Energy cost and optimisation in breath-hold diving

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We present a theoretical model for calculating the locomotion cost of breath-hold divers. Starting from basic principles of mechanics, we calculate the work that the diver has to provide with propulsion for counterbalance the action of the drag, the buoyant force and the weight during the immersion. The basal metabolic rate and the efficiency to transform chemical energy in propulsion are also considered for the calculation of the total energy cost of a dive. The dependency on the diver and dive characteristics and possible optimisations are analysed and discussed. Our results are compared to observation on different breath-hold diving animals. The model confirms the good adaptation of dolphin for deep dives, and it gives some insights for a possible explanation of the exhalation of air before diving observed in seals. A comparison between predicted and observed swim velocities of different breath-hold mammals confirms the importance of the role of the diving reflex.

I. INTRODUCTION

Breath-hold diving animals try to minimize the energetic cost during their dives for gaining time for foraging due to the limited amount of oxygen stored in their lungs. Besides metabolic and physiological adaption (diving reflex), like bradycardia and peripheral vasoconstriction [1, 2], the most efficient method for lowering the energy cost of the dive is the reduction of the total duration of the dive and of the mechanical work necessary for the propulsion. In one side, the energy cost related to the basal metabolic rate is proportional to the dive duration and then it favours a choice of an elevate swimming velocity. In another side, the energy spent for propulsion depends on the drag force during the dive, which increases with the square of the velocity. Beside of the swimming optimisation and hydrodynamics, the thrust work is then efficiently reduced slowing down the swim speed. The choice of the optimal dive velocity is a compromise that takes into account these two aspects and is specific to the characteristics of the diver body and of the typical dive. An additional energy cost reduction is obtained in particular in mammals by alternating active swim and gliding phases during some parts of the dive using the buoyant force and the weight at their advantage [3].

Several studies and observation have been performed on swim strategy of breath-hold diving animals [3–9]. In particular for penguins, which are always positively buoyant and glide only during the ascent phase, a complete force and energy cost analysis have been accomplished and the expression of the optimal velocity during the dive has been found by Sato and collaborators [6, 8, 9]. Energy cost have been also evaluated for trained bottlenose dolphins [4] where however its dependency on the dive velocity and diver body characteristics have not been specifically investigated.

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In this paper we present a complete analysis on the energy cost and its optimisation for breath-hold divers for a general case that can includes gliding phases in the ascending and descending parts of the dive. Starting from the analysis of the involved mechanical forces and some basics consideration of the animal physiology, we predict the energy cost of a typical dive. In particular, we take into account the exact dependency of buoyancy on the depth similarly to Refs. [5–7]. The determination of the gliding regions extension is calculated and it is included in the total energy cost of the dive. The dependency of the energy cost on the different parameters (dive velocity, diver buoyancy and mass, etc.) and its optimisation is investigated. Our findings are compared to observations on dives of different breath-hold animals, in particular on bottlenose dolphin for which several observations on trained exemplars are available.

The article is organised as following. In the next section we present out model to calculate the mechanical work required for a typical dive as function of the diver and the dive characteristics, including the animal metabolism. In the third section we discuss our results and their comparison to observation of dives of breath-hold animals. Section four is our conclusion.

II. MODEL DESCRIPTION

A. Basic assumptions

During a dive in a fluid (sea water in our case), the animal is subject to four forces: the drag, the weight, the buoyant force and the thrust (see scheme in Figure 1). The drag force is caused by the friction of the fluid on a moving body. It is strongly dependent on the module of the body velocity $v = |\boldsymbol{v}|$ and it is always opposite to it ($\boldsymbol{F_d} = -F_d(v)\hat{\boldsymbol{v}}$ with $\hat{\boldsymbol{v}} = \boldsymbol{v}/v$). For typical swim velocities and body masses of breath-hold divers, turbulent regime have to be considered [10] with a dependency of the drag on the square of the velocity, $F_d(v) = Cv^2$,

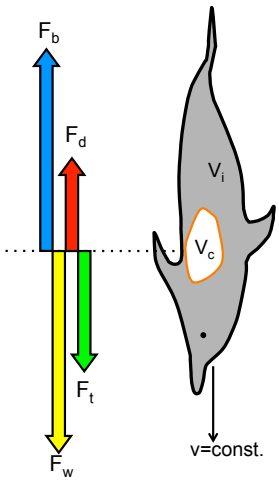

FIG. 1. Scheme of the forces acting on a breath-hold diver (a dolphin in this example.)

where C is a constant that includes the dependency on the diver body characteristics and the Reynolds number at this velocity regime.

