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Energy cost and optimisation in breath-hold diving



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HIGHLIGHTS

- We present a new model for calculating the locomotion cost of breath-hold divers.
- Optimal speed during dive transits is predicted to be a function of dive depth.
- Air exhalation before diving observed in phocid seals is explained.
- An upper limit to the active to passive drag ratio is given for dolphins.
- Neutral buoyancy of divers has been confirmed to be energetically advantageous.

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ABSTRACT

We present a new model for calculating locomotion costs in breath-hold divers. Starting from basic mechanics principles, we calculate the work that the diver must provide through propulsion to counterbalance the action of drag, the buoyant force and weight during immersion. Compared to those in previous studies, the model presented here accurately analyses breath-hold divers which alternate active swimming with prolonged glides during the dive (as is the case in mammals). The energy cost of the dive is strongly dependent on these prolonged gliding phases. Here we investigate the length and impacts on energy cost of these glides with respect to the diver characteristics, and compare them with those observed in different breath-hold diving species. Taking into account the basal metabolic rate and chemical energy to propulsion transformation efficiency, we calculate optimal swim velocity and the corresponding total energy cost (including metabolic rate) and compare them with observations. Energy cost is minimised when the diver passes through neutral buoyancy conditions during the dive. This generally implies the presence of prolonged gliding phases in both ascent and descent, where the buoyancy (varying with depth) is best used against the drag, reducing energy cost. This is in agreement with past results (Miller et al., 2012; Sato et al., 2013) where, when the buoyant force is considered constant during the dive, the energy cost was minimised for neutral buoyancy. In particular, our model confirms the good physical adaption of dolphins for diving, compared to other breath-hold diving species which are mostly positively buoyant (penguins for example). The presence of prolonged glides implies a non-trivial dependency of optimal speed on maximal depth of the dive. This extends previous findings (Sato et al., 2010; Watanabe et al., 2011) which found no dependency of optimal speed on dive depth for particular conditions. The energy cost of the dive can be further diminished by reducing the volume of gas-filled body parts in divers close to neutral buoyancy. This provides a possible additional explanation for the observed exhalation of air before diving in phocid seals to minimise dive energy cost. Until now the only explanation for this phenomenon has been a reduction in the risk of decompression sickness.

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1. Introduction

During their dives, breath-hold diving animals minimise energetic cost to gain time foraging as oxygen stored in their body is limited. Besides plastic physiological adaptations to diving, like bradycardia, reduction and redistribution of the blood flow (Butler

and Jones, 1997; Kooyman, 1985; Kooyman and Ponganis, 1998; Butler, 2004), dive energy cost can be lowered by reducing dive duration and/or the mechanical work necessary for propulsion. Energy cost related to the basal metabolic rate is proportional to dive duration and inversely proportional to swimming velocity. On the other side, energy spent for propulsion depends on the drag force during the dive, which increases with the square of velocity. Besides swimming optimisation and hydrodynamics, thrust work is efficiently reduced by slowing down swim speed. Optimal dive

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velocity is a compromise, taking into account these two elements and is specific to the diver's body characteristics and maximal dive depth. An additional energy cost reduction is obtained, particularly in mammals, by alternating active swimming with prolonged glides using buoyant force and weight to their advantage but also by varying their stroke frequency and/or by using stroke-and-glide swimming (Crocker et al., 1997; Webb et al., 1998; Skrovan et al., 1999; Williams et al., 2000; Davis et al., 2001; Nowacek et al., 2001; Biuw et al., 2003; Sato et al., 2003; Miller et al., 2004; Watanabe et al., 2006; Aoki et al., 2011; Maresh et al., 2014).

In recent years many models have been developed to study energy economy in breath-hold divers, mainly birds and mammals (Wilson, 1992; Skrovan et al., 1999; Hansen and Ricklefs, 2004; Sato et al., 2010; Aoki et al., 2011; Watanabe et al., 2011; Miller et al., 2012). In these studies, energy cost is estimated from first principles from the work of the mechanical forces acting on the diver and the diver's metabolism. A complete force and energy cost analysis has been made for penguins, which are usually positively buoyant and glide only during the ascending phase (Hansen and Ricklefs, 2004; Sato et al., 2010; Watanabe et al., 2011; Miller et al., 2012). In particular Sato et al. (2010) and Watanabe et al. (2011) found the analytical expression of optimal velocity for minimising energetic cost of the dive for this particular case.

In the case of mammals, the problem is more complex due to their alternation of prolonged glides and active swimming phases – crucial for energy balance. For this case, an exhaustive analysis is still missing in the literature. An investigation similar to Sato et al. (2010) for mammals was developed by Miller et al. (2012), though the dependency of buoyancy on depth was not taken into account. Skrovan et al. (1999) produced another analysis where only the average value of the buoyant and thrust forces was considered. A numerical study was also developed by Davis and Weihs (2007) for elephant seals, but in this case it was for a related investigation where the benefit of transit dives with gliding descent is compared to purely horizontal displacement.

