

# Pitching a new angle on elephant seal dive patterns

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**Abstract** Elephant seals are one of the most proficient diving mammals in the world and are also one of the most studied. However, their long periods at sea and pelagic habits make research into their foraging ecology particularly challenging. Most current understanding comes from the use of time-depth recorders (TDRs). We used TDRs that additionally recorded body pitch and roll on four juvenile southern elephant seals (*Mirounga leonina*) foraging over the Patagonian Shelf to describe their diving behaviour and compared them with those of adults, using standard descriptions of elephant seal dive profile types provided by the literature. Over 280 days of diving data showed that dive types were similar to those of adults (types: A, B, C, D, E<sub>b</sub> and E<sub>f</sub>) but that dive types A and C differed slightly, probably because our animals were constrained by bottom topography. Steep dive and return-to-surface angles in all dive types except type B indicate that animals generally attempt to maximize vertical displacement. Horizontal displacement was much greater in type B dives, which indicates a travelling function. Pitching and rolling behaviour lends support to the functions ascribed to the dive types

already described for adult elephant seals, although type E<sub>b</sub> dives are unusual in that the animals appear to be taking prey by up-ending in the benthos.

**Keywords** Elephant seals · Diving behaviour · Dive classification · Body orientation · Patagonia

## Introduction

Despite being air breathers, marine mammals manage to exploit sub-surface food resources by simple breath holding (e.g., Kooyman 1989). The ability to breath-hold for longer periods allows animals to exploit greater depths and therefore profit by using a larger volume of the ocean. Extended breath-hold capabilities are enhanced by particular physiological adaptations (Hindell et al. 1992; Boyd 1997; Hindell et al. 1999, 2000; Bennett et al. 2001; Thornton et al. 2005; Kooyman 2006) but also by larger body size (Irvine et al. 2000; Sato et al. 2007). In addition, behavioural strategies such as passive sinking and burst and glide swimming (e.g., Williams et al. 2000; Williams 2001; Mitani et al. 2010) may reduce energy expenditure and therefore oxygen use.

Elephant seals (*Mirounga* spp.) have extraordinary breath-hold capacities (e.g., Hindell et al. 1992; Hassrick et al. 2010), which are presumably enhanced by their body size (they are the largest pinnipeds in the world), and this, together with a suite of physiological adaptations (Kooyman and Ponganis 1998; Kooyman 2006; Davis and Weihs 2007; Meir et al. 2009; Hassrick et al. 2010), passive sinking (e.g., Mitani et al. 2010) and burst and glide swimming (Williams 2001), has led to them executing the deepest and longest divers of any member of their superfamily, with animals generally exploiting waters over 500 m deep

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(Le Boeuf et al. 1989; Hindell et al. 1991a). The superlative diving capacity of elephant seals has incited great interest, and much of their free-ranging diving behaviour has been intensively studied using time-depth recorders (TDRs) for both the southern, *Mirounga leonina*, and northern, *Mirounga angustirostris*, species (Le Boeuf et al. 1989; Hindell et al. 1991a; Le Boeuf et al. 1993, 2000; Campagna et al. 2000; Hindell et al. 2000; Bradshaw et al. 2004; Campagna et al. 2006, 2007; Bailleul et al. 2007; Biuw et al. 2007; Hassrick et al. 2007; Bailleul et al. 2008; Zeno et al. 2008; Bailleul et al. 2010). Accordingly, diving behaviour has been mainly described using two-dimensional (2D) dive profiles, graphs of depth against time. Six major dive types are generally recognized. Type A dives (Le Boeuf et al. 1992, 1993—also called type 6 by Hindell et al. 1991a)—consist of a ‘V-shaped’ dive profile during which animals descend to a specific depth before returning to the surface immediately. Type B dives (Le Boeuf et al. 1992, 1993—type 4 *sensu* Hindell et al. 1991a)—have a parabolic dive profile with descent rates slowly decreasing until, at the bottom of the dive, when descent rates are zero, the animal reverses the process to return to the surface. Type C dives (Le Boeuf et al. 1992, 1993; Crocker et al. 1994, 1997—also called type 3 by Hindell et al. 1991a; cf. Biuw et al. 2003)—consist of an initial steep descent (in the depth vs time profile), which abruptly changes to a markedly slower, but constant, rate of descent, which continues until the deepest point of the dive when the animal returns to the surface at a constant rate. Type D dives (Le Boeuf et al. 1988, 1993; type 1 *sensu* Hindell et al. 1991a) are characterized by an essentially ‘W-shaped’ dive profile, with distinct and constant rate of both descent and ascent and a clear bottom phase. The bottom phase is, however, distinguished by irregularities as the animal moves up and down the water column. Type E<sub>b</sub> dives (Hassrick et al. 2007—also called type 2 by Hindell et al. 1991a)—are similar to type D dives but the bottom-phase undulations are minimal, whereas type E<sub>f</sub> dives (Hassrick et al. 2007) are similar to type E<sub>b</sub> dives except that they have no discernable variability in bottom depth.

The literature has attempted to interpret the various elephant seal dive types giving specific functionality based on the dive characteristics although authors have not always agreed in this. Type A and type B dives are generally ascribed a travelling function (Hindell et al. 1991a; Le Boeuf et al. 1992, 1993, 2000). Type C dives are mainly considered to comprise periods where animals are resting or digesting food, this occurring during the minimized descent rates (cf. Crocker et al. 1997; Webb et al. 1998; Biuw et al. 2003; Hassrick et al. 2007; Mitani et al. 2010), while type D dives are considered associated with prey detection and/or pursuit (Le Boeuf et al. 2000; Hassrick et al. 2007; Kuhn et al. 2009). The functions ascribed to

type E<sub>b</sub> and E<sub>f</sub> dives are benthic feeding and rest (and/or processing food) in the benthos, respectively (Campagna et al. 2007; Hassrick et al. 2007). One of the difficulties of interpreting dive type function is the relative paucity of information other than depth against time. Previous studies used multiple parameters to investigate seal behaviour [speed (e.g., Hindell et al. 2000; Hassrick et al. 2007), light (e.g., Campagna et al. 2001), temperature (e.g., Hindell et al. 1991b; Campagna et al. 2000; Bailleul et al. 2010) and deploying video (e.g., Williams et al. 1996, 2000; Davis et al. 2001, 2003)], but much of dive function still remains unclear. Mitani et al. (2010), however, recently showed that dive function could be greatly enhanced if body orientation was also recorded.

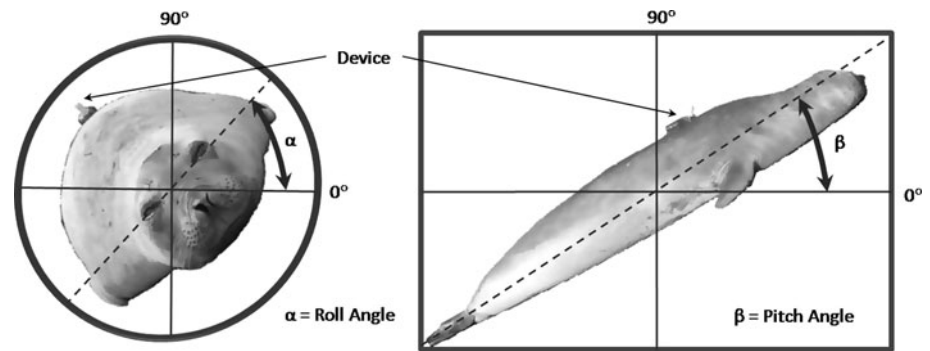
This work examines the diving behaviour of four juvenile southern elephant seals using TDRs that have additional channels recording body orientation (via pitch and roll) to expand our understanding of the foraging behaviour of this species. Unlike the adults, the juvenile elephant seals in our study area commonly forage over the Patagonian Shelf (Campagna et al. 2007) and are therefore constrained to dives of less than about 120 m depth. Our objective was to examine the extent to which juveniles adhere to the well-documented adult patterns and consider, in particular, how their diving patterns might be constrained by the bottom topography.

