

Foraging tactics of Baikal seals differ between day and night

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ABSTRACT: Some pinniped species appear to forage during both daylight and darkness. To determine any differences in the foraging tactics between day and night, we attached data loggers with a newly developed time-scheduled release system to 2 free-ranging female Baikal seals *Phoca sibirica*. The system released the loggers from the seals 24 h after deployment, and allowed us to retrieve the loggers via VHF radio signals. We obtained the first time-series diving data on Baikal seals. The seals dived almost continuously, to an average of 68.9 m, with dives deeper than this (>150 m) being concentrated around dusk and dawn. They showed distinctly different diving patterns between day and night in terms of swimming speed profile and the sequential pattern in maximum dive depth. In the daytime, dives were characterized by higher swimming speeds (mean 1.2 m s⁻¹) and upward-directed acceleration events. At night, dives were shallower around midnight and characterized by lower speeds (mean 0.9 m s⁻¹) and undirectional deceleration events. We suggest that these differences reflect predation on pelagic fishes by seals using visual cues during the day and predation on swarming crustaceans by seals using tactile cues at night.

KEY WORDS: Baikal seal · Foraging tactics · Diving · Release system · Data logger

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INTRODUCTION

Diel variation in foraging behavior is a common feature of diving animals. Penguins, for example, are primarily diurnal foragers (Wilson et al. 1993, Pütz & Bost 1994, Pütz et al. 1998, Bost et al. 2002) while fur seals are generally nocturnal foragers (Croxall et al. 1985, Boyd & Croxall 1992). On the other hand, some pinniped species appear to forage during both daylight and darkness (Kooyman 1975, Le Boeuf et al. 1988, 2000, Feldkamp et al. 1989, Coltman et al. 1997). Different tactics could be used during the day and at night because of changes in the relative importance of the predator's sensory systems and because many aquatic organisms, including pinniped prey, make diel vertical migrations (e.g. Stich &

Lampert 1981, Wurtsbaugh & Neverman 1988, Scheuerell & Schindler 2003). However, little is known about how pinnipeds may change their foraging tactics in response to diel cycles in aquatic ecosystems.

In this respect, Baikal seals *Phoca sibirica* are interesting models. Firstly, they appear to forage almost continuously both day and night (Stewart et al. 1996). Secondly, their prey, such as sculpin fishes and amphipods, are known to undertake pronounced diel vertical migrations in Lake Baikal (Melnik et al. 1993, Pankhurst et al. 1994), probably to escape predators, which are efficient hunters even at substantial depths in the clear waters of Lake Baikal (Gliwicz 1986). Therefore, we would expect Baikal seals to use different foraging tactics during day and at night.

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Time-series data on diving behavior have not previously been obtained for Baikal seals. One practical reason may lie in the fact that animal-borne micro-data loggers require the recapture of animals for data retrieval and the recapture of instrumented Baikal seals in Lake Baikal is almost impossible (Baranov 1996). An exception is satellite-linked telemetry (Stewart et al. 1996); however, such systems can transmit only a limited amount of data (see Fedak et al. 2002). In the present study, we used a newly-developed time-scheduled release system. The system releases micro-data loggers from the seals and allows the loggers to be retrieved via VHF radio signals. Recapture of the seals is therefore not necessary. Our objective in this study was to determine possible differences between the foraging tactics of Baikal seals during the day and those at night.

MATERIALS AND METHODS

We captured 2 female Baikal seals using modified twine gill-nets placed just offshore at the Selenga River Delta (52.47° N, 106.88° E) in Lake Baikal, Russia, during December 2002. The seals (Individuals 1 and 2) were held in captivity at the Limnological Institute aquarium in Listvyanka for about 6 mo. Individual 1 (54.6 kg) and Individual 2 (72.8 kg) were released on the shore in Listvyanka (51.85° N, 104.90° E) on 19 and 22 June 2003, respectively, after the following instruments had been attached to their backs.

