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DETERMINING TRANSMITTER DRAG AND BEST-PRACTICE ATTACHMENT PROCEDURES FOR SEA TURTLE BIOTELEMETRY

T. Todd Jones, Brian Bostrom, Michael Carey, Brittany Imlach, Jon Mikkelsen, Peter Ostafichuk, Scott Eckert, Patrick Opay, Yonat Swimmer, Jeffery A. Seminoff, and David R. Jones

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PREFACE

This Technical Memorandum describes the first comprehensive study to quantify the increased drag induced by attachment of biotelemetry devices to sea turtles. Drag (i.e., fluid resistance) refers to forces that oppose the relative motion of an object. Transmitters attached to the carapace of turtles as well as epibiont-related biofouling of the transmitter or its attachment method can increase hydrodynamic drag and affect lift and pitch during movements potentially altering an animal's swimming behavior or workload. This report provides an empirical description of the increase in drag caused by multiple telemetry attachment configurations on different species of sea turtles. Additionally, we report on studies to determine the best location (i.e. that with the least amount of drag) on a turtles' body for each telemetry attachment configuration.

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EXECUTIVE SUMMARY

All sea turtles are currently listed as threatened or endangered under the U.S. Endangered Species Act of 1973. To identify appropriate conservation management actions for recovering sea turtle populations, we must understand their migration routes, distribution, habitat use, and resource requirements. Electronic transmitter technology (i.e., biotelemetry), such as time depth recorders (TDR), VHF radio and ultrasonic transmitters, satellite-linked (i.e., ARGOS) telemetry tags, and animal-borne video and still cameras, provides researchers with a suite of valuable research tools to address questions about sea turtle ecology, behavior, and physiology. Ultimately, this information can be used to guide effective conservation strategies. The use of electronic tags, however, has the potential to negatively impact the natural behaviors of the animals on which they are attached (Watson and Granger 1998; Wilson and McMahon 2006; Godley et al. 2008; Sherill-Mix and James 2008). Therefore, this study was designed to quantify the drag forces induced by attachment of biotelemetry devices to sea turtles using some of the transmitters and methods of attachment described in the scientific literature.

The project goal was to quantify the drag induced by attachment of biotelemetry devices. We investigated the physical design of the transmitters and placement on turtles in order to determine the best hydrodynamic (least drag) telemetry system. We then theoretically examined the trade-off turtles must make between increasing energy output to maintain velocity and decreasing velocity to cope with added drag. Finally, we determined guidelines for the use of biotelemetry devices establishing low-drag attachment protocols. Casts were made of leatherback (*Dermochelys coriacea*), green (*Chelonia mydas*), and olive ridley (*Lepidochelys olivacea*) turtles ranging in straight carapace length (SCL) from 40.5 to 147.0 cm. These casts were tested in the Boundary Layer Wind Tunnel (BLWT) at the Department of Mechanical Engineering, University of British Columbia, Canada, to determine the drag and lift forces of the turtle casts with and without various biotelemetry packages placed at different locations. The casts were tested across wind speeds of 0.1 to 19.4 m s^{-1} and through 26 degrees of angle of attack. For the multitude of biotelemetry tag trials, we used a wind speed of 16 m s^{-1} (as all casts had reached turbulent boundary layer flow at this speed) and the angle of attack that gave the least drag and lift forces on the cast. For the adult leatherback cast we conducted tag trials over the whole range of capable velocities.

We found that drag coefficients were 0.144, 0.126, 0.192, 0.137, and 0.174 for green (small and large), olive ridley and leatherback (juvenile and adult) casts, respectively. The various tags and attachment configurations caused increases in drag of 0 to 173%. The greatest increases in drag coefficient came from a backpack harness (78% to 173%) on the leatherback casts, a foam drogue used to house transmitters and National Geographic Crittercams (67% to 110%) on the olive ridley cast, and the Telonics VHF radio tags (47% to 53%) on the green turtle casts. In

most cases, the manufacturer whose tags resulted in the smallest increase in drag (< 10%) was Wildlife Computers.

Increases in drag force causes a direct and proportional increase in power output if turtles maintain pre-attachment swim speeds or the turtles must reduce swimming speed. Therefore, the increased drag force caused by the tags has implications for the migratory energetics and welfare of the outfitted turtles. It is important that researchers using biotelemetry devices in their research strive to minimize the added drag forces caused by the devices thus ensuring the applicability of the data to tag-free turtles in the wild and lessening the potential for adverse effects to the turtles.