The weight is of course proportional to the body mass m and the acceleration of free fall g ($\boldsymbol{F_w} = m\boldsymbol{g}$). The buoyant force is its counterpart and is proportional to the body volume V and the fluid density ρ ($\boldsymbol{F_b} = -\rho V\boldsymbol{g}$). The buoyant force changes with the depth due to the parts of the diver body filled with air or other gases (lungs, air cavities, etc.) that changing their volume with the change of the pressure. To take into account this, it is better to rewrite F_b as:

$$F_b = \rho(V_i + V_c)g = mg\left(R_i + \frac{R_c}{1+\frac{\rho g d}{P_0}}\right), \qquad (1)$$

where V_i and V_c represent the incompressible and compressible part of the body volume V, respectively. In addition we introduce the ratios $R_i = \rho V_i/m$ and $R_c = \rho V_c^0/m$, where V_c^0 represent the compressible volume at the surface and were we explicit the dependency on the depth. R_i can be written also with respect to the fluid and average body tissue density ρ_t: $R_i = \rho/\rho_t$.

For a descent to a depth D and return to the surface, the required locomotion cost can be quantified by the calculation of the work W of the thrust force produced by the diver long to the dive path. To reduces W, breath-hold birds, mammals and reptiles (but also freedivers athletes) try to use the buoyant force and the weight in their favour gliding as long as possible. In particular, some mammals like dolphins, seals, etc. let them glide for a part in both descent and the ascent phases of the dive. A typical dive is composed by a first step where the diver makes an effort to descent from the surface. Then it reaches an equilibrium depth where the buoyancy is small enough to be possible to glide to the maximum depth D. Following, the diver makes another effort to ascend from the bottom until a second equilibrium depth from which it let itself gliding to the surface under action of the buoyant force.

The mechanical work for the round-trip can written as

$$W(D) = \int_0^{d_{eqD}} \boldsymbol{F_t}(d)\cdot\boldsymbol{d\ell} + \int_D^{d_{eqA}} \boldsymbol{F_t}(d)\cdot\boldsymbol{d\ell}, \qquad (2)$$

with d_{eqD} and d_{eqA}, are the equilibrium position during the descent and the ascent, respectively and $\boldsymbol{d\ell}$ it the infinitesimal of the dive path.

B. Locomotion cost calculation

For the calculation of the locomotion cost of the dive, we consider purely vertical dives, without horizontal displacement and without considering possible foraging at the bottom or at intermediate depths. In addition we consider that the diver travels to a constant velocity, which is well justified by the observation of velocity profiles of many breath-hold mammals dives [3–5]. In the gilding regions, the velocity can easily modulate by the diver with an intentional increasing of the drag without any additional significant effort. Where the propulsion is necessary, the thrust F_t has to balance the other forces. Considering a constant cruise speed, we have $\boldsymbol{F_t}(d) = -(\boldsymbol{F_b}(d) + \boldsymbol{F_w} + \boldsymbol{F_d})$, where the dependency on the depth comes from buoyancy only. From Eqs. (1-2), and the previous considerations, the total work can be written as

$$\begin{aligned} W(D) = {} & [F_d - mg(1-R_i)]d_{eqD} + \\ & + \frac{mR_cP_0}{\rho}\log\left(1+\frac{\rho g\, d_{eqD}}{P_0}\right) + \\ & + [F_d + mg(1-R_i)](D - d_{eqA}) + \\ & + \frac{mR_cP_0}{\rho}\log\left(\frac{1+\frac{\rho g\, d_{eqA}}{P_0}}{1+\frac{\rho g D}{P_0}}\right). \end{aligned} \qquad (3)$$

We neglect here the work required to accelerate to the cruise velocity $\pm\boldsymbol{v}$ in the round trip, which is equal to $m\ v^2$ and generally much smaller than the total work. We also make the approximation of considering the drag force coefficient being constant during the swimming and the gliding phases.

