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TWO APPROACHES TO COMPRESSING AND INTERPRETING TIME-DEPTH INFORMATION AS COLLECTED BY TIME-DEPTH RECORDERS AND SATELLITE-LINKED DATA RECORDERS

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ABSTRACT

Time-depth recorders sample information about the three-dimensional behavior of diving animals over time and reduce this into just two dimensions, depth and time. Even so, interpretation of the data may still be difficult because of the volume of data and the detail that remains. Comparison of dive "shape" across individuals, geographical locations, or species presents problems because its analysis may involve subjective judgments or arbitrary distinctions. More constraints may be imposed if a telemetry system is used to transmit the data. Here we present two approaches for dive data compression and analysis. The first (applied before storage and transmission) selects the most important time-depth points in a profile where depth *vs.* time trajectories change most significantly. The second (used to either preprocess or postprocess dive information) creates a dimensionless, depth, and duration independent index (TAD), which encapsulates the relevant information from dive profiles on where the diver centers its activity with respect to depth during a dive. Its use facilitates comparison across dives performed at different times or places, within or between individuals or species, irrespective of the duration and depth of their dives. Both can be used to reduce the amount of information sent or stored about dive behavior and can facilitate dive analysis.

Key words: diving behavior, telemetry, data compression, seals, Argos, marine mammals, diving birds.

The study of diving in nature necessarily involves a process of data abstraction. Technology has made it possible to collect information on diving behavior of birds and mammals in nature with unprecedented detail. But the volume of information collected can place unacceptable demands on data storage and transmission and make subsequent analysis difficult. Dive information often

takes the form of a sequence of depths taken at predetermined times using time-depth recorders (TDRs) (Kooyman 1965, 1981; Wilson and Bain 1984). By sampling and recording only depth at regular intervals, TDRs reduce the information about the 3-D spatial behavior of diving animals through time into just two dimensions, depth and time. But even with this simplification, analysis can be difficult because of the quantity of data and detail that remains.

While it is possible to examine each dive in a record individually, it may be useful and often essential to further abstract the data in order to assimilate the information and relate important features to environmental or behavioral factors. Various shape classification and statistical techniques, such as PCA and clustering approaches, have been successfully used to do this (LeBoeuf *et al.* 1988; Hindell *et al.* 1991; McConnell *et al.* 1992; Schreer and Testa 1995, 1996; Sjoberg *et al.* 1995; Brillinger and Stewart 1997; Martin *et al.* 1998; Schreer *et al.* 1998). For these techniques to be effective, they need to use meaningful, easily quantified dive characteristics. It is also important that they be ones that can be done objectively and in an automated way. A number of variables and parameters have been used including combinations of maximum depth and duration of the dive and characteristics such as descent rate, ascent rate, "bottom time," "wiggle factors," and methods of shape classification. Simple scalar variables are particularly useful in this regard.

Additional constraints are imposed by telemetry systems such as satellite-linked data recorders (SLDRs). These can provide information about diving behavior when recording devices are difficult to recover. They can record large amounts of data on board the logger, as can recording-only devices, but the amount of data they can send back is necessarily constrained by size and battery energy. The amount sent may also be limited, as it is with the Argos system, by bandwidth constraints, a result of both communication system limits and the limited time spent by marine mammals at the surface where transmissions can be sent. In these situations, data compression and interpretation are best done on board the SLDR so that the limited amount of data sent will provide an adequate picture of the animal's behavior.

Therefore, methods for selecting key aspects of the data may be useful with both recorded and relayed data and similar approaches may benefit both pre-transmission processing and postcollection analysis of dive information. Any approach used to reduce the number of bits stored or sent about diving behavior will involve either a reduction in redundancy or a loss of detail. The elimination of redundancy is obviously the preferable option, but once the opportunities to do this have been exhausted, fundamental information will be lost. The process becomes one of making decisions about what parts of the information are most relevant and important to the analysis.

Classification and analysis of dive profile "shape" may involve subjective judgments or arbitrary distinctions. In time-depth records, dive shape is usually derived from a sequence of depths taken at regular intervals (typically 10–60 sec) from a depth transducer. When drawn as a function of time, the sequence of depth points form a profile with a shape that can be related to behavioral or ecological factors and compared within or between individuals

or species. While the shape of the profile itself can form a basis of comparison, the information contained within the profile includes data on a complicated set of temporal and spatial relationships. It is possible to break dive profile information down into a number of informative components. One useful one is the allocation of time spent by an animal at the depths encountered during a particular dive. This information is most intuitively conveyed using a histogram where the bar heights indicate the sum of time spent at each depth. Such a representation contains less information than a full dive profile because it lacks information on the temporal sequence of depths attained as the dive progresses. However, even such histograms may require individual inspection and interpretation for each dive and the problem of comparison between dives remains. Therefore, further abstraction may be useful.

