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# Calculating the ecological impacts of animal-borne instruments on aquatic organisms

**T. Todd Jones[1, 2*], Kyle S. Van Houtan[1, 3], Brian L. Bostrom[2], Peter Ostafichuk[4], Jon Mikkelsen[4], Emre Tezcan[4], Michael Carey[5], Brittany Imlach[2] and Jeffrey A. Seminoff[6]**

*[1]NOAA Fisheries, Pacific Islands Fisheries Science Center, Honolulu, HI, USA; [2]Department of Zoology, University of British Columbia, Vancouver, BC, Canada; [3]Nicholas School of the Environment and Earth Sciences, Duke University, Durham, NC, USA; [4]Department of Mechanical Engineering, University of British Columbia, Vancouver, BC, Canada; [5]Michael Carey Photography, Bellingham, WA, USA; and [6]NOAA Fisheries, Southwest Fisheries Science Center, La Jolla, CA, USA*

## Summary

**1.** Animal-borne instruments provide researchers with valuable data to address important questions on wildlife ecology and conservation. However, these devices have known impacts on animal behaviour and energetics. Tags deployed on migrating animals may reduce reproductive output through increased energy demands or cause phenological mismatches of foraging and nesting events. For marine organisms, the only tagging guidelines that exist are based on lift and thrust impacts on birds – concepts that do not translate well to aquatic animals. Herein, we provide guidelines on assessing drag from animal-borne instruments and discuss the ecological impacts on marine organisms. Of particular concern is the effect of drag from instruments to the welfare of the animals and for the applicability of collected data to wild populations.

**2.** To help understand how drag from electronic tags affects marine animals in the wild, we used marine turtles as model aquatic organisms and conducted wind tunnel experiments to measure the fluid drag of various marine turtle body types with and without commercially available electronic tags (e.g. satellite, TDR, video cameras). We quantified the drag associated with carrying biotelemetry devices of varying frontal area and design (squared or tear drop shaped) and generated contour plots depicting percentage drag increase as a framework for evaluating tag drag by scientists and wildlife managers. Then, using concepts of fluid dynamics, we derived a universal equation estimating drag impacts from instruments across marine taxa.

**3.** The drag of the marine turtle casts was measured in wind speeds from 2 to 30 m $s^{-1}$ (Re $3{\cdot}0 \times 10^4$–$1{\cdot}9 \times 10^6$), equivalent to 0·1–1·9 m $s^{-1}$ in seawater. The drag coefficient ($C_D$) of the marine turtles ranged from 0·11 to 0·22, which is typical of other large, air-breathing, marine vertebrates (0·08–0·26). The $C_D$ of tags in reference to the turtle casts was $0{\cdot}91 \pm 0{\cdot}18$ and most tags caused minimal additional drag ($< 5\%$) to adult animals, but the same devices increased the drag for juveniles significantly ($> 100\%$). The sensitivity of aquatic animals to instrument drag is a dynamic relationship between the fluid flow patterns, or $C_D$, and the frontal area ratio of the animal and tag.

**4.** In this paper, we have outlined methods for quantifying the drag costs from animal-borne instrumentation considering the instrument retention time (time to release from the animal) and the activity of the instrumented animal. With this valuable tool, researchers can quantify the drag costs from animal-borne instrumentation and choose appropriate tags for their intended study organism and question. Reducing drag will ultimately reduce the impact on the instrumented animals and lead to greater biological realism in the collected data.

**Key-words:** animal welfare, biotelemetry, cost of transport, hydrodynamic, permit, phenological mismatch, swim velocity, tagging, tracking

## Introduction

Animal-borne instruments (see Glossary, Table 1) play important roles in understanding the behaviour, ecology and physiology of free-ranging animals and their response to ever-changing environmental conditions (see Cooke *et al.* 2004). With the continued loss of biodiversity and the ever-expanding need for data on the basic biology of wildlife and their associated ecosystems, we are likely to see a continued increase in biotelemetry and biologging studies (McMahon, Hindell & Harcourt 2012). Attachment of instruments to animals, however, affects the very data that are sought (e.g. movements, velocity, diel behavioural budgets, energy expenditure).

Along with altering the natural behaviours of tagged animals, the costs of increased drag from carrying tags can lead to reduced fecundity and even survival. A meta-analysis of 84

*Correspondence author. E-mail: todd.jones@noaa.gov

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**Table 1.** Glossary of terms used in paper

| Terms | Definitions |
|---|---|
| Electronic tags | The full suite of animal-borne instruments and attachments that log, transmit or receive information; for example, time-depth recorders, satellite tags, VHF radio and ultrasonic transmitters, accelerometers, and animal-borne cameras as opposed to identification tags that are made of steel or plastic and are generally engraved with an identification code |
| Biotelemetry | Devices that record or transmit information on the biological parameters of the organism to which they are attached. For instance, the body temperature or heart rate of the organism |
| Biologgers | Archival data loggers that can record biotic data (e.g. body temperature or heart rate) and abiotic data (e.g. depth, light level, environmental temperature). These electronic tags must later have the data downloaded from them; a common example is a time-depth recorder (TDR) |
| Locational telemetry | Specifically tags that transmit radio or acoustic signals that can be detected by stationary antennas or orbiting satellites. These tags are typically used for locational ($x$, $y$ coordinate) data but may also transmit (upload) other logged data |
| **disclaimer* | As our interest is in the added drag from devices to aquatic macrovertebrates, we did not distinguish between the various electronic tags listed above as in many cases tags perform combinations of these functions and are similar in shape and attachment methods; therefore, we collectively refer to them as instruments, attachments, or tags. For detailed definitions see Cooke *et al.* (2004) |