## Materials and methods

### Deployment of devices

We deployed experimental multi-sensor data loggers on juvenile southern elephant seals that registered bi-axial body position (pitch and roll) (see below) (Fig. 1) as well as depth, temperature and light at 5-s intervals (cf. Wilson et al. 2008). All instruments were calibrated by being rotated through all combinations of pitch and roll on a specially prepared angle-calibrating frame (see Liebsch 2006 for details), while pressure transducer calibration took place in the Institut für Meereskunde (Kiel, Germany) pressure tanks. Angle accuracies were better than 2°, while depth could be resolved to within 0.2 m. Five 2- to 3-year-old juvenile seals were instrumented at Punta Delgada (42.8°S, 63.6°W), Península Valdés, Argentina (where the animals had been marked since birth), during July 2004 (two males), August 2005 (one of each sex) and January 2007 (one female), and the devices were recovered approximately 2 months later. The seals were also instrumented with satellite tags (SPOT5; Wildlife Computers, Redmond, WA; <http://www.wildlifecomputers.com>) to determine their foraging routes (as part of a wider study—see Campagna et al. 2007) and to facilitate recovery of the devices by indicating

**Fig. 1** Schematic representation of body orientation and measures of roll and pitch angles (note the location of the electronic device on the southern elephant seal body)



when and where the animals came back to Península Valdés. Procedures to deploy and recover instruments were as those described in previous works (see Campagna et al. 1995, 1999). All loggers were placed between the shoulder blades of the animals on the upper back and oriented in the same way to ensure that recorded signals were comparable in the different animals.

### Analysis

We used custom-made programs, MT-Dive and MT-Route (Jensen Software Systems, Laboe, Germany) and SNOOP (Freeware), to conduct a preliminary survey of all the dives of each animal and thus to identify and categorize the bouts of each dive type, according to definitions following Le Boeuf et al. (1992) and Hassrick et al. (2007). Then, we randomly selected dives in the middle of bouts displaying, as far as possible, all dive types, to act as a basic description of the dive parameters. In order to facilitate categorization of dive types (and bouts), we also looked for differences in pitch and roll as a function of dive profile (see below). Following Schreer et al. (2001), seals were taken to be at the bottom of a dive whenever the depth exceeded 80% of the maximum depth reading for that dive. Phases between the water surface and the points of inflection defining the bottom phase were deemed to be descent or ascent phases. Dive type classification was primarily based on that documented by Le Boeuf et al. (1992) and Hassrick et al. (2007), using their criteria, and assessed visually with the caveat that, where pitch and/or roll parameters indicated particular dive categories, these were used to inform decisions on dive types. The classification was later confirmed and contextualized in time and space, particularly with regard to the water depth in which the animals were foraging, using geographic position data obtained from the PTTs (platform transmitter terminals). PTT information indicated whether the animals were travelling rapidly and therefore likely commuting rather than foraging, while water depth with respect to dive depth proved particularly important for us to assess whether dives terminated at the seabed or not. The pitch and roll angles were defined relative to the

horizontal where both pitch and roll were taken to be 0° (Fig. 1). Statistics of pitch and roll were calculated for each phase (descent, bottom and ascent) of the different dive types.

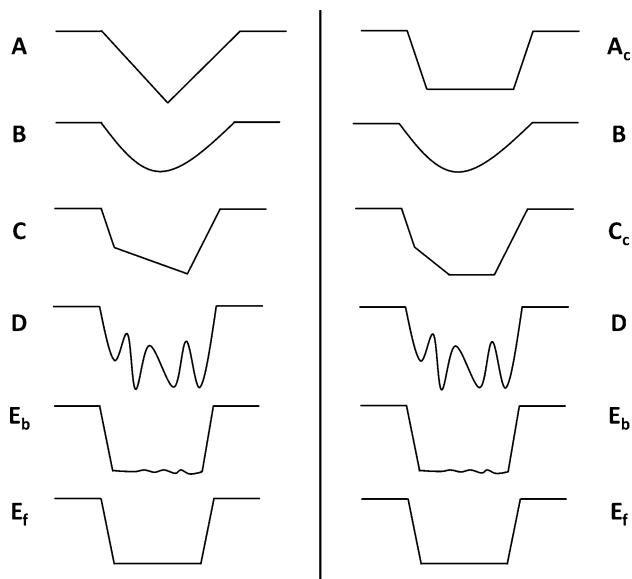
We analysed a total sample of 220 dives (10 dives from each animal of every recognized dive type—see later) performed by four of the instrumented animals contained within a total of 280 days of records available to us (except for the juvenile female, which did not make  $E_f$  or C dive types). The animal equipped in 2007 was not included in the analysis, because there were only 2 days of records. We selected 10 dives of each dive type per animal to give us a reasonable amount of idea of variance but also because we strived for equal samples from each dive types even though some dive types (e.g., Types C and  $E_p$ ) were rare.

### Statistics

We used linear mixed-effects model (LME) fit by restricted maximum likelihood (REML) to control for individual variation and test for significance of fixed effects and differences in body orientation and diving parameters. Mixed-effects models were used for all comparisons using data from individual dives, and individual (ID) was considered as a random-effects subject term. Model residuals were assessed for approximate normality. All statistical analyses were performed using the open-source statistical package R version 2.8.1 (R Development Core Team 2009), specifically using *lme4* package, with a level of significance of  $P < 0.05$ .

### Results

All studied seals remained over the Patagonian Shelf in depths of generally less than 120 m for the duration of the monitored period (see Figs. 2, 4 in Campagna et al. 2007). The constant depth of the dives, which primarily reflected the depth of the sea (something we were able to ascertain using the PTT positional information), provided a stable baseline for the bottom phase of almost all dive types recorded.