Here, we first present a technique for data compression that retains the salient features of dive profiles by selecting the time-depth points in a profile where trajectories change most rapidly. Then we describe a dimensionless index of dive shape (Time Allocation at Depth index, or TAD). TAD is independent of the depth and duration of the dive and encapsulates the relevant information from the dive profile on where, in the range of depths encountered in a dive, the diver has concentrated its activity. Its use facilitates comparison across dives performed at different times or places, within or between individuals or species. These two independent approaches can reduce the amount of information sent or stored about dive behavior by logging devices and can facilitate dive analysis. The TAD can be used to either preprocess dive information before transmission from SLDRs or to postprocess recorded dive information. The use of the index can also provide information on the maximum vertical speed adopted by animals without examining each dive individually and making subjective judgments about when to terminate ascent and descent phases.

METHODS

Finding Dive Profile Inflection Points

We developed an approach to compressing dive profile information from time-depth records that selects the time-depth points where the dive trajectory changes most rapidly (Fig. 1). The profile can be reconstructed by joining the selected points with straight lines. Only these time-depth points are stored for transmission or recovery along with the maximum depth point and its associated time. Any number of points can be chosen depending on the constraints of bandwidth and the resolution required. Along with the selected points, a residual is calculated that provides a measure of how far the abstracted trajectory deviates from the full resolution profile as collected by the device. For example, if the SLDRs collect depth information every four seconds, 150 points would be collected during a 10-min dive. This represents 1,200 bits of information if depths are stored with a resolution of 8 bits. By way of example, using the algorithm, this could be reduced to 80 bits plus another 8 bits for the residual index for a 4-point profile (including three selected

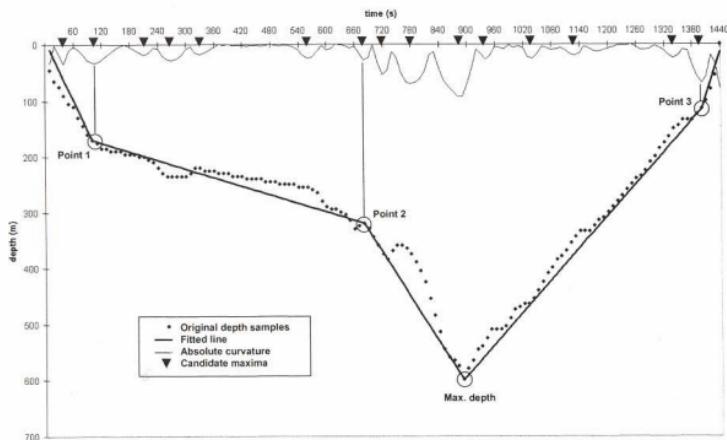


Figure 1. Time-depth profile of single dive of adult female southern elephant seal from South Georgia. Data from records presented by Boyd and Arnborn (1991). Depth readings taken every 10 sec through approximately 16-min dive shown as points. Upper solid line plots smoothed second derivative of depth samples at each recorded point. Dotted line connects three points chosen by algorithm and point of maximum depth. Arrows indicate temporal position of potential points corresponding to local maxima of curvature. See text for further explanation.

pairs, the maximum time-depth pair plus the bits for the start- and end-times of the dive). The fidelity of this representation varies with the shape of the dive profile. Simple V-shaped or trapezoidal profiles will have smaller residuals than some more complex shapes.

The algorithm for selecting these profile points is executed at the end of each dive. It is simple enough to run in a very short time, even on fairly basic processors running a high level language such as "C." The first step is to find the points in the dive where the profile deviates most from a straight line. Following the application of a simple 1-2-1 smoothing filter ($d_i^* = (d_{i-1} + 2d_i + d_{i+1})/4$), the second difference of the smoothed depths is calculated at each point ($d_i'' = d_{i-2}^* - 2d_i^* + d_{i+2}^*$). The absolute value of d'' (shown as the top line in Fig. 1) is used as the measure of curvature at each point. A list of candidate points is then created by finding the local maxima of the absolute curvature. In addition, the point at which the maximum depth occurs is always included in the profile. The remaining three profile points are determined by selecting all combinations of three points from the candidate list and evaluating for each the residual error between the profile created and the original full-resolution profile. The set of three candidate points that minimizes the residual is chosen to represent the dive. If the shape of a dive is complex with lots of changes in trajectory ("wiggles") the algorithm will select

only the most abrupt, missing others. This lack of fit will result in a higher residual.

The Time Allocation at Depth Index (TAD)

This index uses the concept of dive *time-depth area*, defined as the area enclosed by the dive profile trajectory and the line of zero depth (effectively the integral of the dive depth over the duration of the dive). The index is based on the calculation of an achievable *time-depth area* for a dive using an estimate of a rate at which animals can change depth, hereafter referred to as vertical speed (VS). This may be less than, or equal to, the swimming speed through the water. (Throughout this paper, it is important to keep in mind that we consider VS only in relation to dive profiles and that this rate is distinct from swimming speed or the rate of movement through the water. It is equal to swimming speed only in dives where the animal swims vertically. Also, note that we are describing dives in simple terms. There is no consideration of which dive depths and durations might be useful or "optimal." This sort of "optimality" argument is used only in the discussion of the choice of swimming speed (see below) and angle).