Researchers will not have available the means to test the additional drag force directly when purchasing tags or outfitting turtles in the field. Therefore the following recommendations will help to ensure that drag forces from biotelemetry devices are minimized:

- The frontal area of the tags should be reduced and the tags should have a low profile,
- the tags should have a tear drop shape,
- the antenna length and diameter should be minimized,
- the tags should not be placed at the peak height of the carapace, and
- adhesives should be minimized and use of base plates or building up of material avoided.

While it is highly recommended that drag forces for long-term deployment tags are minimized for the welfare of the turtles, special considerations should be made for tags that cause large drag increases (i.e., upwards of 50% to 100%) but are not intended for extended deployments (e.g., National Geogrpahic Crittercam deployments of < 5 days) or studies on small scale home ranges in which locomotion does not dominate the turtle's diel activity.

INTRODUCTION

Background

All sea turtles are listed as threatened or endangered under the U.S. Endangered Species Act (ESA) of 1973. To identify appropriate conservation management actions for recovering sea turtle populations, we must understand their migration routes, distribution, habitat use and requirements, as well as characteristics of the environment in which they exist, both within the U.S. and internationally. Electronic transmitter technology (i.e., biotelemetry), such as time depth recorders, VHF radio and ultrasonic transmitters, ARGOS-linked satellite tags, and animal-borne video and still cameras, provides researchers with a suite of valuable research tools to address questions about sea turtle ecology, behavior, and physiology. For example, satellite-linked transmitters equipped with data loggers and pressure sensors can provide information on turtles' vertical and horizontal movement patterns over time, as well as the amount of time spent in different locations and/or depths, thereby generating valuable insights on the habitat requirements of turtles. Technological improvements in instrument design, including better reliability, miniaturization, longer battery life and data recording capacity, as well as improved attachment methods and simplified data analysis tools have led to the broader applicability in the use of such tools on marine turtles and a concurrent increase in tag use over the last two decades.

Electronic tags are clearly valuable tools for sea turtle ecological research, although considerations for the potential to affect the well-being and natural behaviors of the research subject must be made (Watson and Granger 1998; Wilson and McMahon 2006; Godley et al. 2008; Sherill-Mix and James 2008). Historically, to help ensure that these effects are minimized, a transmitter weight limit has been used as a guide to limit the size of the transmitter packages attached to sea turtles. For example, the U.S. National Marine Fisheries Service (NMFS) requires that total weight of transmitter attachments must not exceed 5% of the body mass of the animal. The '5%' rule is the standard recommendation and commonly used in telemetry studies (Cochran 1980), however the 5% rule came from acceptable loading weight in bird tracking studies where lift and gravity are the dominating forces. The rule was meant to keep the increased power output of the bird to carry the device < 5% (Aldridge and Brigham 1988). The justification or basis for choosing 5% in terrestrial or aquatic animals is not discussed in the literature (Caccamise and Hedin 1985). While the 5% rule has been a reasonable guide to indirectly keep transmitters small, it is important to note that sea water is three orders of magnitude more dense than air, gravity is basically non-existent, and thus drag forces or resistance more directly reveal impacts to aquatic organisms. While weight has provided a reasonable guideline to indirectly keep transmitter packages small, the hydrodynamic characteristics of transmitter packages more directly reveals the potential effects to marine animals. Drag (i.e., fluid resistance) refers to the force that opposes the relative motion of an object through a fluid (liquid or gas). Instruments attached to the outside of turtles, and subsequent biofouling, can increase hydrodynamic drag, affect lift (the force perpendicular to drag in the vertical plane), and pitch (forces causing the tilt of the animal down or up). For example, Watson and Granger (1998) performed wind tunnel tests on a juvenile green turtle (*Chelonia mydas*) cast and found that at small flow angles representative of straight-line swimming, a transmitter (Telonics ST-6) mounted on the carapace increased drag by 27-30%, reduced lift by less than 10% and increased pitch moment by 11-42%. Consequently, these types of instruments negatively affect the swimming efficiency of sea turtles. Energy consumption, reduction of speed during migratory or long-distance movements, and potential for increased entanglement probability are several of the issues that must be analyzed when considering whether to attach a device, what type of device, and which attachment type will be used on a sea turtle. Additionally, the potential effects of the biotelemetry devices on the natural behavior of turtles are an important consideration (Eckert 1999).

