Three-Dimensional Diving Behavior of a South American Sea Lion (*Otaria flavescens*)

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Abstract

Even though the use of time-depth-recorders (TDRs) has dramatically increased knowledge about pinniped diving behavior, recent studies have shown the limitations of two-dimensional plots of time and depth in interpretation of animal activity. Recently, new technologies have become available allowing collection of more dive parameters so that dives can be depicted in three dimensions. This study uses information collected by a multiple-channel dead reckoner (tracking recorder) to provide detailed information on movements in space of a male South American sea lion (*Otaria flavescens*) in Patagonia, Argentina. The information was analyzed using an area-interest-index (AII), which reflects the directionality of movement. The AII was calculated for a complete foraging trip where the middle part showed the highest values, indicative of foraging activity. Activity estimations based on three-dimensional dive profiles (four dimensions with speed) showed good agreement with the calculated AII. The use of the AII is thus a promising tool for the determination of activity of marine animals over varying spatial scales.

Introduction

Determination of animal activity at sea has generally been hindered by the lack of information on animal movement in three-dimensional space so that behaviors cannot be assigned to specific areas. However, in recent years advances in technology have allowed collection of information that allows animal movements to be determined in more than the conventional two dimensions of depth over time (Harcourt et al. 2000; Davis et al. 2001, 2003, 2004; Hindell et al. 2002; Mitani et al. 2003).

Relatively little is known about the distribution at sea and diving behavior of the South American sea lion (*Otaria flavescens*), knowledge to date being almost exclusively limited to lactating females equipped with satellite tags and time-depth recorders (Werner and Campagna 1995, Campagna et al. 2001). We hypothesized that use of a compass together with measures of speed and dive depth would allow a much more comprehensive insight into dive behavior than the standard dive depth versus time approach. This study details recent investigations on a single male sea lion using a dead reckoner (tracking recorder) to reconstruct the three-dimensional route during a foraging trip, to detail the applicability of the method as well as to provide insights as to what types of behaviors can be elucidated by this approach. An activity index based on analysis of track tortuosity was created and applied to the route. Individual three-dimensional dive profiles are also provided to exemplify specific activities observed at different stages of the trip.

Methods

As part of a larger project studying the foraging ecology of South American sea lions conducted at Peninsula Valdés, Chubut, Argentina, eight subadult males from the breeding colony of ca. 250 males at Punta Norte were equipped with dead reckoners (Driesen and Kern GmbH, Bad Bramstedt, Germany) in November 2003. Animals were immobilized using a combination of tiletamine and zolazepam (Telazol®), which was delivered intramuscularly by darting the animals. A detailed description of this procedure is in Campagna et al. 2001. Approval for this procedure was given by the Dirección de Fauna and Subsecretaría de Turismo de la Provincia del Chubut. Although five units were recovered (see Müller et al. 2005), we only managed to obtain appropriate data for the complete foraging trip from a single animal. This is important for dead reckoning applications because the start and end positions must be known to correct for drift (Wilson et al. 2002). As a result, we will only consider further the data from this single animal. The recovered device recorded time, depth, swim speed, compass heading (in three dimensions), and tilt angle (pitch and roll, 0-70 degrees off the horizontal) at a sampling interval of 10 seconds. This relatively low sampling rate was chosen to try

and ensure that the complete foraging trips could be recorded before the memory was full. Animal speed was determined by using two medium-separated 20 bar pressure transducers, one that recorded hydrostatic pressure directly and another that recorded hydrostatic pressure plus an additional component derived from the pressure produced by the forward motion of the animal underwater. For this a small paddle projected into the water from the device. The paddle was linked via an axle to another arm, set at 90 degrees to it, running longitudinally up the length of the device. The end of this second arm articulated with a small plate that rested on the medium-separating membrane of one of the pressure transducers. Water pressure from the front as the animal swam caused the paddle to be pushed back and thus, via the axle, caused the plate to be pushed with more force down onto the membrane (cf. Wilson et al. 2004). This resulted in a higher pressure being recorded from one pressure transducer than the other. Subtracting the value of one transducer from the other produced an output that was proportional to swim speed. This was calibrated in situ by plotting the pressure sensor's swim component against the known speed when the animal dived or returned to the surface; simple trigonometry allowed us to calculate this using rates of change of depth and pitch angle. The resulting regression was then used to derive swim speed when the animal swam horizontally. The compass used was a solid-state system sensing tri-axial magnetic field strength. Methods for determination of heading are based on known pitch and roll angle and are detailed in Mitani et al. (2003). The three-dimensional route could be determined using the stored data and was reconstructed using custom-written software (MT-Route from Jensen Software Systems, Laboe, Germany). The route was corrected for drift using two procedures, by incorporating the known start and end point of the trip and by correcting for depth inconsistencies. In a first iteration of the route, the known start and end points were made to accord with the calculated positions by assuming that any errors were due to drift resulting from a constant current displacing the animal to the extent shown over the full course of the foraging trip (R.P. Wilson et al. unpubl.). We then used bathymetry data, with a resolution of 10 m, and superimposed the first iteration onto the map, noting where the maximum depth reached by the animal exceeded that of the seabed. The nearest likely point for the animal to be, in terms of depth, was then allocated to that position and all subsequent positions corrected to accord as if the error occurred due to drift (see above).