bird tagging studies indicates that tagged birds have a marked increase in energy expenditure and are less likely to nest (Barron, Brawn & Weatherhead 2010). Further, Bowlin *et al.* (2010) suggest that the increased load (weight) and drag due to transmitters explain the reduced returns of instrumented birds. Bird tagging studies have long followed the 5% rule, where transmitter mass must be within 5% of the bird's body mass (Cochran 1980; Barron, Brawn & Weatherhead 2010) to allow sufficient lift and thrust for take-off and flight, and this concept pervaded into tagging studies of terrestrial and aquatic organisms. While this may have helped to reduce the impacts on flying birds, where lift and gravity dominate, for marine organisms, the transmitter mass has less an effect on the organism, due to buoyancy, than does the overall increase in drag (Watson & Granger 1998; Hanson 2001; Wilson *et al.* 2004; Jones *et al.* 2011). For example, identification tags that weigh less than a few grams increased required power output in penguins by 24% (Culik, Wilson & Bannasch 1993) and tag antennas increased the drag of penguins by upwards of 70% (Wilson *et al.* 2004). Royal penguins (*Eudyptes schlegeli*) outfitted with biologgers that weighed <1% of their body mass were less likely to continue their breeding attempt, had increased foraging trip durations and decreased fat stores from controls (Hull 1997). Dorsal fin attachments to small cetaceans such as harbor porpoises (*Phocoena phocoena*) increase drag up to 70% (Hanson 2001) and pinnipeds (grey seal; *Halichoerus grypus*) carrying back-mounted satellite tags had drag increases of 10–14% (Hazekamp, Mayer & Osinga 2010). Pop-up satellite tags (PSATs) that are slightly buoyant increased the cost of transport in eels by 26% (Methling *et al.* 2011) and caused a twofold increase in swimming cost (Burgerhout *et al.* 2011) with both studies citing that PSAT drag prevented eels from completing breeding migrations in the wild. These examples together suggest, in marine applications, that the drag of a tag is of more consequence than the mass to the well-being of the animal and applicability of the data to untagged animals. Nevertheless, the need for an understanding of the basic biology of federally and internationally protected species, such as marine turtles, has led to a growth in tagging studies (see Godley *et al.* 2008). In the United States alone, there has been a tripling in permits and permitted tagging over the last decade (Fig. 1a). At present, 50 publications per year report some form of instrumentation attached to marine turtles alone (Fig. 1a). Marine turtles are highly migratory throughout their development, making long-distance migrations as developing juveniles and transoceanic migrations as breeding adults (Fig. 1b). Therefore, long-term attachment of instruments with high drag costs may have considerable ecological implications.

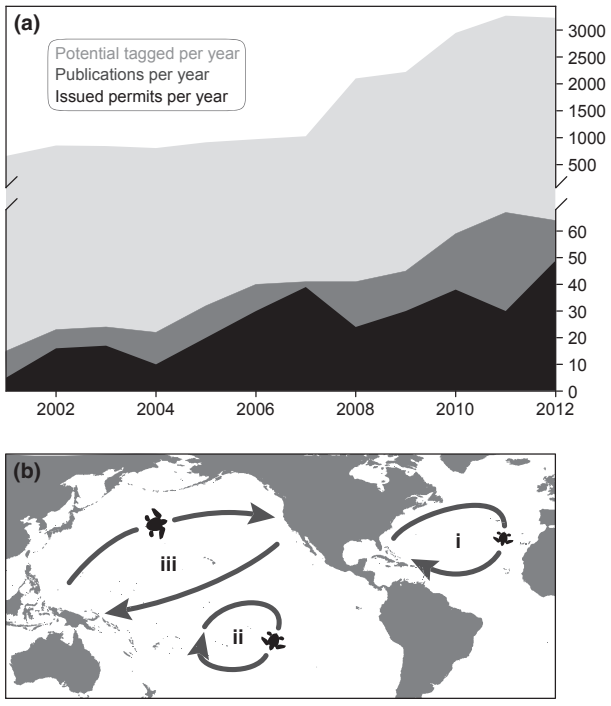


**Fig. 1.** (a) Three shaded areas depict total permits issued per year (black) for marine turtle biotelemetry attachments in the United States (e.g. satellite, TDR, etc.), the total potential for tagged marine turtles per year in the United States (light grey), and the total number of publications (grey) that include some form of biotelemetry attachment to marine turtles (e.g. satellite, TDR, etc.). (b) Map depicting long-distance and local migrations of marine turtles: (i) Life-history specific ontogenetic migrations as found in juvenile *C. mydas* and *C. caretta* turtles in the North Atlantic gyre, (ii) insular migrations as found in *C. mydas* and *E. imbricata* turtles of the western Pacific and (iii) transoceanic migrations between foraging and breeding grounds for Pacific *D. coriacea* populations.