Existing Telemetry Use & Attachment Methods

Increasing our understanding of sea turtle habitat use and migratory behavior has been enabled by the use of a variety of animal-borne telemetry systems attached to wild turtles. The priority has been to maximize the data per deployment while minimizing the effects on the turtles. Biotelemetry systems date back to the 1970's (Carr et al. 1974). Systems have been as simple as tethered balloons or 30 cm diameter floats attached to a 24 m tether and pulled by turtles as they swim (Carr et al. 1974), to more recent use of very high frequency (VHF) radio and ultrasonic transmitters, archival time-depth-recorders (TDRs), and satellite-linked telemetry (Timko and Kolz 1982; Mendoca 1983; Eckert et al. 1986; Duron-Dufrenne 1987; Eguchi et al. 2006; Seminoff and Jones 2006; Godley et al. 2008; Rice and Balazs 2008). Cameras (in waterproof housings) attached to marine animals (Marshall 1998), have also been used in sea turtle studies to help show short-term behaviors such as foraging (Heithaus et al. 2002; Seminoff et al. 2006) and internesting movements and mating (Reina et al. 2005). Presently, the most widely used biotelemetry tag in sea turtle studies are via ARGOS satellite technologies. Satellite transmitters were first used on loggerheads (*Caretta caretta*) in 1982 (Stoneburner 1982; Timko and Kolz 1982) and their use increased rapidly in the new-millennium with nearly 350 studies (peer-reviewed publications, abstracts, and technical reports) to date (Godley et al. 2008). Biotelemetry systems are attached to the carapace of sea turtles in myriad ways, and generally, the attachment strategies for hard-shelled turtles differ substantially to that of the leatherback (*Dermochelys coriacea*), which possess a less keratinized carapace. For example, with hard-shelled turtles, attachment techniques include; direct attachment by drilling through the marginal scutes and using zip ties to attach the instrument (ultrasonic, Seminoff et al. 2002), direct attachment to the central scutes using fiberglass cloth and polyester resin or epoxy (satellite and TDR, Balazs et al. 1996), subdermal insertion (Ogden et al. 1983), and tethering of a telemetry drogue or self-releasing data logger (PAT tag) bolted along the trailing edge of the carapace (Epperly et al. 2007) or with baseplate epoxied on the carapace (Swimmer et al. 2002, 2006). In contrast, attachment procedures on leatherback turtles have included the use of a backpack-style harness (Eckert and Eckert 1986), tethering by attachment to the caudal peduncle (Morreale et al.

1996), direct attachment to the longitudinal ridges (Southwood et al. 1999; Lutcavage et al. 2002; Fossette et al. 2008; Byrne et al. 2009), and suction cups (Reina et al. 2005).

These studies have provided researchers with insight into the biology and ecology of sea turtles that were not otherwise obtainable. Nonetheless, a lack of quantifiable measurements of the effect such instrument packages or attachment methods may have on turtle energy budgets or behavior is generally lacking. Part of this lack of information is driven by a general lack of understanding of turtle energy budgets. Recent studies have begun to address these limitations in our understanding of sea turtle biology. For example, turtles are constrained to a tight metabolic budget (Wallace and Jones 2008), therefore increases in locomotory costs (due to biotelemetry) represents a major portion of their energy budget, and for regional populations such as the eastern Pacific leatherback, which is resource stressed, increases in energy costs might cause a reduction in ecological fitness (Wallace et al. 2006). Other studies have shown that reductions in food resources can delay reproduction (Limpus and Nicholls 1988). Furthermore, 75% of all tagging studies take place on internesting females (Godley et al. 2008), that are often already compromised energetically due to egg production and long migratory routes. Therefore nesting females may be severely affected, energetically speaking, by carrying devices that increase drag force yet these animals are the most ecologically precious to sustaining sea turtle populations.

It is important to bear in mind that increases in drag require a proportionate increase in energy expenditure (power output) by the turtle to overcome the added drag force if the turtle is to maintain velocity underwater. Alternatively, the turtle must swim at a reduced speed, which may result in negative impacts on foraging or timing of migratory events (Wilson and McMahon 2006; Fossette et al. 2008). Consequently, it is important that we continue to improve sea turtle-borne telemetry packages and attachment methods to reduce the potential for negative effects on the turtles. Ideally, such systems should always be as small and streamlined as possible and located in areas that minimize hydrodynamic perturbation (Wilson and McMahon 2006).