An area-interest-index (AII) was used to describe animal activity at sea (Fig. 1). It relates the total horizontal distance traveled between two points ("a" through to "e") to the direct distance between the first and the last point (F):
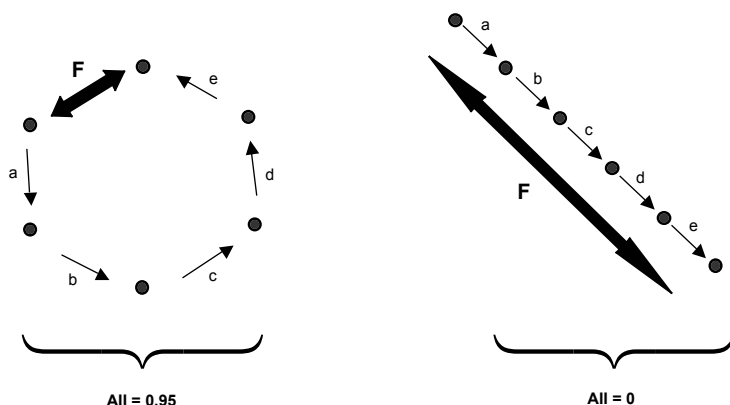
Figure 1. Calculation of the area-interest-index (AII) over six successive points illustrating concentrated movement in a small area (left) and highly directional movement (right).

A high AII value corresponds to a convoluted track whereas low values indicate more directional movements. Because of the long duration of the trip the data were thinned out so only every tenth data point was included in the calculation of the AII, which spanned five successive points and thus was calculated over a time interval of 360 seconds. In order to see the change in AII over time the trip was divided into intervals, each covering 5% of the total time, and an inverse polynomial curve was fitted to the means of the AII for each interval.

Results

During the 16 day foraging trip the sea lion made 2,163 dives, of which 1,849 (85.5%) were square (U-shape) dives (cf. Le Boeuf et al. 1988). The mean dive depth was 62.5 m (SD 29.1 m) with mean duration being 4.7 min (SD 1.6 min). From Punta Norte the animal headed eastward toward the shelf break, turning north just before reaching the 100 m depth contour, and finally turning southwest on return to the colony (Fig. 2). The AII was highly variable, but an inverse polynomial curve fit through the means of each time interval showed that the index increased over time reaching a maximum at about five days into the trip and then declining again toward the end of the trip (Fig. 3). AII values less than 0.2 were found in the first 10% and the last 25% of the trip with the middle part showing greater AII values.

