

Three-dimensional resting behaviour of northern elephant seals: drifting like a falling leaf

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During their long migrations through the Pacific, northern elephant seals, *Mirounga angustirostris*, never haul out on land and they rarely spend more than a few minutes at a time at the surface. They are almost constantly making repetitive, deep dives, raising the question of when do they rest? One type of dive, the drift dive, characterized by a time-depth profile with a phase of lower than average descent speed is believed to be a resting dive. To examine the behaviour of seals during drift dives, we measured body position and three-dimensional diving paths of six juvenile seals. We found that seals rolled over and sank on their backs during the drift phase, wobbling periodically so that they resembled a falling leaf. This enabled seals to drastically slow their descent rate, possibly so that negatively buoyant seals can rest without ending up in the abyss. This reduces the work required to return to the surface to breath, and allows them time to rest, process food or possibly sleep during the descent phase of these dives where they are probably less susceptible to predation.

Keywords: northern elephant seals; drift dives; three-dimensional diving behaviour

1. INTRODUCTION

Pinnipeds have secondarily adapted to an aquatic existence, yet most species spend considerable periods of time onshore, where they can rest free from predators. Northern elephant seals (*Mirounga angustirostris*), however, are out to sea for 2–8 months at a time during long-distance migrations, where seals never haul out and spend 83–90% of their time at sea underwater

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(Le Boeuf *et al.* 1989). Seals are usually only at the surface for 2–3 min breathing intervals between dives of ca. 20 min (Le Boeuf *et al.* 1989, 1992). Therefore, it has been suggested that elephant seals do not rest at the surface, but that they may rest during deep dives while reducing locomotion cost (Crocker *et al.* 1997).

Different dive shapes of elephant seals may have different functions (Le Boeuf *et al.* 1992). ‘Drift’ dives are one of the dive types that might be food processing and/or resting dives in elephant seals (Crocker *et al.* 1997). Drift dives include a rapid descent phase (C1) followed by a prolonged phase of slower descent (C2), followed by a fairly rapid ascent to the surface (C3) (Le Boeuf *et al.* 1992). In the unusual cases when seals are positively buoyant, they drift upwards during the C2 drift phase. It was initially thought that seals switched from active swimming to passive gliding at the start of C2 (Crocker *et al.* 1997), but flipper stroke recordings from an animal-borne video camera suggest that negatively buoyant seals probably stop stroking long before C2 begins (Davis *et al.* 2001). If so, then the cause of the significant change in the descent rate is a mystery. Recently, drift dives have gained attention because they can be used to infer foraging success by comparing the vertical speed during C2 to determine whether seals are changing their body composition and therefore their buoyancy (Crocker *et al.* 1997; Biuw *et al.* 2003). Despite this attention, little is known about the biomechanics of seals during the drift phase. Therefore, we monitored three-dimensional diving behaviour including stroking activity and body position during the drift dives of northern elephant seals, so we could determine what causes the change in descent rate and gain some insight into the function of these dives.

2. MATERIAL AND METHODS

In April and November 2005, six juvenile northern elephant seals were captured at Año Nuevo State Reserve, California, USA, and fitted with a data logger containing speed, depth, temperature and tri-axial acceleration and magnetometry sensors (three-dimensional data logger: W1000L-3MPD3GT; 26 × 178 mm, 146 g; Little Leonardo, Japan), and satellite transmitters. Seals were released offshore or from the coast of Monterey Bay south of the capture site. When the seals returned to land, the data loggers were retrieved. Data were analysed for diving behaviour including stroking rates and three-dimensional movements (Mitani *et al.* 2003). GPS tracking data from a satellite transmitter (Mk10-AF, Wildlife Computers, USA) deployed on two seals in November were used to match bathymetry with the reconstructed three-dimensional dive paths from the three-dimensional data logger. For further details, see the electronic supplementary material.

Using swim speed and depth data, typical drift dives were defined as dives where C2 represented greater than 40 per cent of the total duration of the dive and had constantly low vertical speed (mean < 0.4 m s⁻¹) with continuous descent and continuously low swim speed (mean < 0.5 m s⁻¹) (modified from Biuw *et al.* 2003).