Tag attachments have been shown to increase the drag of marine animals (Watson & Granger 1998; Hanson 2001; Wilson *et al*. 2004; Hazekamp, Mayer & Osinga 2010; Jones *et al*. 2011) likely leading to increases in energy expenditure (Wilson & McMahon 2006). It is this balance between energy in and energy out that ultimately determines growth, reproduction and survival. Therefore, the effect of tagging on the energetics of animals should be quantified and then considered over the expected attachment duration (see Wilson & McMahon 2006). To help understand how drag from electronic tags affects marine animals in the wild, we used marine turtles as model aquatic organisms and (i) measured the drag characteristics of their body forms and grouped them by drag coefficient ($C_D$), (ii) correlated the frontal area ($cm^2$) and carapace length of the turtle groups and scaled drag force across juvenile and adult carapace length, (iii) quantified the drag associated with carrying biotelemetry devices of varying frontal area and design form with turtle carapace length, (iv) generated contour plots depicting percentage drag increase as a framework for evaluating tag drag by scientists and wildlife managers, and (v) detailed the ecological implications of drag from animal-borne instrumentation and developed an universal application of this study for other marine taxa.

## Materials and methods

### LITERATURE AND PERMIT SURVEY

We conducted a literature search from 2000 through November 2012 using ISI Web of Science. Our search included the topic word 'sea turtle' and one of the following topic words: satellite, time-depth, radio, crittercam, animal-borne and acceleration. We examined the results and removed false positives and duplicates. The permits issued per year and potential tagged turtles per year in the United States came from the National Marine Fisheries Service APPS data base (https://apps.nmfs.noaa.gov), United States Fish and Wildlife Service, and state agencies (Florida Fish & Wildlife Conservation Commission, South Carolina Department of Natural Resources).

### WIND TUNNEL TRIALS

#### *Casts*

Eleven fibreglass casts were constructed from frozen or stuffed leatherback (*Dermochelys coriacea*, Vandelli 1761), green (*Chelonia mydas*, Linnaeus 1758), hawksbill (*Eretmochelys imbricata*, Linnaeus 1766) and olive ridley (*Lepidochelys olivacea*, Eschscholtz 1829) marine turtle carcasses. The front flippers were removed at the radiocarpal joint, and the rear flippers were positioned at zero angle of attack along the anteroposterior axis (see Jones *et al*. 2011). The front flippers are the propulsion creating the thrust needed to overcome the drag of the rigid body; therefore, by removing the flippers, we measure the drag of the rigid body which the flippers must match in thrust for the turtle to move (Watson & Granger 1998; Jones *et al*. 2011).

#### *Frontal area*

Frontal Area (FA) of the casts (for drag coefficient determinations) and six additional turtles [for FA to straight carapace length (SCL) correlations] were calculated using photographs (Nikon D-90 camera; Nikon Inc., Melville, NY, USA) taken head-on with a measuring scale for reference. Photographs were then uploaded to Adobe Photoshop® (Adobe Systems Incorporated, San Jose, CA, USA) to calculate area based on the defined pixel area from the reference.

#### *Test facilities*

Drag of the turtle casts was measured in the large boundary layer and Parkinson wind tunnels in the Department of Mechanical Engineering, University of British Columbia, Canada. The tunnels are capable of wind speeds up to 35 m $s^{-1}$ with test sections of 4 and 0·7 $m^2$, respectively. The generated wind speeds are uniform across the test section except for a boundary layer near the tunnel walls (<5 cm).

#### *Drag measurements*

Casts were attached to a sting mount which in turn attached to a two-axis, air-bearing force balance mounted below the wind tunnel. The forces exerted on the casts by the wind are transferred by the sting to the force balance where drag was measured as the force parallel to the wind direction. The drag force $F_D$ on a blunt body of frontal area $A$ ($m^2$), moving through a fluid of density ρ (kg $m^{-3}$) at speed $U$ (m $s^{-1}$), is denoted as $F_D = 0{\cdot}5\ \rho C_D A U^2$, where the drag coefficient $C_D$ is unitless and describes the drag force that is characteristic of the blunt body and can be solved for by $C_D = F_D/0{\cdot}5\ \rho U^2 A$. Matching Reynolds numbers ($Re$) allows the calculation of air speeds that are representative of swimming speeds (Reynolds similarity law; Vogel 1996); thus, $(U_{sw}/\nu_{sw})\nu_a = U_a$, where $\nu$ is the kinematic viscosity of the fluid ($m^2$ $s^{-1}$) and the subscripts $_{sw}$ and $_a$ represent sea water and air. Therefore, air speeds in the wind tunnel (at 25 °C) of 2–30 m $s^{-1}$ are equivalent to swimming speeds of 0·1–1·9 m $s^{-1}$ in sea water. The casts were tested over 25° angle of attack (α) to determine the angle of lowest $C_D$; then, all subsequent tests were conducted at that angle (α = 0). The dependence of $C_D$ on Re becomes weak in turbulent flow (Tritton 1988). Therefore, we measured $C_D$ from 2 to 30 m $s^{-1}$ for the smaller casts (<40 cm SCL) and from 2 to 20 m $s^{-1}$ for the larger casts (>40 cm SCL) and averaged the drag coefficients over the plateau (where $C_D$ became independent of Re) for each cast, and then, the casts (or species) were grouped based on $C_D$ similarity. The drag coefficient of the casts was then measured with various commercially available electronic tags attached to the carapace.

#### *Note*

Complete experimental details are provided in Jones *et al*. (2011).