A selection of individual dives considered to be typical of three different parts of the foraging trip is shown in Figs. 4-6. All two-dimensional
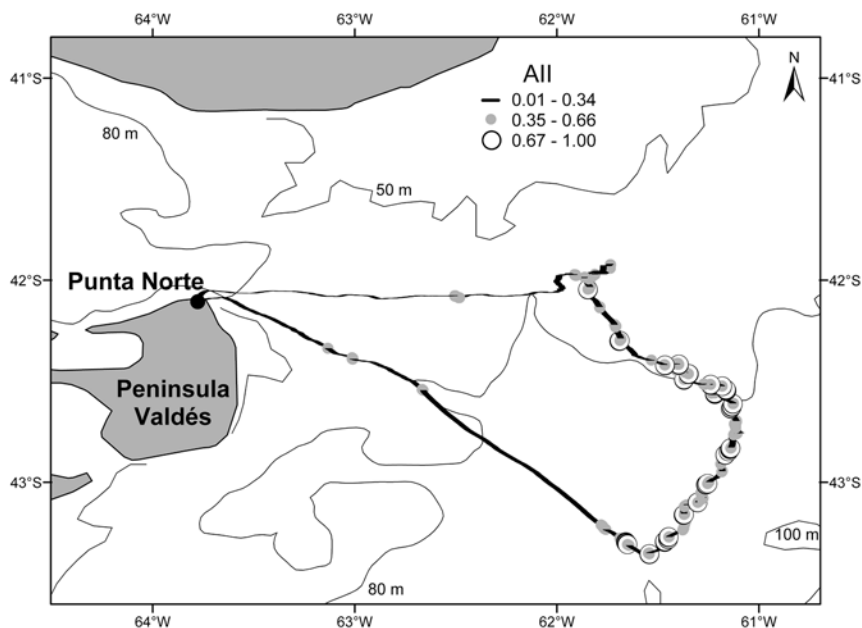
Figure 2. Map showing the route of the foraging trip performed by a male South American sea lion. For each dive only one AII value (corresponding to the start time of the dive) is depicted. The AII was calculated over five successive points with only every tenth data point being used in the calculation.