3. RESULTS

We identified 45 drift dives from four of the six juveniles. Mean depth and duration of drift dives were 373.1 ± 55.4 m and 23.1 ± 1.9 min, respectively. Seals dived almost vertically and stroked continuously in the beginning of drift dives (figure 1a). They stopped stroking and began a prolonged glide during C1 in 39 drift dives. As pitch angle became shallower than 26.4 ± 5.4°, C2 began at a mean depth of 221.1 ± 17.4 m (93.5–348 m). Mean duration of C2

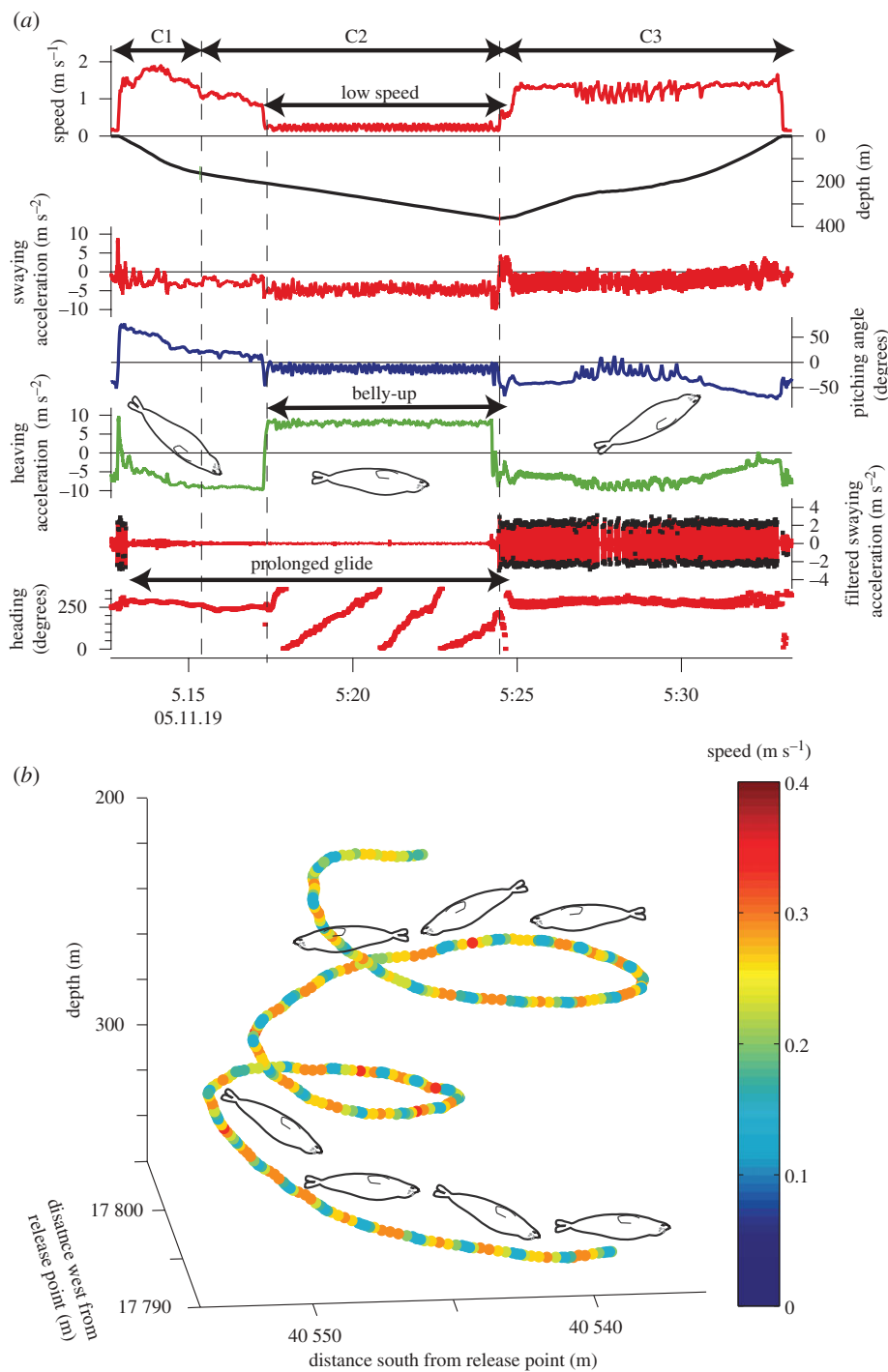


Figure 1. (a) Behavioural sequence and (b) three-dimensional trajectory during belly-up phase of a typical drift dive of northern elephant seal juvenile. Seals stroked regularly and dived vertically in the beginning of the drift dive. Filtered swaying acceleration showed that seals stopped stroking and began gliding down owing to negative buoyancy in the middle of C1 continuing through C2. When pitching angle turned positive, the low-speed and belly-up phase started. During this phase, the seals' body wobbled in a cycle of about 10 s duration.