### DATA ANALYSIS

We correlated FA with SCL ($FA = aSCL^b$) for 4 *D. coriacea* and 13 Cheloniidae (*C. mydas*, *E. imbricata* and *L. olivacea*) specimens. *D. coriacea* specimens ranged in length and FA from 35 to 148 cm SCL and 0·019 to 0·471 $m^2$, respectively. The Cheloniidae specimens ranged in length and FA from 21 to 94 cm SCL and 0·012 to 0·179 $m^2$, respectively. We then scaled drag across carapace length by combining drag, the correlation for FA with SCL (Dermochelyidae and Cheloniidae), and the corresponding $C_D$ for species groups (*D. coriacea*, *C. mydas* and *E. imbricata* and *L. olivacea*) in the following equation, $F_D = 0{\cdot}5\ \rho C_D(aSCL^b)U^2$. We then generated contour plots of drag (isodrags) of 5%, 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90% and 100% depicting the increased drag caused by attachments based

on their shape (square or tear drop) and FA when attached to turtles, $A = (2\ F_D)/(\rho C_D U^2)$. The $C_D$ for square tags was estimated by $C_{Dtag} = (C_{Dturtle,tag} - C_{Dturtle})/(A_{turtle}/A_{tag})$, where subscripts $_{turtle}$ and $_{tag}$ refer to the turtle body and the attachment (see Watson & Granger 1998), respectively. Fairing or making tags tear drop shaped reduces drag by a third (Obrecht, Pennycuick & Fuller 1988; Jones *et al.* 2011); thus, to produce the isodrags for tear drop tags, we multiplied the $C_D$ of the squared tags by 0·66. Tags were applied to the second central scute as is commonly done in tagging studies; however, tag placement can change drag characteristics (see Jones *et al.* 2011). The data generated from this study have been deposited online and are available from the Dryad Database (Jones *et al.* 2013).

The outcome is isodrags that depict the percentage increase in drag caused by tags of known FA on turtles of known SCL. The plots can be read based on percentage increase in drag, that is, increasing FA of tag with increasing SCL for set drag percentage. Or from the standpoint of the turtle, if a turtle is of known SCL, what size tag can be used while maintaining drag below a given percentage. And from the standpoint of the tags, if a tag has known FA, what size turtle can it be applied to, so that drag remains below a given percentage. This will allow researchers to understand the drag characteristics from all viewpoints and allow more informed research planning.

## Results

### DRAG

The drag of the marine turtle casts was measured in two-degree increments from −12 to +12 degrees of pitch (angle of attack α) from the transverse axis to determine the angle that produced the minimum drag coefficient (α = 0) (Fig. 2a), and then, set to their respective α = 0, the casts were tested at wind speeds ranging from 2 to 30 m $s^{-1}$ (Fig. 2b). Angles greater or less than α = 0 led to increases in $C_D$ (Fig. 2a), with a small plateau or neutral zone of ± 4 degrees from α = 0. The increase in $C_D$ is due to the increased frontal area of the casts at angles other than 0. The wind speeds were representative of Re of $3{\cdot}0 \times 10^4$ to $1{\cdot}9 \times 10^6$ for the smallest cast in the lowest wind speed to the largest cast in the highest wind speed. From 2 to 8 m $s^{-1}$ (equivalent to 0·13–0·51 m $s^{-1}$ in sea water), the drag coefficients of all casts had plateaued and were no longer sensitive to further increases in wind speed (Fig. 2b), suggesting turbulent boundary layer flow. The average Re for casts entering the transition to turbulent flow was $2{\cdot}1 \pm 1{\cdot}5 \times 10^5$; this is less than the typical Re transition of $5 \times 10^5$ (Hoerner 1965); however, we calculated Re based on SCL which is less than the total length of the animal, and as turtles are airfoil shaped, the local Re was probably higher than what we calculated.

Specimens of *C. mydas* had the lowest $C_D$ (0·13 ± 0·02) of the turtle groups and were most sensitive to increased drag from instrumentation. The measured drag coefficient of seven commercially available squared tags (from Wildlife Computers, Redmond, WA 98052, USA; Telonics, Mesa, AZ 85204, USA; and Desert Star Inc., Marina, CA 93933, USA) was 0·91 ± 0·18. Not all of the tags were appropriate for the 11 turtle casts (because of the carapace shape or overall size of turtle); thus, we conducted a total of 34 tag trials out of a possible 77 combinations. The frontal area to straight carapace

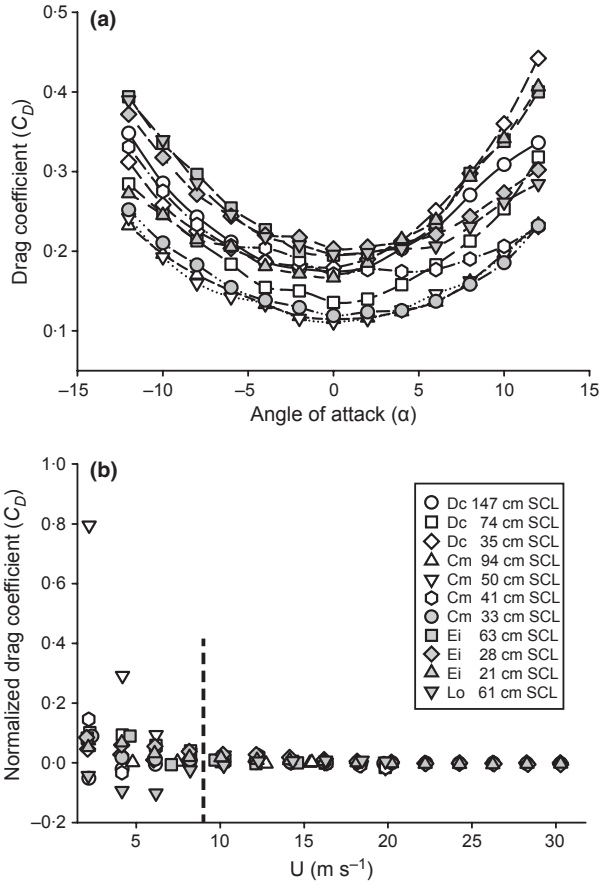


**Fig. 2.** (a) Drag coefficient of the 11 marine turtle casts measured through ± 12 degrees of pitch (angle of attack α) in turbulent flow (>8 m $s^{-1}$). (b) The drag coefficient of the 11 marine turtle casts measured through wind speeds of 2–30 m $s^{-1}$ at the angle of attack with lowest $C_D$ (α = 0) determined from panel (a) – the dashed line denotes the transition where all of the casts had reached turbulent boundary layer flow. The *y*-axis in (b) was normalized to the average $C_D$ for each cast in turbulent flow, and the figure legend is true for both panels.