time-depth profiles are similar in being U-shaped and differing only in maximum depths attained. The time-AII profiles, on the other hand, show obvious differences between these dives. The differences become even more apparent in the three-dimensional presentations of these dives. The first dive, taken from the beginning of the trip, has a low AII value of around 0.2 and shows very directional movement through all phases of the dive with a relatively constant, high speed (Fig. 4). The two dives with higher AII values from the middle part of the trip (Figs. 5 and 6) are much less directional in all phases of the dive. The last dive shows extremely convoluted movements during the bottom phase (Fig. 6). In the latter two dives the speed during the bottom phase is much slower and more variable than in the first dive.
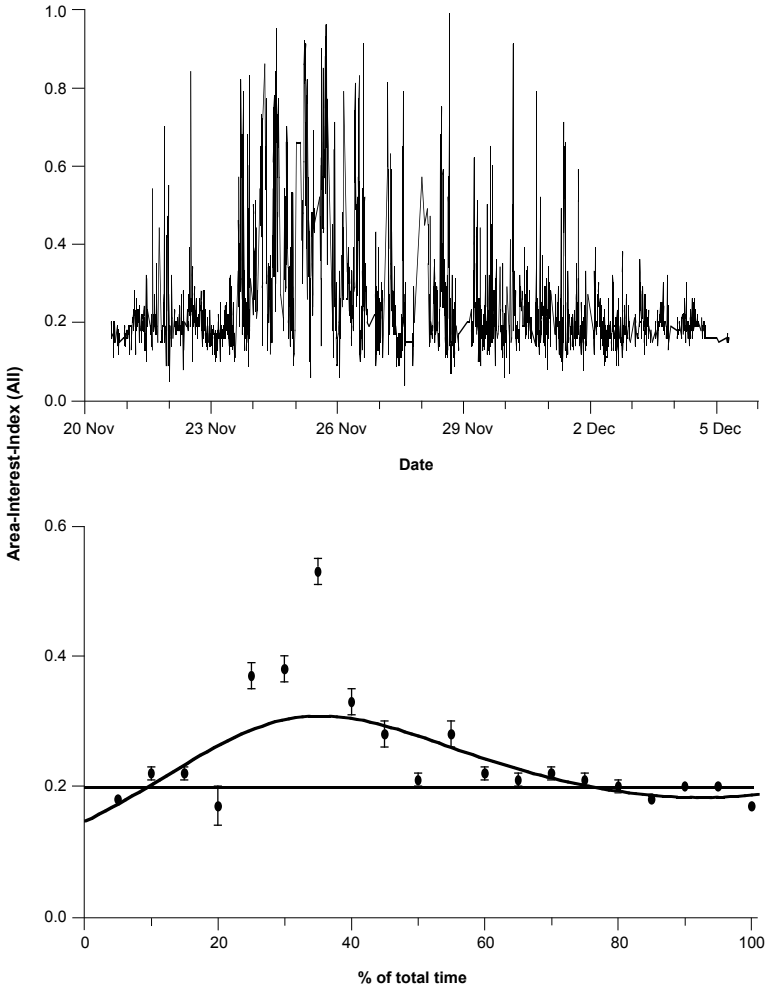