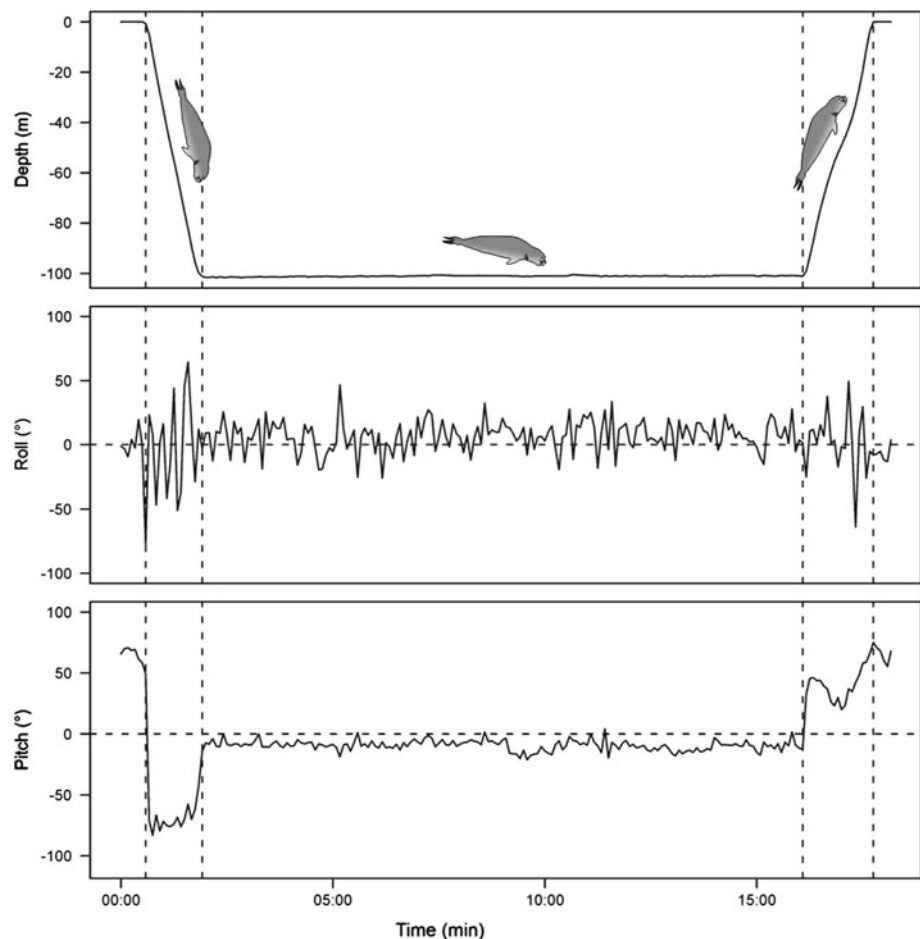


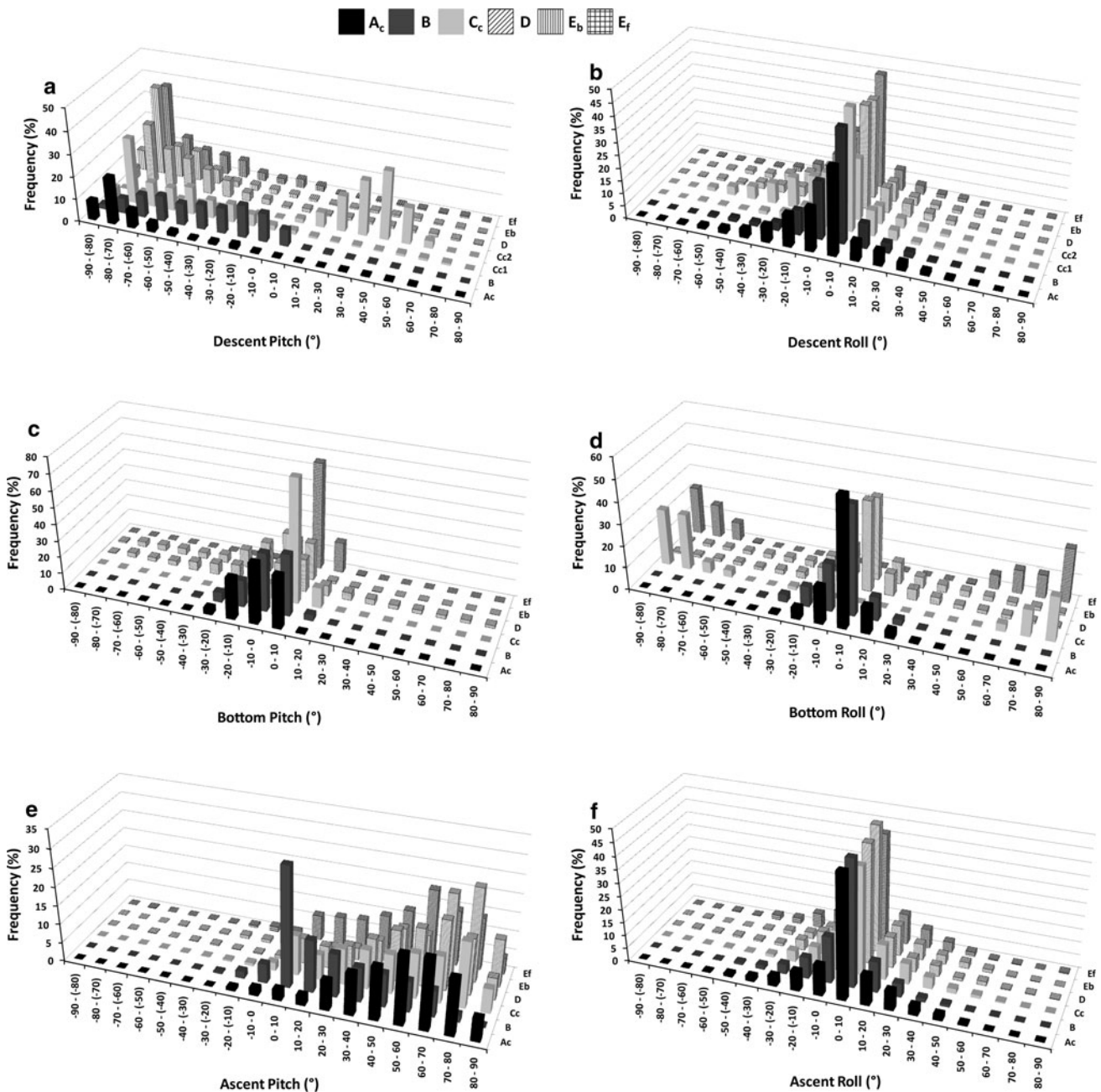
**Fig. 2** Schematic diagram of the dive profiles of elephant seals (the vertical axis represents depth, while the horizontal shows time) according to types described by Le Boeuf et al. (1992) and/or Hassrick et al. (2007) (left panel) and those found during our study (right panel)

### Dive types

We observed no conventional ‘type A’ dives. However, we ascribed a particular dive type to the conventional ‘type A’ dive type (Fig. 2—A<sub>c</sub>) even though our type A had a distinct bottom phase (Fig. 3), which is not the case in standard type A dives (Le Boeuf et al. 1992, 1993) (cf. Fig. 2). We attribute the distinct bottom phase to the animal reaching the seabed and maintaining travel (see later). The relatively invariant depth profile during the bottom phase, which coincided with water depths at the dive locality, in tandem with the pitch and roll angles, made a very strong case for the juvenile elephant seals to be travelling along the seabed at this time. The relatively shallow water depth at the sites of these dives led us to propose that these dives are simply likely to be the functional analogues of the typical type A dives, despite having different profiles. Thus, we describe our ‘type A’ as ‘type A<sub>c</sub>’ (type A constrained). Type A<sub>c</sub> dives were characterized by continuous rolling during all three diving phases: descent, bottom phase and ascent (Fig. 3). During the descent, the mean pitch angle was relatively stable (Table 1; Fig. 4a), while the roll varied

**Fig. 3** Dive depth, roll and pitch angles of a type A<sub>c</sub> dive. The orientation of the elephant seals helps illustrate body posture