Depending on the maximum depth of the dive and the diver characteristics, the equilibrium depths exist if

$$R_i + \frac{R_c}{1+\frac{\rho g D}{P_0}} + F_d < 1 < R_i + R_c + F_d \quad \text{for } d_{eqD}, \qquad (4)$$

$$R_i + \frac{R_c}{1+\frac{\rho g D}{P_0}} - F_d < 1 < R_i + R_c - F_d \quad \text{for } d_{eqA}. \qquad (5)$$

If these conditions are satisfied, the descent and ascent equilibrium depths d_{eqD} and d_{eqA} are

$$d_{eqD,A} = \frac{P_0}{\rho g}\frac{mg(R_c + R_i - 1) \pm F_d}{mg(1-R_i) \mp F_d}. \qquad (6)$$

Depending on the existence or not of the equilibrium depths in the interval $[0, D]$ we can recognise different cases:

Case A: Both d_{eqD} and d_{eqA} exist (the diver partially glide in the descent and the ascent).

Case B: Only d_{eqD} exists (the diver never glide during the ascent).

Case C: Only d_{eqA} exists (the diver never glide during the descent).

Case D: No equilibrium depth exists and $F_w > F_b + F_d$ for any considered depth (the diver is always negatively buoyant, and it glides for the entire descent).

Case E: No equilibrium depth exists in the interval $[0, D]$ and $F_b > F_w + F_d$ for any d in $[0, D]$ (the diver is always negatively buoyant, and it glides for the entire ascent).

Case F: No equilibrium depth exists in the interval $[0, D]$, and $F_f > \max(F_b(0) - F_w, F_w - F_b(d))$ for any d in $[0, D]$ (no gliding phase is present, the drag is dominant).

For the case A, where both equilibrium positions exist, from the combination of Eq. (3) with Eq. (6) we can obtain the explicit formula of W. Similar expressions of W for cases B and C can be obtained substituting one of the equilibrium depth with one of the extremes of the $[0, D]$ interval: $d_{eqA} = 0$ for B and $d_{eqD} = D$ for C.

In cases D and E, the diver glides for the entire descent and ascent phase, respectively, and it has to use its self-propulsion for the whole opposite phase. No dependency of any equilibrium depth is then present, leading to the simple formulae

$$W^{D,E}(D) = F_d D \pm mg(1-R_i)D \mp \frac{mP_0R_c}{\rho} \log\left(1 + \frac{\rho g D}{P_0}\right). \tag{7}$$

Case F is a peculiar case where the drag is so strong that no gliding phase is present at all. The work expression is even simpler than cases D and E and it can be formally obtained from $W^D + W^E$ leading to $W^F(D) = 2F_dD$. We note that in this case the work for a vertical dive is the same of the work required for an equivalent horizontal displacement where only the drag is relevant. Another remark is that case F is complementary to case A. The conditions to have one of the other cases are related to the different dive parameters. In particular it can be demonstrated that if

$$F_d > \frac{\rho g D}{2P_0} \frac{mgR_c}{1 + \frac{\rho g D}{P_0}} \tag{8}$$

we cannot have d_{eqD} and d_{eqA} simultaneously in the interval $[0, D]$ for any value of R_i and then case A is impossible.

C. Total metabolic energy cost and its optimisation

In the previous section we studied the work spent by a hold-breath diver to reach a defined depth and coming back to the surface taking into account exclusively the mechanical aspects. In this section we consider also the diver metabolism. For this, more than the thrust work, the relevant quantity is the total energy E that includes the basal metabolic rate and the efficiency to transform chemical energy on thrust. E can be decomposed in two parts $E = E_m + E_t$ where $E_m = B\ T$ is proportional to basal metabolic rate B and the elapsed time during the dive T, and where $E_t = W/\varepsilon$ is proportional to the dive mechanical work over the efficiency ε to transform the chemical energy into forward thrust. ε depends on the efficiency ε_p to transform the muscular movement to thrust and on the metabolic efficiency ε_m to transform chemical energy into muscular work, with $\varepsilon = \varepsilon_p\varepsilon_m$.

