Revisiting the energetics of porpoising in penguins

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Some insist penguins porpoise to save the energy at high speeds. Some believe penguins porpoise to breathe without losing their speed. Others think penguins porpoise to watch predators in the air and on the shore. The present proposal is introduction of equations of motion: a penguin is treated as a particle; the conventional aerodynamics and hydrodynamics is used; added mass is incorporated to capture the effect due to splash; constant power is assumed. As the penguin dashes out of the water, it sprays water around: the added mass in the water is assumed as an impact, whilst the added mass in the air is neglected; no wave resistance is incorporated, because penguins are quite streamlined. Parameters are determined so as to explain the existing field data. The results show the following facts: penguins lose horizontal speed in the air because of inclined flight-trajectory; porpoising consumes more energy than steady-state swimming on the same-speed basis.

1. INTRODUCTION

Some marine animals are known to leap out of the water, challenge a ballistic flight for a short duration, and dive into the water: this behavior is porpoising. The point is that the combination of high-power and short duration might result in smaller energy consumption than steady locomotion. Some insist that steady-state swimming energetically costs more than porpoising at and above the so-called 'crossover' speed in high-drag inducing environments (Au & Weihs, 1980, for example). The observations, however, do not support the existence of the crossover speed (Fish & Hui, 1991, Yoda *et al*., 1999); marine animals do porpoise at much slower speeds than the crossover speed. A compromise is to believe animals do porpoise to breathe without losing their travelling speed (Hui, 1987, Fish & Hui, 1991). But porpoising behavior has not evolved in all the potential species, or not all the individuals in one species do porpoise (Yoda *et al*., 1999). Our question is if porpoising is energy conserving in any sense or not.

So far there are only analyses of equilibrium and no former works that deal with the dynamics of porpoising. The aim of this study is, from a theoretical point of view, to re-examine arguments on the criterion about energy consumption in this intermittent locomotion. By use of mechanics of a particle as well as elementary knowledge of aerodynamics and hydrodynamics, we derive the equations of motion for porpoising and steady-state swimming, and carry out numerical and theoretical comparisons in required powers by porpoising and steady-state swimming on the same-speed basis. This theory leads us to the orthodox: porpoising is not energy conserving locomotion.

Structure of this paper is as follows: in THEORY we derive the basic equations; in NUMERICAL RESULS AND DISCUSSION we present the numerical results on the aerial phase as well as the comparison of energetics in porpoising and steady-state swimming; in THEORETICAL IMPLICATION we mathematically annotate the inefficiency of porpoising observed in the numerical results; in CONCLUSION we summarise our findings.

2. THEORY

2.1 DESCRIPTION OF A PORPOISING CYCLE

We treat a marine animal as a particle of mass m; we incorporate added mass to capture the effect due to splash or impact. The related Reynolds numbers are around 10^5 to 10^6 in the air and 10^6 to 10^7 in the water.

Porpoising consists of the aerial and swimming phases. We assume porpoising is periodic: starting from the initial condition and returning to the initial condition in the end of a cycle. We show the schematic diagram in Fig.1. We take the Cartesian coordinate (x, z), where $\mathbf{v} = (u, w)^T$ is the velocity vector with respective components. We assume a flat sea surface just upon x-axis.

We describe one cycle like this: at the time $t = 0$ an animal leaps out of the water with $\mathbf{v} = \mathbf{v}_0$ at an angle θ, which we shall call the emergence angle; it flies as described by the equation of motion in the air; at $t = t_s$ it dives into the water with $\mathbf{v} = \mathbf{v}_s$; at the diving instance the velocity is immediately decelerated by the impact, which is dealt with by introducing added mass; the animal changes its mode of locomotion to swimming with $\mathbf{v} = \mathbf{v}_d$ and accelerates itself to the final condition $\mathbf{v} = \mathbf{v}_f$; then it leaps out of the water with splash and immediately loses its speed down to $\mathbf{v}_0$; the effect of splash is dealt with by added mass again; this is the end of one cycle and at the same time the start of the next cycle. In due course we also use scalar forms: $v_0 = |\mathbf{v}_0|$, $v_s = |\mathbf{v}_s|$, $v_d = |\mathbf{v}_d|$, and $v_f = |\mathbf{v}_f|$.