Consider the three dives shown in Figure 2a. The angle of the lines with respect to the horizontal represents the rate of change of depth, or vertical speed, VS. In the top (trapezoidal or "square") dive, the animal proceeds to the maximum depth at a constant relatively high VS, spends some time at the maximum depth and returns to the surface, again at the same constant rate. In the center (V-shaped) dive, the animal proceeds to the maximum depth at a lower rate and then ascends to the surface using the same rate. In the lower (tooth-shaped) dive, the animal spends much of its time near the surface and only briefly (at the same relatively high VS) descends to and ascends from the maximum depth, spending little time at that depth. Assume a vertical swimming angle with respect to the sea surface, and that the VS in the first and last dive are those that are the maximum sustainable or sensible for some reason. The histograms of Figure 2b indicate the amount of time spent in each depth bin. In terms of time allocation at depth, the trapezoidal dive represents the case where the maximum possible time is spent at the maximum depth encountered in that dive, given a maximum VS. The V-shaped dive represents a case where equal time is spent at all depths encountered, and the tooth-shaped dive a case where maximum time is spent at minimum depth with the minimum time spent going to and returning from the maximum depth.

The *time-depth area* of these idealized dives is obviously a function of dive profile shape. Given some set VS, the *time-depth area* is greatest in the trapezoidal dive and least in the tooth-shaped dive. If the animal were able to ascend and descend more rapidly, it could spend relatively more time at the bottom or top of the dive and have an increased scope to apportion dive time with respect to depth. That is, given a particular maximum depth and duration, greater area is achievable as vertical speed increases. If the animal could

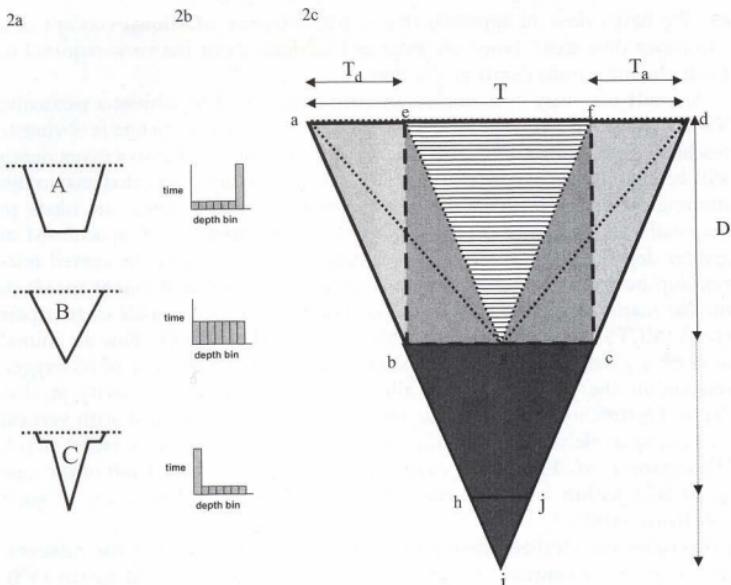


Figure 2. Part 2a shows diagrams of three theoretical dive profiles representing maximum time spent at greatest depth (A), equal time spent at all depths (B), and maximum time at minimum depth (C); part 2b presents histograms of the time spent at each depth of equivalent dives in 2a; 2c is a diagram of areas used in development of the TAD index (see text).

reach very high VS, the trapezoidal dive could approach a rectangular section and thus achieve the maximum possible area for its duration. This would yield the maximum proportion of time at the chosen maximum depth. In tooth-shaped dives, the animal would minimize the time-depth area, apportioning least time at depths other than just below the surface.

Because the maximum achievable area is a function of depth, duration, and the sustainable VS, an index based simply on time-depth area would necessarily vary as a function of these parameters. Given limits to VS, dives inevitably become more V-shaped as the maximum depth of a dive increases or duration decreases. A greater fraction of the time is spent travelling to and from depth and more is spent spread across the depths encountered.

Necessary Dive Area

We set out to devise an index that would provide a measure of time allocation at depth during a dive and yet be independent of depth and duration to facilitate broad comparison across different situations, individuals, species,

etc. We have taken an approach that depends on the additional concept of a "necessary dive area," based on some assumptions about the time required to reach the maximum depth of the dive.

Animals may vary both angle and swimming speed to achieve a particular VS. At any given swim speed, the most rapid rate of depth change is obviously reached by swimming vertically. The fastest speed sustainable to a given depth will be a complicated function of the depth (in the same way that maximum running speed is a function of distance covered). Higher speeds are likely to be possible to shallower depths while only lower speeds could be achieved to greater depths. There is no single limiting speed. However, the curved relationship between the power requirements of swimming at different speeds in marine mammals makes it likely that there is a minimum cost of transport speed (MCTS) for most animals. This is the speed that will allow an animal to reach a given depth having consumed the minimum amount of its oxygen reserves in the process, thereby allowing more oxygen for activity at that depth. Optimality arguments suggest that this speed combined with vertical swimming angle would yield the greatest time or activity at a target depth (Thompson *et al.* 1993). The available data suggest that this minimum-cost speed falls within a limited range for seals from about 1.3 to 2.6 m sec⁻¹ (Williams 1999).