After these consideration we can write the expression for the total energy E cost for a dive as

$$E(D, v) = B\ \frac{2D}{v} + \frac{W(D, v)}{\varepsilon}. \tag{9}$$

Here we show explicitly the dependency on the velocity v from the drag and the diving time $T = 2D/v$. Due to the reliance of W on d_{eqD} and d_{eqA}, which depend on the drag force proportional to v^2, in the general case we have a non-trivial relationship between E and v. This is not completely true in cases D, E and F, where a simpler expression for $E(D, v)$ can be found due to absence of any equilibrium depth in the expression of W.

Any breath-hold diver will have the tendency to minimise E adopting an optimal cruise velocity. For simple cases D and E, were the diver is always negatively or positively buoyant, the minimisation of Eq. (9) with respect to v taking into account equations (7) leads to the optimal cruise velocity

$$v^{best} = \sqrt[3]{\frac{\varepsilon B}{C}}. \tag{10}$$

This expression has been previously found by Sato and collaborators [6] for the study of the optimal speed of emperor penguins, which are always positively buoyant. Due to their average tissue density smaller than seawater and their small drag coefficient comparer do their mass, penguins dives enter in the case E, where $F_b - F_w > F_f$ and for which Eq. (10) is valid.

For case F, the expression of the optimal speed is slightly different due to the thrust work required for both descent and ascent then the denominator C in Eq. (7) has to be replaced by $2C$. N.B. this is also the optimal velocity for an horizontal displacement.

No analytical formula of v^{best} can be obtained for the other cases and numerical methods has to be applied for solving the equation $\partial E/\partial v = 0$. For case A in particu-

lar, this corresponds to solve the equation

$$-\frac{BD}{v^2}+\frac{DC}{\varepsilon}v+2\frac{mP_0R_c}{\rho}\frac{C^2v^3}{m^2g^2(R_i-1)^2-C^4v^4}=0. \tag{11}$$

Solutions of Eq. (11) and the analysis of the general expression of the dive energy cost (Eq. (9)) are discussed in the following sections where theoretical predictions are compared to observations on breath-hold divers.

III. RESULTS AND DISCUSSION

A. Locomotion work and gliding regions

Some general consideration can be done on the formulae of W for the different cases. For any expression of W a linear contribution on F_d is present, as for a horizontal displacement. For the simple cases D and E a linear dependency on m, R_c and R_i is also present. For cases A,B and C we have a more complex dependency on these parameters because of the presence of $d_{eqD,A}$ (Eqs. (6)). Variation of m, R_c, R_i and F_d values imply in facts the existence or not of the two equilibrium in the $[0, D]$ range and then the case it has to be considered for the work calculation.

Compared to the other parameters, only F_d can be easily varied modulating the swim speed. The ratio $R_c = \rho V_c^0/m$ can slightly modulate inhaling more or less air before diving but is generally much less than the unity [2]. A decreasing of R_c causes a reduction of W (except for extreme negatively buoyant divers as case D) and it can be obtained exhaling before diving. As counterpart, this operation reduces sensitively the amount of available stored oxygen penalizing the maximum achievable depth or time of the dive. However, it could be the explanation of the peculiar practice of different seals species that are observed to exhale before diving [11, 12] as discussed in Ref. [13].

The ratio R_i, equal to the ratio between the sea water and the average body tissue densities ρ/ρ_t, is generally close to the unity. From Eqs. (6) we can see that small variations of R_i can drastically change the value of the equilibrium depths and then the dive work. R_i can tuned varying the lipid content of the diver body, as seasonally happens in elephant seals [5, 7].