relationships for Dermochelyidae and Cheloniidae were $6 \times 10^{-6}$ $SCL^{2{\cdot}24}$ ($R^2 = 0{\cdot}99$, $n = 4$) and $5 \times 10^{-5}$ $SCL^{1{\cdot}79}$ ($R^2 = 0{\cdot}90$, $n = 13$), respectively. All of the drag results are summarized in Table 2.

### READING AND INTERPRETING DRAG COSTS

Using the data in Table 2, we derived isoplots of drag, or isodrags, to quantify the increased drag caused by animal-borne instrumentation on marine turtles. Figure 3 lists frontal area of tags in $cm^2$ on the *y*-axis and SCL of turtles in cm on the *x*-axis. Thus, researchers and managers can estimate the increase in drag caused by a tag by:

1 Measuring the FA of the tag as width (cm) multiplied by height (cm) – this information is available on the specifications sheet of commercial tags online – or by simply measuring the tags.
2 Determining whether the tag is square (flat front, sharp or slightly rounded edges, rectangular or square in total dimensions) or tear drop (bulbous head with narrowing trailing posterior) shaped.

**Table 2.** Drag equation coefficients and frontal area to carapace length relationships

| Reference | Coefficient | SD | *n* |
|---|---|---|---|
| $C_D$ of squared electronic tag | 0·91 | 0·18 | 34 |
| $C_D$ of tear drop electronic tag | 0·64 | 0·13 | 34 |
| $C_D$ of *C. mydas* (turbulent) | 0·13 | 0·02 | 27 |
| $C_D$ of *D. coriacea* (turbulent) | 0·17 | 0·02 | 23 |
| $C_D$ of *E. imbricata*/*L. olivacea* (turbulent) | 0·18 | 0·02 | 31 |
| Reference | Equation | $R^2$ | *n* |
| Dermochelyidae (FA to SCL) | $(6 \times 10^{-6}\,SCL^{2·24})$ | 0·99 | 4 |
| Cheloniidae (FA to SCL) | $(5 \times 10^{-5}\,SCL^{1·79})$ | 0·90 | 13 |

SD is standard deviation; *n* is total number of trials (drag coefficient) or number of turtles (FA to SCL relationships).

3 Matching the FA of the tag on the *y*-axis for the appropriate panel in Fig. 3 [e.g. for a squared tag on *C. mydas*, use panel 2(f)].

4 And continuing along the *x*-axis until reaching the SCL (in cm) of the intended length of the instrumented turtle.

This will give the estimated drag increase to the turtle for carrying the tag. This is an estimate as the increased drag will vary on an individual basis because of the variability in $C_D$ within a species, variability in the correlation of FA to SCL for turtles and variability in the $C_D$ of the tag (Table 2). Furthermore, tags of different manufacturers will vary slightly and may include water channels or other features. While these differences may cause small changes to the drag characteristics, they will be minor in comparison with the overall shape

