© 2014. Published by The Company of Biologists Ltd | The Journal of Experimental Biology (2014) 217, 4229-4236 doi:10.1242/jeb.108225

RESEARCH ARTICLE

Bottlenose dolphins modify behavior to reduce metabolic effect of tag attachment

Julie M. van der Hoop[1,2,*], Andreas Fahlman[3], Thomas Hurst[2], Julie Rocho-Levine[4], K. Alex Shorter[5], Victor Petrov[6] and Michael J. Moore[2]

ABSTRACT

Attaching bio-telemetry or -logging devices ('tags') to marine animals for research and monitoring adds drag to streamlined bodies, thus affecting posture, swimming gaits and energy balance. These costs have never been measured in free-swimming cetaceans. To examine the effect of drag from a tag on metabolic rate, cost of transport and swimming behavior, four captive male dolphins (*Tursiops truncatus*) were trained to swim a set course, either non-tagged (*n*=7) or fitted with a tag (DTAG2; *n*=12), and surface exclusively in a flow-through respirometer in which oxygen consumption ($\dot{V}_{O_2}$) and carbon dioxide production ($\dot{V}_{CO_2}$; ml kg^{-1} min^{-1}) rates were measured and respiratory exchange ratio ($\dot{V}_{O_2}/\dot{V}_{CO_2}$) was calculated. Tags did not significantly affect individual mass-specific oxygen consumption, physical activity ratios (exercise $\dot{V}_{O_2}$/resting $\dot{V}_{O_2}$), total or net cost of transport (COT; J m^{-1} kg^{-1}) or locomotor costs during swimming or two-minute recovery phases. However, individuals swam significantly slower when tagged (by ~11%; mean ± s.d., 3.31±0.35 m s^{-1}) than when non-tagged (3.73±0.41 m s^{-1}). A combined theoretical and computational fluid dynamics model estimating drag forces and power exertion during swimming suggests that drag loading and energy consumption are reduced at lower swimming speeds. Bottlenose dolphins in the specific swimming task in this experiment slowed to the point where the tag yielded no increases in drag or power, while showing no difference in metabolic parameters when instrumented with a DTAG2. These results, and our observations, suggest that animals modify their behavior to maintain metabolic output and energy expenditure when faced with tag-induced drag.

KEY WORDS: DTAG, Respirometry, Drag, Bio-logging, Transmitter, Cost of transport, Tagging

INTRODUCTION

Bio-telemetry and bio-logging devices ('tags') allow for direct measurements of movement and behavior in free-ranging animals. These technologies have been especially useful for the study of marine animals, which perform the majority of life functions out of view. Tag data have provided insights into the physiology, spatial ecology, acoustics and kinematics of marine animals, and have been used in combination with other measures (e.g. prey field sampling, genetics, oceanography) to interpret the role of a tagged animal in its environment. As technologies have improved, the cost and size of tags have been reduced, whereas sensing capabilities have increased. This has led to growth in the number and diversity of tags and study subjects (Kooyman, 2004; Crossin et al., 2014), as well as scientific efforts to deploy tags: the number of permits issued in the United States for tagging studies on marine turtles alone has tripled in the last decade (Jones et al., 2013).

However, the attachment of external devices is not benign (for reviews, see e.g. Wilson and McMahon, 2006; McMahon et al., 2011). Whereas animal-specific rules intended to minimize tag impact have been established, e.g. that bird tags should not exceed 3 or 5% of the animal's body mass (Vandenabeele et al., 2012), there currently exist few guidelines for aquatic, terrestrial or flying mammals (American Society of Mammalogists, 1998). Of 559 published studies having deployed bio-logging tags on free-ranging marine mammals from 1965 until 2012, only 2.5% addressed device influence, and only 1% focused on cetaceans (T. McIntyre, personal communication). The difficulty of establishing suitable controls by quantifying behavior and energetics from untagged animals at the same resolution as tagged animals probably limits the ability to perform such investigations (Shorter et al., 2014).

For marine mammals, hydrodynamic drag is of primary concern, where tag volume, shape, position and presence (and if so, size) of an antenna can significantly affect drag loading (Bannasch et al., 1994; Culik et al., 1994; Wilson et al., 2004; Jepsen et al., 2005; Vandenabeele et al., 2012). In an experimental study, Skrovan et al. (Skrovan et al., 1999) showed that instrumented dolphins experience higher drag loading, especially when tags are quite large compared with the subject. To minimize the impact to the animal, design and analysis tools [e.g. computer-aided design (CAD) and computational fluid dynamics (CFD)] and physical models are used to estimate and predict drag coefficients and force balances of tag subjects with a given tag position or orientation (Bannasch et al., 1994; Pavlov et al., 2000; Ianov, 2001; Pavlov and Rashad, 2012; Jones et al., 2013; Shorter et al., 2014).

Although these studies have provided useful estimates of the effect of drag from instruments, the models do not capture the full dynamics of a free-swimming animal. *In situ* measurements are required to determine how changes, such as body undulation, unsteady flow and tag movement (i.e. sliding) affect forces and moments on an animal, and to directly couple the effect of tag drag with changes in energy consumption. Previous studies on drag manipulation in marine mammals have shown changes in metabolic cost measured directly via respirometry (Feldkamp, 1987), or indirectly by metabolic heat production (Cornick et al., 2006). It is therefore reasonable to assume that increased drag from an instrument could translate into an increase in metabolic cost (Boyd et al., 1997; Jones et al., 2013). Using the doubly labeled water

[1]Massachusetts Institute of Technology-Woods Hole Oceanographic Institution Joint Program in Oceanography/Applied Ocean Science and Engineering, 77 Massachusetts Avenue, Cambridge, MA 02139, USA. [2]Woods Hole Oceanographic Institution, 266 Woods Hole Road, Woods Hole, MA 02543, USA. [3]Texas A&M University Corpus Christi, 6300 Ocean Drive, Corpus Christi, TX 78412, USA. [4]Dolphin Quest Oahu, 5000 Kahala Avenue, Honolulu, HI 96816, USA. [5]University of Michigan, 2350 Hayward, Ann Arbor, MI 48109, USA. [6]University of Michigan, 2355 Bonisteel Boulevard, Ann Arbor, MI 48109, USA.