To visualise the dependency of dive work on R_i, we plot in Figures 2 and 3 the thrust work for a particular subject of bottlenose dolphin with a mass of 177 Kg, a lung volume of 8.5 l (data from Ref. [4]) where we artificially vary the value of R_i for two different dive conditions. In Figure 2 we consider a dive to a maximum depth of 100 m and with a cruise velocity of 1.8 m/s. In Figure 3 we consider a dive to a maximum depth of 25 m and with a cruise velocity of 4 m/s, i.e. where the drag is much more important. F_d is calculated using the drag constant value $C = 4.15$ kg/m reported by Skrovan and coworkers [4]. Different values ranges of R_i corresponds to different cases of dive. If the drag and the maximal depth are respectively small and large enough (see Eq. (8)), case A is possible, we can have both equilibrium depths and a minimum of W is uniquely present, always in case A. This are the conditions of Figure 2. At the W minimum, the corresponding values of these equilibrium depths are around the middle-depth: $d_{eqD,A} = D/2 \pm \Delta d_{eq}$ with Δd_{eq} depending on m, R_c and F_d. If the drag intensity is high and/or the maximal depth is small (as in Figure 3) the difference of the two equilibrium depth can be larger than D. Then case A is substitute by case F that correspond to a region of R_i values where the total work is minimal and strictly equal to $2DF_d$.

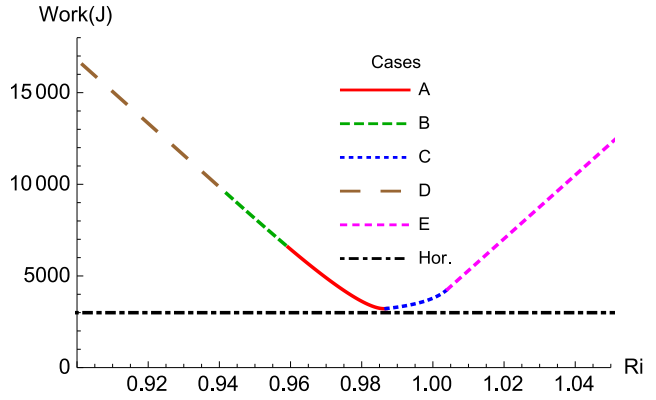

FIG. 2. Plot of the thrust work as function of R_i for a bottlenose dolphin diving to a maximum depth of 100 m with a speed of 1.9 m/s. See text for details.

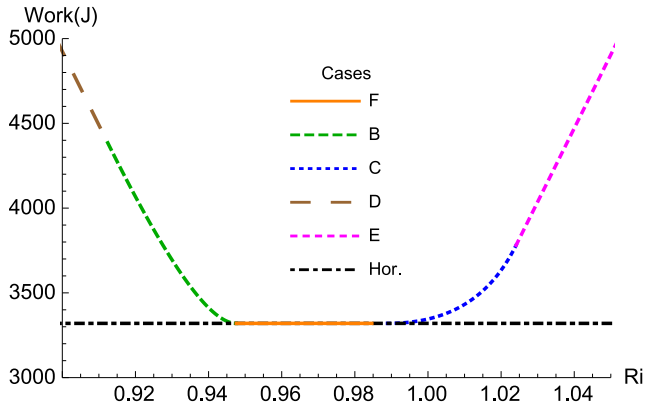

FIG. 3. Plot of the thrust work as function of R_i for a bottlenose dolphin diving to a maximum depth of 25 m with a speed of 4 m/s. See text for details.

For the considered dolphin exemplar, from the buoyancy at different depth the value of R_i is estimated to be $R_i^{meas} = 0.981$ [4] . This value results to be very close to the minima of W for this specific dive. More precisely, we can calculate from Eqs. (3-6) that R_i^{meas} is ideal for dives with maximum depths close to 35.2 m.

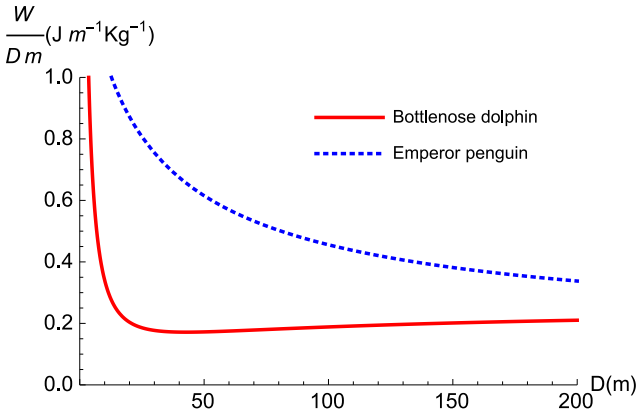

FIG. 4. Locomotion cost per unit of covered distance and diver body mass as function of the dive depth for bottlenose dolphins and emperor penguins.