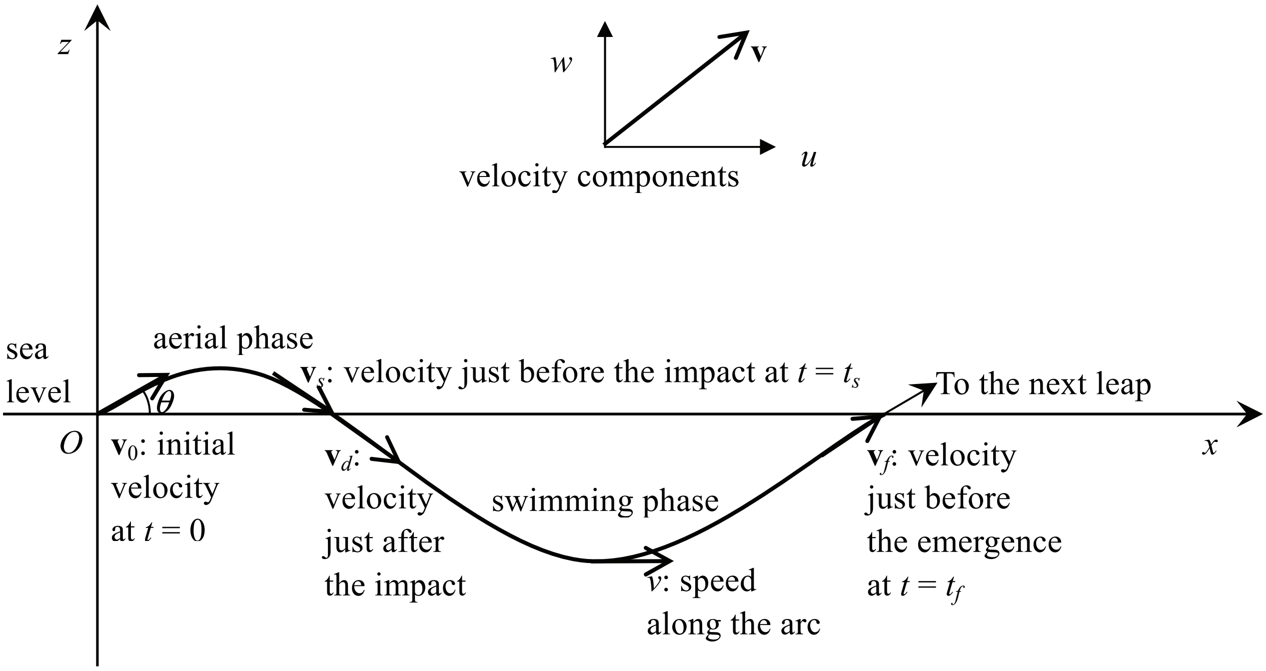


Fig.1 Schema for one cycle of porpoising

The aerial phase is a ballistic flight. Gravitation and resistance due to the air act on an animal, and hence the equation of motion in the air is given by

$$d\mathbf{v}/dt = -g\mathbf{j} - \delta|\mathbf{v}|\mathbf{v}, \tag{1}$$

where $\mathbf{j} = (0,1)^T$; g designates the acceleration due to gravitation; δ is the parameter related to the aerodynamic drag given by

$$\delta = \rho_a S_b C_D / 2m,$$

where ρ_a, S_b, and C_D denote the air density, the frontal area of the animal, and the form drag coefficient, respectively. We deal with the case of the flippers folded. The trajectory in the air is almost a parabola. If we neglect resistance due to the air, we get $2v_0\sin\theta/g$ as a fairly accurate estimate for the duration in the air.

At the interface between air and water we consider the effect due to added mass of water to model impact at the time of dashing into water and splash at the time of leaping out of water. Almost instantly an animal is decelerated from v_s, the terminal speed in the air, to v_d, the initial velocity in the water: $mv_s = m(1+a)\, v_d$, where a denotes the ratio of the added mass to the body mass. Hence we have the relation $v_d = \ \ v_s/(1+a)$. When the animal leaps out of the water, the splash takes away a part of the momentum. This consideration connects v_f, the terminal velocity in the water, to v_0, the initial velocity in the air: $v_0 = v_f/(1+a)$. According to typical field data of Adélie penguins (Yoda *et al.*, 1999), v_f is 2.8[m/s] just before the emergence, while v_0 is 2.6[m/s] just after the emergence. In case of Adélie penguins, this measurement leads us to the conclusion that the fraction a is 0.077.