We used 2 types of micro-data loggers. A multi-sensor data logger (UWE1000-PD2GT: 22 mm in diameter, 124 mm in length, 92 g in the air; Little Leonardo) with a memory of 32 Mb and 12-bit resolution, recorded swimming speed, depth and temperature at 1 s intervals, and 2 D accelerations (for detecting flipper movement and body angle) at 1/16 s intervals (see details in Sato et al. 2003). A digital still-picture logger (DSL-380DTV: 22 mm in diameter, 138 mm in length, 73 g in the air; Little Leonardo) with a memory of 2 Gb, recorded depth and temperature (12-bit resolution) at 1 s intervals, and still-color images (370 × 296 pixels) at a pre-programmed sampling interval of 30 s after a pre-programmed start time of 2 h. Because the DSL does not contain a light source (e.g. flash), the sampling intervals and start time were selected to use all of the memory (ca. 1300 images) during daylight hours.

The data loggers were attached to a float of copolymer foam, in the top of which a VHF radiotransmitter with a 45 cm semi-rigid wire antenna was embedded (Fig. 1). A plastic cable connected to a time-scheduled release mechanism (Little Leonardo)

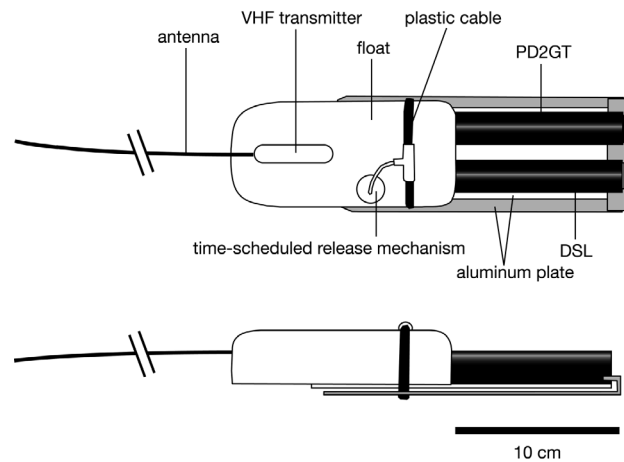


Fig. 1. Top and side views of micro-data logger system (PD2GT). DSL: digital still-picture logger

bound the package to an aluminum plate, which was glued onto the seals with a quick-setting epoxy resin. The release mechanism included a timer that was activated 24 h after attachment. Once the release mechanism had been activated, the plastic cable was severed by an electric charge from the battery of the device, and the whole buoyant package was released from the seals. The package floated to the surface of the lake and was located via VHF radio-signals. The total weight of the system was 360 g in the air (approx. 0.6% of the body mass of a Baikal seal).

The PD2GT logger uses a 2-axis acceleration sensor that measures both dynamic acceleration (such as propulsive activities) and static acceleration (such as gravity). Swaying accelerations often contained low-frequency variations that were assumed to be the result of various turning and rolling movements by the seals. These were separated using a 0.1 Hz highpass filter (IGOR Pro, WaveMetrics). The remaining peaks and troughs with absolute amplitudes greater than 0.5 m s^{-2} were considered to be stroke activities of the seals (Sato et al. 2003). Surging accelerations are affected by both the forward movements of the seal and gravity (Tanaka et al. 2001, Yoda et al. 2001). High-frequency variations in the surging acceleration record were believed to be caused by flipper movements (Sato et al. 2003). Surging acceleration was filtered out using a 0.1 Hz lowpass filter (IGOR Pro). When the seal is still or moving at a constant speed, the gravity vector will change in response to its body angle, which can thus be calculated (Tanaka et al. 2001, Sato et al. 2003). Swimming speed was calculated using the number of rotations per second (rev s^{-1}) of an external, anteriorly-mounted propeller. The rotation value was converted to actual swimming speed (m s^{-1}) using a calibration line that was calculated for each individual from a linear regression of

rev s^{-1} against a second independent method of calculation, which used the body angle and vertical speed (as determined from the depth recorder). This second method is only reliable for steeper body angles, and hence we used only the absolute value of the angles over 45° in our calculations (see details in Sato et al. 2003).

Based on the sensor's absolute accuracy, a dive was defined as any excursion below the surface to a depth of >2 m. Each dive was subdivided into a descent phase (from the beginning of a dive to the time of the first ascent), an ascent phase (from the depth of the last descent to the end of dive), and a bottom phase (the time between the end of descent and beginning of ascent) (Le Boeuf et al. 1988). Statistical analysis was performed using Stat View (SAS Institute). Values for statistical significance were set at $p < 0.05$. Means (± 1 SD) are reported.