**Fig. 4** Frequency histograms of the *descent*, *bottom* and *ascent* pitches and rolls displayed by four juvenile elephant seals according to dive type (keyed on the top of the figure)

over about 80° (Table 1; Fig. 4b) with particularly regular low-frequency roll oscillations (approximately three cycles per minute ≈4.4°/s) (Fig. 3). Once at the ocean floor, mean body angle indicating a slightly ‘nose down’ attitude (Table 1; Figs. 3, 4c) over what appeared to be generally relatively flat bottom contours, as suggested by constant depth (Fig. 3). During this phase, rolling occurred over less than 70°, with nearly 60% of the records in the range of 0°–10° (Fig. 4d). During the ascent, the pitch was significantly less acute than during the descent indicating a ‘head-up

position’ at a mean of 51° (LME:  $F_{75,1} = 61.23, P < 0.0001$ ; Table 1; Figs. 3, 4e). Similar to the descent, ascending seals rolled in a series of oscillations (over a range of about 80° again) at a rate of approximately three cycles per minute (≈4°/s) (Table 1; Fig. 3).

The type B dives were clear in our data (Fig. 5) and exhibited rolling movements similar to those observed during the descent and bottom phases of type A<sub>c</sub> dives (Table 1; LME:  $P_{(Descent)} = 0.22$ ; LME:  $P_{(Bottom)} = 0.19$ ), although during the ascent, the mean roll was significantly

**Table 1** Summary statistics (Mean (SD) and [Max., Min.]) of pitch and roll angles for the different dive types in *Mirounga leonina*

	Type A <sub>c</sub>	Type B	Type C <sub>c</sub>	Type D	Type E <sub>b</sub>	Type E <sub>r</sub>
<b>Pitch</b>						
Descent	−65.5 (31.8) [43.3, −81.8]	−41.4 (27.1) [32.5, −82.5]	−57.0 (33.5) [48.9, −89.4] 38.5 (12.5) [63.6, 5.5]	−59.0 (33.9) [45.5, −86.1]	−67.6 (33.7) [46.6, −87.9]	−63.2 (29.3) [47.1, −88.2]
Bottom	−13.9 (5.1) [2.5, −36.2]	−11.4 (7.7) [10.6, −32.8]	−5.3 (2.9) [8.2, −13.8] 2.6 (2.3) [9.5, −4.1]	−10.6 (35.2) [77.3, −87.3]	−25.1 (21.6) [23.5, −90.0]	−3.9 (2.6) [5.4, −11.1] 5.0 (3.2) [15.8, −3.3]
Ascent	51.0 (19.3) [73.5, −8.0]	21.5 (22.5) [60.1, −14.2]	44.4 (19.1) [75.6, −10.5]	48.9 (20.8) [74.1, −5.0]	57.7 (23.5) [78.6, −21.9]	45.8 (17.6) [73.4, −5.6]
<b>Roll</b>						
Descent	−8.0 (22.9) [35.9, −52.5]	−5.3 (16.3) [33.6, −47.7]	−3.2 (16.8) [38.0, −39.4] −16.2 (25.6) [46.4, −66.6]	−5.7 (20.4) [34.2, −49.5]	−7.7 (19.1) [35.1, −43.4]	−6.2 (16.5) [33.7, −44.1]
Bottom	−1.4 (11.1) [34.7, −38.4]	−4.4 (11.3) [27.4, −40.0]	79.8 (3.8) [86.8, 59.8] −84.1 (2.8) [−75.7, −90.0]	−2.6 (27.5) [79.6, −87.5]	−1.4 (30.5) [80.7, −90.0]	74.8 (3.4) [81.8, 58.1] −87.0 (3.7) [−73.9, −90.0]
Ascent	−0.9 (19.3) [39.1, −41.4]	−3.29 (15.9) [31.8, −37.5]	0.7 (18.7) [43.6, −39.3]	−1.3 (19.3) [34.7, −37.9]	0.6 (18.1) [40.7, −36.0]	−2.8 (19.9) [41.5, −45.1]

As explained above, the descent phase of type C<sub>c</sub> dives is divided into two stages, which were analysed separately. And also, during the bottom time of the dive types C<sub>c</sub> and E<sub>r</sub>, we analysed separately when the animals lay on one flank or the other

lower than that in type A<sub>c</sub> dives (LME:  $F_{75,1}(\text{Ascent}) = 5.80$ ,  $P = 0.018$ ). There was no clear mode in pitch angle during the descent (Fig. 4a) and, after an initial descent phase of  $\sim -90^\circ$  position (head down), the animals, overall, orientated their bodies more horizontally than during the descent phases of A<sub>c</sub> dives (cf. Figs. 3, 5). During the bottom phase, the body was angled down slightly with little variation (Table 1; Fig. 4c). During these dives, the seals were clearly not tracking the seabed, as evidenced by the existence of deeper preceding or succeeding dives. During ascent, body pitch showed a clear mode between  $0^\circ$  and  $10^\circ$  (Fig. 4e), indicating the seals travelled close to horizontally, with 57% of the values between  $0^\circ$  and  $30^\circ$ .

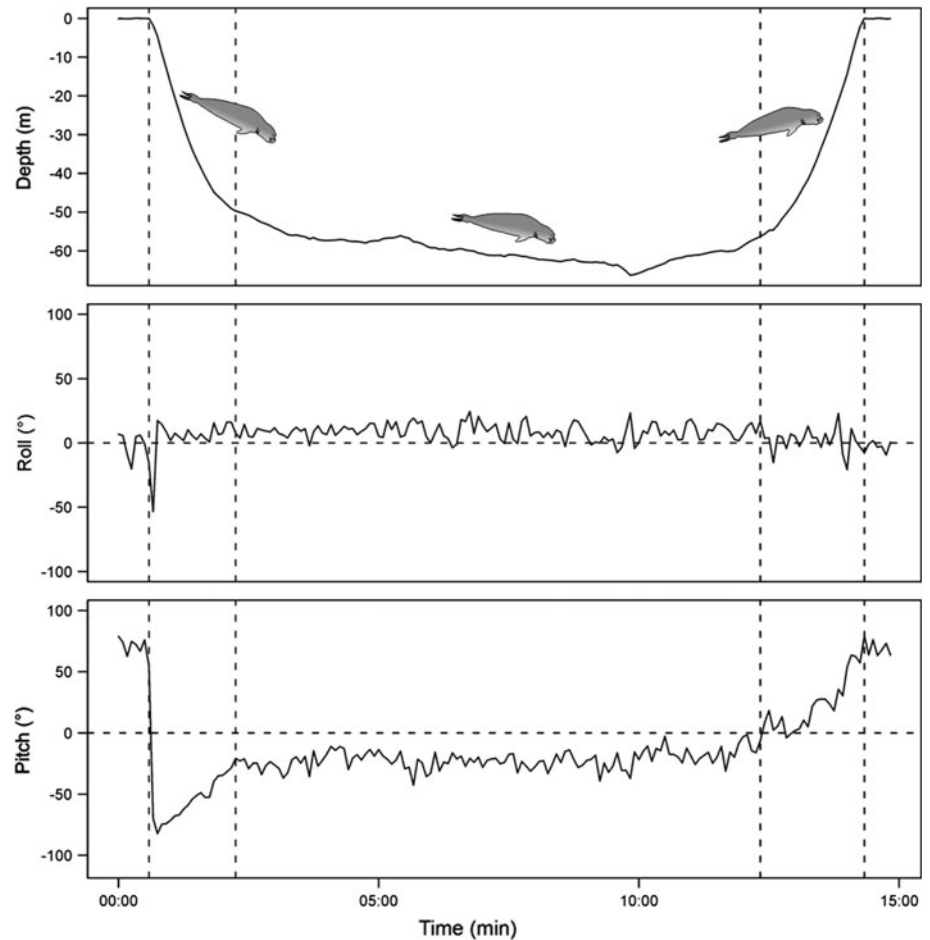
We recorded dives that were superficially similar to the standard type C dives (Fig. 2). The main feature in our dives, and shared by the classic type C dive, was the drifting phase during the descent. A notable difference, however, was that our individuals followed the descent phase by a period on the seabed where the seals remained motionless, lying on either their left or right sides in a manner similar to E<sub>r</sub> dives (see below) (Figs. 2, 6, 9). Our dives had a first stage in the descent with a nose-down attitude similar to that of type D dives (LME:  $P = 0.15$ ; Table 1) until a depth of  $70 \pm 15$  m, followed by a period where the rate of change of depth decreased dramatically during which the seals rolled onto their backs and adopted a ‘head-up’