The next is the swimming phase. To make the arguments simple we assume that densities of animals and sea water are the same and that animals become free from gravitation in the water. Let us introduce the total velocity v along the swimming path. We also assume an effectively straight swimming-path, and neglect its curvature effects. As a matter of course $u \leq v$, and hence the analysis of v gives us a clue to the upper bound of a horizontal velocity. The basic equation of motion in the water assumes the form:

$$m\mathrm{d}v/\mathrm{d}t = T - D,$$

where T and D denote thrust and hydrodynamic drag, respectively. Since thrust is generated by the flapping motion of flippers, thrust exhibits periodic fluctuations. The fluctuations in thrust can be treated by a high order approximation, but this affects the velocity a little. At the same time fluctuations are periodic, and hence their time averages are zero anyway. Our argument depends on the time-averaged values in the end. Hence we neglect the fluctuations, although T can be a function of time. This is quasi-steady treatment. Since the mechanical required-power, P, is equal to Tv, we substitute P/v for T in the equation of motion; dividing the equation by m, we obtain the specific version of the equation of motion:

$$\mathrm{d}v/\mathrm{d}t = p/v - \alpha v^2 - p^2/\beta\gamma^2 v^4, \qquad (2)$$

where p, α, β and γ denote the specific required-power and the parameter related to form drag, the parameter related to induced drag and the ratio of thrust to lift, respectively; the parameters are defined in the following:

$$\alpha = \rho_w\{S_b C_D + S_w C_{D0}\}/2m,$$

$$\beta = \rho_w S_b e\pi A/2m,$$

where ρ_w, S_w, C_{D0}, e, and A designate the water density, the flipper area, the form drag coefficient of the flipper, Oswald's wing efficiency, and the aspect ratio of the flipper, respectively. This formalism is within the realm of the conventional wing theory.

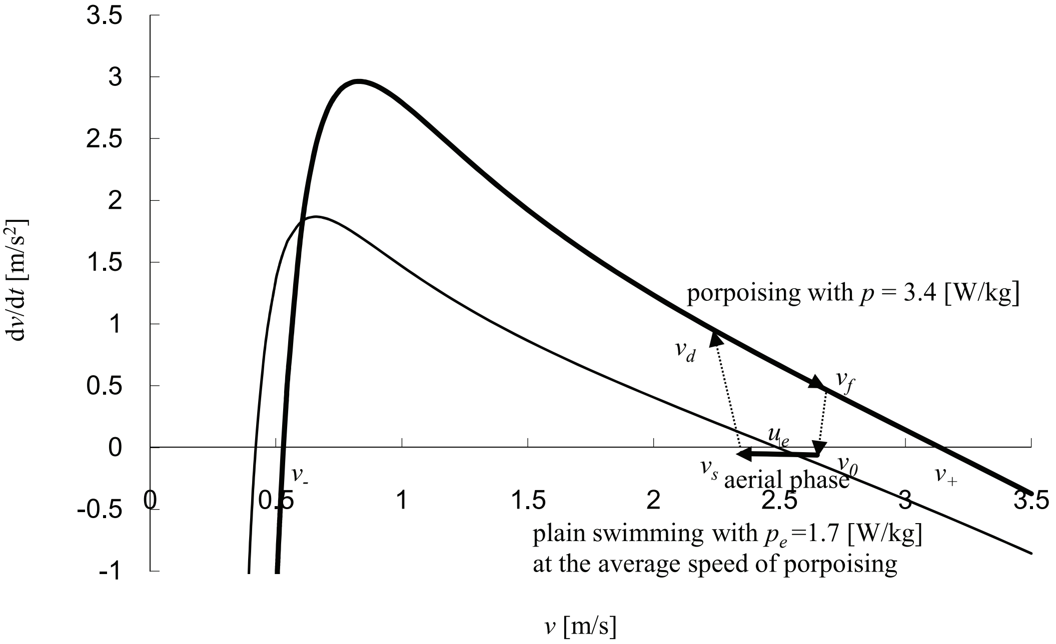


Fig. 2 Phase portrait of porpoising and swimming

Figure 2 shows typical examples of the phase portrait, *i.e.*, (v, dv/dt) plot, of porpoising and swimming by use of the parameters given in the next subsection. The mechanical required power is assumed to be kept constant during continuous process. Two curves represent swimming modes under the condition of constant required-powers. This is a fairly realistic assumption. The curves go into the deceleration region, lower half, at low speed due to v^{-2}-proportional lift-induced drag as well as at high speed due to v^2-proportional profile drag. A curve becomes located upward for swimming with higher required-power. The aerial phase is actually too close to the abscissa, and hence the line is depicted exaggeratedly away from the axis in Fig.2.