This study quantifies the drag induced by attachment of biotelemetry devices to sea turtles using the various transmitters and methods of attachment. We attempt to be comprehensive in scope by testing physical design of the transmitters, placement on turtles, and methods of attachment in order to determine the manner and location where an attachment will have the least influence. Results of various manipulations are reported, as well as recommendations on configurations which result in the least amount of drag.

Project Goals

- Measure the drag coefficient and drag force of sea turtles with and without transmitter packages.

- Determine low-drag attachment protocols and guidelines for the use of biotelemetry devices on sea turtles.
- Estimate the energetic cost of carrying telemetry packages and how drag increases may affect sea turtles ecologically.

MATERIALS & METHODS

Turtle Casts

Fiberglass casts were made from carcasses of a juvenile and adult leatherback turtle, olive ridley turtle (*Lepidochelys olivacea*), and a juvenile and sub-adult green turtle (see Table 1 below for dimensions). The carcasses were held in a deep freeze and were obtained from the Department of Zoology, University of British Columbia (juvenile leatherback turtle), Moss Landing Marine Laboratory (adult leatherback turtle) and NMFS-Southwest Fisheries Science Center (olive ridley turtle and green turtles). The front flippers were removed from the carcasses at the radiocarpal joint (wrist) and the remaining stub was sutured to prevent bleeding. The front flippers are the propulsion creating the thrust force needed to overcome drag force of the rigid body (Watson and Granger 1998). Therefore, by removing the flippers, we measure the drag force of the rigid body, which the front flippers must match in thrust force for the turtle to swim.

TABLE 1
Area and dimension data on the 5 casts used in the wind tunnel experiments. The symbol given for each turtle is used throughout all the figures.

Turtle	Symbol	Frontal area (m^2)	Planform area (m^2)	SCL (cm)	SCW (cm)	Mass (kg)
leatherback (adult)	◇	0.445	1.050	147.0	105.0	unknown
leatherback (juvenile)	□	0.077	0.337	74.0	49.0	43.0
olive ridley	○	0.080	0.290	60.5	57.0	28.0
green (large)	△	0.051	0.214	49.5	44.0	12.0
green (small)	▽	0.046	0.147	40.5	37.0	7.0

The carcasses were measured and a plywood box was built for each carcass leaving a minimum 10 cm space between the carcass and box walls. Wooden pegs were placed in the bottom of the box and used to support the turtle, carapace down, with the plastron as close to horizontal as possible. The carcass was covered with petroleum jelly and placed in the box. Plaster of Paris (hemihydrated calcium sulfate; DAP Inc., Baltimore, MD) was mixed and poured into the box to the carapace-plastron junction. This was allowed to dry for several hours and then the exposed plaster was covered in petroleum jelly and one layer of wax paper was laid down on the set plaster. Another layer of plaster was then poured into the box until the plaster measured 10 cm thick at the highest point of the plastron. Twenty-four hours later, the two halves of the plaster mold were opened and the carcasses were removed. One piece of plaster of paris had the impression of the dorsal half of the turtle and the other piece was an impression of the ventral half. The petroleum jelly was cleaned from the impressions and they were sprayed with 3 coats of a clear enamel (lacquer) allowing each coat to dry between applications. The impressions were waxed and buffed twice using carnauba based car wax (Turtle Wax©, Westmont, Illinois).

The impressions were lightly painted with a coat of polyester resin mixed 250:1 with methyl ethyl ketone peroxide (catalyst) then 6 oz fiberglass cloth was laid in the impressions and painted until thoroughly soaked. The fiberglass was allowed to completely dry and then two layers of 1 oz fiberglass matt were laid in and painted with resin. After 24 hours, the casts were popped from the impressions. The fiberglass which came out of the impressions and did not represent turtle anatomy was trimmed off and one piece of 6 oz cloth was placed around the junction of the two halves to hold the cast together. Each cast was fitted with a 5.04 cm outer diameter aluminum pipe from the head of the turtle down the central axis and out the posterior end (i.e. through the end of the carapace and tail). This pipe extended a minimum of 10 cm out the posterior end of the turtle (Figure 1, below). The anterior end of the pipe was fitted with a tapered copper bung, which was then used to lock the cast onto the cantilever arm of the sting balance (see below; Sting balance).