Consider the idealized dive profiles shown in Figure 2c. For the moment, let us assume a constant VS and that the rates of descent and ascent (VS), shown in the dive represented by polygon *abcd*, represent the MCTS and vertical travel. In that case, the dive *abcd* represents the situation where the animal has maximized time at the greatest depth reached during that dive. In the dive *agd*, the animal chooses a slower VS so that it reaches the maximum depth and then immediately returns to the surface producing a V-shaped profile. In this case, the animal spends minimal time at maximum depth and spreads its time equally across all depths. This same uniform time at depth distribution could be generated in any dive where the profile is triangular (either symmetrical or non-symmetrical) or one made up of a set of triangles that extend across all depths (*i.e.*, "W-shaped"). The dive *aegfd* represents the case where the animal spends the maximum time very near the surface and minimal time travelling to and at the maximum depth of the dive. Of these, the profile *(abcd)* produces the greatest total *time-depth area*. The fraction of this area represented by the time spent travelling to and from the bottom is the area contained by the triangles *abe* + *cdf*. The remaining area (represented by the rectangle *bcef*) is the fraction of the *time-depth area* remaining after the time required for travel is removed. This area is maximized when the animal proceeds directly to the maximum depth of the dive (D) at VS. Dive *aegfd* encloses the minimum area and the dive *agd* an intermediate area.

The *time-depth area* thus provides an indication of how the animal spends its time during the dive with respect to depth. However, that area is clearly a function of both the maximum depth and duration of the dive and it would therefore not provide a simple index of time allocation. Also, deeper dives necessarily involve more travel time and will become more V-shaped (*e.g.*, dive

ahjd) reaching the limit where the greatest area possible, given some set VS, is the area of the triangle *aid*. To avoid this problem we condition the index by subtracting the "necessary travel area" (hereafter termed travel area) from each dive. For example, for dive *abcd*, the areas of *abe* + *dc* (the travel area) are subtracted leaving the area of rectangle *bce*. In this case, where the animal descends and ascends at VS, it spends the maximum possible time during the dive at the maximum depth. We could subtract the same (in this case notional) area from dive *agd*, which would leave a smaller area. If the same process were done for dive *aegfd*, the remainder would be zero. In each case, the ratio of the realized remaining area for that particular dive, to the maximum possible remaining area as for dive *abcd*, represents how much of the possible dive area was realized after travel to and from the maximum depth. We have called this ratio the TAD index.

Expressed simply:

$$\text{TAD index} = \frac{\text{actual dive area} - \text{travel area}}{(\text{area of "maximum dive trapezoid"}) - \text{travel area}} \quad (1)$$

where the area of "maximum dive trapezoid" (equivalent to area of *abcd* in Fig. 2c) is set by dive duration, depth, and the time taken to travel to depth. Travel area is the area of a triangle with a height equal to the maximum depth of the dive and a base equal to travel time at the set speed, *S*.

In algebraic terms and as implemented operationally:

$$\text{TAD} = \frac{A_a - A_t}{((D \cdot T) - A_t) - A_t} \quad (2)$$

$$= \frac{\sum_{i=2}^n ((d_i + d_{i-1})/2) \cdot t - A_t}{(D \cdot T) - 2A_t} \quad (3)$$

where

$$A_a = \text{actual dive area} = \sum_{i=2}^n ((d_i + d_{i-1})/2) \cdot t$$

$$A_t = \text{travel area} = \frac{1}{2} T_t \cdot D^2 / S$$

d = individual depth readings from the TDR during the dive

t = sampling time interval of TDR

D = maximum depth of dive

T = total duration of dive

T_t = travel time = *T_a* + *T_d* = time to ascend and descend at rate *S*

S = a set average VS or rate of change of depth

note: *S*, *D*, and *T* must be in the same units of distance and time (e.g., m and sec).

This index takes values from 1 when the dive area is maximum, given the set speed *S* as in Fig. 2a (A) to 0.5 when the dive is V-shaped as in Figure 2a (B) or some variant of this such as saw-toothed, and approaches 0 for tooth-shaped dives as in Figure 2a (C) where the animal spends its time just below

the surface and swims to and from the maximum depth at S . Values outside this range are obtained when the animal's average VS speed exceeds S when travelling to and returning from depth.