Steady-state swimming, the equilibrium, corresponds to the point of $\mathrm{d}v/\mathrm{d}t = 0$ in the phase plane. There are two possibilities: one at low speed v_- and another at high speed v_+; the equilibrium at high speed alone is stable and feasible. Suppose a disturbance drifts the animal toward higher velocity condition away from the high-speed equilibrium, then deceleration due to drag immediately acts to retain the equilibrium; and *vice versa*. The equilibrium at $v = v_-$ exhibits an adverse mechanism, and hence the velocity drifts from v_-.

On the other hand, porpoising is intermittent and switches over between deceleration in the air and acceleration in the water. The average velocity to be attained is below v_+, the value at the steady state of swimming with higher required-power. Therefore many have been puzzled by the existence of high-power intermittent locomotion.

2.2 MATERIAL AND METHODS

We choose Adélie penguins, partly because there are ample laboratory and field data available (Culik *et al.*, 1994, Yoda *et al.*, 1999 for example), partly because they are free from Gray's paradox.

As for the aerial phase we use Runge-Kutta method to numerically integrate (1) by use of the following parameters: $m = 4.4$ [kg], $\rho_a = 1.225$ [kg/m³], $S_b = 0.0314$ [m²], $C_D = 0.03$.

In the numerical experiments we use the following values: $\gamma = 0.5$; $\rho_w = 1025$ [kg/m³]; $S_w = 0.028$ [m²]; $C_{D0} = 0.01$; $e = 0.8$; $A = 11.2$.

The power has the upper bound. This is determined by the stall of hydrofoils or the physiological limit. Suppose $C_{L\max} = 1.5$, we obtain the upper bound as large as 236 [W]. Suppose the maximum output of around 100 [W/kg] per muscle-weight basis and flipper muscle amounting around 10% of the total mass, we obtain the upper bound as large as 44 [W]. Therefore we use 50 [W] as the upper bound in the numerical experiments. We can analytically integrate the governing equation (2) with constant p (see Appendix).

3. NUMERICAL RESULTS AND DISCUSSION

3.1 THE AERIAL PHASE

Figure 3 shows the summary of numerical calculations of (1) against various emergence angle θ at the initial velocity $v_0 = 2.6$ [m/s].

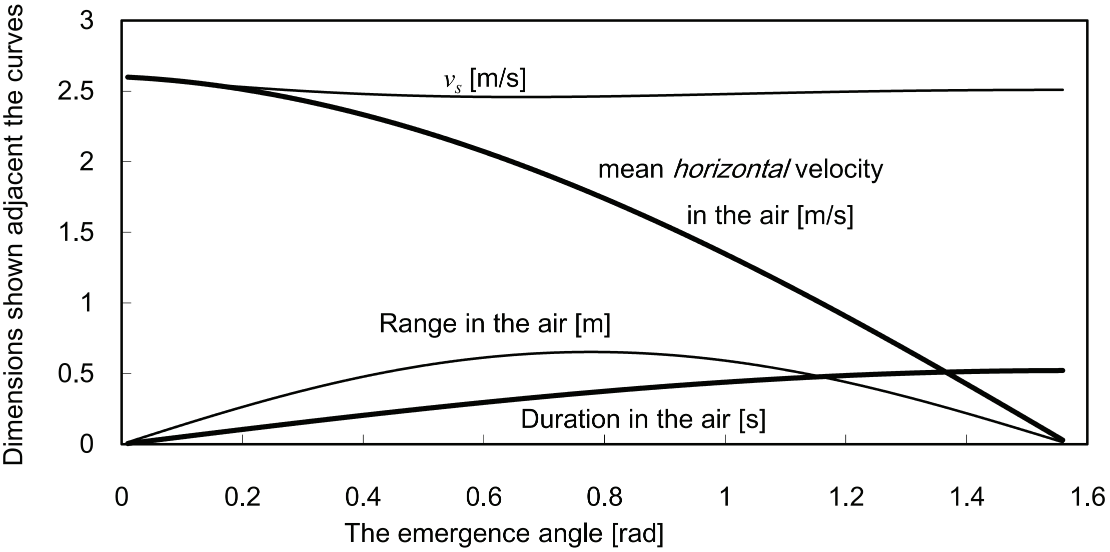


Fig. 3 Numerical results of aerial phase

As shown in Fig.3 v_s , the speed just before the impact, is slightly smaller than v_0 and almost constant against various θ. This fact has misled us to erroneous belief that speed does not drop in the aerial phase. But Fig.3 also shows the tendency that the mean *horizontal* velocity $<u>$ significantly decreases in proportion to $\cos\theta$. Since $<u>$ corresponds to the travelling speed, the aerial phase is the decelerating phase in porpoising.