*Author for correspondence (jvanderhoop@whoi.edu)

Received 18 May 2014; Accepted 13 October 2014

List of symbols and abbreviations

A_w	wetted surface area
BP	barometric pressure
C_D	profile drag coefficient
COT	cost of transport
COT_{min}	minimum cost of transport
COT_{net}	net cost of transport
DTAG	digital acoustic recording tag
D_d	dolphin body drag
D_t	tag drag
D_T	total drag
F_e	excurrent fraction of O_2
F_i	incurrent fraction of O_2
LC	locomotor costs
PAR	physical activity ratio
P_L	locomotory power
RER	respiratory exchange ratio
Rh	relative humidity
U	speed
$\dot{V}_{CO_2}$	rate of carbon dioxide production
$\dot{V}_e$	excurrent flow rate
$\dot{V}_{O_2}$	rate of oxygen consumption
WVP	water vapor pressure
η	efficiency
ρ	fluid density

method, Costa and Gentry (Costa and Gentry, 1986) found an average 19% increase in oxygen consumption in female Northern fur seals at sea over a number of weeks, when wearing a tag estimated to increase drag by up to 70%. To our knowledge, no investigations of this kind have been carried out with cetaceans.

As tag designs progress (Balmer et al., 2014; Shorter et al., 2014), it is crucial to quantify the impact of a tag on the subject and to determine whether amelioration is required. Here, the modeled increase in drag created by a tag is combined with an experimental study of the energetic cost of swimming with and without a tag. A conventional drag model is used to quantify the effect of different swimming speeds and forces on power output, and to provide insight into the experimental results. It is hypothesized that the added drag from the tag will result in increased energetic output during the swimming task. This hypothesis is tested using experiments with four trained bottlenose dolphins (*Tursiops truncatus* Montagu 1821) that perform a series of swimming tasks when wearing and not wearing a bio-logging tag (Digital Acoustic Recording Tag, DTAG2; Johnson and Tyack, 2003). Metabolic parameters and swimming speed of the animals were measured to determine the energetic and behavioral effects of instrumentation on a small cetacean. This work presents an experimental design for the direct measurement of behavioral modifications created by bio-logging tags on cetaceans for the first time.

RESULTS

The conceptual model illustrates tradeoffs between swimming speed and drag forces when wearing and not wearing a tag (Fig. 1A). Individuals swam significantly slower (by 11%; $F_{1,14}$=7.24, P=0.0176) when wearing a tag (mean±s.d. 3.31±0.35 m s^{-1}) than when non-instrumented (3.73±0.41 m s^{-1}; Fig. 2C). No individual variation in swimming speed was detected ($F_{3,14}$=2.79, P=0.0794). Because of this observed decrease in swimming speed when wearing a tag, the model predicts an average change in drag of −4.1 N (range from −13.3 to 0.4 N) or −7% (range from −20.5% to 9.3%) when instrumented (Fig. 1A, blue=tag versus black=no tag). Had individuals maintained the faster swimming speeds observed during the non-tagged trials, the modeled drag force would have increased by 10.1 N (8.2–11.6 N) or by 15% (12.9–16.3%; Fig. 1A, red). Estimates of power output between non-tagged and tagged trials at their observed speeds were not significantly different (Fig. 1B, blue, black; Student's *t*-test, T_{17}=1.12, P=0.279). However, maintaining a faster swimming speed with the increased drag loading created by the tag would require the animal to significantly increase power output during swimming, by 29–59% (Fig. 1B, red; Student's *t*-test, T_{17}=–2.22, P=0.041). Slowing down to observed speeds reduced potential drag loading by 14.3 N (7.7–24.8 N) and power expenditure by 530 W (270–920 W) or 41.7% (26.8–61.5%).

During the experiment, respiratory gases were measured for four male bottlenose dolphins (Table 1) from 11 to 15 November 2012. From this, metabolic rate was calculated before, during and after the animals completed a set swimming protocol, either non-instrumented (n=7) or while wearing a DTAG2 (Fig. 3; n=12). The number of trials per individual and the order in which they were performed are listed in Table 1. Across individuals, no significant linear trends in swimming $\dot{V}_{O_2}$ (P=0.130–0.581; R^2=0.08–0.96) or speed (P=0.147–0.465; R^2=0.21–0.59) with trial number were apparent.

Individuals showed no difference in oxygen consumption rate ($\dot{V}_{O_2}$; ml O_2 kg^{-1} min^{-1}) when wearing versus when not wearing a tag during rest, swim (Fig. 2A) or two-minute recovery phases (Table 2). Oxygen consumption rates were significantly different between individuals for all phases ($F_{3,14}$=4.85, 4.07, 9.11; P=0.0162, 0.0285, 0.0013, respectively). The slopes and intercepts of the respiratory exchange ratio (RER, $\dot{V}_{O_2}/\dot{V}_{CO_2}$) throughout the recovery period did not significantly differ between tag and no-tag conditions (Table 2), and significant individual variability was evident in the slopes ($F_{3,14}$=4.37, P=0.0228) but not the intercepts ($F_{3,14}$=1.46, P=0.268) of the recovery RER. Measured RER values for resting (1.00±0.02)

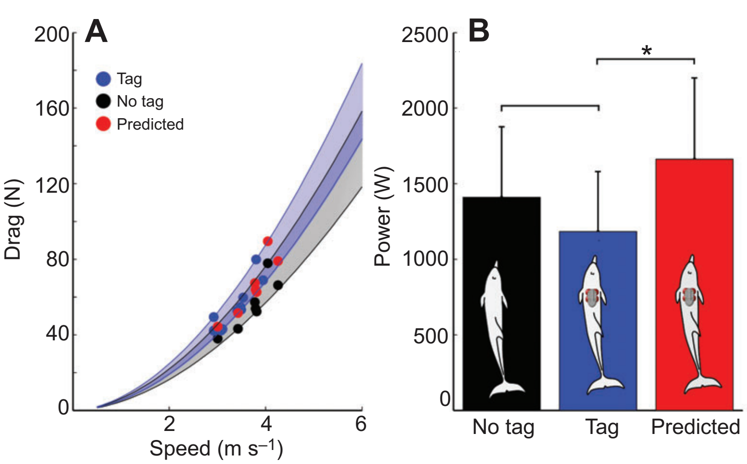

Fig. 1. Bio-logging tags increase the drag forces experienced by bottlenose dolphins. (A) Envelope of the drag force (N) estimated for the four bottlenose dolphins in this study when not wearing (black) and wearing (blue) bio-logging tags across a range of swimming speeds (lines; m s^{-1}) and for specific observed swimming speeds (dots; m s^{-1}). Red dots reflect the predicted drag loading in the tagged condition if individuals maintained their non-tagged swimming speed. (B) Mean ± s.d. power output (W) estimated for when (blue) wearing a tag, swimming at observed speeds; and (black) not wearing a tag, swimming at observed speeds; and predicted for when (red) wearing a tag, if individuals had maintained their non-tagged swimming speed.