attitude (Table 1; Fig. 6). At this time, the animals began rolling over about  $110^\circ$  (Fig. 6) with a frequency of almost 4 oscillations per minute ( $\approx 7.5^\circ/\text{s}$ ; Table 1; Fig. 4b). All lateral roll movements in the second stage of these descents showed animals adopting a mean left-hand roll (mean:  $-16.2 \pm 25.6^\circ$ ; Fig. 4b). During the bottom phase, the seals apparently remained immobile, lying on one side or the other (Table 1; Fig. 6) so that roll values had a bimodal frequency (Fig. 4d). The strong implication is that, at this time, the animals were lying on the seabed so we describe our ‘type C’ dives as ‘type C<sub>c</sub>’ (type C constrained). During the ascent, the pitch was about  $45^\circ$  though variance was high (Table 1; Fig. 4e) and the roll ranged up to about  $80^\circ$  (Table 1; Fig. 4f).

Type D dives occurred in our data set where the most obvious feature related to body movement during the bottom phase where great variation was apparent in both roll and pitch angles (roll range:  $170^\circ$ , pitch range:  $170^\circ$ ) (Table 1; Fig. 4c, d) which varied in tandem with the substantial variation in depth, or ‘wiggles’ (mean =  $7.7 \pm 3.5$  m). Descent and ascent phases were either direct or parabolic (Fig. 7).

Type E<sub>b</sub> dives were apparent in our data in which the most obvious feature was the high level of change in pitch and roll during the bottom phase [pitch range over  $110^\circ$ , most of which occurred in the ‘head-down’ attitude

**Fig. 5** Dive depth, roll and pitch angles of a type B dive. The orientation of the elephant seals helps illustrate body posture

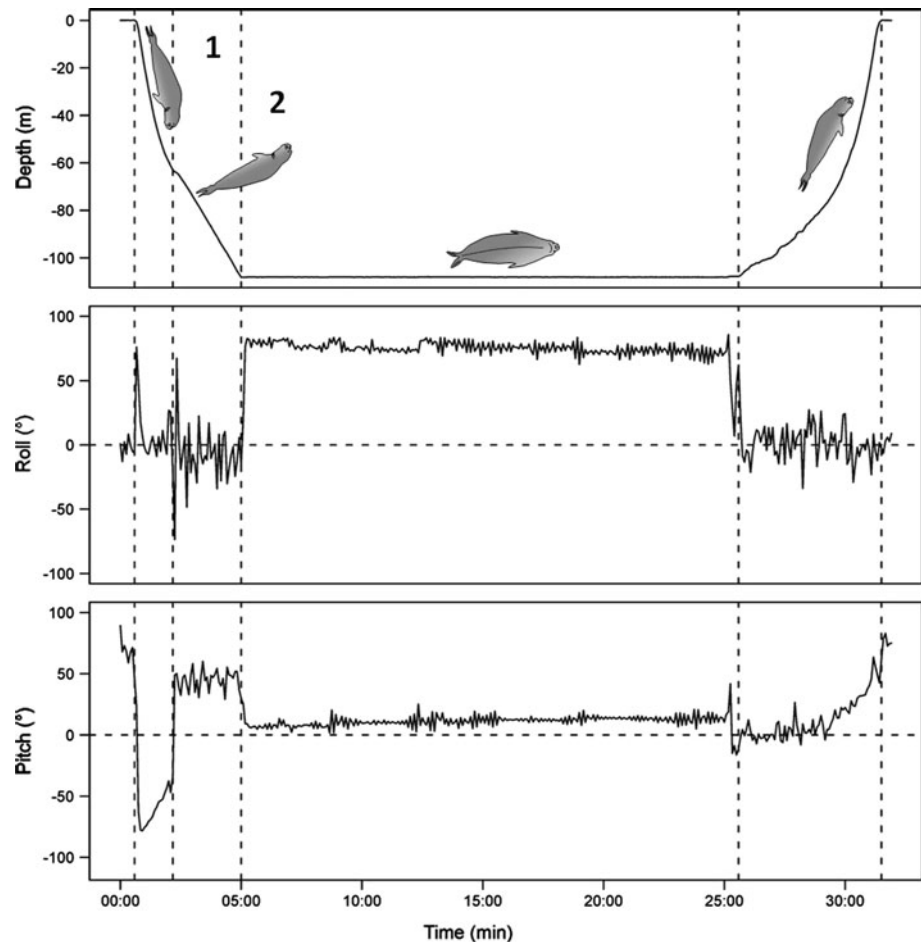


(Fig. 4c), roll range over  $170^\circ$  (Fig. 4d)], with no substantial change in dive depth (Fig. 8). In particular, animals occasionally pointed virtually directly down while the roll angles changed continuously (Fig. 8). The cumulated effect of all these behaviours, which differed from the type  $A_c$  dives, resulted in markedly lower mean values of pitch and significantly greater roll ranges, during the bottom phase (LME:  $F_{72,1}(\text{Pitch}) = 96.41$ ,  $P < 0.0001$ ; LME:  $F_{72,1}(\text{Roll Range}) = 687.54$ ,  $P < 0.0001$ ). Although both pitch and roll angles were similar between these two dive types during the descent phase (LME:  $P_{(\text{Pitch})} = 0.24$ ; LME:  $P_{(\text{Roll})} = 0.99$ ), the average values of pitch in the ascent of type  $E_b$  dives were significantly higher than those of type  $A_c$  dives (LME:  $F_{72,1}(\text{Pitch}) = 9.00$ ,  $P < 0.0037$ ; LME:  $P_{(\text{Roll})} = 0.25$ ). Thus, although the dive profiles were superficially similar between both dive types (Fig. 2), there are noticeable differences in body positions adopted by the seals (Figs. 3, 8).