was 11.6 ± 1.4 min, which accounted for $50.1 \pm 2.4\%$ of dive duration. During C2, relatively few flipper strokes were performed (1.7 ± 2.2 stroke min^{-1} ; $0\text{--}0.2$ Hz). After increasing to maximum in the beginning of C1, swim speed decreased gradually. Swim speed then declined rapidly and remained lower than 0.5 m s^{-1} until C2 ended. This period of low swim speed was observed during every C2; however, the low-speed phase did not start at the beginning of C2 in 29 drift dives. Instead, the low-speed phase started

when the seals' pitch angle changed from positive to negative ($n = 44$). In all drift dives, seals rolled over and changed their body orientation from the normal ventral-down position to a 'belly-up' position, and kept this posture for 8.1 ± 1.2 min (1.2–16.4 min) during C2. The belly-up phase and the low-speed phase started simultaneously ($n = 43$). This belly-up phase began at a mean depth of 266.6 ± 10.2 m (137.5–394.75 m), and accounted for $69.7 \pm 8.2\%$ of the C2 segment, and $92.7 \pm 4.4\%$ of the low-speed

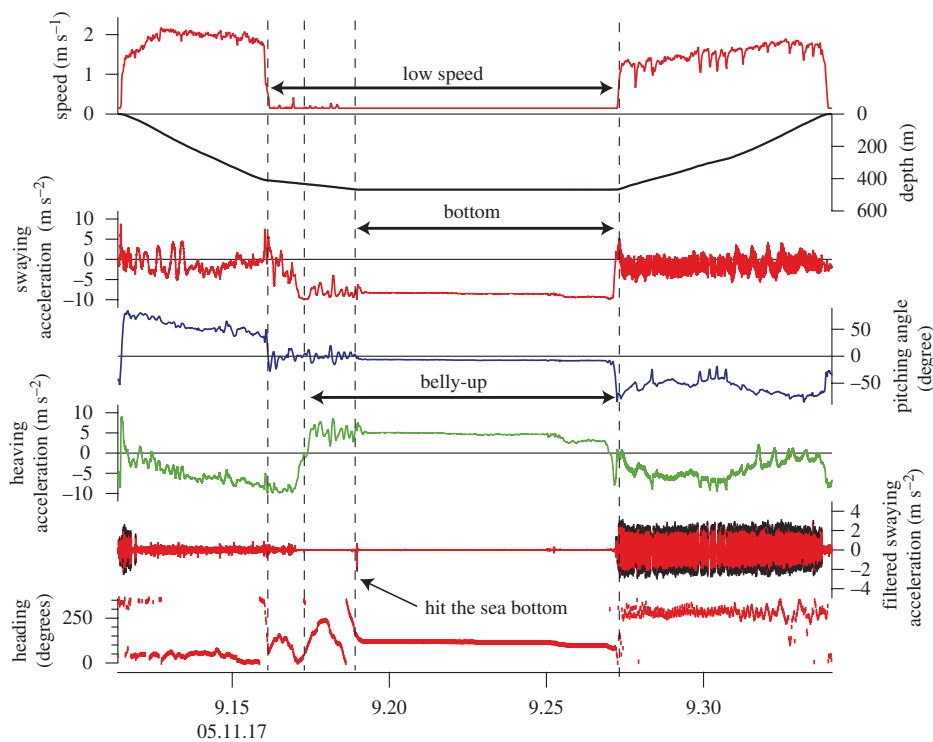


Figure 2. Behavioural sequence of an 'additional dive'. During the belly-up phase, the seal hits the sea bottom and then remained immobile for over 5 min, suggesting that the seal may have been sleeping during the belly-up drift phase.

phase. Almost as soon as the belly-up phase ceased, seals started ascent ($n = 44$). During the belly-up phase, almost no flipper strokes were performed, and the body wobbled slowly by pitching and yawing in all drift dives. A line drawn through the seal's long axis would trace circles at the head and tail, in a cycle of about 10 s (mean 11.7 s, range: 8–32 s) as seen in the oscillation of pitch angle (figure 1*a*), similar to the precession of a spinning top, without the spin. The reconstructed three-dimensional paths during belly-up phase showed four different types of trajectories: circular ($n = 34$, figure 1*b*), fluttering ($n = 3$), both ($n = 6$) and straight ($n = 2$).

4. DISCUSSION

Our data reveal that seals drifted down like a falling leaf, displaying periodic body precession and circular and/or fluttering trajectories without flipper stroking during the belly-up phase ('falling-leaf' phase) in 43 of 45 drift dives. Others have suggested that ceasing stroking and drifting down passively at the beginning of C2 allows elephant seals to use the oxygen and energy no longer required for aerobic locomotion for food processing (Le Boeuf *et al.* 1992; Crocker *et al.* 1997). Gliding will reduce locomotion costs, but prolonged gliding is also observed during C1 in drift dives, and in other dive types (Davis *et al.* 2001). Therefore, the cessation of flipper stroking does not distinguish the drift phase from the descent phase of other dive types. Instead, C2 is characterized by a falling-leaf phase.