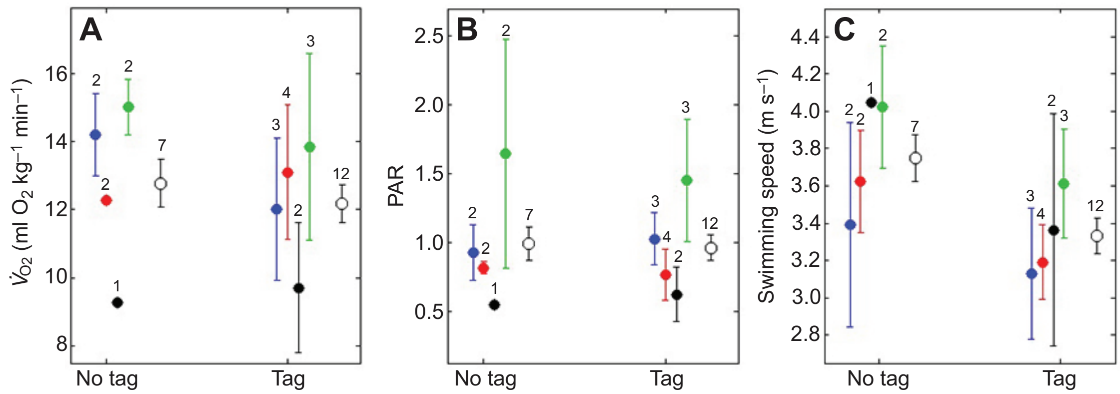

Fig. 2. Bio-logging tags do not significantly affect the metabolic rate of bottlenose dolphins, but tagged dolphins swim at significantly lower speeds. (A) Individual mean ± s.d. (Kolohe, blue; Liko, red; Lono, black; Nainoa, green) and marginal mean ± s.e.m. (white) oxygen consumption rates ($\dot{V}_{O_2}$; ml O_2 kg^{-1} min^{-1}). (B) Physical activity ratios (PAR, nondimensional) measured during swimming, and (C) swimming speeds (m s^{-1}) of four bottlenose dolphins, when not wearing and when wearing a bio-logging tag.

were significantly greater than during swimming (0.96±0.01; T_{36}=7.430, P<0.001); there was no significant difference in RER between swimming and recovery (0.97±0.01; T_{36}=−1.9405, P=0.060).

Whereas individuals had significantly different physical activity ratios (PAR; $F_{3,14}$=7.12, P=0.0039), being the energetic cost of a specific activity over the resting metabolic rate, there was no significant effect of wearing a tag (Fig. 2B, Table 2). This parameter indicates that on average the swimming task increased $\dot{V}_{O_2}$ by a factor of 2.01±0.89 over resting values. Although it was expected, individual total and net cost of transport (COT_{tot}, COT_{net}; J m^{-1} kg^{-1}) were not significantly greater when wearing (COT_{tot}=1.32±0.01, COT_{net}=0.612±0.095) than when not wearing a tag (COT_{tot}=1.18±0.12, COT_{net}=0.371±0.385; T_3=1.49, 1.41; P=0.116, 0.125, respectively; Table 2). Similarly, mean individual locomotor costs (LC) were not significantly higher in tagged (0.47±0.10) than in non-tagged trials (0.32±0.32, T_3=0.993; P=0.197; Table 2).

Pre-exercise resting metabolic rates were measured when individuals were fasted and when they had been fed up to 6.2 kg of a mix of herring, capelin and squid, depending on the time of day. Individuals had significantly higher resting oxygen consumption rates ($\dot{V}_{O_2}$) when fed (n=28; mean±s.d. 6.65±1.73 ml O_2 kg^{-1} min^{-1}) compared with fasted (n=10; 4.34±0.53 ml O_2 kg^{-1} min^{-1}; $F_{1,33}$=21.44; P<0.001). There was no significant difference in RER ($F_{1,33}$=1.58; P=0.217) between fasted (0.994±0.019) and fed (1.00±0.0203) rest periods. Significant individual variability was observed in resting $\dot{V}_{O_2}$ ($F_{3,33}$=5.45; P=0.0037) and RER ($F_{3,33}$=3.38; P=0.0298). As such, individuals were fed during the experimental trials (n=19).

DISCUSSION

When faced with higher drag loading, either naturally (Williams, 1989), experimentally (Cornick et al., 2006), or inadvertently (van der Hoop et al., 2014), marine mammals have been shown to (1) increase swimming effort by increasing fluke stroke rate and/or amplitude (Williams, 1989; Cornick et al., 2006; Aoki et al., 2011), (2) reduce the use of stroke-and-glide gaits (Cornick et al., 2006) and (3) alter the speed and angle of dive ascents and descents (Boyd et al., 1997; van der Hoop et al., 2014). Experiments have shown drag-attributed reductions in average swimming speed in Steller sea lions fitted with harnesses, increasing body drag by 23% (Cornick et al., 2006), and in maximum swimming speeds by attaching drag collars to bottlenose dolphins (Lang and Daybell, 1963) and wooden blocks to Antarctic fur seals (Boyd et al., 1997; Lang and Daybell, 1963).