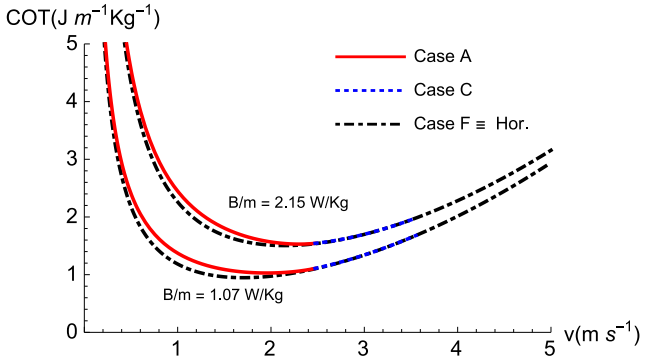

FIG. 5. Cost of transport as a function of the dive velocity v for a bottlenose dolphin diving to a maximum depth of $D = 100$ m. The presence of the equilibrium depths (different cases) depends on the value of v (both equilibrium depths present: case A; only one present in the ascent: case C; none present: case F).

To see its adaption for dives of different maximal depths D, in Figure 4 we plot the thrust work per unit of covered distance and diver body mass as function of D. As we can observe that, except for superficial dives, the locomotion cost normalized to the covered distance and diver mass is almost constant demonstrating a good adaption of dolphin's body characteristics for deep dives. For comparison, we plot the normalized locomotion cost for emperor penguins, where we consider a particular exemplar with $m = 30$ Kg, $V_0 = 4$ l and $C = 0.6$ kg/m (data from Ref. [6]) and where we assume the same cruise velocity of 1.8 m/s. As witten above, due to their low average tissue density compared to the salty water, $R_i = \rho/\rho_t = 1.007$ [6], emperor penguins are always positively buoyant at any depth and they are included in case E, with a complete gliding ascent. As expected from Figure 2, in the case of the penguin the thrust work is larger, and decrease progressively with the depth showing a worse global energy economy than dolphins.

Eqs.(6), can be used also to predict the depths where the dolphin should start to glide and the percentage of the glide phase distance with respect to the total dive length. For a well define dive to 100 m of the same dolphin exemplar, Skrovan and collaborators observed a descending glide phase starting from a depth of $d_{eqD}^{meas.} = 67.5$ m preceded by a swimming phase with a cruise velocity of 1.7 m and an ascending glide phase from $d_{eqA}^{meas.} = 5.5$ m and a preceded by a swimming phase with a cruise velocity of 1.9 m. From Eq. (6) we obtain the predicted values that result to be $d_{eqD} = 30.5$ m and $d_{eqA} = 8$ m, significantly different from the measured values. However, considering the drag of instrumented dolphins, about 40 N at these velocities [4], we should observe almost any gliding phase except for the very end of the dive. The problem is in fact more complex because carrying instruments could affect the animal behaviour in an non trivial way as discussed in Ref. [14].

B. Swim velocity and optimisation

As announced in the previous sections, the choice of the swim velocity is a crucial point for the total energy cost due to the basal metabolism, which contribution is proportional to the total diving time, and the drag, which increases with the square of the velocity. In this section we consider the case of bottlenose dolphin, for which observation on trained exemplars of purely vertical dives without foraging are available [4, 15], i.e. the ideal conditions to compare our model.

In addition to m, R_i, R_c and C from Ref. [4], we consider here the basal metabolic rate for bottlenose dolphins per unit of mass $B/m = 2.15$ W/Kg from Ref. [16], and the metabolic and propulsion efficiencies $\varepsilon_m = 0.25$ and $\varepsilon_p = 0.86$ from Ref. [17]. For ε_m we consider here the aerobic efficiency. This is justified by post-dive blood lactate measurements in dolphins [15] that shows an increasing of anaerobic process only after significantly long dives (longer than 200 s) not considered here. During the dives, dolphins are actually subject to strong bradycardia (reduction of the heart rate down to 63.4% [15]) with an expected substantial reduction of B. To roughly take into account the diving reflex, we consider also the expected value of E corresponding to half of the value of the basal metabolic rate reported in literature ($B/m = 1.07$ W/Kg), which is also about the basal metabolism expected by the Kleiber's law [16, 18].