RESULTS

The time-scheduled release mechanism worked as planned, and the packages were successfully retrieved on both attempts. The 2 packages were found 34.7 km (51.5° N, 104.95° E) and 24.8 km (51.70° N, 105.17° E) away from the release point of the seals, 4 h and 2.5 h after activation of the release mechanism, respectively. Both seals swam offshore to the opposite bank of the lake. The PD2GTs provided 20 h of data including 174 dives for Individual 1, and 20 h including 162 dives for Individual 2. The dive depths of the first 10 dives for Individual 1 and the first 11 dives for Individual 2 were shallower (range 3 to 8 m) than those of the following dives. Therefore, we suspected that these dives might have been influenced by the instruments' deployment and shallower water depths, and thus removed these data from further analyses. Over all of the dives used in the analysis ($n = 315$), the mean and maximum dive depths and durations were 68.9 ± 53.3 m and 245 m, respectively, and 6.0 ± 2.8 min and 13.5 min, respectively, for Individuals 1 and 2. The DSL deployed on Individual 1 provided only 700 images (ca. half of the memory) due to water leakage into the device; no image showed prey. The DSL provided 1315 images for Individual 2, among which 1 image showed a pelagic sculpin (*Comephorus* spp.) (Fig. 2), the primary prey of Baikal seals (Thomas et al. 1982).

Both the instrumented seals dived almost continuously during the recording period (Fig. 3), with similar proportions of diving time (Individual 1 78%, Individual 2 82%). Deeper dives occurred near dusk, with dive depth decreasing and then increasing again toward dawn for both seals (Fig. 3). The seals velocity changed

abruptly during dives (Fig. 4). Steep accelerations to speeds greater than the mean $+3$ SD swimming speed (1.75 m s^{-1}) detected by the speed sensor were termed 'acceleration events'. Deceleration to less than the mean -3 SD swimming speed (0.36 m s^{-1}) were termed 'deceleration events'. Acceleration and deceleration events were accompanied by changes in the body angle (Fig. 4). Individuals 1 and 2 swam upward (i.e. body angle >0) in 78% ($n = 45$) and 83% ($n = 105$) of the acceleration events, respectively, and in 85% ($n = 252$) and 52% ($n = 172$) of the deceleration events, respectively. Acceleration events occurred at significantly shallower depths and within narrower depth ranges (Individual 1 mean 37.2 ± 14.6 m, range 10 to 67 m, $n = 45$; Individual 2 mean 32.2 ± 12.9 m, range 3 to 58 m, $n = 105$) than deceleration events (Individual 1 mean 60.2 ± 48.6 m, range 3 to 205 m, $n = 252$; Individual 2 mean 76.2 ± 51.4 m, range 3 to 234 m, $n = 172$) in both seals (Mann-Whitney *U*-test: Individual 1, $p < 0.01$; Individual 2, $p < 0.0001$). The prey image obtained by DSL was taken during an acceleration event. Both seals showed distinctly different diving patterns between day and night in terms of the sequential pattern in the maximum depth of dive and the occurrence of acceleration and deceleration events (Fig. 3). Therefore, dives fell into 2