A more intuitive way of looking at this index value is that it represents the mean of where, in the range of depths in the water column encountered on a given dive, the animal has centered or focused its activity. It takes the value of 0.5 when: (1) the mean depth of the non-travel time (hereafter called *working depth*) is midway between the surface and the maximum depth, or (2) the animal spends equal time at all visited depths regardless of how it does this (*i.e.*, symmetrical, skewed, or "multiple V"- shaped dives). The index value approaches 1 when the animal moves to and from the maximum depth in the minimum time at S and remains at that depth (*i.e.*, when a dive is as "square" as it can be). Dives that involve excursions through a part of the range of depths encountered ("wiggles") are manifest by a reduction in the index proportional to the mean of the depths over which their time was spread. The index approaches 0 when the animal spends its time very near the surface, spending only the time it takes to travel at S to visit the maximum depth (as a person with a snorkel might). The index gives no measure of the dispersion of the activity across depth. That is, a TAD value of 0.5 indicates only the mean fraction that the working depth is of the maximum depth and says nothing about how widely spread or skewed across depth it is. Additional bits are required to describe these characteristics, and in some cases it might be useful to compute and send them. When the animal has exceeded the set speed, the index can take larger positive or negative values than 1 or 0. If the index is greater than 1, the animal must have traveled to and from depth more quickly than S (*i.e.*, VS > S); if it is less than 0, the animal must have traveled to and from the maximum depth at a VS > S after spending most of the duration of the dive near the surface. Such situations may be relatively uncommon, but may be of interest.

The index has an internal instability as dives approach the maximum depth achievable for their duration. These are likely to be "spike" dives where the animal swims vertically down and immediately back up at S . Indeed, square, V-, and tooth-shaped dives do become indistinguishable in these circumstances, approaching equal time spent at all depths. Near the maximum depth for a given duration and set speed, the *time-depth areas* for all types of dive converge, *i.e.*, the numerator and denominator of equations (1) or (3) both tend towards 0. The index, therefore, can not discriminate between such dives. In practice, however, this leads to no ambiguity because the maximum depth and duration will also always be known. Furthermore, such dives are likely to be relatively rare (if interesting). This same approach can be used to postprocess dives with complicated profiles as sampled by TDRs, using equation (3).

The process of subtracting the area equivalent to necessary travel time to reach maximum depth makes the index insensitive to depth and duration of dives and/or the ratio of depth and duration. Realizing this insensitivity depends on choosing the appropriate vertical travel speed. *A priori*, the most obvious choice for S is the MCTS, for the reasons mentioned above. However,

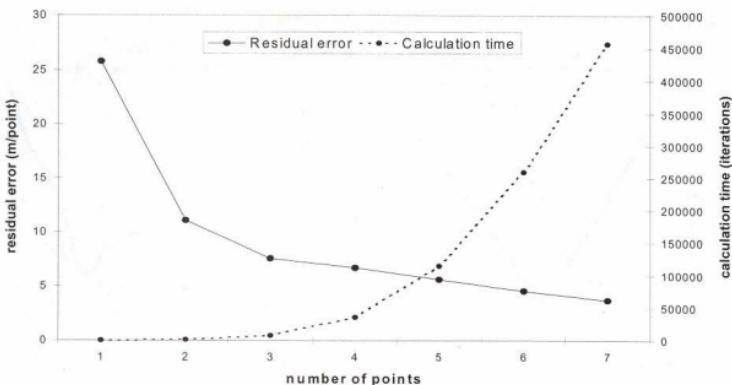


Figure 3. Example of the effect of choice of number of points included in profile on residual error and calculation time when applying algorithm to reduce data used to describe time-depth profiles.

with postcollection processing of the data, a range of speeds can be investigated. This process is discussed below.

RESULTS

The utility of these two approaches was tested and investigated in several ways. We tested it by postprocessing data from TDR records obtained from northern (*Mirounga angustirostris*) and southern (*Mirounga leonina*) elephant seals (see Acknowledgments for details). The method of selecting dive trajectory inflection points was implemented in SLDRs and deployed on southern elephant seals and gray seals (*Halichoerus grypus*) starting in 1997. The TAD index has also been applied retrospectively to dive data obtained from SLDRs (using area data generated by the inflection point method). The index was implemented on board SLDRs built by SMRU and deployed with collaborators starting in 1999.

Inflection point selection—The algorithm for returning inflection points can be set to return any number of points, depending on the resolution required and bandwidth or storage constraints. In SLDRs, we have used the algorithm to select three inflection points in each dive for transmission along with the maximum depth and its time of occurrence. There is a trade-off between the fidelity of the profile returned and energy cost of computation (a function of the time taken to select the points) and the cost of sending the data. Figure 3 presents data from SMRU's SLDR on this trade-off. The final choice will depend on both scientific and technical criteria within each deployment.

Characteristics of TAD index—Figure 4a-f provides a set of selected dive profiles from an elephant seal TDR record of about 3,000 dives where depth was sampled at 10-sec intervals (Boyd and Arnbom 1991) by a Mark XIII