Figure 3. **The change in area-interest-index (AII) over the course of the complete foraging trip (above) and AII means for time intervals (each covering 5% of total time) with an inverse polynomial curve fit ($y = 1/(6.8017923 - 0.2313366x + 0.0045242x^2 - 0.0000024x^3)$, $r^2 = 0.5$, below).**
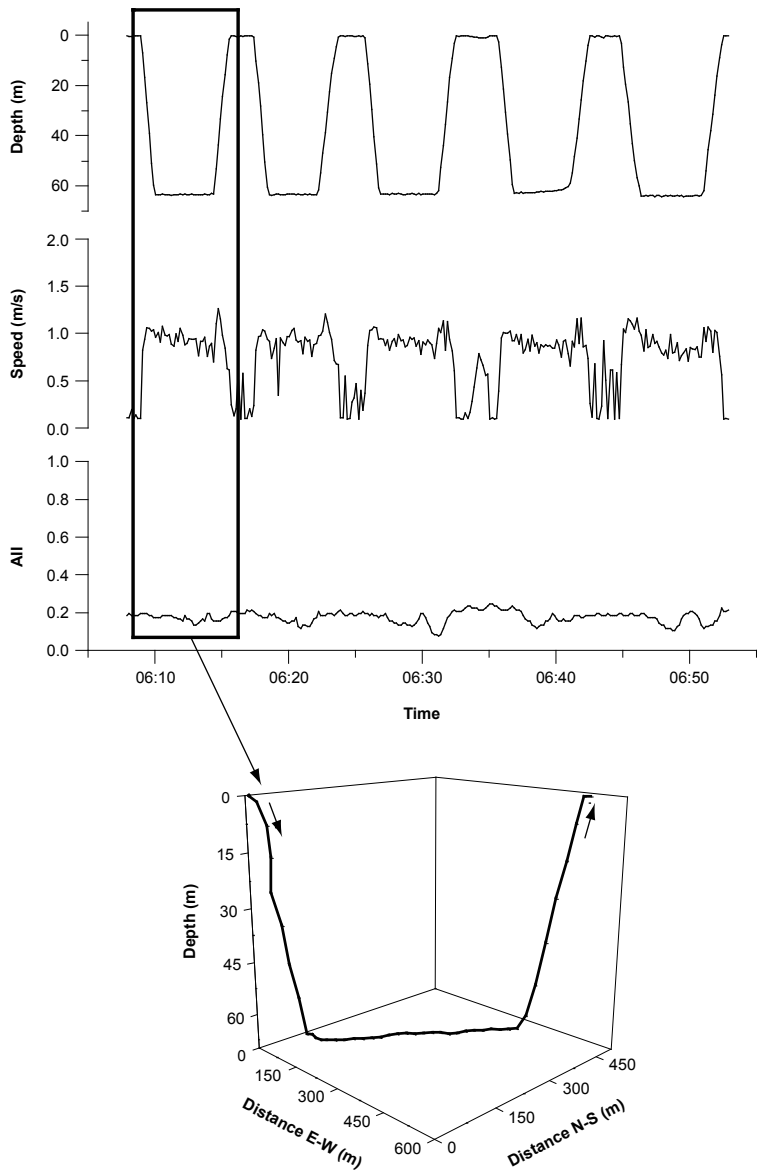
Figure 4. Example of dives from the beginning of the foraging trip with relatively constant speed throughout the dives and low AII values. The three-dimensional dive path of the framed dive is depicted below.
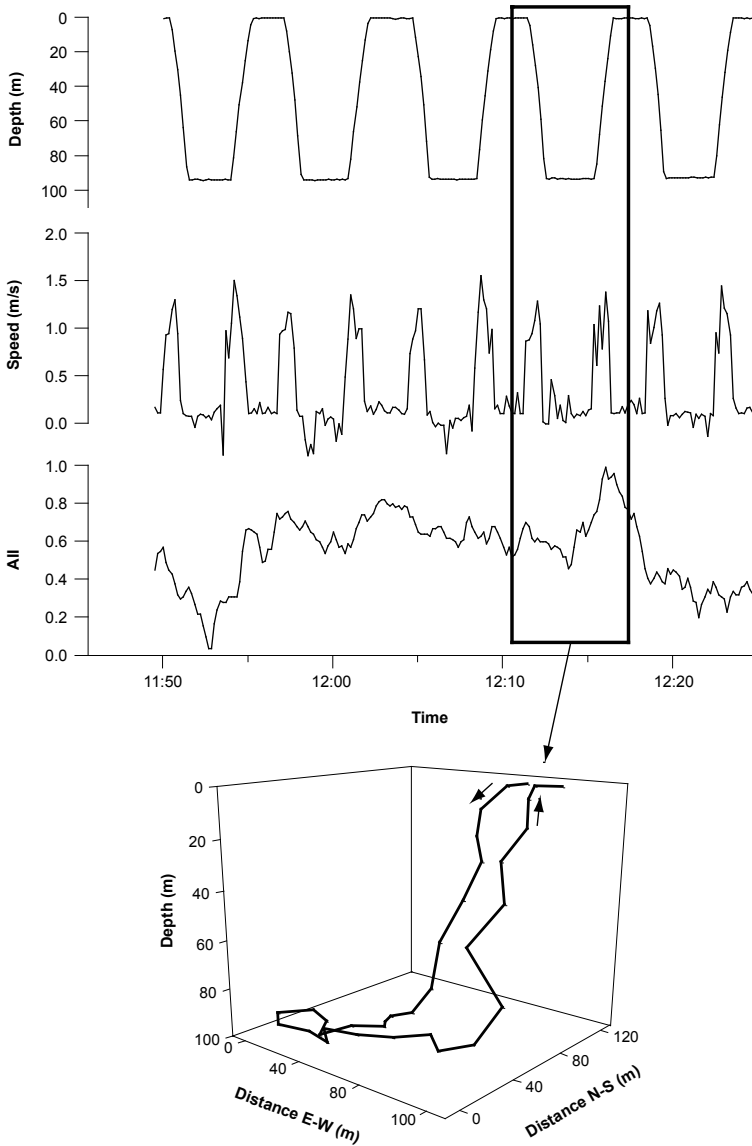
Figure 5. Example of dives from the middle part of the foraging trip with slow speed throughout the dives and variable AII values. The three-dimensional dive path of the framed dive is depicted below.
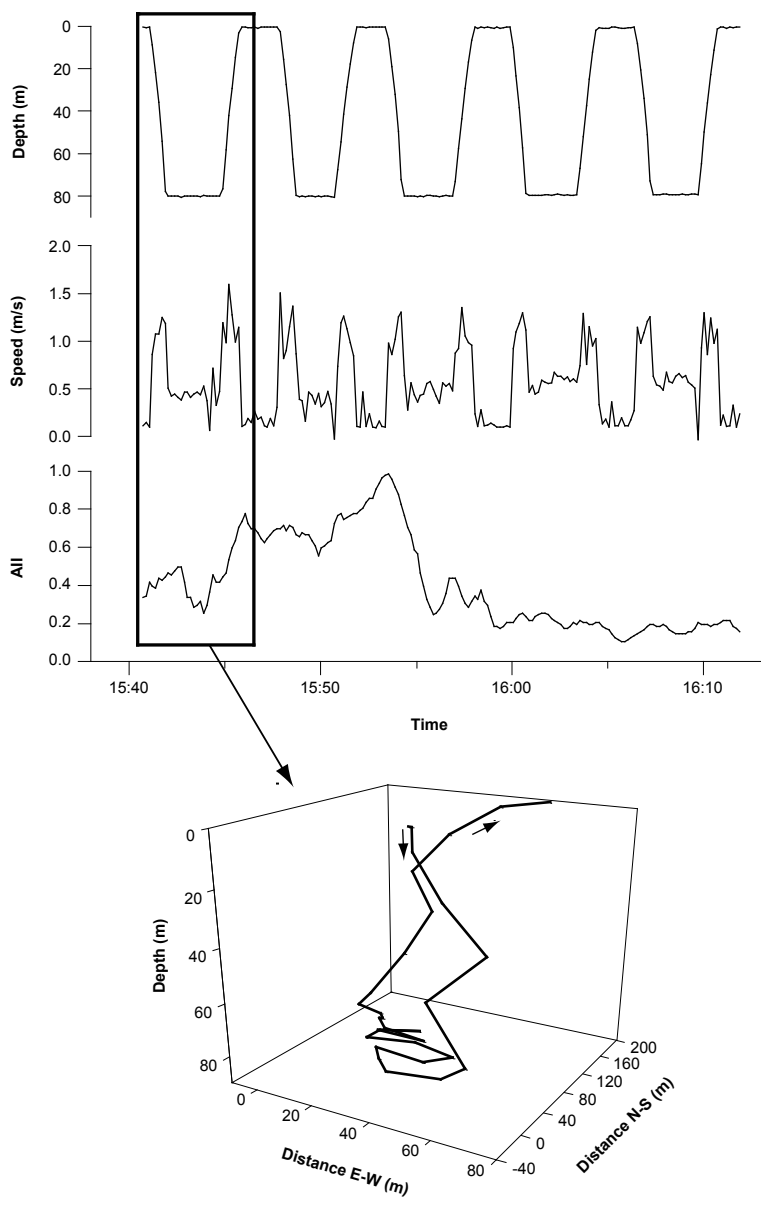
Figure 6. Example of dives from the middle part of the foraging trip with variable speed and AII values throughout the dives. The three-dimensional dive path of the framed dive is depicted below. Note the convoluted path in the bottom phase of the dive.