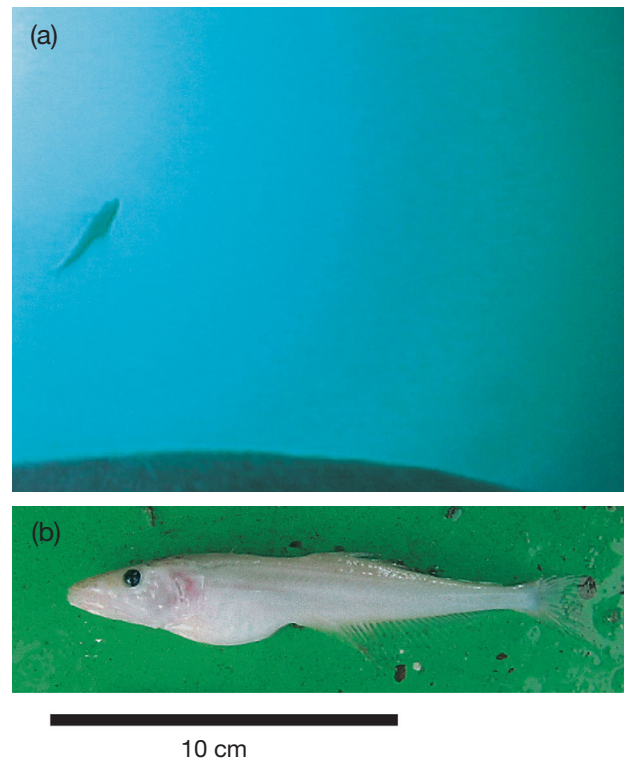


Fig. 2. Pelagic sculpins *Comephorus* spp., the primary prey of *Phoca sibirica*. (a) *Comephorus* spp. (taken with digital still-picture logger attached to Individual 2 at 14:32 h at 54 m depth, looking forward over the seal's back), (b) *C. baicalensis* caught by a trawl

