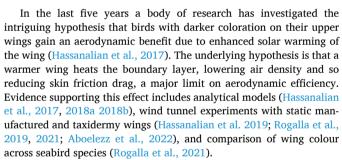Forum Article

Little prospect of colour-based drag reduction underwater

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In the last five years a body of research has investigated the intriguing hypothesis that birds with darker coloration on their upper wings gain an aerodynamic benefit due to enhanced solar warming of the wing (Hassanalian et al., 2017). The underlying hypothesis is that a warmer wing heats the boundary layer, lowering air density and so reducing skin friction drag, a major limit on aerodynamic efficiency. Evidence supporting this effect includes analytical models (Hassanalian et al., 2017, 2018a 2018b), wind tunnel experiments with static manufactured and taxidermy wings (Hassanalian et al. 2019; Rogalla et al., 2019, 2021; Aboelezz et al., 2022), and comparison of wing colour across seabird species (Rogalla et al., 2021).

Recently, similar suggestions have been made for large swimming organisms, hypothesizing that colour-based drag reduction could be a functional explanation for dark dorsal coloration in many sharks, rays, billfish, whales, dolphins and penguins. Hassanalian et al. (2019b) proposes that solar radiation absorbed by the integument when the animal swims near the water surface heats the boundary layer, reducing skin friction drag concluding: "the black colour on the top of these marine organisms is very efficient in terms of drag reduction". Using simulations of the turbulent flow around flat plates and two-dimensional animal models, the authors suggest drag reduction due to colour of up to 11%. This magnitude of drag reduction requires substantial warming of the skin surface, and the benefit is a more modest (ca. 1%) if the boundary layer is kept 5 °C above ambient temperature. Tenorio et al. (2022) make similar claims for penguins: "this study shows conceptually that dark coloration in penguins could be a significant influence on water drag". As penguins travel 0.5–1 m below the water surface and dive much deeper (Ainley and Wilson 2023), the argument is extended to include potential drag benefits during dives using body heat acquired when the animal is resting on the surface.

We feel that drag reduction through solar warming is much less likely to be a strong selective pressure on the coloration of swimming than flying animals for the following reasons:

i) Non-negligible warming of darker dorsa by sunlight could only occur in water if the organism remains relatively stationary on or very near the water's surface for tens of minutes.
ii) Movement underwater or in moving water would cause any heat gained to be lost much more rapidly than in air.
iii) Swimming near the surface of the water is more expensive than swimming at depth, and this cost is much higher than any claimed energetic savings from dark pigmentation.

We expand on these points below.

When electromagnetic radiation is absorbed, energy is converted to another form, often thermal energy, which is why objects warm up in strong sunlight. Dark pigmentation is unlikely to aid substantially with absorption of thermal energy when an animal is under water, unless it is very near the surface. Dark coloration is caused by high absorption of all wavelengths of visible light (electromagnetic radiation with wavelengths in the region 300–700 nm). At longer wavelengths melanic pigments responsible for dark colour in most marine species are increasingly reflective (Rogalla et al., 2021). At sea level around 55% of the energy from direct sunlight lies at infra-red wavelengths above 700 nm (Stuart-Fox et al., 2017). After some radiation is reflected off the water surface, absorption of visible and infrared radiation by water is

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much greater than absorption by air, and crucially absorption strongly increases with wavelength. This is why the sea looks blue – because long-wavelength red light is absorbed much more readily than short-wavelength blue light. This rise is very steep, the absorption co-efficient of pure water is around 0.30 m^{-1} for red light at 600 nm, 2 m^{-1} at 700 nm and over 20 m^{-1} for much of the infra-red spectrum (Kirk 1994, p57). If we take light of wavelength 700 nm, then an absorption coefficient of 2 m^{-1} implies that intensity will have dropped to 82% of surface values at a depth of 10 cm in pure water, 37% after 50 cm, and 14% at 1 m (Denny 1993). Absorption will be even more rapid the more dissolved and suspended material there is in the water. Thus, dark pigmentation can increase warming through exposure to direct sunlight in air, but this effect is reduced rapidly by submergence in water, even in near-surface waters.