For an easier comparison with previous studies, instead of E it is more useful consider the cost of transport for units of mass and covered distance $COT = E/(mD)$. In Figure 5 we plot the COT for the same dolphin subject considered in the previous section for a dive with D and the $B/m = 2.15$ and 1.07 W/Kg. Changes of the dive velocity determine the existence or not of the equilibrium depths. In the particular case of dolphin dives, cases A, C and F have to be taken into account. We remember that

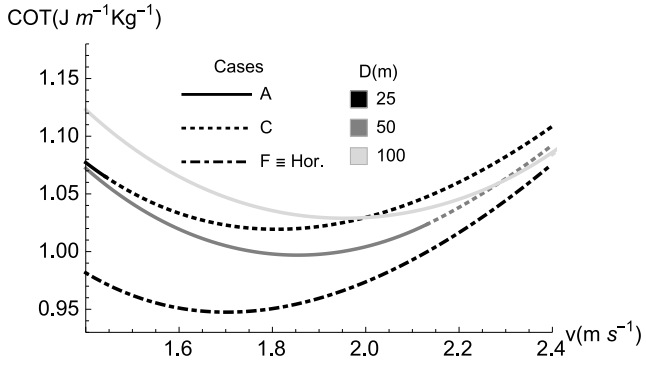

FIG. 6. Zoom of the minimum region where the dependency on D and the comparison with the horizontal displacement case is more visible.

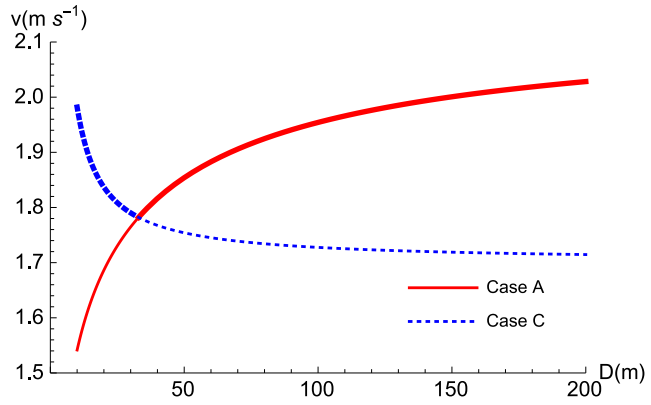

FIG. 7. Optimal velocity dependency on the dive maximal depth. Solution case A or C has to be considered. Both cases are represented and the pertinent values of v^{best}, which depends on D, is indicated by the thick lines.

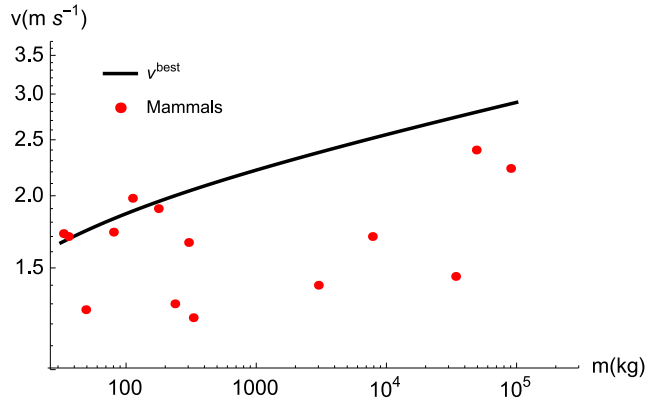

FIG. 8. Velocities of the breath-holder swimmer for a dive 100 m depth as function of diver mass mass. Theoretical predictions are compared to available observations in mammals.

case F is equivalent to the purely horizontal displacement that we report for any value of v and already considered in the literature (see ref. [16] as ex.).