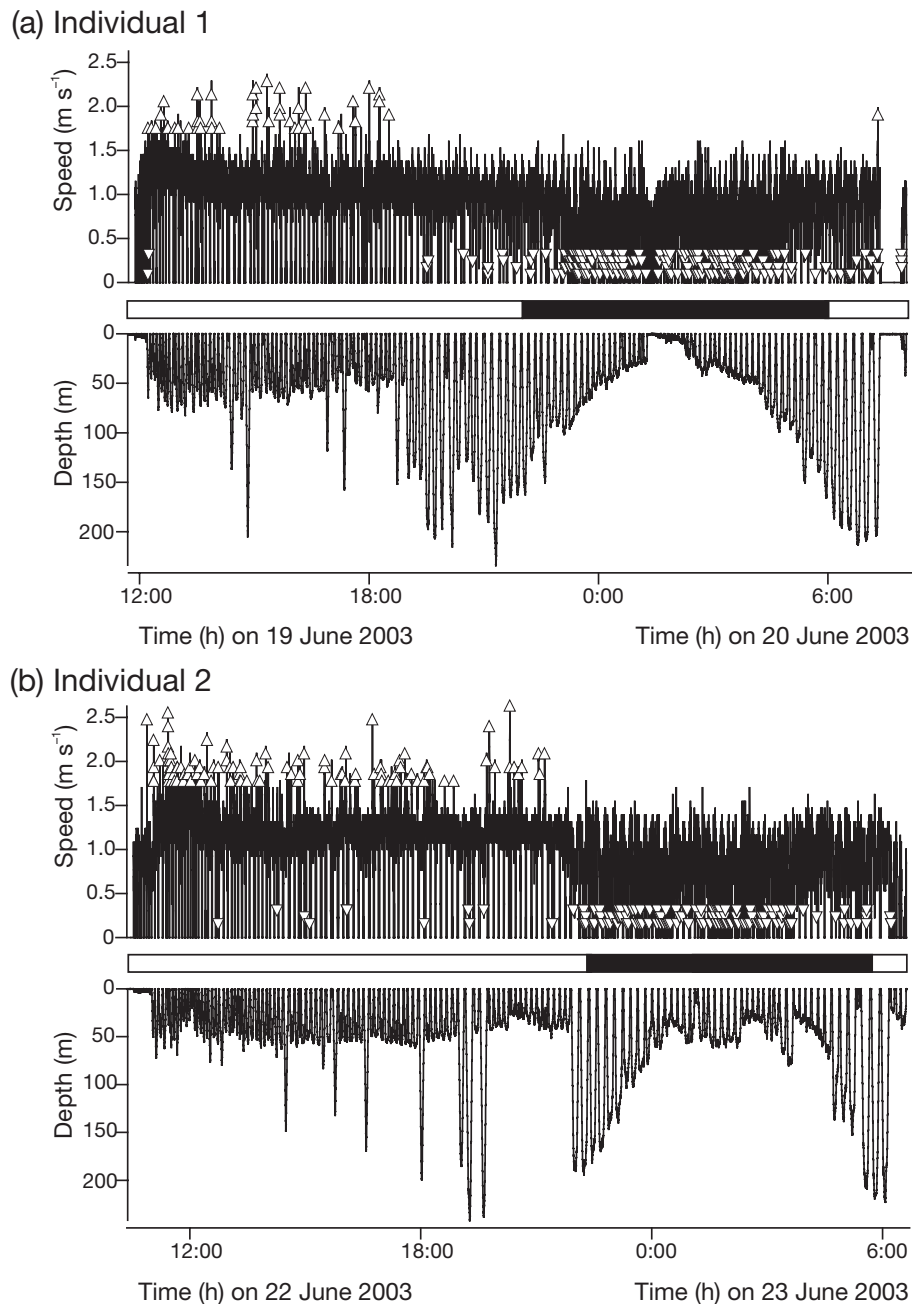


Fig. 3. *Phoca sibirica*. Swimming speed (upper graphs) and dive profiles (lower graphs) in relation to time of day for (a) Individual 1 and (b) Individual 2. (Δ ∇) Acceleration and deceleration events, respectively (see 'Results' for definition of events). Horizontal bars: daytime (white) and nighttime (black)

discrete categories, day dives and night dives, based on the local sunset and sunrise time (22:22 and 05:41 h, respectively).

During day dives, the swimming speed of the seals increased rapidly from 0 m s⁻¹ at the surface to a constant value (mean 1.1 ± 0.2 and 1.2 ± 0.3 m s⁻¹ for Individuals 1 and 2, respectively) (Table 1, Fig. 4a). Acceleration events interrupted the velocity record during the bottom phase of dives. There was no signifi-

cant difference in the speeds of day dives for both individuals between descent, bottom and ascent phase (1-way ANOVA: Individual 1, $p = 0.06$; Individual 2, $p = 0.25$) (Table 1). During the night dives, seals decelerated gradually until the beginning of the bottom phase, which was characterized by low speed (mean 0.8 ± 0.1 m s⁻¹ for both individuals) with a series of deceleration events (Table 1, Fig. 4b). The speeds of night dives were significantly different between

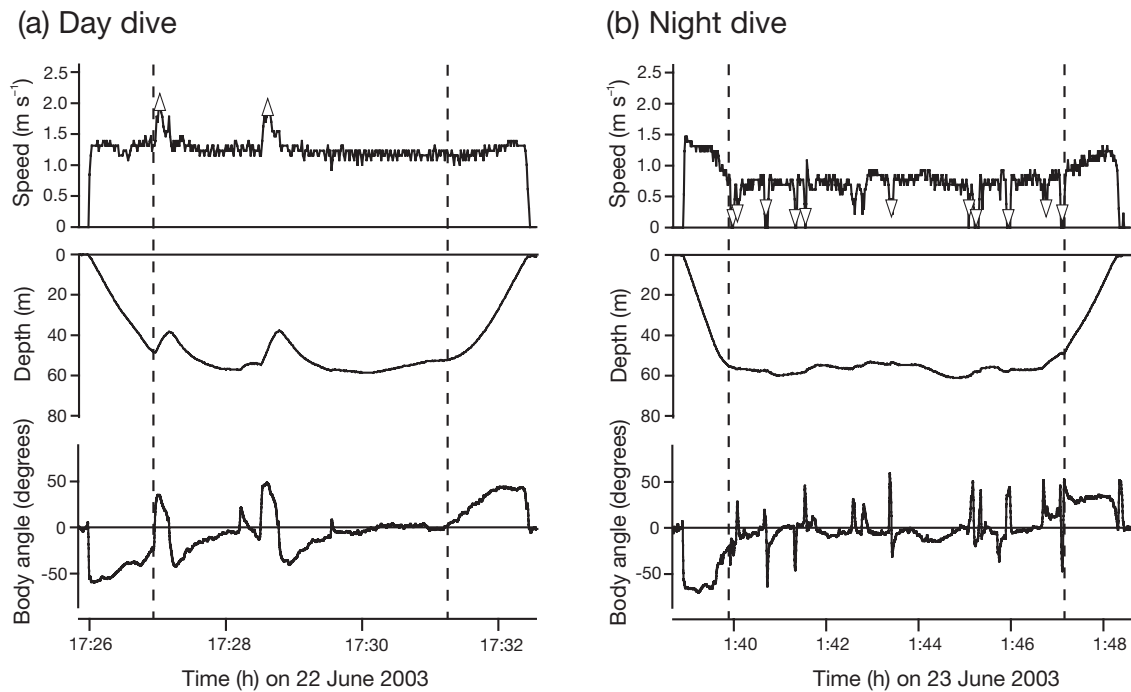


Fig. 4. *Phoca sibirica*. (a) Typical day dive; (b) typical night dive, showing swimming speed, dive depth and body angle (i.e. angle between long axis of seal's body and water surface, with positive values indicating ascent and negative descent). (Δ) Acceleration (upward) and deceleration (downward) events, respectively (see 'Results' for definition of events). Vertical dashed lines separate dive into 3 phases: descent, bottom and ascent