In this work, it was expected that metabolic rate would significantly increase due to additional drag loading from wearing a tag. Instead, (1) an observed 11% reduction in swim speed when wearing the tag (Fig. 2C), (2) a lack of any significant effect on measured metabolic parameters (Fig. 2A,B) and (3) the reduced power output predicted by the model at slower swimming speeds (Fig. 1B) all suggest that tagged animals modulate their behavior to maintain energy expenditure when faced with greater drag forces. Individuals slowed to the point where the tag yielded no increases in drag or power (Fig. 1B). Similar reductions in speed have been associated with drag from tags or other instruments. Blomqvist and Amundin (Blomqvist and Amundin, 2004) found significantly reduced activity levels in tagged bottlenose dolphins, in which fast-swimming behaviors significantly increased following tag removal. Similarly, bottlenose dolphins instrumented with a particularly large tag (14 kg, ~22% of frontal area; Davis et al., 1999) swam on average 9–10% slower than when non-instrumented (Skrovan et al., 1999), and drag collars of various diameters reduced maximum swimming speeds by 36% in bottlenose dolphins (Lang and Daybell, 1963).

Table 1. Body sizes, resting metabolic rates and order of experimental trials

Individual	Length (m)	Girth (m)	Mass (kg)	Wetted surface area (m^2)	Mean ± s.d. fed RMR (N trials)	Experimental trial order (N trials)
Kolohe	2.61	0.44	186.9	2.3	6.33±1.54 (7)	CTTCT (5)
Liko	2.54	0.40	160.6	2.2	7.95±1.49 (8)	CTTTCT (6)
Lono	2.73	0.47	249.5	2.9	6.96±1.39 (6)	TCT (3)
Nainoa	2.46	0.41	165.6	2.2	5.22±1.43 (7)	CTTTC (5)

Measured body length, girth (m) and mass (M, kg), calculated wetted surface area (m^2), mean ± s.d. resting metabolic rate (RMR; ml O_2 kg^{-1} min^{-1}) calculated over N fed trials and the order of N experimental trials (C=Control; T=Tag) for four male bottlenose dolphins. Wetted surface area was calculated from mass as A_M=0.08$M^{0.065}$ from Fish (Fish, 1993), based on a number of odontocete species.

The Journal of Experimental Biology (2014) doi:10.1242/jeb.108225

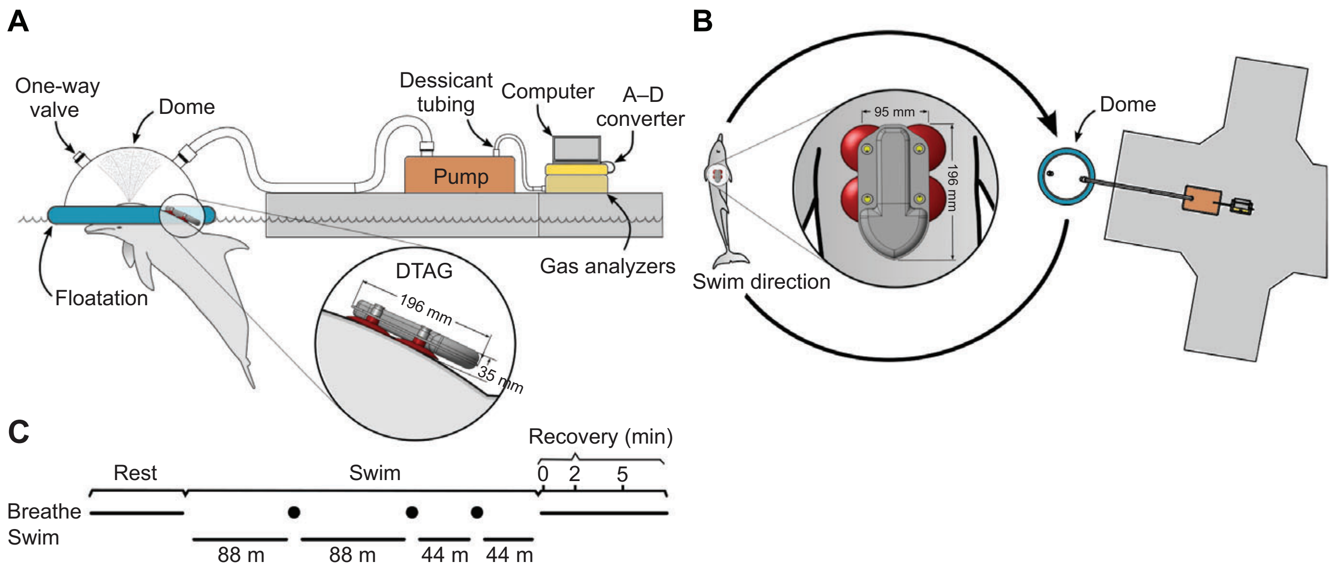

Fig. 3. Experimental setup. (A) Dockside setup of a bottlenose dolphin wearing a DTAG2 in the respirometry system (see the Materials and methods for full description), (B) the 44 m swimming track departing from and returning to the respirometry dome, and (C) the phases over which respirometry-based oxygen consumption rates were measured from four bottlenose dolphins Thick horizontal black lines represent time periods during which individuals were breathing in the respirometer (Breathe) or performing the swimming task of specific distances (Swim). Black dots represent pauses between specific laps in which individuals returned to the respirometer for two to three breaths.

Optimal swimming speed is a function of drag, but not of buoyancy or dive depth (Suzuki et al., 2014), and is proportional to (resting metabolic rate/drag)$^{-3}$ (Alexander, 1999; Sato et al., 2010). Based on this relationship, the influence of tag-related drag should have decreased optimal swimming speeds in our experimental animals by 1.8% on average. Given that (1) the dolphins in this study were swimming at speeds much greater than optimal (observed 2.9–4.3 m s^{-1} versus estimated optimal 1.6–1.9 m s^{-1}), (2) metabolically optimal (within 10% of COT_{min}) speeds of bottlenose dolphins are 1.9–3.2 m s^{-1} (Yazdi et al., 1999) and (3) drag increases with the square of speed, it is not surprising that a greater reduction in speed was observed.