$$\text{Horizontal travel efficiency} = \frac{(2 \times A) + D}{(2 \times C) + D}$$
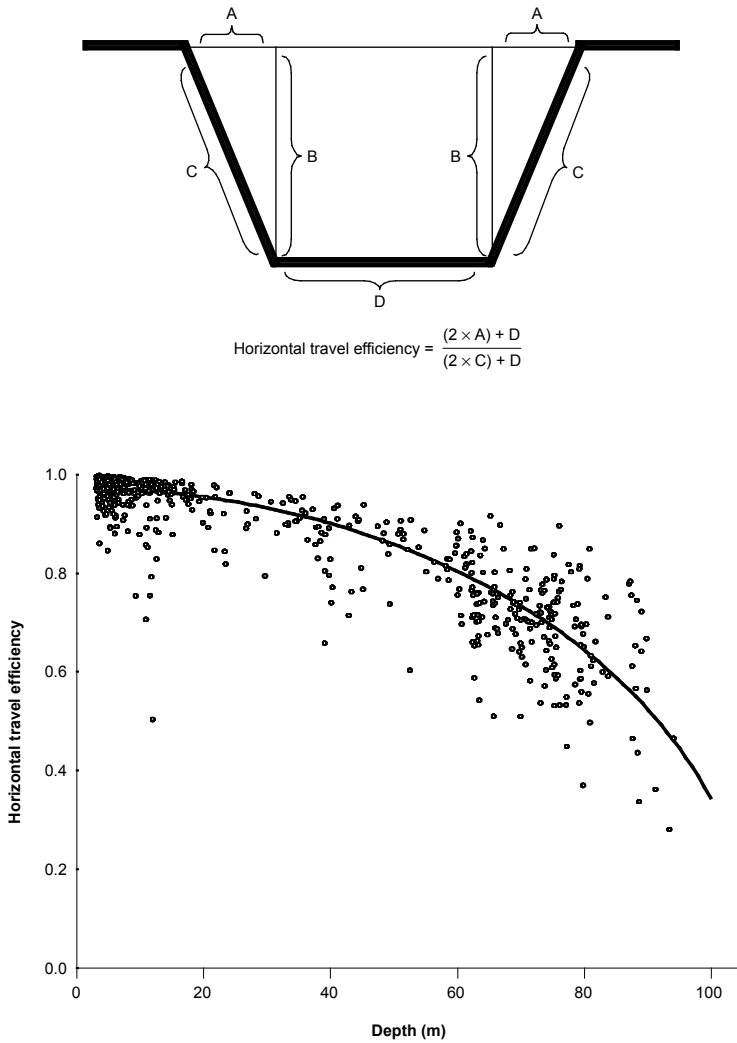