These arguments are supported by recent empirical work studying sun-basking in fish by Nordahl et al., (2018). First temperature loggers painted black or white were submerged under 4 mm of water in an outdoor pool exposed to bright sunlight. The black-painted loggers achieved very slightly higher temperatures (0.17 °C peak value of mean excess). The authors repeated this experiment with black and white physical models of a fish at a depth of 5–10 mm, and the effect of colour was reported for be further reduced. Then temperature loggers that could record depth, ambient water temperature and core body temperature were implanted in carp (*Cyprinus carpio*, of both dark and lighter morphs) and these fish released into a large outdoor tank. Fish were scored as sun-basking when in the top 35 cm of the water column for longer than 20 min. Basking fish did acquire body temperatures higher than the ambient temperature and dark morph individuals were on average warmer, but by small amounts (at most 0.2 °C – interpreted from their Figure 3). These thermal increases are much smaller than those of flat plates warmed by a heat lamp a few mm under the water surface (Hassanalian et al., 2019b).

On the evidence above, an aquatic organism would need to remain on or very near the surface for a period of several tens of minutes at least for basking in the sun to increase dorsal temperature appreciably. While empirical investigation is warranted, the behaviour of sharks, dolphins and penguins does not seem to allow for this. Even shallow swimming species travel from A to B at depths greater than a few cm (Yoda et al., 1999). When foraging, penguins generally rest with dorsal parts above the surface for only short periods between dives (Ainley and Wilson 2023). During resting periods metabolic rate increases (Stahel and Nicol 1982) and penguins often shiver (Kooyman et al., 1971) to generate heat as conduction, convection and evaporative cooling cause them to lose heat from outer layers. Very few large aquatic animals seem to display the basking behaviour that would be required to appreciably heat body surfaces above ambient water temperature (e.g. sunfish *Mola mola* Nakamura et al., 2015). Remaining still at the surface for periods of time might increase the vulnerability of organisms such as penguins to predation.

Furthermore, and critically, any movement of the animal (or water-currents moving past the animal) would quickly reduce any excess warming of dorsal surfaces. One reason for this is the very high thermal conductivity of water. A motionless animal in calm conditions will lose heat over 20 times as fast into water as into air at the same temperature. However, as soon as something starts moving, heat loss through forced convection dominates heat loss through conduction. For an organism about 1m long traveling at a modest 1ms^{-1} heat loss is 1000 times greater than it is for the same object when still (interpreted from Figure 8.3 and 8.5 of Denny 1993). The faster the organism swims, the greater the convective heat loss to the water around it. Thus, any small temperature differential between an individual's integument and the surrounding water that built up when basking on or near the surface of water, would be lost very quickly if the animal begins to swim through the water. This is confirmed by Ponganis et al. (2003) who showed sub-feather temperatures in Emperor penguins decreased from 31 to 35 °C during rest periods to 15.0 °C on average during dives.

As well as cooling the skin of the animal, these thermal processes also take heat away from the boundary layer in proximity to the organism. It is warming of this layer by the organism that is critical for the colour-based drag reduction hypothesis. Rate of heat loss will in increase with the thermal conductivity of the fluid (which is over 20 times as high in water than air: Denny 1993: p155). However, it is also affected by the thickness and stability of the boundary layer, with rate of heat loss increasing with both the Prandtl and Reynolds numbers (see Monteith and Unsworth 2008 for an introduction to these quantities as descriptors of the physics of movement through fluids). Both of these are typically at least an order of magnitude higher in air than water (Denny 1993: p155). The relative contributions of these factors to overall heat loss will differ with the size, shape and speed of the organism. However, for a flat planar surface, at sizes and velocities relevant to marine mammals and bird, heat transfer rate will be approximately 200 times higher in water than air: Denny (1993) p155, Campbell and Norman (1998) p101. , See also Vogel (1996) for a detailed description of the physics of animals moving in air and water.