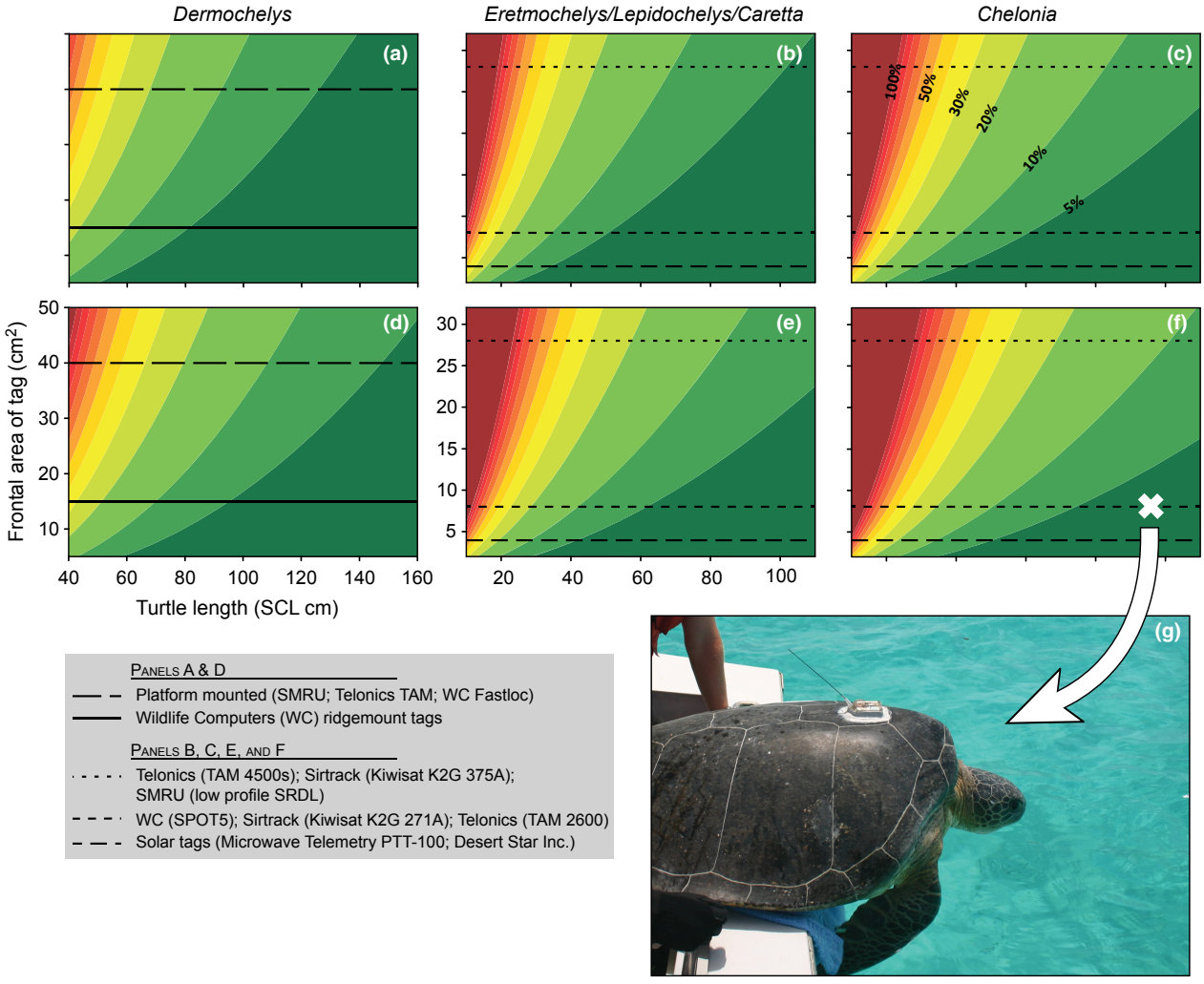


**Fig. 3.** Percentage increase in drag associated with electronic tags (measured as frontal area of tag in $cm^2$; *y*-axis) attached to marine turtles (measured as straight carapace length in cm; *x*-axis). Isodrags are given for increases in drag of 5%, 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90% and 100%. A particular shade represents the continuum of drag between isodrags (e.g. 0–5% drag is depicted by the dark green shading). Isodrags of 5%, 10%, 20%, 30%, 50% and 100% are labelled in panel (c). The isodrags in panels a–c are for tear drop shaped tags with smooth or rounded edges and in panels d–f for squared tags with hard edges. The solid and dashed horizontal lines represent frontal areas of commercially available tags as listed in the figure legend. Panels a and d are for *D. coriacea*, panels b and e are for *E. imbricata* and *L. olivacea* (and suggested for *C. caretta* and *L. Kempii*) and panels c and f are for *C. mydas*. The white X in Panel (f) marks the estimated drag increase (<5%) from a Wildlife Computers SPOT5 tag attachment on a 95-cm SCL *C. mydas* caught in the Dry Tortugas (Florida, USA) – panel (g). The photograph was taken by Kristen Hart (USGS) with permission under NMFS Permit No. 13307-02, FL Fish and Wildlife Conservation Commission Marine Turtle Permit 176, and Dry Tortugas Scientific Research Permit DRTO-2008-SCI-0008.

(square vs. tear drop) and most importantly the FA of the tag. Antenna area can also be added to estimate total FA of the tag, and stiff antennas that do not bend backward when the turtle is swimming (e.g. radio tags) can add an additional 10–15 $cm^2$ (Jones *et al.* 2011).

We did not directly measure loggerhead (*Caretta caretta*, Linnaeus 1758) or Kemp's ridley (*Lepidochelys kempii*, Garman 1880) turtles; however, we suggest that they be included with the *E. imbricata* and *L. olivacea* $C_D$ group because of their similar body shape, relatively large head and rough carapace (Poh *et al.* 2008).

## Discussion

### ENERGETIC AND PHENOLOGICAL CONSEQUENCES OF DRAG

Evolutionary adaptations allowed large, air-breathing, macrovertebrates (i.e. turtles, birds, and mammals) to invade the marine environment where they have successfully navigated the oceans for nearly 50–100 million years (Pritchard 1997; Baker *et al.* 2006; Perrin, Würsig & Thewissen 2009). These adaptations led to streamlined bodies, as noted by their $C_D$, and efficient thrust producing flippers that have permitted marine animals, such as the turtles, to make transoceanic migrations between breeding and foraging grounds (Benson *et al.* 2011) or as developing juveniles in oceanic gyres (Carr 1986) (see Fig. 1b). It is therefore not surprising that the hydrodynamics of their body forms are sensitive to biological fouling (Logan & Morreale 1993) or tag attachments (Watson & Granger 1998; Hanson 2001; Wilson *et al.* 2004; Hazekamp, Mayer & Osinga 2010; Jones *et al.* 2011) (see Fig. 3). The energetic cost of carrying transmitters and the effects to the animal's behaviour, ecology and physiology, however, are rarely considered, let alone quantified (Casper 2009; McMahon, Hindell & Harcourt 2012).