Type  $E_f$  dives were also present in our data and had roll angles during the descent phase that were similar to those of type  $E_b$  dives although pitch angles were significantly lower (Table 1; LME:  $P_{(\text{Roll})} = 0.62$ ; LME:  $F_{62,1}(\text{Pitch}) = 7.35$ ,  $P = 0.0087$ ). During the bottom phase, however, the depth

values were extremely stable and seals spent most of their time in the slightly head-up position (Table 1; Fig. 9) and lying either on their left or on right side (Figs. 4d; 9) with minimum variance in roll and pitch angles for any particular bottom phase (Table 1). For example, in a typical left roll bottom phase, the mean roll was  $-87.0 \pm 3.7^\circ$ . This preference for one side or another gave rise to a clear bimodal distribution of roll angles (Fig. 4d). This one-sidedness was a common feature of both dives  $E_f$  and  $C_c$ , with the pitch and roll angles being statistically indistinguishable between them during the bottom phase (LME:  $P_{(\text{Pitch})} = 0.80$ ; LME:  $P_{(\text{Roll})} = 0.49$ ). The distinguishing feature between the two dive types was, however, in the descent phase, which was clearly different in the values of pitch and roll angles (LME:  $F_{72,1}(\text{Pitch}) = 498.13$ ,  $P < 0.0001$ ; LME:  $F_{72,1}(\text{Roll}) = 8.36$ ,  $P = 0.0054$ ), and also in shape (Figs. 2, 6, 9). The ascent phase of both dive types was similar (LME:  $P_{(\text{Pitch})} = 0.74$ ; LME:  $P_{(\text{Roll})} = 0.10$ ). Importantly, while the shapes of the  $E_b$  and  $E_f$  dive types (Figs. 8, 9; 1st window) appear similar in the ‘depth versus time’ profile, this similarity disappears in the roll and pitch signals during the bottom phase (Figs. 8, 9; 2nd and 3rd windows, respectively; Table 1).

**Fig. 6** Dive depth, roll and pitch angles of a type  $C_c$  dive. The orientation of the elephant seals helps illustrate body posture



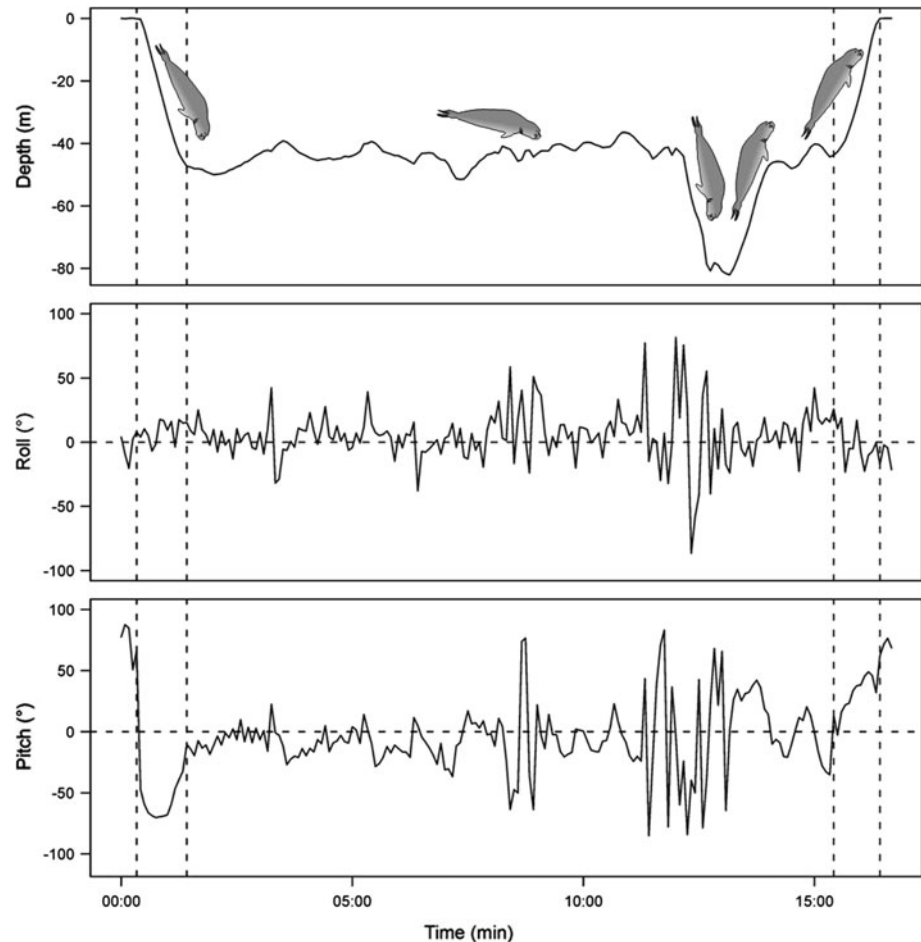
## Discussion

Our results derived from juveniles showed that these animals appear to have similar dive types to the adults although there were obvious differences in type A and C dives, where our animals had clear bottom phases, something that does not occur in adults. Our explanation for this is that the bottom topography of the Patagonian Shelf precludes the juvenile elephant seals from following the descent phase to ‘completion’ (cf. Campagna et al. 2007). Instead, the time nominally allocated to the latter part of the descent in the adults is simply spent on, or near, the bottom in bottom-constrained juveniles. In Le Boeuf et al. (2000), type E dives are grouped into both travelling dives (over the continental shelf) and benthic foraging dives. Our results suggest that  $A_c$  dives are primarily for travel, although they may also be involved in (generally unsuccessful) search for food. Indeed, it seems unlikely that elephant seals commuting along the seabed (cf. Campagna et al. 2007) would not consider prey if opportunistically encountered. Certainly, the body pitch position recorded was always inclined slightly towards the bottom [see Table 1; Fig. 3 (in particular, the graph of the pitch values during the bottom phase)].

In fact, the characteristics of the bottom phase in our data seem to give the best clue as to the functions of the various dive types. In both type  $C_c$  and  $E_f$  dives, the depth of the bottom phase showed strikingly little variance, while at the same time, the animals either lay on one side or the other with no rolling (Figs. 4d, 6, 9). We note also that Hassrick et al. (2007) reported no measurements for speed at this time in  $E_f$  dives. All these suggest very strongly for a resting function at this time (see Hassrick et al. 2007). The second, slow descent phase of type  $C_c$  dives would therefore appear to be an extension of this because it is clear from the angle during this part that the seals are not travelling in the direction their body is pointing since the animals were on their backs with the body angled upward. This posture presumably increases the drag coefficient and results in a decrease in the rate of descent. Mitani et al. (2010) reported similar behaviour for the northern elephant seal, and although their work implies that their animals descend tail-first (which also appears the case in their figures), it is not explicit about this. The ‘head-down’ posture during the initial part of the descent phase (Fig. 6) is reported as occurring in tandem with active stroking (cf. Mitani et al. 2010 for northern elephant seals) and is presumed to take



**Fig. 7** Dive depth, roll and pitch angles of a type D dive. The orientation of the elephant seals helps illustrate body posture