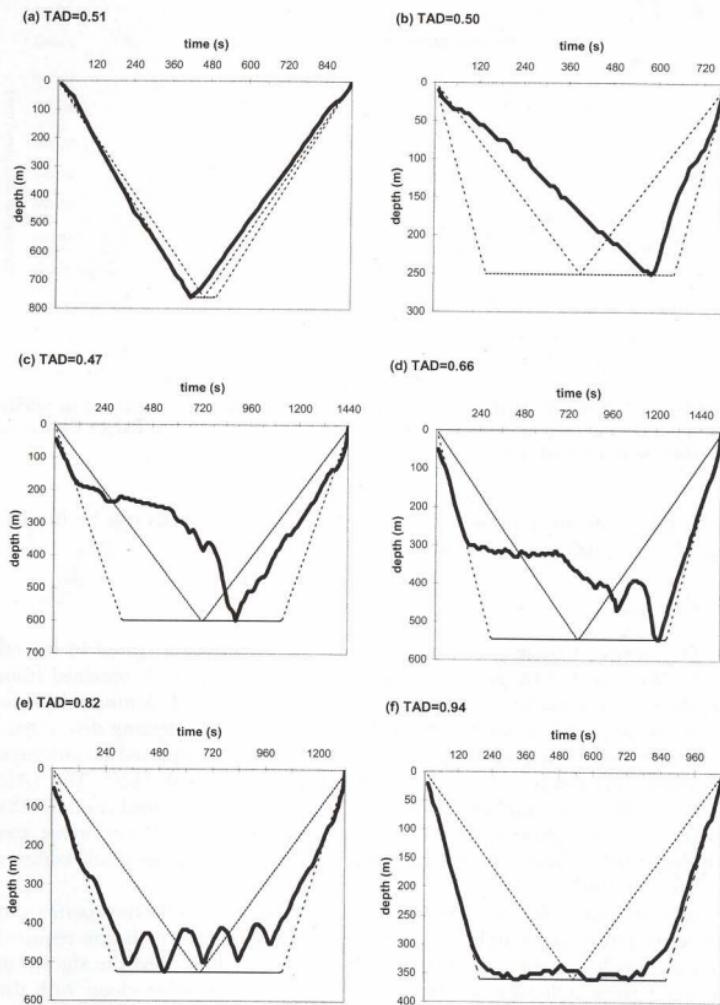


Figure 4. Six examples of dives taken from records of Boyd and Arnbom (1991) which produce a range of TAD index values between 0.5 and 1.0. Dotted lines show idealized dives of corresponding maximum depth and duration that have TAD values of 0.5 and 1.0 with speed parameter (S) of 1.8 m sec^{-1} .

TDR (Wildlife Computers, Seattle, WA). Index values are presented next to each graph based on a speed parameter (S) of 1.8 m sec^{-1} . The dives are ordered by TAD value. These dives were chosen to cover a range of depths and shapes from trapezoidal through to tooth-shaped. The index varies in a stable and predictable way and is insensitive to depth and duration.

The effect of varying the speed parameter—It is apparent that if an S is chosen that is faster than animals can attain, then for relatively short, deep dives the index values will have a lower upper limit than those for shallow dives. Figure 5 shows the effect of different estimates of S on three sets of synthetic dives and on actual dives. In Figure 5a–c, dives were constructed, for a nominal VS of 1.8 m sec^{-1} , to produce index values of 0, 0.5, and 1.0, respectively across a range of depth/duration ratios from long and shallow to short and deep. When the estimate of S is “correct” at 1.8 m sec^{-1} (Fig. 5a) the index is correct across all depth/duration ratios. When the estimate is too high (Fig. 5b) the index calculated for short and deep dives is biased downwards towards 0.5. When the estimate of S is too low the index takes a hyperbolic form around the estimated S (Fig. 5c).

Assuming that a real data set contains a spread of true index values (at least between 0.5 and 1), this behavior can be used to check the plausibility of any estimate of S . Figure 5d–f shows the distribution of the TAD values of an elephant seal from the data obtained by Boyd and Arnborn (1991), using the same three estimates of S . The distributions for $S = 10.0 \text{ m sec}^{-1}$ (Fig. 5e) and $S = 1.0 \text{ m sec}^{-1}$ (Fig. 5f) show the behavior expected for over- and under-estimates of S , respectively; whereas for $S = 1.8 \text{ m sec}^{-1}$ (Fig. 5d) there is no observable bias with respect to depth/duration, suggesting that this value of S is close to the “true” maximum VS. The value of 1.8 m sec^{-1} is near the estimated MCTS for a seal of this size (Williams 1999) whereas 1 m sec^{-1} is below the vertical speed displayed in a significant number of dives. Note that while the lower edge of the distribution remains relatively unaffected by speeds faster than those commonly used (V-shaped dives will generate a value of 0.5 regardless of chosen speed), the upper edge of the distribution falls away from 1 as dives get deeper and/or shorter. This happens because the assumption of a high speed, in effect, requires dives with an index of 1 to approach a rectangular profile with *time-depth areas* approaching $D*T$. Short and/or deep dives will necessarily deviate from this to a greater extent than shallow and/or long dives. With an S value of 1.8 m sec^{-1} , index values are spread evenly and broadly within the range $0.5 < \text{TAD} < 1$. When an artificially low speed is selected, many values of $\text{TAD} > 1$ or < 0 are generated. It might seem tempting to choose for S the value that delivers a spread of TAD values that show no trend with depth or duration. However, while it is true that a regression line drawn through the points when $S = 1.8 \text{ m sec}^{-1}$ has a slope not significantly different from 0, the reasons for this are a result of the distribution of TAD values near 1 (see discussion below).