Here we present a new model for breath-hold diving for a general case which can include the presence of prolonged gliding phases in both ascent and descent. We begin with analysis of the mechanical forces involved and their exact dependency on depth. We calculate length of the gliding phases and take it into account to evaluate dive locomotion cost. Moreover, by including some basic consideration of the animal physiology, we also predict the energy cost of a typical dive. We study the dependency of locomotion and energy cost on the different parameters (dive velocity, diver buoyancy, mass, etc.) and their optimisation. We then compare this with observations of real dives in different breath-hold diving animals, in particular the bottlenose dolphin, for which several vertical-dive measurement from trained individuals are available.

In the following section of this paper we present our model to calculate mechanical work and total energy cost required for a typical dive as a function of the diver and the dive characteristics, including animal metabolism. In the third section we discuss our results and how they compare with observations of real dives. The fourth section is our conclusion.

2. Model description

2.1. Basic assumptions

We calculate dive energy cost from first principles from the work of the mechanical forces acting on the diver and their dependency on depth, as did Wilson (1992), Skrovan et al. (1999), Hansen and Ricklefs (2004), Sato et al. (2010), Aoki et al. (2011), Watanabe et al. (2011), and Miller et al. (2012). During a dive in a fluid (sea water in our case), the animal is subject to four forces: drag, weight, the buoyant force and

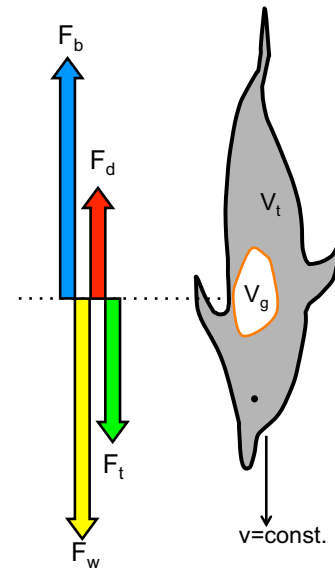


Fig. 1. Scheme of the forces acting on a breath-hold diver (a dolphin in the sea in this example) moving with a velocity v in a liquid. Forces are thrust F_t , drag F_d , buoyant force F_b and weight F_w . V_g indicates the volume of the gas-filled parts of the diver body (mainly the lung, oral cavities, etc.) compressible with pressure changes. V_t indicates the volume of the liquid and solid parts of the diver body (body tissues), which do not change significantly in volume when the pressure increases.

thrust (see scheme in Fig. 1). Drag is caused by friction and the pressure gradient differential. It is strongly dependent on the body velocity $v = |\mathbf{v}|$ and always opposes it ($F_d = -F_d(v)\hat{\mathbf{v}}$ with $\hat{\mathbf{v}} = \mathbf{v}/v$).

Weight is proportional to body mass m and the acceleration of free fall \mathbf{g} ($F_w = m\mathbf{g}$). The buoyant force is its counterpart and is proportional to body volume V and the fluid density ρ ($F_b = -\rho V\mathbf{g}$). The buoyant force changes with depth due to the presence of gas-filled parts of the diver's body (lungs, oral cavities, etc.) whose volume V_g varies with the pressure ($PV_g = \text{const.}$). To take into account the effect of V_g variations, it is better to rewrite the magnitude of the buoyant force F_b as a function of the depth d as:

$$F_b = \rho(V_t + V_g)g = mg \left(R_t + \frac{R_g}{1 + \frac{\rho g d}{P_0}} \right), \quad (1)$$

where V_t represents the volume of the tissue of the diver's body comprising liquids and solids which is considered constant at any depth, due to its small variation with pressure, as well as the water density ρ . We also introduce the ratios $R_t = \rho V_t/m$ and $R_g = \rho V_g^0/m$, where V_g^0 represents the gas-filled body parts volume at the surface. R_t can also be written with respect to fluid density ρ and average body tissue density ρ_t : $R_t = \rho/\rho_t$. The use of the ratios R_t and R_g instead of the volumes V_t and V_g has the advantage of allowing us to investigate the dependency of locomotion cost and other pertinent quantities on the different parameters independently (or almost) from the specific mass of the diver.

Locomotion cost required to descend to a maximal depth D and return to the surface can be quantified by the calculation of the work W of the thrust force produced by the diver along to the dive path. In order to reduce W , breath-holding animals (and also human freediver athletes) use the buoyant force and weight in their favour by gliding for as long as possible. In particular, some mammals such as dolphins and seals glide for large parts of both descending and ascending dive phases. For these mammals, a typical dive is composed of a first step where the diver makes an effort to descend from the surface. Then it actively swims down to a depth d_D (descent critical depth), where the buoyancy is small enough to

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