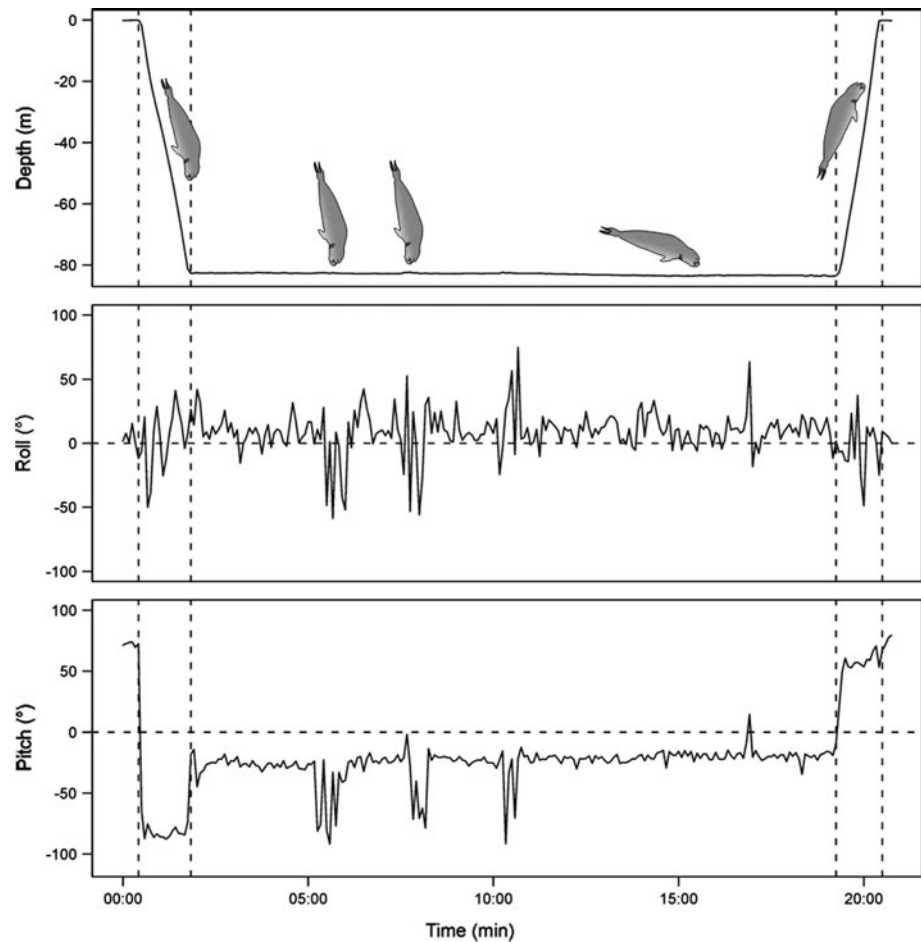
the seal to the point where negative buoyancy allows passive sinking. Mitani et al. (2010) report that these decreased rates of descent occur at depths that are so great that encounters with predators are unlikely (Mitani et al. 2010). Importantly though, our animals adopted this phase at a mean depth of 70 m, considerably less than the mean value of 221 m reported by Mitani et al. (2010). In the case of southern elephant seals at least, this would seem too shallow to escape predators. It is notable that both type  $C_c$  and  $E_r$  dives also tended to occur after a series of dives likely to be foraging (see below), suggesting this behaviour may be an analogue to pelagic drift or processing (digesting) dives observed in adult elephant seals (cf. Crocker et al. 1997; Webb et al. 1998; Biuw et al. 2003, 2007; Bailleul et al. 2007; Hassrick et al. 2007). Perhaps the difference between Mitani et al.'s (2010) drift depths and ours is simply a measure of the difference in buoyancy between the animals in the two groups with neutral buoyancy being achieved at shallower depths in our animals.

The high variance in depth and both pitch and roll in the bottom phase of type D dives indicate that our type D dives are characterized by foraging, as previously proposed by the literature (Le Boeuf et al. 1988; Hindell

et al. 1991a; Le Boeuf et al. 2000; Kuhn et al. 2009). Active pursuit of prey would seem to be the most likely explanation for the high variance, and it would be useful to know what speeds these animals reach during this process. The steep dive angle (with means of *ca.* 60–70°) of type D dives, with little variance, can be treated via simple trigonometry to show that the vertical displacement is over 90% of the absolute (angled) dive trajectory on the descent, which suggests for a dive functionality intending to maximize vertical displacement. Type D dives also show a marked regular rolling from side to side, which may enhance the animals' visual fields and thus increase the chances of spotting prey given that the bottom phases of this dive type indicate that is highly likely to be associated with hunting and/or the pursuit of prey (see below).

The bottom-phase behaviour of type  $E_b$  dives contrasts that of type D dives. Not only do  $E_b$  dives have much smaller variance in depth in general [which is assumed to be because the animals are tracking the seabed (Campagna et al. 2007; Hassrick et al. 2007)], but they also have a much more left-hand skewed distribution of pitches (cf. Fig. 4c) that are not accompanied by a change in depth. Thus, it would appear

**Fig. 8** Dive depth, roll and pitch angles of a type  $E_b$  dive. The orientation of the elephant seals helps illustrate body posture



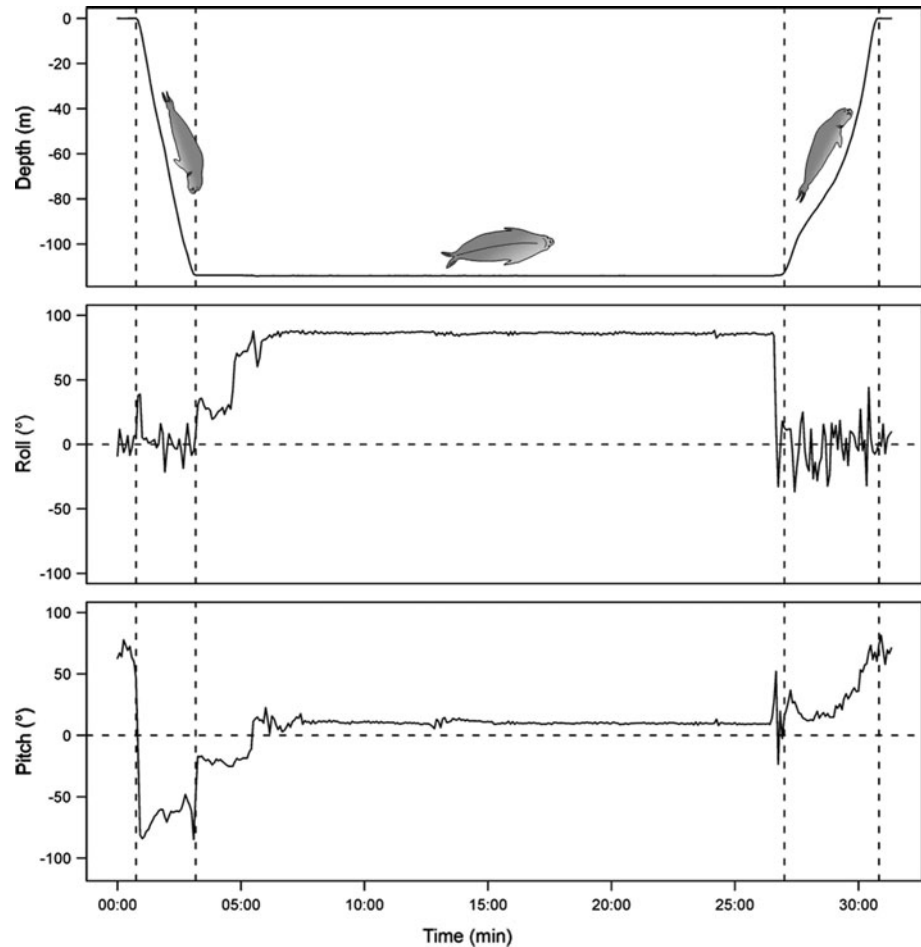
that animals periodically ‘up-end’, much as do dabbling ducks, on the seabed, and we assume that this behaviour is associated with the seals locating and feeding on benthic and/or buried prey (cf. Campagna et al. 2007). The fact that steep pitch angles during the bottom phase are not associated with any descent (unlike those of type D dives—cf. Figs. 7, 8) lends support to this. Importantly, the apparent similarity between the profiles of the  $E_b$  and  $A_c$  dive types in our data set is superficial because pitch and rolls values for  $E_b$  dives (Fig. 8) show likely feeding on the seabed manifest in the up-ending behaviour, whereas no such thing occurs in  $A_c$  dives (Fig. 3) where the main function appears to travel and possibly (unsuccessful) search for food.