These properties of TAD were also found when investigated in other lower resolution data sets (*i.e.*, 30-sec period sampling of depth) in northern and southern elephant seals and also in the SLDR-derived records from gray seals

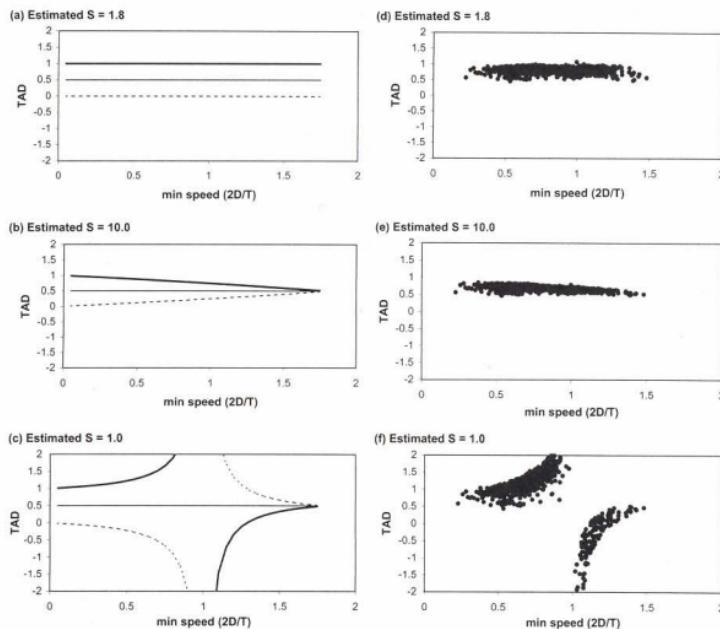


Figure 5. Response of TAD index to variation of speed parameter for a set of simulated (a–c) and actual (d–f) dives. Parts (a)–(c) show response in set of simulated dives of index values of 1.0, 0.5, and 0.0 over range of ratios of depth to minimum speed required to accomplish dives, expressed as ratio of depth to duration ($2D/T$). Thick, thin, and dotted lines represent simulated “trapezoidal,” “V-shaped,” and “tooth-shaped” dives, respectively. Examples show results at three choices of speed parameter (S): (a) 1.8 m sec^{-1} (actual value used in generating simulated dive areas), (b) 10 m sec^{-1} , and (c) 1 m sec^{-1} . That is, we chose S values above and below “true” vertical speed used to generate areas of simulated dives. Plot shows that when S is “true” value part (a), index is independent of ratio of depth and duration as well as depth or duration independently. Whereas, when it is not, parts (b) and (c), index changes in predictable ways with respect to ratio of D/T (see text). Parts (d)–(f) show response of TAD to ratio of depth and duration of 1,000 actual dives taken from data from Boyd and Arnborn (1991). Pattern follows that demonstrated by simulated dives. When speed parameter S is set at 1 m sec^{-1} , a value lower than observed, index values produce a hyperbolic distribution with many values >1 or <0 . When speed value is set to 1.8 m sec^{-1} , a value close to estimated minimum cost speed (MCTS) for elephant seals, values are largely spread between values of 1 and 0.5. When S is set impossibly high, values of TAD near 1 or 0 cannot be achieved for deep/short dives. In practice, setting S deliberately low or high and moving it towards realistic values generates clear indication of descent and ascent speeds that animals tend not to exceed. As soon as values of S are chosen that fall below those that occur in data, a clear signal is generated as a result of hyperbolic nature of index. Overestimates of S cause TAD values of deep dives to drift away from 1 in conspicuous, but not “explosive,” way.

around the UK coast (see Acknowledgments for details). The data from gray seals differed from that of the elephant seals in that they were sent back using the data point selection algorithm described above and were therefore computed on a subset of the dive data. In all cases the index performed as described above, in terms of its general behavior and independence to depth and duration.

The procedure of computing the TAD was implemented on SLDRs deployed on gray seals captured in 1999 on the coast of Brittany. Here, the dive area was computed using the 4-sec sampling resolution employed by these tags. In this deployment the maximum depth and duration are sent for a sample of dives along with the actual dive area (A_s), which is computed at the end of each dive and sent back to the data base with 6-bit resolution. The index is then computed from the values stored in the database and displayed interactively in the visualized data using MAMVIS (Fedak *et al.* 1996). This package provides the capability to vary the chosen S . By sending back (A_s) rather than TAD, we can postprocess the data, making it possible to vary the speed parameter S retrospectively and use the displayed index to investigate distributions of ascent and descent speed over the course of the deployment.

DISCUSSION

The method for selecting dive inflection points has proved to be a useful tool for data compression where storage or transmission limitations impose significant constraints. Such a procedure is necessary when transmitting dive information in order to reduce energy requirements and to avoid bandwidth limitations. However, it might also be of value in TDRs or other recorders where data storage limitations may develop from extremely long-term recordings, or when other sorts of information need to be stored. Most dive profiles can be approximated with 10–20 points with little loss of information. The real cost of the process involves any energy demands of the additional processing necessary and the extra volume of additional batteries, if required.