As we can observe, for $B/m = 2.15$ W/Kg the optimal velocity is around $v^{best} = 2.3$ m/s. This value is significantly different from the observed value around 1.8 m/s [4]. The smaller cruise speed could be caused by the additional drag due to the instruments carried by the dolphins no considered here but also by the diving reflex as discussed above. From the data reported in Ref. [4] a drag constant value of $C = 16.9$ kg/m can be extracted for instrumented dolphins that lead to the very low value of $v^{best} = 1.3$ m/s, which is also in contrast with the observations. When the basal metabolic rate value of $B/m = 1.07$ W/Kg is considered for taking into account the diving reflex an optimal velocity of $v^{best} = 1.95$ m/s is obtained, very close to the measured values. With these considerations and the observation that a large drag constant value is also in contrast to the measured equilibrium depths, we can conclude that i) the additional drag due to the carried instruments could be overestimated and ii) the diving reflex plays an important role. These statements are corroborated from one side from the the direct observation of the heart rate reduction [15] in diving dolphins and from another side from recent studies that indicate a swim speed reduction of only 11% for instrumented dolphins [14], that however carry different apparatus than in Ref. [15]. For simplicity, for the following calculations we will take the value $B/m = 1.07$ W/kg without considering any additional drag.

The dependency of the COT on the maximal depth of the dive is marginal, as it can be observed in Figure 6 where we plot the COT for dives with $D = 25, 50, 100$ m close to the minimum, the more sensitive region on D variation. The dependency the optimal dive velocity on the maximal depth can be studied from the exact solution of $\partial E/\partial v = 0$. The solution $v^{best}(D)$ is presented in Figure 7.

For deep dives, we are in case A when for depths, less than 54 m in this particular case, we are in case C (no glide in the descent). For each case, $v^{best}(D)$ is calculated and it results slightly varying in the 1.8 and 2.0 m/s range, similarly to the observations.

C. Mass dependency of the optimal dive velocity

A more general comparison can be done considering the dependency on the diver mass of the optimal velocity v^{best}. Similarly to Ref. [8], we introduce a mass dependency on the different parameters of Eqs. (3–9). For the drag constant C we consider a variation on $m^{3/5}$ from the dependency of the diver surface ($m^{2/3}$) and the drag coefficient ($m^{-1/15}$). For the basal metabolic rate we take the classic dependency on $m^{2/3}$ from the Kleiber's law. From observations [2] and basic principles, it is difficult to make an estimation of the variation of the lung volume

with the mass. We consider then no dependency on m for R_c as for the efficiency ε.

In Figure 8 we plot v^{best} relative to a dive of $D = 100$ m as function of m for a large range of diver masses, all corresponding to case A with presence of both equilibrium depths. As we can observe, contrary to Watanabe and co. [8], no exponential law can be extrapolated. We compare our predictions with the observed velocities of mammals that generally glide in both ascending and descending phases from Ref. [8]. In comparison with measurements our prediction are systematically higher for large masses. This can be caused by a particularly strong diving reflex for large mammals as well as the rude approximations in our model where we considered active and passive drag coefficients equal. However, our predictions well reproduced the general trend for large m and it is quite in agreement for small values.

IV. CONCLUSIONS

We presented a theoretical model for analyse dives of breath-hold animals. Starting from the first principle forces acting on the diver, we calculated the work of the thrust to evaluate le energetic locomotion cost of the dive. Considering simple cases with a constant cruise velocity during the dive we were able to take into account the presence and extension of gliding phases during the ascent and descent and their influence on the total locomotion cost. We analyse its dependency on the different dive parameters, namely the diver body characteristics (mass, lung volume, buoyancy, etc.) and the dive characteristics (cruise velocity and maximum depth). We found that for the body characteristics of bottlenose dolphins, in particular the ratio between the body tissue volume and their mass are well optimise for deep dives, contrary to the case of emperor penguins. From the dependency of the locomotion cost on the lung volume, we also could provide a possible explanation on the observed and counterintuitive exhalation of air from seals species before diving.

For the calculation of the total energy cost of the dive, we also included the basal metabolism and efficiency for transforming chemical energy in propulsion. In particular, we studied the dependency of the total dive cost with respect to the cruise velocity and the optimal swim speed to minimise it. The energy cost of the dive, once normalized with the covered distance, results to be almost independent on the reached maximum depth with a similar behaviour for the case of a purely horizontal displacement. Comparisons between our finding and observation on breath-hold mammals suggest that the diving reflex could play an important role on the choice of the cruise velocity during diving.

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