Figure 7. Calculation of the horizontal travel efficiency of a dive (above) where C and D are the actual distances traveled (including the vertical component), A is the horizontal distance covered during the descent and ascent phases, and B is the depth of the dive. Actual data from the trip made by the sea lion are given below.

Discussion

The results of this study highlight the advantage of incorporating information on three-dimensional behavior and movements in the determination of animal activity at sea and the association of these activities with specific areas. The sea lion in this study foraged on the Patagonian shelf, as has been shown for other males from Peninsula Valdés (Campagna et al. 2001; unpubl. data). The combination of position and area-interest-index shows that only the middle part of the trip (in terms of distance covered) is characterized by consistently high AII values. Both the outward and inward legs of the trip show mainly low AII values (indicative of directional movement), but each covers approximately the same distance as the middle part, suggesting that the sea lion employs a strategy of comparatively fast and directional travel to foraging grounds in order to maximize the time available for foraging. This division of time at sea into distinct travel and foraging phases has also been noted in southern elephant seals (*Mirounga leonina*) (McConnell and Fedak 1996) and Antarctic fur seals (*Arctocephalus gazella*) (Bonadonna et al. 2000). The travel function of these parts of the trip is further supported by inspection of individual three-dimensional dive profiles. During these apparent travel dives the animal shows very straight movements during all phases of the dive, with only minor changes in speed during the entire dive. The reduction in speed at the surface does not necessarily reflect the actual swim speed of the animal, as the device was located on the sea lion's head and therefore was not able to measure speed at the surface. In addition, the location of the device led to a high variability in speed measurements, as movements of the head do not necessarily reflect movements of the body. Therefore the measured speed might not always correspond to the actual swim speed, although the overall changes in speed are assumed to be generally correct.

High AII values are a reflection of localized movements and thus depict areas that are of particular interest to the animal. For the South American sea lion, these areas are most likely foraging spots. Again, the three-dimensional dive profiles support this, as the observed movements, especially during the bottom phase, can be highly convoluted. This suggests that the animal dives down to the bottom (at approximately the same speed as during travel dives) and then slows down in order to search for prey. The slow speed supports earlier studies which showed that South American sea lions mainly feed on benthic-demersal prey (George-Nascimiento et al. 1985, Koen Alonso et al. 2000). However, as the sampling interval increases, the probability of recording short events such as speed bursts during pursuit of fast-moving prey will decrease (see Ropert-Coudert and Wilson 2004 for a discussion of the errors involved in this). Thus, data logging devices sampling at high frequencies would be beneficial for a detailed study of the pursuit and capture of prey (Davis et al. 1999, Williams et al. 2004).

The time-depth profiles in combination with the AII imply that the sea lion at least partially performs square dives while traveling. Because the movement during a dive can be divided into a horizontal and a vertical component, the most efficient strategy for travel dives in which the horizontal component is to be maximized would be to make shallow parabolic dives as observed in, e.g., penguins (Wilson 1995). For a constant dive duration the horizontal distance traveled will decrease with increasing depth, as a greater proportion of the dive is allocated to the vertical component of the movement. This can be illustrated by calculating the horizontal travel efficiency, which is the horizontal distance actually traveled divided by the total distance traveled, including the vertical component (Fig. 7). As the vertical component increases with depth, the horizontal efficiency decreases because the horizontal movement along the bottom becomes a smaller fraction of the total movement. Such a reduction in efficiency not only leads to a loss of time for the animal but also to an apparently unnecessary expenditure of energy. However, swimming along the bottom may confer advantages that cannot be easily measured. It may allow the animal to feed on an opportunistic basis, if prey is encountered, which could be of particular importance after long periods of fasting on land when the foraging grounds are far from land. In addition, if a sea lion is close to the seabed it may reduce the risk of being detected by predators such as sharks, as these often approach and attack their prey from below and behind (Tricas and McCosker 1984, Crespi-Abril et al. 2003, Lucifora et al. 2005). Ultimately, however, the possible advantages of swimming along the bottom will be eventually limited by the animals' diving capacity and the bathymetry.

In conclusion, the analysis of a sea lion foraging trip using an index of activity showed that, in terms of distance covered, the major part of the trip was spent traveling. However, more than half the time was spent performing more localized movements at lower speed, suggesting foraging activity. This is supported by the three-dimensional dive profiles that reveal substantial differences in movements during travel and foraging dives. The obtained results emphasize that incorporation of three-dimensional data on movements is particularly useful for determining activity of animals at sea as well as inferring the function of different dive types.

Acknowledgments

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