We can quantify the energetic cost of carrying tags from measurements of drag, estimates of tag attachment duration and the presumed activity of the animal (i.e. migrating turtles vs. local foraging or home range movements). However, it is difficult to document changes in behaviour, as our baseline for comparison is other tagged animals with different tag types or tagging protocols (Fossette *et al.* 2008; Byrne *et al.* 2009), and this does not get around the issue of 'measurement affects performance' (Wilson, Grant & Duffy 1986; Wilson & McMahon 2006). Therefore, researchers, at a minimum, should consider the physical consequences of increased drag. Figure 3(f) shows that a tear drop tag with a FA of 8 $cm^2$ increases drag <5% on marine turtles >60 cm SCL but the drag costs for the same tag increase to >20% and >100% for turtles of 30 cm and 15 cm SCL, respectively. It is important to note that increases in drag cause a proportional increase in power output of the tagged animal, described by $P = F_D U$ or $P \propto C_D U^3$; therefore, increases in drag require an increase in power output by the animal, or the animal's swimming velocity will decrease.

Many migratory animals operate close to their maximum ceiling for migration distance based on their resource acquisition and storage ability (Hays & Scott 2013); consequently, small increases in drag may compromise their ability to complete the journey. For example, a tag deployed for 1 year on a migrating animal will increase the individual's yearly energy budget proportionally to the percentage increase in drag or by the increased time in reaching its destination as a result of decreases in swim speed. Recent studies suggest, however, that marine organisms maintain optimal swimming speed ($U_{opt}$) despite increased drag to maintain timing of migratory events such as spawning (Burgerhout *et al.* 2011; Methling *et al.* 2011). For animals on long-distance migrations, such as *D. coriacea* making year-long (10 000 km) migrations to arrive at foraging grounds that last just a few months (Benson *et al.* 2011) or eels migrating 6 000 km from the European coast to the Sargasso Sea to spawn (Burgerhout *et al.* 2011), decreases in swim velocity could lead to phenological disruptions of ephemeral foraging (Jones *et al.* 2011) and spawning events (Burgerhout *et al.* 2011; Methling *et al.* 2011). Therefore, a turtle (e.g. *D. coriacea*) on a year-long migration across the Pacific (see Benson *et al.* 2011, for example) carrying a platform-mounted transmitter that increased drag by 43% (Jones *et al.* 2011) would then consume 143% of its typical migratory energy budget. The extra energy needed to overcome drag costs during migration could possibly come from fat stores that were intended for reproduction (see Methling *et al.* 2011), which could translate to reducing the reproductive output of the tagged animal.

### ESTIMATING DRAG ACROSS TAXA

We can estimate the increase in drag from animal-borne instruments to many marine taxa by scaling drag relative to the animal's frontal area and drag coefficient. The Reynolds similarity law states that the drag force can be estimated from the unitless drag coefficient as long as the objects (animals) in question have similar shape and are tested at equivalent Reynolds numbers for the medium representing turbulent flow (Hoerner 1965; Vogel 1996). Marine taxa, such as turtles, birds and mammals, have drag coefficients ranging from 0·08 to 0·26 (Stelle, Blake & Trites 2000; Hanson 2001; Lovvorn *et al.* 2001; Hazekamp, Mayer & Osinga 2010; Jones *et al.* 2011; Pavlov & Rashad 2012; this study) and assuming that the flow patterns around attached instruments are similar, then the percentage increase in drag for attachments to large marine vertebrates can be estimated by $\%\Delta\ drag = (((C_{Dtag}FA_{tag})/FA_{animal})/C_{Danimal})100$, where subscripts $_{tag}$ and $_{animal}$ refer to the attachment and the animal body, respectively. Obrecht, Pennycuick and Fuller (1988) found a drag coefficient of 0·72 for a squared tag (FA = 0·0012 $m^2$) attached to several different bird species (bald eagle *H. leucocephalus*, tundra swan *C. columbianus*, snow goose *C. caerulescens* and mallard *A. platyrhynchos*), and Hanson (2001) found drag coefficients ranging from 0·69 to 1·04 for tags (FA = 0·0018–0·0031 $m^2$) attached to an adult male harbor porpoise. Both of these studies corroborate with our finding of a $C_D$ of 0·91 ± 0·18 for squared tags tested over similar speeds on 4 different species (body types) of marine turtle. This gives further confidence in

the assumption that the fluid dynamics of instruments are similar when attached to animals within a narrow $C_D$ band (e.g. the marine taxa listed above) and in use of the universal equation for estimating drag costs of animal-borne instruments.

For instance, from the equation above, we can estimate that a small squared tag (FA = 0·0011 $m^2$; $C_D$ = 0·91) would increase the drag of a Gentoo penguin (*P. papua*, *c.* 50 cm, 3·4 kg, $C_D$ = 0·07, FA = 0·02 $m^2$) (Bilo & Nachtigall 1980) by 72% and of a juvenile green turtle (*C. mydas*, 33 cm SCL, 4 kg, $C_D$ = 0·12, FA = 0·032 $m^2$) by 26%; however, the same tag on a large stellar sea lion (*E. jubatus*, 2·37 m, 185 kg, $C_D$ = 0·10, FA = 0·194 $m^2$) (Stelle, Blake & Trites 2000) would increase drag by only 5%. The estimation for *P. papua* is directly corroborated by Bannasch, Wilson and Culik (1994) who measured the drag increase from a similar sized tag on casts of *P. papua* and *P. Antarctica* (chinstrap penguins) and found that the tag increased drag by 52–71%. Applying the same tag parameters (FA = 0·0011 $m^2$; $C_D$ = 0·91) to a grey seal (*Halichoerus grypus*, <2 m, *c.* 100 kg, $C_D$ = 0·108, FA = 0·08 $m^2$) gives a drag increase of 11·6%, and this estimation is corroborated by the simulation of Hazekamp, Mayer and Osinga (2010) who simulated the increased drag from squared tags on grey seals to range from 10 to 14%. While the penguin and juvenile turtle in question are similar in mass, length and FA, the lower $C_D$ of the penguin makes it much more sensitive to increased drag from instruments. The seal and sea lion also have low drag coefficients; however, their large frontal areas (0·08 and 0·194 $m^2$, respectively) relative to the frontal area of the tag (0·0011 $m^2$) greatly reduce the drag costs from carrying the instrument. Computer simulations of the drag induced from dorsal fin attachments on small cetaceans suggest that hydrodynamically designed tags with reduced frontal area may keep drag increases below 4% (Pavlov & Rashad 2012). The sensitivity of aquatic animals to instrument drag is a dynamic relationship between the fluid flow patterns ($C_D$) and the frontal area ratio of animal and tag.