The swimming speeds of experimental trials were within routine swimming speeds of *T. truncatus* in aquaria (1.2–6.0 m s^{-1}; Fish, 1993) and while free-swimming (1.6–5.6 m s^{-1}; Rohr et al., 2002). Experimental studies have determined minimum COT (COT_{min}) to occur at 2.1 and 2.5 m s^{-1} (Williams et al., 1993; Yazdi et al., 1999). Although dolphins in this study swam above reported COT_{min} speeds (at 2.9–4.3 m s^{-1}), they remained in the metabolically optimal range of swimming speeds for 33% of trials and showed a comparable average COT of 1.28 J m^{-1} kg^{-1} [compared with 1.29 and 1.16 J m^{-1} kg^{-1} (Williams et al., 1993; Yazdi et al., 1999)].

In this experiment the animals were required to swim completely submerged in order to capture all breaths in the respirometry dome (Fig. 3), thereby limiting the duration of the swimming phase. Previous studies (Taylor et al., 1987; Williams et al., 1993) conducted exercise tests on a number of mammal species over a minimum of 3 to 5 minutes, although $\dot{V}_{O_2}$ half times have yet to be established for marine mammals. As such, the swimming trials conducted in this experiment probably do not allow individuals to reach steady-state oxygen consumption.

Whereas the tagged and untagged metabolic parameters measured during the experiment did not differ, they agree with previous studies on bottlenose dolphins. Mean fasted (4.34±0.53 ml O_2 kg^{-1} min^{-1}) and fed (6.65±1.73 ml O_2 kg^{-1} min^{-1}) resting metabolic rates (Table 1) fall within the range of those reported over the last 60 years (4.0–7.6 ml O_2 kg^{-1} min^{-1}; see table 3 in Yazdi et al., 1999). It is not surprising that individuals showed different levels of physical fitness,

Table 2. Oxygen consumption rates, physical activity ratios, respiratory exchange ratios and costs of transport

	No tag	Tag	$F_{tag\ (1,14)}$	P_{tag}
Resting $\dot{V}_{O_2}$ (ml O_2 kg^{-1} min^{-1})	7.04±1.71	7.01±2.10	0.08	0.787
Swim $\dot{V}_{O_2}$ (ml O_2 kg^{-1} min^{-1})	13.2±2.2	12.4±2.4	0.46	0.508
Recovery $\dot{V}_{O_2}$ (ml O_2 kg^{-1} min^{-1})	13.4±2.4	13.7±3.5	0.01	0.922
PAR	2.10±1.11	1.96±0.79	0.04	0.840
RER slope	(7.60±7.33)E-6	(9.13±8.17)E-6	0.08	0.781
RER intercept	0.967±0.017	0.961±0.013	0.69	0.419
Total COT (J m^{-1} kg^{-1})	1.18±0.12	1.32±0.14	1.493[a]	0.116[b]
Net COT (J m^{-1} kg^{-1})	0.371±0.385	0.612±0.095	−1.44[a]	0.125[b]
Locomotor cost contribution (%)	0.32±0.32	0.47±0.10	−0.993[a]	0.197[b]

Mean ± s.d. oxygen consumption rates ($\dot{V}_{O_2}$) during rest, swim and recovery phases; physical activity ratio (PAR); slopes and intercepts fit to the respiratory exchange ratio (RER) during post-exercise recovery; total and net cost of transport (COT); and the contribution of locomotor costs to COT in four male bottlenose dolphins performing a swimming task while not wearing and while wearing a bio-logging tag. Test (*F* and *t*) and *P* statistics are for the effect of tag in two-way ANOVA with no interaction.
[a]t_3 value; [b]*P* value.

as evidenced by significant individual variability in the effect of exercise on oxygen consumption rates (PAR) and recovery from exercise (slope of RER). It was expected that total and net COT would be greater for each individual when wearing a tag, given the decrease in speed and no difference in metabolic rate. High variability in both $\dot{V}_{O_2}$ and swimming speed probably affects the ability to detect statistically significant differences. However, mean COT_{tot}, COT_{net} and locomotor cost contributions are increased when tagged (Table 2); net COT in particular is nearly double in instrumented individuals. COT was one of the few metabolic parameters that was not significantly different between individuals, which reinforces the frequent use of this measure for inter-individual and inter-species comparisons (Tucker, 1970; Schmidt-Nielsen, 1972; Williams, 1999). Tagged (6.52±1.42 W kg^{-1}), non-tagged (7.83±1.66 W kg^{-1}) and predicted (9.22±1.99 W kg^{-1}) power estimates fall well within the range (0.3–23.7 W kg^{-1}) of mass-specific power estimates for *T. truncatus* using a variety of modeling methods across speeds 1–6 m s^{-1} (reviewed by Fish et al., 2014). Power may be separately estimated from O_2 consumption rates, in which tagged (5.72±0.27 W kg^{-1}) and non-tagged power (4.54±0.26 W kg^{-1}) are slightly greater than those calculated in Yazdi et al. (Yazdi et al., 1999), but within the range of power measured at higher speeds (2.9 m s^{-1}) in Williams et al. (Williams et al., 1993). The disparity in power estimates from mechanical models and oxygen consumption measurements is an issue that remains unresolved in the field (Daniel, 1991).

Importantly, failure to demonstrate a statistically significant difference in metabolic parameters does not allow for the complete dismissal of instrument effects on metabolic rate, especially when considering limited sample sizes. It is possible that reduced swimming speeds observed in this study might be due to factors other than instrument drag and energy economy, potentially limiting the application of these results to wild populations. Interpretation of the swimming task by the dolphins might have been variable, as the discriminatory stimulus provided to animals was for a ‘fast swim’, although not at a specific pace. Individuals may have experienced additional wave drag from near-surface swimming (Hertel, 1969), required by the experimental protocol and limited by the depth of the study site.