Also shown in Fig.3 is the relation between the duration in the air, t_s, and θ. The duration in the air is said to have close connection to inhalation. Hui (1987) reports that penguins leap out of the water at the emergence angle between 25° and 45°, most frequently at 32.2°. Hui suggests that penguins make most of porpoising as inhalation. Penguins need typically 0.24 [s] for one inhalation. To assure more than 0.24 [s], it is necessary to leap out at θ greater than around 25°. The emergence angle θ has the lower bound determined by the minimum duration enough for inhalation and the upper bound determined by searching for the maximum range; there is another trade-off to determine the emergence angle, which is annotated in the next section, *i.e.*, THEORETICAL IMPLICATION. To assure more than 0.24[s], it is necessary to leap out at θ greater than 0.475 [rad]; this bound corresponds to 27.2°. As a consequence $<u>$ is less than or equal to 2.24 [m/s], which is more than 13.8% decrease compared to the initial speed. The most frequent observation at 32.2° corresponds to 16.3% loss in $< u >$ against v_0.

Let us annotate the relation between the range, the horizontal travelling-distance, and θ in Fig.3. The calculated maximum range is 0.653 [m] attained at $\theta = 0.778$ [rad], which is slightly smaller than $\pi/4$. This θ may stand for the upper bound of the emergence angle. In this case the flight duration is 0.367 [s], but $<u>$ is as slow as 1.78 [m/s]; this is 31.5% decrease compared to the initial speed.

In between the lower and upper bounds of the emergence angle, the mean horizontal velocity significantly decreases compared to the initial velocity, $v_0 = 2.6$ [m/s]: $1.78 \le <u> \le 2.24$. This is the main and novel finding in the analysis of the aerial phase.

3.2 PORPOISING CYCLE

The following results are based on the common initial data: $t_s = 0.279$ [s], $<u> = 2.13$ [m/s], $v_s = 2.46$ [m/s], and $v_d = 2.29$ [m/s] calculated by setting $\theta = 32.2^{\circ}$ after the most frequent observation (Hui, 1987); the terminal condition is fixed at $v_f = 2.8$ [m/s] after the field observation (Yoda et al., 1999).

We shall introduce the same-speed basis comparison. It is appropriate to define the speed u_e in steady-state swimming to be compared with porpoising by the weighted mean:

$$u_e = <u>r + <v>(1 - r), \tag{3}$$

where r and $<v>$ denote the intermittency and the average velocity in the swimming phase of porpoising, respectively; the intermittency is defined by t_s/t_f. We obtain $t_f - t_s$ and $<v>$ analytically (see Appendix). The time-averaged value of the specific required-power $<p>$ is defined and derived by

$$<p> = p(t_f - t_s)/t_f = p(1 - r),$$

while p_e, the specific required-power for steady-state swimming at u_e, is given by (see Appendix)

$$p_e = \frac{\beta\gamma^2}{1 - \sqrt{1 - 4\alpha/\beta\gamma^2}} u_e^3. \tag{4}$$

Figure 4 is the summary of numerical results to be compared with the observation (Yoda et al., 1999). According to the field data, penguins do porpoise at this situation. Everything is plotted against the required power bounded by 50 [W], the supposed physiological maximum, and 13.9 [W], the required power for steady-state swimming at $u_e = 2.8$ [m/s].

Let us take a look at the time-averaged value of the specific required-power $<p>$ in porpoising. From the lower bound of P to around 20 [W], $<p>$ is smaller than 3.15[W/kg], that is the value of steady-state swimming at 2.8 [m/s]; $<p>$ takes the minimum value 2.91 [W/kg] with the required power of 14.4 [W] and $r = 0.111$. This reduction in specific power is due to partial success of porpoising, although u_e becomes less than 2.8[m/s]. As the required power increases beyond this point, $<p>$ gradually increases.

