals and tri-axial geomagnetism at 1 s intervals, in addition to depth, swim speed and temperature at 1 s intervals. A still-picture camera (22 mm diameter, 138 mm length and 73 g; Little Leonardo Co.) was also attached to individuals 1–4, but the images obtained were not used in this study. The devices were incorporated into a package for instrument recovery (Watanabe et al., 2004), which was composed of a time-scheduled release mechanism (Little Leonardo Co.), float and VHF transmitter (Advanced Telemetry Systems Inc., Isanti, MN, USA). The package weighed 360–370 g (with camera) or 270 g (without camera), accounting for 0.4–0.9% of body mass of the animals. The package was attached to the fur on the back (approximately in the center) of the seals using epoxy resin, before the seals were released. Once the package detached from the animals after a 1–3 day free-swimming period, it was located using VHF signals and recovered by a boat.

Data were analyzed using the software Igor Pro (WaveMetrics Inc., Lake Oswego, OR, USA) with the package Ethographer (Sakamoto et al., 2009). Drift dives were readily identified from the diving records based on the characteristic depth profile and unusually low swim speed (Figs 2, 4). The start point of the drift phase during a drift dive was defined as the point where the rate of depth change became constant (which closely corresponded to the point where swim speed dropped below the stall speed of the sensor) (Fig. 4). Pitch angles of the animals were estimated from low-frequency signals of longitudinal acceleration (Sato et al., 2003). Relative swimming speed measured by a propeller sensor was converted to actual swim speed ($m\ s^{-1}$) using the within-data calibration method (Sato et al., 2003), which compared propeller rotation values with the speeds calculated from depth change and pitch angle. According to the calibration equations, stall speed of the sensors (i.e. the speed below which the propeller does not rotate) was 0.04–0.10 $m\ s^{-1}$. In addition, for individuals 3–5 for which tri-axial accelerations and tri-axial geomagnetism were recorded, roll angle and heading were calculated using the 3D path program (Narazaki and Shiomi, 2010).

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#### Competing interests
The authors declare no competing or financial interests.

#### Author contributions
Y.Y.W., E.A.B. and N.M. designed the research. Y.Y.W. and E.A.B. conducted the fieldwork. Y.Y.W. analyzed the data and wrote the paper with input from E.A.B. and N.M.

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