phases for both individuals (1-way ANOVA: Individuals 1 and 2, $p < 0.0001$) (Table 1) and a Fisher's PLSD (protected least-significant difference) post hoc test showed that the speed during the bottom phase was significantly lower than that during the descent (Individuals 1 and 2, $p < 0.0001$) or ascent (Individuals 1 and 2, $p < 0.0001$) phases. Comparisons of the diving behavior during the day and at night revealed that day dives had higher swimming speeds (Mann-Whitney U -test: Individuals 1 and 2, $p < 0.0001$) and higher stroke frequencies (Mann-Whitney U -test: Individuals 1 and 2, $p < 0.0001$) than night dives (Table 1). The number of acceleration events per dive was significantly higher during day dives than night dives (Mann-Whitney U -test: Individuals 1 and 2, $p < 0.0001$), while the number of deceleration events per dive was significantly higher during night dives than day dives (Mann-Whitney U -test: Individuals 1 and 2, $p < 0.0001$) (Table 1).

DISCUSSION

The results presented here are, to our knowledge, the first time-series data on the diving activity of free-ranging Baikal seals. They indicate that there is a distinct difference in the diving behavior of Baikal seals during the day and at night. We hypothesize that

these differences in the diving behavior are related to different foraging tactics employed during the pursuit and capture of different prey. The diet of Baikal seals is thought to comprise primarily pelagic sculpins commonly known as golomyankas (*Comephorus baicalensis* and *C. dybowskii*), benthic sculpins such as *Cottocomephorus grewingki* and *C. comephoroides* (Thomas et al. 1982, Pankhurst et al. 1994) and amphipods such as *Macrohectopus branickii* (Melnik et al. 1993).

Day dives were characterized by a relatively constant speed interrupted by acceleration events (Fig. 4a). An image taken during an acceleration event showed a prey, *Comephorus* spp. (Fig. 2) suggest that seals sometimes actively chase pelagic fishes during the day. Both seals swam upward during most acceleration events, suggesting that seals use vision to search for silhouetted prey against the brighter water overhead (Fig. 2a). The use of a back-lighting effect to detect and capture prey has been observed in Weddell seals *Leptonychotes weddellii* (Davis et al. 1999). Additionally, attacks on *Comephorus* spp. from below may prevent pelagic fishes from escaping, since these have dorsally located eyes with a restricted visual field dorsally (Fig. 2b) (Pankhurst et al. 1994). In the present study, each acceleration event lasted on average 7 s, and the seals swam on average 11 m during this period. This suggests that,

Table 1. *Phoca sibirica*. Dive variables (means \pm SD) during day and night dives for each individual. See 'Results' for definition of acceleration and deceleration events. Mann-Whitney *U*-test was used to test for differences between day and night dives; 1-way ANOVA was used to test for differences between descent, bottom and ascent. **p* < 0.0001. ns: not significant