In Fig.4 the average horizontal speed u_e in porpoising monotonically decreases, as P and accordingly r increase. This is because the aerial phase, or the deceleration phase, dominates the locomotion. Hence u_e also decreases, as P and r increase. This in turn has p_e monotonically decrease, as P and r increase. As a

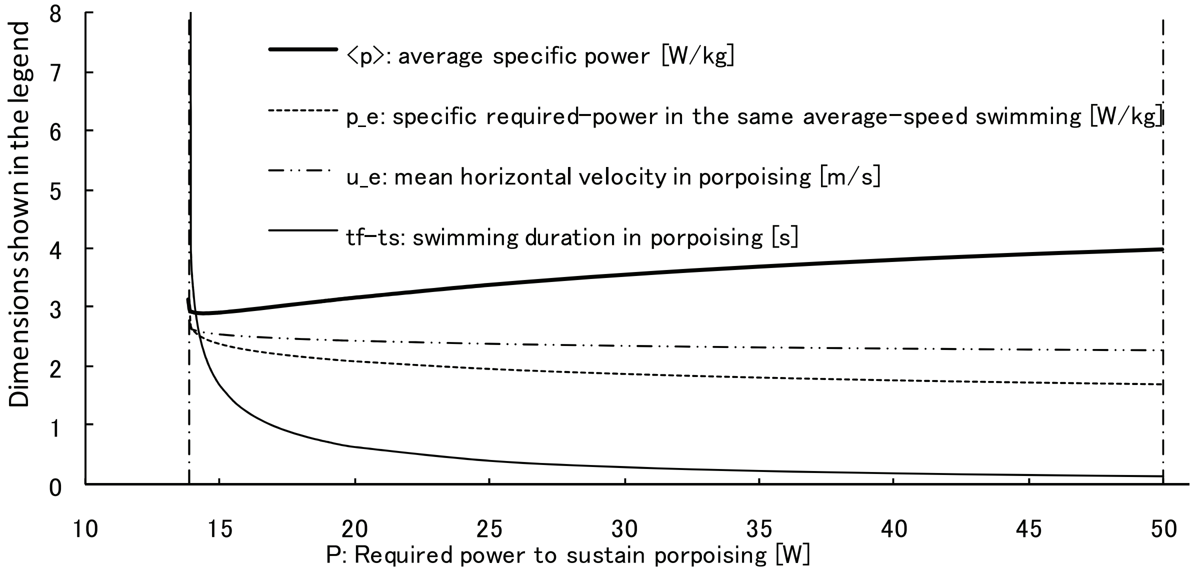


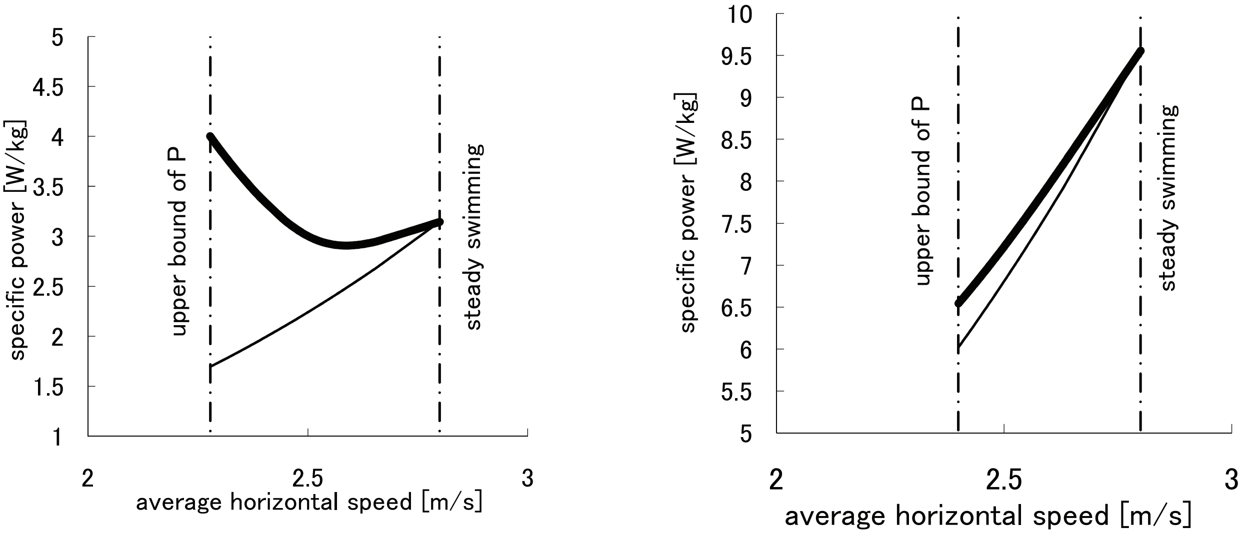
Fig.4 Summary of numerical results

result $<p>$ is always greater than p_e, and hence porpoising is found to be less efficient than steady swimming on the same-speed basis.