The observed behavioral impacts of tag-associated drag remain applicable to wild animals. In certain scenarios, wild animals might be able to modulate their swimming behaviors without affecting fitness (prey capture, or competition with non-tagged conspecifics). However, animals might not be able to reduce their top velocities or acceleration; especially during high-speed pursuits chasing active prey (Aguilar Soto et al., 2008), the energetic cost due to extra drag would be considerable. In a social context, cohesion is often maintained between tagged and non-tagged members of a social group (Wursig, 1982), which would require increased power output and metabolic cost by tagged individuals to sustain pace (Fig. 1A,B). It is likely that tradeoffs between managing additional energy expenditure are balanced with the demands that foraging and social behaviors require: despite 13% and 10% slower ascent and descent rates during dives, respectively, Northern elephant seals with added drag experienced 65% increases in field metabolic rate (Maresh et al., 2014). The short-term nature of the suction cup archival tags used here provides confidence that any metabolic or behavioral tag effects would occur over an extremely short proportion of a subject’s life and that these effects would probably not carry over after the tag has fallen off. In addition to these concerns of animal welfare and scientific ethics, data reliability must be considered: it is crucial to ensure that tagged individuals exhibit normal behaviors for measurements to be meaningful and representative of the remainder of the population (e.g. Wilson and McMahon, 2006).

Although the scope of this study limits the creation of hard design rules with respect to tag size and increased drag loading, the results presented here continue to support the argument for the creation of tags that minimize drag loading on the animal. The tag used in this study is an older generation model, the DTAG2. Modeled and measured drag forces on the current DTAG3 model have been described by Shorter et al. (Shorter et al., 2014), in comparison with two alternative model designs. The current DTAG3 is one-third smaller than the DTAG2 (frontal area 24 cm^2), with smaller suction cups (4.5×1.5 cm, diameter × height) holding the tag close to the attachment surface, thereby minimizing lift forces. A more streamlined urethane housing containing all of the tag elements (electronics, VHF and flotation) minimizes geometric disruptions in the flow around the housing, reducing drag forces. Similar to previous papers on tag design (Bannasch et al., 1994; Culik et al., 1994; Hazekamp et al., 2010; McMahon et al., 2011; Jones et al., 2013), the study by Shorter et al. (Shorter et al., 2014) suggests that tag designs should: (1) minimize frontal cross-sectional areas and maintain a smooth exterior to reduce drag; (2) cover suction cups or other exposed features to reduce flow stagnation and wake generation; and (3) reduce lift by minimizing the attachment area and by adding flow channels or spoilers to reduce differences in flow speed above and below the housing, or redirect flow to counter lift.

In order to establish acceptable limits of drag associated with instrumentation (e.g. the 3% or 5% rules for birds), additional studies investigating the degree of impact of different amounts of drag loading are required and are underway.

CONCLUSIONS

Wearing a tag during the prescribed swimming task presented in this work resulted in no detectable effect on the oxygen consumption rate of bottlenose dolphins. Behavioral changes in the form of reduced swimming speed appear to be a mechanism by which individuals avoid increased energy expenditure from tag-induced drag. Further studies to (1) measure differences in energy consumption when swimming at consistent, established speeds; (2) identify thresholds below which tag size does not affect metabolic cost; and (3) investigate individual response to increased drag via modulation of kinematics and swimming speed are currently underway and will better link the potential tradeoffs observed in this study.

MATERIALS AND METHODS

CFD and conceptual model

A conceptual model was used to compare theoretical drag forces on instrumented and non-instrumented dolphins. Dolphin body drag (D_d; N) was estimated based on the conventional model of a turbulent flat plate (Hoerner, 1965; Webb, 1975; Fish and Rohr, 1999) with specific dimensions and estimated surface areas of the four dolphins used in the experiment (Table 1). The additional drag force imparted to the animal by the DTAG2 was estimated with computational fluid dynamics (CFD) simulations using STAR-CCM+ (version 9.04). This commercial code (STAR-CCM+, 2014) solves the transport equations for continuity and three-dimensional (3D) momentum on a very fine 3D mesh. The two-layer Reynolds–Averaged Navier–Stokes (RANS) approach for the solution of the k-ε transport equations was used to model turbulence (Rodi, 1991; STAR-CCM+, 2014). All simulations used trimmed cell mesh (9.6 m cells) with an extra mesh refinement in the region located under the tag and a prismatic cell layer at the wall (Fig. 4A). In order to achieve comparable simulation results to those presented by Shorter et al. (Shorter et al., 2014), the overall simulation domain consisted of a 1.7-m-long duct with a 0.4 m × 0.4 m square cross-section. During all of the simulations, the tag was located 1 m from the inlet with real wall (no slip) flow conditions

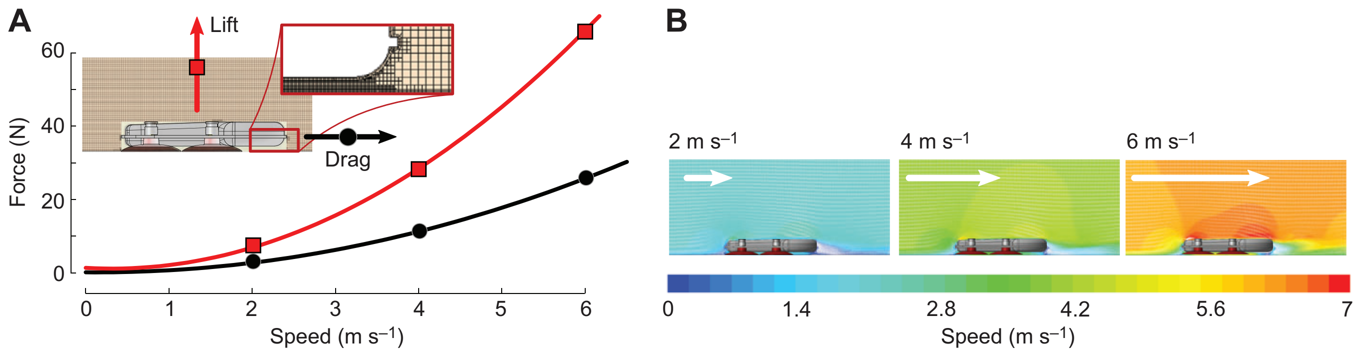

Fig. 4. Lift and drag forces on a DTAG2 increase with speed. (A) Lift (red) and drag (black) forces (N) on a DTAG2, and (B) flow visualization at uniform velocity profiles of 2, 4 and 6 m s^{-1} from computational fluid dynamics (CFD) simulations using STAR-CCM+ (version 9.04) over 9.6 m cells, with extra mesh refinement in the region located under the tag (A). See main text for further CFD details.

on the lower wall, and ideal wall (free slip) conditions on the side and upper walls. Mesh sensitivity was performed using three different meshes (coarse, medium and fine) with 2 million, 9.6 million and 18 million cells, respectively. Variation in drag and lift forces from medium to fine mesh was ~1%. To estimate the inlet velocity profile effect, sensitivity analyses were performed on a shorter domain with the tag located 0.15 m from the inlet using two velocity profiles, fully developed and uniform, both with mean flow velocities of 4 m s^{-1}. The drag and lift forces from simulation with the fully developed flow were 15% and 10% lower than from uniform flow, respectively. Simulations using a uniform velocity profile were then conducted at mean flow velocity profiles of 2, 4, 6, 8 and 10 m s^{-1}. For all simulations, the side forces were considered as self-compensating, because of the tag symmetry. A polynomial function was used to interpolate forces at flow speeds between simulated points (Fig. 4B).