The primary difference between  $E_b$  and  $E_f$  dives is apparent in the pitch and roll during the bottom phase with  $E_b$  dives showing up-ending behaviour with great variability in roll (Fig. 8; Table 1), features that are absent in  $E_f$  dives. Notably, both dive types show no major changes in diving depth and therefore no real changes in the dive profile. By contrast, pitch and roll angles for  $E_f$  dives (Figs. 4c, d, 9) most likely correspond to rest and/or processing of food during the bottom phase. In such dives, which are well documented in juvenile northern elephant seals by Hassrick

et al. (2007), individuals remain motionless (see Hassrick et al. 2007) while lying on one of their sides.

The bottom phase of type  $A_c$  and type B dives (although both are momentary, especially in the case of  $A_c$  type dives) shows low variability in both pitch and roll values, indicating a straight-line course with no prey encounter to cause the animals to deviate substantially. This accords generally with the idea of the travelling function of type A and B dives suggested by Le Boeuf et al. (1992, 1993, 2000) and Hassrick et al. (2007) (cf. Hindell et al. 1991a). The slight ‘head-down’ position adopted by the elephant seals during the type  $A_c$  and B dives could, however, indicate that these dives may also have a ‘search’ (but no prey ‘find’) function (cf. Hindell et al. 1991a; Le Boeuf et al. 1992, 1993). Descent angles of type  $A_c$  dives are as steep as those of D type dives (Fig. 4a) which would tend to indicate that, here too, animals are attempting to maximize vertical displacement, perhaps to give them most rapid access to depths where foraging can occur. We note though that Hassrick et al. (2007) found type A dive angles to be considerably shallower than ours, something that lent support to their interpretation of these dives to be travelling. However, these authors found that juveniles of the northern species (*Mirounga angustirostris*) used much steeper descent angles

**Fig. 9** Dive depth, roll and pitch angles of a type E<sub>f</sub> dive. The orientation of the elephant seals helps illustrate body posture



than adults on type A dives and proposed that this was because of differences in buoyancy that forced juveniles to use steeper descent angles and greater stroke frequencies (Hassrick et al. 2007). The precise form of power use in relation to work done to overcome buoyancy, and the consequences of this for the vertical cost of transport will likely determine the optimum angle to descend (cf. Wilson et al. 2011). In contrast to our type A<sub>c</sub> dives, the type B dives, with the parabolic form to the descent (Fig. 5), had a steep initial descent angle, which rapidly flattened out with an overall mean descent angle that was only about 41°, some 25° less than type A<sub>c</sub> dives, so that these dives incur a horizontal displacement that is 75% of the absolute dive trajectory on the descent, implying that a primary function of this dive type may be in horizontal displacement or travelling. Certainly, the substantial difference in dive pitch between type B dives and all others (Fig. 4a, c, e) implies a markedly different functionality between these dives and any of the others. The initial steep descent angle during type B dives can be explained because it may serve to get the seal quickly through the surface waters where it has positive upthrust (*sensu* Wilson et al. 1992) (Webb et al. 1998; Biuw et al. 2003). These dives also show less variance in the roll angles than the other dive types (Fig. 4b, d, f). Type B dives

also have return-to-surface angles that are some 25° shallower than all other dive types which, again, would suggest for a different functionality for this dive type. Assuming that the seals travel in the direction that their bodies indicate then, all other things being equal, simple trigonometry would indicate that during most dives except type B, animals incur a vertical displacement that is about 78% of the absolute (angled) dive trajectory on the ascent. The comparable figure for type B dives is only 37%. Thus, dives of type A<sub>c</sub>, C<sub>c</sub>, D and all Es would seem excellent for displacing the animals rapidly between the allocated bottom depth and the surface. Conversely, type B dives incur a horizontal displacement that is 93% of the absolute dive trajectory on the ascent, whereas the comparable figure of all other dive types is about 63%. Thus, again, type B dives seem well suited for allowing the animals to travel horizontally, while the return-to-surface angles of other dive types serve to get the animal quickly and efficiently (with minimal horizontal displacement) to the surface to breathe.

This study indicates that juvenile southern elephant seals from Península Valdés engage in diving behaviour that is similar to that of adults. Differences can be mainly attributed to the constraints of the bottom topography, but certain

features that have emerged by using the accelerometers to define body pitch and roll appear to be new to this species. Most notable of these is the ‘up-ending’ behaviour that appears during the bottom phase of  $E_b$  dives. This indicates that juvenile elephant seals forage on truly benthic as well as pelagic prey (cf. Campagna et al. 2007). Thus, accelerometer data suggest that several unique behaviours can ‘hide’ behind the same dive shape (e.g.,  $A_c$ ,  $E_b$ , and  $E_f$  dive shapes; Figs. 3, 8, 9), highlighting the importance of having this information to study the diving behaviour, in general, and to conduct a functionality-based classification of dives in particular.

Knowledge on the underwater behaviour of elephant seals has been primarily based on indirect information provided by dive depth and duration statistics together with some data on estimated swim speeds (Thums et al. 2008), although Crocker et al. (1997) were able to explore dive functionality in greater detail by examining the order of bouts. Accelerometers, such as those used here to determine animal pitch and roll, improve our ability to interpret behaviour. For example, it was known that type C dives have a drifting down phase (Crocker et al. 1997; Biuw et al. 2003, 2007; Hassrick et al. 2007), but it was not until Mitani et al. (2010) identified the ‘belly-up’ posture of animals during such dives that the true nature of descent phases became apparent. Although work with time-depth recorders has had a pivotal role in making a first step into the interpretation of the behaviour of diving animals, the measurement of body angle has now been shown important in shedding light on the function of the different dive types exhibited by elephant seals. The use of accelerometers has already proven itself for helping determine behaviour of a number of animal species (e.g., Yoda et al. 1999; Sato et al. 2003; Ropert-Coudert et al. 2004; Watanabe et al. 2005; Kato et al. 2006; Gómez Laich et al. 2008; Shepard et al. 2008). As information on body orientation using static acceleration values progresses into that using dynamic acceleration for measures of limb and body movement (e.g., Watanabe et al. 2005; Mitani et al. 2010), we expect the process of understanding the function and value of the different dive types of marine endotherms to progress still further.

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