The total swimming time in porpoising is less than three seconds; the corresponding intermittency r is in between 0 and 0.048. In the aquarium the total duration t_f takes the value around 10 [s]; using the same estimate for t_s, we obtain $r = 0.028$. Penguins apparently swim longer than possible porpoising cycle-time. From an energetic point of view, porpoising with such a small intermittency is much the same as steady-state swimming.

The next consideration is to see how the magnitude of drag affects porpoising. We carry out the numerical analysis in which we double and triple the hydrodynamic drag, *i.e.*, α. Two extreme results are shown in Fig. 5; the result of doubled drag shows the tendency between (A) and (B) of Fig. 5. On the same drag basis the steady-state swimming always consumes less energy than porpoising. The intermittency r monotonically increases from 0 at $<v> = 2.8$ [m/s], as $<v>$ decreases.

As a matter of course the low-drag porpoising consumes less energy than the high-drag swimming. But it is not confirmed in the fields that every penguin porpoises to approach the water surface, *i.e.*, the high-drag environment due to the existence of wave drag.



(A) Plain calculation with the same setting for Fig. 4. (B) Calculation with drag tripled.

Fig. 5 Numerical results for drag augmentation
Bold lines for porpoising; thin lines for steady-state swimming

4. THEORETICAL IMPLICATION

To consider the meaning of Fig. 5 we deduce the criteria for the relation $<p> > p_e$, where $<p>$ is $p(1-r)$ Multiplying (2) by v and integrating this with respect to time t from t_s to t_f, one obtains the relation below.

$$\frac{{v_f}^2-{v_d}^2}{2}=p(t_f-t_s)-\int_{t_s}^{t_f}\left(\alpha v^2+\frac{p^2}{\beta\gamma^2 v^4}\right)v\mathrm{d}t,$$

or divided by t_f

$$p(1-r)=\frac{1}{t_f-t_s}\int_{t_s}^{t_f}\left(\alpha v^2+\frac{p^2}{\beta\gamma^2 v^4}\right)v\mathrm{d}t(1-r)+\frac{{v_f}^2-{v_d}^2}{2t_s}r, \tag{5}$$

where the first and second terms on the right-hand side correspond to the time-averaged specific power against drag, hereinafter referred to as $<p_d>(1-r)$, and the time-averaged loss of energy in the air, respectively. At $r = 0$ the first term on the right-hand side of (5) tends to p_f, *i.e.*, (4) with v_f for u_e. Therefore in the vicinity of $r = 0$ (5) behaves as follows.

$$p(1-r)\to p_f(1-r)+\left.\frac{\mathrm{d}<p_d>}{\mathrm{d}r}\right|_{r=0}r+\frac{{v_f}^2-{v_d}^2}{2t_s}r+O\left(r^2\right), \tag{6}$$

The second term on the right-hand side of (6) is negative. On the other hand substituting the right-hand side of (3) for u_e in (4) and expanding it with respect to r in the vicinity of $r = 0$, one obtains

$$p_e\to\frac{\beta\gamma^2}{1-\sqrt{1-4\alpha/\beta\gamma^2}}\left\{{v_f}^3-3{v_f}^2\left(v_f-<u>\right)r\right\}+O\left(r^2\right)=p_f-3p_f\left(1-\frac{<u>}{v_f}\right)r+O\left(r^2\right), \tag{7}$$

because $<v>$ becomes equal to v_f at $r = 0$. Subtracting (7) from (6), we are led to the final result:

$$<p>-p_e\to\left\{\frac{{v_f}^2-{v_d}^2}{2t_s}+\left.\frac{\mathrm{d}<p_d>}{\mathrm{d}r}\right|_{r=0}-3p_f\left(\frac{<u>}{v_f}-\frac{2}{3}\right)\right\}r+O\left(r^2\right), \tag{8}$$

as r tends to 0. Therefore $<p> > p_e$, if the following holds.

$$\frac{{v_f}^2-{v_d}^2}{2}>\kappa p_f-\left.\frac{\mathrm{d}<p_d>}{\mathrm{d}r}\right|_{r=0}t_s, \tag{9}$$

where

$$\kappa=3\left(\frac{<u>}{v_f}-\frac{2}{3}\right)t_s.$$

This κ has the upper bound, because $<u> < v_0\cos\theta < v_f\cos\theta$ and $t_s < 2v_0\sin\theta/g < 2v_f\sin\theta/g$ hold: after some algebra and calculus in our case $\kappa < 0.175$. Although magnitude of the derivative term is explicitly unknown, t_s is usually very small; hence the second term on the right-hand side of (9) affects not too much. This result implies that porpoising is energy-consuming locomotion because of the loss of kinetic energy in the air; in our numerical simulations this loss is apparently greater than 17.5% of the specific power due to steady-state swimming on the same-speed basis.