When the number of inflection points stored or sent falls to the level of four points (three selected depth/time points and the maximum depth/time point), as we have chosen to meet the power and bandwidth restrictions of transmission, some loss of information and resolution is inevitable. However, even with this reduced resolution, crude dive shapes are retained and some commonly occurring shapes are easily recognizable. For example, trapezoidal, symmetrical and asymmetrical V-shaped, or other simple polygonal shapes such as "drift dives" (Crocker *et al.* 1997) are easily detected and represented with small residuals. But even with this extreme data compression, only a limited number of dives can be transmitted from a reasonably small package. In the SLDRs deployed by SMRU, a combination of transmission formats is used to provide synoptic behavioral coverage. Combinations of randomly sampled "detailed" dives (*i.e.*, those represented by four inflection points and duration); "index" dives (*i.e.*, those represented by maximum depth, duration, average swimming speed, and *time-depth area*); and six-hourly summaries of

behavioral state (*i.e.*, % time diving, % time hauled out, mean maximum depth, and duration of dives) are sent in order to build a comprehensive picture of behavior. Combinations of data of these types can obviate some of the losses of extreme compression.

The TAD has proved useful for purposes of both data compression and post-data-collection analysis. In terms of compression, it extracts information on where the animal has focussed its activities within the range of depths encountered during the dive. This information, combined with bathymetry for the diving location, can provide clues to the type of prey being sought. High index values near 1 are indicative of an animal concentrating its activity at the bottom of the dive (*i.e.*, performing a dive with maximum bottom time) and possibly seeking prey there. Conversely, an animal exploring opportunities across a range of depths may be expected to allocate time to a wider range of depths and have lower TAD values. An animal travelling from place to place may angle down to the bottom or some other "interesting" depth and spend equal times at all depths of a dive. Such behaviors will return TAD values nearer to 0.5. Values of below 0.5 are indicative of activity near the surface with only brief excursion to maximum depth.

The TAD obviously delivers far less information than a full dive profile because it contains no information on the sequence of depths encountered or information on the time spent at particular depths. But its simple, scalar nature should make it useful in correlative analyses in combination with other behavioral or geographical variables. It also provides a simple, objective variable easily combined with others for use in clustering or PCA techniques (Schreer and Testa 1996). Often, little of the detailed information in TDR records is presented in papers. Ironically, the use of the index might lead to more information rather than less being presented.

The choice of the speed parameter—We have demonstrated how the choice of S may have an influence on the TAD value, both in terms of maximizing its independence from depth and duration and in increasing its power to highlight variations in behavior. Depth and duration independence may help to identify general patterns of dive characteristics in relation to behavior across habitats, seasons, or individuals over long TDR records. For example, deeper dives necessarily become more V-shaped so that a relationship between dive type and travelling speed might be obscured by dive-depth variability. Because the index is insensitive to depth, this complexity can be avoided.

As we described above, the final calculation of the index can be done after the data are collected. (TDRs return all time-depth pairs. With SLDRs, the full resolution *time-depth area* can be returned along with maximum depth and duration.) The choice of S can therefore be varied and the consequences of the choice inspected to search for an appropriate value. The most generally useful value is probably the MCTS. It can be argued that choice of swimming speeds above this value by the animal suggests some necessity for speed that balances the extra oxygen cost. Thus, choosing an estimate of MCTS for the speed parameter should offer an opportunity to detect these circumstances. Values above 1 might imply that there was some behavioral requirement to hurry

such as a transient source of food. Alternatively, a negative value might suggest behavior where the animal is suddenly required to descend rapidly after being active at very shallow depths. The choice of the MCTS as the speed parameter will make such events conspicuous.

Examining the range of values taken by the index when S is varied can also provide information on the maximum vertical speed adopted by animals without making decisions about when to terminate ascent and descent phases of individual dives. As shown in Figure 5, if S is progressively reduced until the values of TAD are most evenly spread between 0.5 and 1, this speed is likely to be the greatest VS commonly chosen by the animal for descent and ascent. If the speed selected is too low, the many values above 1 will be very conspicuous. If the speed is too fast, relatively few dives will generate TAD values as high as 1. If S is realistic, the upper bound on the values will be spread just below the value of 1 across all depths and durations. Alternatively, examining a plot of depth against duration for all dives can provide an *a priori* value for S . Such a plot will show a lower bound where a given depth could no longer be reached during the duration of a dive. The speed given by this edge will approximate the speed that gives the most even spread of TAD values between 0.5 and 1 and the one that will provide TAD values independent of depth and duration.

We suggest that these two approaches have potential utility when used with other techniques for classifying dive shape and extracting behavioral information collected by dive recorders (see Schreer *et al.* 1998; Schreer *et al.*, in press). The concept of the TAD can be augmented to include other measures of dispersion and skew and thereby be made more specific, albeit at the cost of using more bits to encode. We hope both prove useful for finding relationships with oceanographic parameters, daily and seasonal change, and other behavioral features that can be made available by TDRs and SLDRs and we welcome feedback from anyone who tries to use them.

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