Parameter	Day dives		Night dives
Individual 1			
n	100		64
Dive depth (m)	89.6 \pm 60.9	*	45.4 \pm 38.6
Dive duration (min)	5.7 \pm 2.6	ns	5.6 \pm 3.1
Swimming speed (m s ⁻¹) for:			
dive	1.1 \pm 0.1	*	0.8 \pm 0.1
descent (m s ⁻¹)	1.1 \pm 0.1	} ns	0.9 \pm 0.1
bottom (m s ⁻¹)	1.1 \pm 0.2		0.8 \pm 0.1
ascent (m s ⁻¹)	1.1 \pm 0.2		1.0 \pm 0.1
Stroke frequency (Hz) for:			
dive	1.39 \pm 0.31	*	1.03 \pm 0.13
descent (Hz)	1.61 \pm 0.36	} *	1.49 \pm 0.32
bottom (Hz)	1.24 \pm 0.51		0.86 \pm 0.29
ascent (Hz)	1.24 \pm 0.45		1.01 \pm 0.28
Acceleration events dive ⁻¹	0.46 \pm 0.82		*
Deceleration events dive ⁻¹	0.36 \pm 0.95	*	3.36 \pm 3.76
Individual 2			
n	106		45
Dive depth (m)	60.3 \pm 49.5	ns	70.0 \pm 47.5
Dive duration (min)	5.4 \pm 2.6	*	8.2 \pm 2.9
Swimming speed (m s ⁻¹) for:			
dive	1.2 \pm 0.3	*	0.9 \pm 0.1
descent (m s ⁻¹)	1.2 \pm 0.2	} ns	1.0 \pm 0.2
bottom (m s ⁻¹)	1.2 \pm 0.3		0.8 \pm 0.1
ascent (m s ⁻¹)	1.2 \pm 0.2		1.1 \pm 0.1
Stroke frequency (Hz) for:			
dive	1.70 \pm 0.44	*	1.36 \pm 0.14
descent (Hz)	1.37 \pm 0.45	} *	1.21 \pm 0.23
bottom (Hz)	1.57 \pm 0.65		1.19 \pm 0.32
ascent (Hz)	1.98 \pm 0.45		1.92 \pm 0.27
Acceleration events dive ⁻¹	0.98 \pm 1.35		*
Deceleration events dive ⁻¹	0.21 \pm 0.79	*	3.33 \pm 2.82

during the day, seals may detect prey from this distance visually, although it is possible that the prey may flee to avoid predation and increase the pursuit distances of the seals. The lower depth limit of acceleration events we recorded was 67 m. While this depth may indicate the limit of prey distribution, it is also possible that it is the maximum depth at which seals can detect prey visually.

Night dives had 2 notable characteristics: one was the swimming speed profile, with slower speeds than during the day, and a series of deceleration events during the bottom phase (Fig. 4b); the other was the sequential pattern of the maximum dive depth throughout the night (Fig. 3); this pattern was not likely to have been affected by the proximity of the bottom of the lake because both seals were estimated to be swimming offshore, where the bottom is over 1000 m deep, and no flat-bottomed dives were recorded during the period. These 2 observations sug-

gest that the night dives observed in this study might correspond to foraging dives focused on swarming amphipods such as *Macrohectopus branickii*. Wilson et al. (2002) showed that penguins feeding on small swarming crustaceans tend to slow their speed during prey exploitation, whereas those feeding on larger fishes tend to increase speed. Maximum swimming speed underwater is dependent on body size, with larger animals being able to swim faster (Peters 1983). *M. branickii* is a small animal (< 30 mm) and known to form aggregations (Melnik et al. 1993). Such crustaceans would lead the seals to slow down their swimming speed to optimize foraging efficiency (Wilson et al. 2002). Deceleration events could correspond to capture and ingestion of the amphipods. These events occurred primarily during the night at greater depths and within wider depth ranges than acceleration events which were observed exclusively during the day, suggesting that the seals may rely on senses other than vision to locate and capture prey at night. Dehnhardt et al. (1998, 2001) suggested that harbor seals *Phoca vitulina* may use their whiskers to gain hydrodynamic information resulting from movement of prey. Tactile sensation may be of primary importance to Baikal seals foraging on swarming amphipods, since hydrodynamic object-detection may be better over shorter distances. Amphipods in Lake Baikal are known to undergo a vertical diel migration that brings them close to the surface at night (Melnik et al. 1993). Both of the Baikal seals dived deeper near sunset (Fig. 3), which could be the time at which the vertically migrating amphipods become more readily available as they move upward in the water column. After sunset, dive depths decreased, increasing again toward dawn, presumably in response to the vertical migration of the amphipods. Such tracking of vertically migrating prey has been documented for Antarctic fur seals *Arctocephalus gazella* (Croxall et al. 1985) and northern elephant seals *Mirounga angustirostris* (Le Boeuf et al. 1988).

In conclusion, in the summer, Baikal seals showed different foraging tactics during the day and at night. During the day, they accelerated upward during dives to track and chase pelagic fishes from below, possibly using vision. At night, they changed dive depths to presumably track swarming crustaceans engaged in

diel vertical migrations. The seals decelerated during these nighttime dives possibly to capture crustaceans using non-visual sensory mechanisms such as their whiskers.

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