The occurrence of the falling-leaf phase and its concomitant reduction of travel cost is consistent with the two main hypothesized functions of drift dives, food

processing and resting. Another possible function of some drift dives is prey searching because the high turning rates during the falling-leaf phase resemble a search pattern (Fauchald 1999). Although the belly-up orientation would prevent seals from looking up to find prey backlit by downwelling illumination, it could make it easier to look down and see bioluminescent prey against the dark depths. If the circular trajectory in drift dives did serve as prey searching, then the falling-leaf phase should be observed in other dive types, such as w-shaped foraging dives. Therefore, we scanned all three-dimensional trajectories, and discovered 59 'additional dives' from four seals that contained a falling-leaf phase (additional dives). Although they did not meet the strict drift dive definition, 47 of them were very similar to typical drift dives. For further details, see the electronic supplementary material. Only 12 of the additional dives were similar to other types: either a u-shaped dive ($n = 7$), or flat dive bottom after the falling-leaf phase ('drift-and-bottom-rest dives', $n = 5$, figure 2).

In total, 102 dives contained a falling-leaf phase ('falling-leaf dives'; consisting of 43 drift dives and 59 additional dives). Ninety-four falling-leaf dives (41 drift dives and 53 additional dives) occurred temporally close to other falling-leaf dives, similar to the drift dive bouts reported by Crocker *et al.* (1997). Body rotation and wobbling were also observed during the drift phase of adult female elephant seals during foraging migrations (although it is only confirmed by two-axis acceleration data, right-to-left and tail-to-head; Y. Mitani *et al.* 2003, unpublished data). If all drift dives contain the falling-leaf phase, it is unlikely to function as prey searching, because drift dives during foraging migrations peaked in the early

morning, after the cessation of shallow foraging dives that occurred during the night (Crocker *et al.* 1997). Also, drift-and-bottom-rest dives in this study suggest that seals may not even be alert during the falling-leaf phase. Two seals that performed these five drift-and-bottom-rest dives rotated into the belly-up orientation and then hit the sea bottom as confirmed by a spike in the acceleration data and matching of dive depth and local bathymetry (confirmed by GPS tracking data). After reaching the sea floor, seals laid immobile for 4.8 ± 3.1 min (0.6–8.0 min). In each case of drift-and-bottom-rest dives, the seal did not seem to be searching or even to be alert during the falling-leaf phase, because there was no reaction to the sudden shock upon contact with the sea floor. Therefore, it appears that the function of the falling-leaf phase is not searching, but rather food processing and/or resting.

To optimize the resting time during deep dives, seals must avoid ending up too deep, because it costs time and energy to return to surface. By changing their pitch angle, seals increase their drag substantially, slowing their descent rate dramatically compared to the descent rate when they are gliding in a head forward position. By slowing their descent rate, they increase the time available for rest during the drift phase without having to spend considerable energy actively swimming to the surface from a deeper depth.

Our data showed that seals could slow their descent rate without belly-up rotation, but only when pitch angle is close to zero (the electronic supplementary material, figure S1c). The function of belly-up posture is unclear, but if seals were unconscious and not actively maintaining their body orientation, the thicker blubber layers on their ventral surface compared to their dorsal surface may cause the body to roll belly-up during passive gliding. Sleep in captive aquatic mammals is usually studied by recording the electroencephalogram or eye closure, measurements that are difficult if not impossible to make from deep-diving mammals. Alternatively, sleep can be distinguished from wakefulness using behavioural criteria: a period of sustained quiescence in a species-specific posture or site, with reduced responsiveness to external stimulation (Rattenborg *et al.* 2000). In this study, northern elephant seals showed inactivity with no flipper strokes and a stereotypical belly-up posture in drift dives. Additionally, seals displayed reduced responsiveness to stimulation in falling-leaf phase when they hit the sea floor.

Le Boeuf *et al.* (1989) suggested that sleeping near the bottom of dives would provide security when faced with near-surface predators. The belly-up drift phase does not start until seals reach at least 135 m. The upper 150 m is where seal predators, such as killer whales (mean maximum dive depths: 140.8 ± 61.8 m, Baird *et al.* 2005) and white sharks (99% of time < 50 m, Weng *et al.* 2007), spend most of their

time. The prolonged glide of elephant seals starts before reaching this level, but seals maintain their nose-first body orientation and a high rate of descent, permitting them to get out of the danger zone relatively quickly. Once seals exited the dangerous depths, the belly-up drift phase began. Drifting belly-up at deeper depths permits resting in a safe zone below predators, but prevents seals from drifting too deep, thereby reducing the cost of ascent.

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