Total drag (D_T) on an individual was the theoretical drag on each dolphin body (D_d), plus the contribution of the tag (D_t) when applicable:

$$D_T = D_d + D_t \,, \quad (1)$$

$$D_T = \frac{1}{2}\rho U^2 A_M C_D + D_t \,, \quad (2)$$

where ρ is fluid density (seawater; 1025 kg m^{-3}); U is swimming speed (m s^{-1}); A_M is the wetted surface area of each dolphin calculated from mass (M) as in Fish (Fish, 1993) ($0.08M^{0.065}$; Table 1); and C_0 is the profile (Blake, 1983; van der Hoop et al., 2014) drag coefficient.

Locomotory power (P_L; W) was estimated for each drag condition (tag and no tag) as:

$$P_L = \frac{D_T U}{\eta} \,, \quad (3)$$

with an efficiency factor η of 0.15 (Fish, 1993; Fish and Rohr, 1999).

Drag augmentation factors (see e.g. Fish, 1993; Fish and Rohr, 1999) were omitted as theoretical drag forces from the basic model alone agreed with those of post-parturition female (Noren et al., 2011) and non-instrumented bottlenose dolphins (Skrovan et al., 1999) estimated by glide deceleration. Locomotor power requirements were similar to those calculated by Fish (Fish, 1993) with a hydromechanical model [i.e. following Chopra and Kambe (Chopra and Kambe, 1977)].

The model was populated with observed swimming speeds of individuals in tagged and non-tagged conditions. This conventional illustrates our hypothesis and supports our experimental setup and approach by (1) estimating the drag forces and power requirements likely experienced during experimental swimming trials; and (2) assessing the potential energetic benefits achieved by reducing swimming speed when wearing a tag.

Experiment

To test the null hypothesis that wearing a tag does not affect metabolic rate, cost of transport, or swimming behaviors, four captive male *T. truncatus* (Table 1) were trained to perform a fully submerged swim around a set course and surface exclusively in a metabolic dome (Fig. 3), either non-instrumented or while wearing a bio-logging tag (DTAG2; Fig. 3). The individual determined the pace of the swimming task, i.e. swimming speed was not prescribed, and no speed target was provided. The order of tagged versus control (i.e. non-tagged) trials was determined randomly, and was made more random by certain trials being unusable when an individual breathed outside of the dome. Metabolic rate was measured for the duration of each trial, consisting of pre-exercise rest, swim and recovery phases. Animals were inactive under the respirometry dome during rest and recovery phases (Fig. 3C). The swimming course consisted of a 44 m circumference oval loop departing from and returning to the dome (Fig. 3B). Each trial consisted of six laps (Fig. 3C): two double laps, separated by two to three breaths in the respirometer, and two single laps, again separated by two to three breaths between excursions. The swimming phase was 1–1.5 min in duration, with average breath hold durations of 19 s (range 10–28 s). Animals were reinforced throughout the trial with positive encouragement and tactile stimulation, and with up to 1.8 kg of a mix of capelin, herring and squid 5 min into the recovery phase. Tags were attached by hand on the dorsal midline halfway between the blowhole and dorsal fin.

Tags

The DTAG2 is a bio-logging tag equipped with depth and temperature sensors, three-axis accelerometers and magnetometers sampling at 50 Hz, and two hydrophones sampling at 192 kHz (Johnson and Tyack, 2003). A polyethylene casing houses the electronics, a syntactic foam float to provide positive buoyancy, a VHF radio beacon with a 44 cm antenna for tracking and four 6.3×2 cm (diameter × height) suction cups for attachment (Fig. 3A,B). The fully assembled tag weighs 350 g in air and has a frontal area of 38 cm^2, ~3% of the frontal area of the smallest tagged dolphin based on girth.

Respirometry

A floating transparent acrylic dome (59 l internal volume; Stock no. 02-PD250CA-1687, California Quality Plastics Inc., Ontario, CA, USA) with circumferential buoyancy was used to collect respiratory gases and determine the rate of oxygen consumption ($\dot{V}_{O_2}$; ml O_2 min^{-1}) and carbon dioxide production ($\dot{V}_{CO_2}$; ml CO_2 min^{-1}) by flow-through respirometry (Fig. 3A). A mass flow-meter (Flow Kit Model FK500, Sable Systems International, Las Vegas, NV, USA) pulled air into the dome through a tube (~1 l volume) connected to a low-resistance one-way valve at flow rates between 400–500 l min^{-1}. A subsample of this gas was passed via Nafion tubing to fast-response O_2 and CO_2 analyzers (ML206, Harvard Apparatus, Holliston, MA, USA), with data recorded at 20 Hz and saved to a laptop computer. The gas analyzers were calibrated before and after the experiment, using a commercial mixture of 5% O_2, 5% CO_2 and balance N_2; and before and after each experimental trial, using ambient air.

Whereas the mass flow meter automatically corrected to standard temperature and pressure (STP), post-processing was required to correct all volumes to standard temperature, pressure and dryness (STPD). Flow was corrected for humidity by:

$$\text{Flow} = \frac{(\text{BP} - \text{WVP})}{\text{BP}} \,, \quad (4)$$

where BP was the average daily barometric pressure and WVP is water vapor pressure estimated from the Antoine equation using the average daily air temperature (grand mean 25.4°C, daily range 21–29°C). Relative humidity (Rh) was assumed to be 100% in the dome due to regional air humidity measurements (grand mean 66.2%, daily range 44–97%) and the effect of exhalation. Assuming 90% Rh instead of 100% Rh resulted in a difference of 0.3% for flow rate and 0.5% for instantaneous $\dot{V}_{O_2}$, indicating little sensitivity to this parameter.