Finally, if marine animals swim near the surface to benefit from colour-based drag reduction, then the benefit must exceed the increased cost of swimming near the surface compared to deeper in the water. The main reason for this is the extra work that has to be done against gravity in creating a wave on the surface of the water. The only paper that seems to offer data on how deep is deep enough to avoid this problem is Hertel (1966). On the basis of empirical measurement of towed solid bodies, this paper estimates that cost of swimming should rise steeply for depths shallower than 2.5 body diameters. On theoretical grounds, Hoerner (1965) estimated this critical depth to be above 5 body-diameters. This accords well with observation that Adélie penguins (with a body diameter of ca. 0.3 m) execute traveling dives at a depth of 0.9m (Yoda et al., 1999). The higher cost of surface swimming has been measured for some live animals. Baudinette and Gill (1985) measured the oxygen consumption of little penguins (*Eudyptula minor*) swimming in a flume. They estimated metabolic costs were 50% higher when swimming on the surface than when swimming underwater. The size of the flume was such that the measured underwater swimming speeds where still likely elevated by proximity to the surface. Similar measurements for sea otters (*Enhydra lutris*) suggested swimming at the surface required 70% more power than swimming submerged (Williams 1999). Similarly, Watanabe et al. (2019) estimated the surface swimming to be between 29 and 155% more expensive than swimming deeper.

The energetic advantage of swimming underwater is well-known in human competitive swimming (Tor et al., 2015; Born et al., 2022). Animals similarly seem to select swimming depths that minimise the cost of swimming near the surface. Williams et al. (1992) reported on experiments designed to measure the energetic cost of swimming in bottlenose dolphins. Dolphins were trained to follow a boat but could select their own depth in the water. The authors report that the "*dolphins preferentially swam about 1m (>2.5 body diameter) below the water surface during the swimming tests. At this depth the augmentation in drag from surface waves is reduced.* Surface intervals were limited to respiratory periods and accounted for <10% of the experimental period".

From the measurements described above, it seems that swimming on or near the surface increases the energetic cost of transport by at least 50%. By comparison the modelling study of Hassanalian et al. (2019b) estimated 7–12% reductions in swimming drag for whales and dolphins – on the basis of black coloration giving a 30 °C increase in surface temperature due to solar warming. Tenorio et al. (2022) take a similar approach and claim that black coloration in penguins can raise feather surface temperatures by up to 40°, and this can lead to drag reductions of up to 18% in penguins swimming at over 2ms^{-1} (see Fig. 9). However, observed solar warming in living swimming organisms has been much more modest. While Tenorio et al.'s principal aim in these analyses may have been bioinspiration for design of vehicles, this paper also offered empirical measurements of penguin surface temperatures that were 2 °C warmer than the water. Similar modest warming was found in an

experimental study of basking behaviour in pike (Nordahl et al., 2020). These authors defined basking behaviour as being stationary in a surface position for more the 5 min. They estimated that basking under artificial sunlight in their aquarium allowed the fish to raise their temperatures by 0.4–1.2 °C compared to the surrounding water at 4 cm and 7 cm respectively. Under these modest temperature increases the modelling work suggests drag reduction of less than 1%, which we argue would be offset by the increased cost of swimming near the surface and quickly lost when the animal starts swimming.

In conclusion we argue that dark coloration in large fast-swimming marine organisms is likely to produce a much lower drag reduction through solar warming than previous modelling studies have implied. But even if the most optimistic estimates of this drag reduction are true, they would be dominated by the increase in drag that would be experienced by any organism swimming near enough the surface to benefit from solar warming. The evolutionary drive for the dark coloration in aquatic organisms must lie chiefly in other mechanisms.

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