This formalism also offers another implication of the emergence angle. At the upper bound of κ the emergence angle is 26.7°. As the emergence angle becomes larger than $\cos^{-1}(2/3)$, *i.e.*, 48.2°, κ becomes negative. Penguins leap out of the water at the emergence angle in between these boundary values; they porpoise so that $<p>$ is not much too greater than p_e.

5. CONCLUSION

We summarise our finding concisely as follows:

(1) We present the dynamics of porpoising as a set of ordinary differential equations;
(2) The longer penguins stay aloft, the smaller the horizontal speed becomes;
(3) On the same-speed basis porpoising consumes more energy than stead-state swimming;
(4) One cycle of porpoising is several seconds long, but penguins actually stay much longer in the water;

(5) We present the criterion for the superiority of steady-state swimming to porpoising on the same average-speed basis.

APPENDIX

The relation between the specific power and the speed of steady-state swimming is given by solving (2) with dv/dt = 0: this leads us to the quadratic equation with respect to p; the immediate solution is (4).

Noting dt = dv/(the right-hand side of (2)), we obtain the following relation:

$$\mathrm{d}t = \frac{v^4 \mathrm{d}v}{\alpha\left(v_+^{\ 3} - v^3\right)\left(v^3 - v_-^{\ 3}\right)},$$

where

$$v_\pm = \sqrt[3]{\frac{p}{2\alpha}\left\{1 \pm \sqrt{1 - \frac{4\alpha}{\beta\gamma^{\ 2}}}\right\}}.$$

Using this, we obtain the swimming duration by

$$\begin{aligned}\int_{t_s}^{t_f} \mathrm{d}t &= \int_{v_d}^{v_f} \frac{v^4 \mathrm{d}v}{\alpha\left(v_+^{\ 3} - v^3\right)\left(v^3 - v_-^{\ 3}\right)} \\ &= \frac{1}{3p\sqrt{1 - 4\alpha / \beta\gamma^{\ 2}}} \\ &\times \left[v_+^{\ 2}\left\{\frac{1}{2}\ln\left|\frac{v_f^{\ 2} + v_+ v_f + v_+^{\ 2}}{v_d^{\ 2} + v_+ v_d + v_+^{\ 2}}\right| + \sqrt{3}\tan^{-1}\left(\frac{\sqrt{3}v_+\left(v_d - v_f\right)}{2v_f v_d + v_+ v_f + v_+ v_d + 2v_+^{\ 2}}\right) + \ln\left|\frac{v_d - v_+}{v_f - v_+}\right|\right\}\right. \\ &\left. - v_-^{\ 2}\left\{\frac{1}{2}\ln\left|\frac{v_f^{\ 2} + v_- v_f + v_-^{\ 2}}{v_d^{\ 2} + v_- v_d + v_-^{\ 2}}\right| + \sqrt{3}\tan^{-1}\left(\frac{\sqrt{3}v_-\left(v_d - v_f\right)}{2v_f v_d + v_- v_f + v_- v_d + 2v_-^{\ 2}}\right) + \ln\left|\frac{v_d - v_-}{v_f - v_-}\right|\right\}\right].\end{aligned}$$

In the very same manner we obtain the arc length of the swimming path by

$$\begin{aligned}\int_{t_s}^{t_f} v\mathrm{d}t &= \int_{v_d}^{v_f} \frac{v^5 \mathrm{d}v}{\alpha\left(v_+^{\ 3} - v^3\right)\left(v^3 - v_-^{\ 3}\right)} \\ &= \frac{1}{3p\sqrt{1 - 4\alpha / \beta\gamma^{\ 2}}}\left\{v_+^{\ 3}\ln\left|\frac{v_d^{\ 3} - v_+^{\ 3}}{v_f^{\ 3} - v_+^{\ 3}}\right| - v_-^{\ 3}\ln\left|\frac{v_d^{\ 3} - v_-^{\ 3}}{v_f^{\ 3} - v_-^{\ 3}}\right|\right\}.\end{aligned}$$

Dividing the arc length by the swimming duration, we obtain <v>, the average velocity in the swimming phase of porpoising.

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