The accuracy of the respirometry system was determined by simultaneous N_2- and CO_2-dilution tests (Fahlman et al., 2005), in which differences between the observed and expected values were within 2%. Addition of CO_2 confirmed minimal losses by dissolution in seawater (Fahlman et al., 2005). The effective volume of the system was 53 l, including the volume of the respirometer and the plastic hose to the analyzers (Bartholomew et al., 1981). With a flow rate of 450 l min^{-1}, this resulted in a time constant of 0.11 min. The time required to reach a 95% fractional transformation to a new steady state was 3.2 times this time constant, or 21 s (Fahlman et al., 2004).

From measured gas concentrations, $\dot{V}_{O_2}$ (ml O_2 kg^{-1} min^{-1}) was calculated as:

$$\dot{V}_{O_2} = \frac{\dot{V}_e \times (F_i - F_e)}{1 - F_i(1 - RQ)}, \quad (5)$$

where $\dot{V}_e$ is the excurrent flow rate; F_e and F_i the excurrent and incurrent fractions of O_2, respectively; and RER the respiratory exchange ratio ($\dot{V}_{CO_2}/\dot{V}_{O_2}$) (Koteja, 1996). Mass-specific average $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ were calculated for each phase by dividing the integrated instantaneous O_2 consumption or CO_2 production rates, respectively, over the duration (min) of the rest, swim (entire duration; i.e. time spent submerged and at the surface) and the first two minutes of the recovery (0–2 min after exercise) phase. Least-square linear regression analysis on the two-minute recovery phase RER was used to determine whether drag loading had an effect on the initial anaerobic metabolism (intercept) or the rate of return to resting values (slope).

The physical activity ratio (PAR; nondimensional) was calculated to detect the energetic cost of a specific activity over an individual's reference level (resting metabolic rate). In doing so, PAR controls for daily variability and for individual size and energy efficiency (Schutz et al., 2001). This method differs from the concept of metabolic equivalents (METs) only in that the resting energy expenditure is measured rather than estimated (Schutz et al., 2001; Byrne et al., 2005). PAR was calculated as the ratio of $\dot{V}_{O_2}$ during the swimming period and the pre-exercise rest period of a given trial.

Mass-specific cost of transport (COT; J m^{-1} kg^{-1}) describes the energetic cost of covering a unit distance per unit mass (Schmidt-Nielsen, 1972) and was calculated as the average mass-specific metabolic rate during the swim and two-minute recovery phases combined (ml O_2 kg^{-1} min^{-1}; the exercise metabolic rate) divided by average swimming speeds (m s^{-1}). The average energy conversion for lipid, protein and carbohydrate sources of 20.1 J ml^{-1} O_2 was used (Schmidt-Nielsen, 1997).

Both maintenance costs and locomotor costs (LC) contribute to cost of transport. The net cost of transport (COT_{net}; J m^{-1} kg^{-1}) can be calculated to provide a measure of locomotor cost normalized for both body mass and swimming speed (Williams, 1989; Rosen and Trites, 2002):

$$COT_{net} = \frac{(\text{Exercise metabolic rate} - \text{Resting metabolic rate}) \times \text{Energy conversion factor}}{\text{Swimming speed}}. \quad (6)$$

The contribution of LC to COT is then COT_{net} divided by COT. It is hypothesized that COT and COT_{net} would be greater and that LC would have larger contributions to COT in tagged trials.

Statistical analysis

To test whether individuals became conditioned to the respirometry apparatus or experimental protocol, linear models were fitted to swimming $\dot{V}_{O_2}$ and swimming speed versus trial number for each individual. Two-way ANOVA without interaction were used to test for the effect of individual and feeding condition (i.e. fasted or fed) on resting oxygen consumption rates ($\dot{V}_{O_2}$; ml O_2 kg^{-1} min^{-1}) and RER in rest periods. Two-way ANOVA without interaction were also used to test for the effect of wearing a tag on each individual's oxygen consumption rates ($\dot{V}_{O_2}$) during the three trial phases (rest, swim, recovery) and PAR, and on least-square linear regression slopes and intercepts of RER over the recovery phase. Two-sample *t*-tests were used to compare RER between resting and swimming, and between swimming and recovery periods. One-sided paired *t*-tests were used to determine whether average COT, COT_{net} and LC for each individual were significantly greater when tagged versus not tagged. Swimming speed was estimated by dividing the distance of the swimming track (44 m) by the time required for an individual to complete each lap or set of laps. Two-way ANOVA without interaction were used to test whether swimming speeds of each individual were significantly different in tagged than in non-tagged trials. All data processing, statistical analyses and modeling were coded in MATLAB (R2011a; MathWorks, Inc., Natick, MA, USA).

Acknowledgements
The authors give special thanks to Dolphin Quest Oahu, whose dolphin interactive facility at The Kahala Hotel & Resort served as a crucial, controlled research environment for this study. The collection of these data for the benefit of wild populations would not have been possible without the support of Dolphin Quest, their expert animal behaviorists and the amazing animals in their care. The study protocol was approved by WHOI Institutional Animal Care and Use Committee.

Competing interests
The authors declare no competing financial interests.

Author contributions
J.v.d.H., A.F., K.A.S., V.P., J.R.-L. and M.J.M. developed concepts; J.R.-L. directed animal husbandry and training; J.v.d.H., A.F., K.A.S., V.P., T.H. and J.R.-L. performed experiments and simulations; J.v.d.H. and A.F. processed and analyzed data; J.v.d.H., A.F., K.A.S., V.P., T.H., J.R.-L. and M.J.M. wrote the manuscript.

Funding
This project was funded by the National Oceanographic Partnership Program [National Science Foundation via the Office of Naval Research, N00014-11-1-0113]. Dolphin Quest provided kind support of animals, crew and access to resources. J.v.d.H. was supported by a Postgraduate Scholarship from the Natural Sciences and Engineering Research Council of Canada.

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