### OTHER CONSIDERATIONS

Instruments that induce large increases in drag (e.g. large animal-borne cameras) but are designed to pop-off in several days may have minimal effects on the energetics and phenological relationships of the instrumented animal. Jones *et al.* (2011) calculated that an animal-borne camera, causing upwards of 100% increase in drag, attached to a marine turtle for 3 days would augment its yearly energy budget by <1%. Thus, researchers may weigh drag cost against the applicability of the collected data, for instance how might the increased power output by the animal to overcome drag costs alter dive depth and duration or time spent in various activities. Marine turtles are also known to adjust their lung volumes and dive depths to take account of attachments that alter their buoyancy (Hays, Metcalfe & Walne 2004); therefore, decreasing the drag and mass from instruments increases the biological realism and applicability of collected data to tag-free individuals.

Studies involving sessile or local movements of aquatic animals may need to consider the increased drag not from an energetic standpoint but perhaps from depredation. The instrumented animal may spend a large percentage of its diel activity resting and slowly moving while foraging (i.e. low energy activities) but instruments with high drag reduce the top velocity and acceleration of the instrumented animal, possibly leaving the animal more vulnerable to depredation. This is described by $a = (F_T - F_D)/m$ where $a$ is acceleration (m $s^{-2}$), $m$ is mass (kg), $F_T$ and $F_D$ are thrust and drag (kg m $s^{-2}$), and $F_T$ is assumed to be at a maximum to escape the predator. Therefore, aquatic animals instrumented with tags that have high drag costs may have increased mortality.

As animal-borne instruments become smaller, there is an ever increasing emphasis on tracking juvenile life-history stages; however, juvenile animals that passively migrate in currents (see Fig. 1b) or spend prolonged periods at the surface may be susceptible to wind drift. Drag is proportional to the density of the medium and the square of the velocity. In a situation with an ocean current of *c.* 1 m $s^{-1}$ and a wind speed of *c.* 20 m $s^{-1}$, the proportional force from the current would be twice that of the wind. Assuming 10–20% of the animal and tag are above the water line (exposed to the wind), then the generated wind force would be 5–12% of the current force. This small but off direction force could have large impacts over the course of migration for small turtles (Scott, Marsh & Hays 2012), perhaps blowing them off-course (Monzón-Argüello *et al.* 2012) and making it difficult to compare tracks of instrumented animals with drift models. In larger or older animals that remain submerged or where the exposed portion is 1% or less of their total, then wind drift would play a minimal role.

Researchers must also consider their attachment techniques. Excessive adhesives increase the frontal area of the tag attachment and thus increase the drag, especially if adhesives are used to build up the sides or armour tags. The added drag from adhesives can be calculated with Fig. 3 by adding the increased frontal area (thickness and width of adhesive base) to the FA of the tag (*y*-axis of Fig. 3). There also may be a trade-off involved with epibionts and tag attachments. Marine turtles are different to some other tracked taxa (e.g. birds, pinnipeds) in that they can have high levels of natural biofoulers (e.g. barnacles) (Hayashi & Tsuji 2008). Simulations suggest that the barnacles can cause substantial increases in drag (Logan & Morreale 1993); therefore, removal of barnacles within the tag footprint prior to equipment attachment may offset the increased drag from instrumentation.

## Conclusion

With the continued use of animal-borne instrumentation to monitor wildlife (Cooke *et al.* 2004), there is a need to understand and reduce the adverse effects to the animals. This includes less stressful capture techniques, reduced handling time, and consideration of instrument drag and retention time. Researchers need to have clear objectives and choose instruments that will provide data with minimum ecological impact. Of concern is the effect of drag to the welfare of the instrumented animals and for the applicability of collected data to wild populations. In this paper, we have outlined

methods for quantifying the drag costs from animal-borne instrumentation considering the instrument retention time (time to release from the animal) and the activity of the instrumented animal. We have also shown how this information can be applied across taxa. The colour scheme in Fig. 3 of green (0–20% drag increase), yellow (20–50% drag increase) and red (>50% drag increase) is meant as a qualitative recommendation; however, researchers and managers need to use their specific knowledge of the study animals, habitat and activity to make informed decisions of what is acceptable on an individual basis. With this valuable tool, researchers should strive to reduce the drag from animal-borne instrumentation, which will ultimately reduce the impact on the instrumented animals and lead to greater biological realism in the collected data.

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## Data accessibility

Data generated from this study have been deposited in the Dryad repository: http://dx.doi.org/10.5061/dryad.921k0 (Jones *et al*. 2013).

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