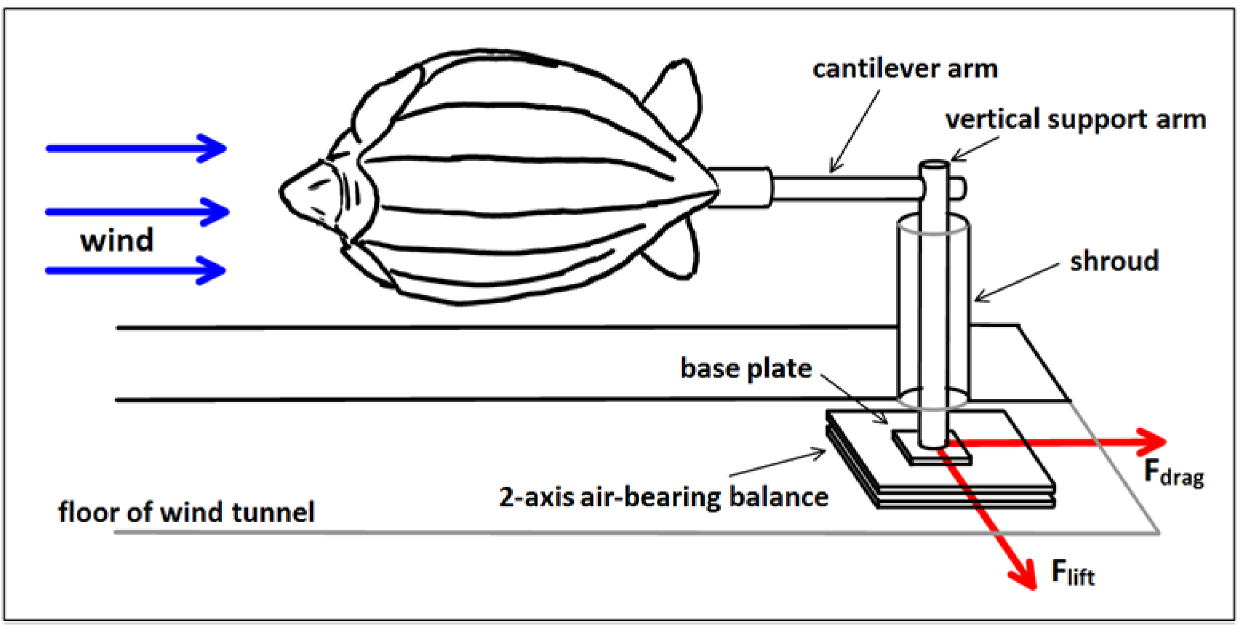

FIGURE 1
Schematic of the sting balance system including the turtle cast, cantilever arm, vertical support arm, shroud, base plate, and balance. The stand inserts into the leatherback turtle cast from the posterior or wake of the turtle cast. The stand goes down through the shroud and floor and is bolted to a two-axis air-bearing force balance below the wind tunnel floor.

Frontal and Planform Area

The frontal area was calculated using photographs taken with a Nikon D-90 12.3 megapixel camera (Nikon Inc., Melville, New York) with a 28-200 mm lens at 65 mm. The photos were shot in the RAW format and were not compressed. The camera was set on a tripod mount (91.5 cm in front of the cast) and a t-square ruler was used to align the camera down the center line of the sting balance assembly to which the turtle cast was attached. The distance from camera to object and the macro lens setting used minimized barrel distortion. The photograph was taken from directly in front of a turtle so that the outline of the turtle seen in the image would be equivalent to a transverse section through the turtle at the point of its largest area. The area the turtle covered in the image was equivalent to the frontal area that a fluid would encounter. A measuring device (imperial tape measure) was placed in the field of view at the same distance that the transverse section would occur. Similar images were taken perpendicular to the wind direction so that the area of the largest coronal section could be measured. These pictures were taken from above the carapace looking down and represent the planform area.

The photos were then uploaded into Adobe Photoshop® (Adobe Systems Incorporated, San Jose, CA, USA) and the measuring device in the images was used to calculate the length per pixel which could then be converted to area per pixel. We then outlined the turtles, filled in the outline in black, and overlaid this shape on a white background. The number of black pixels was then counted using the histogram feature of Adobe Photoshop® which was converted to area since the area per pixel was known.

Tags and Tag Codes

We used a combination of ARGOS-linked satellite tags (Wildlife Computers, Redmond, WA 98052, USA; Telonics, Mesa, AZ 85204, USA; Sirtrack, North Liberty, Iowa 52317, USA), VHF radio tags (Telonics), and ultrasonic tags (Sonotronics, Tucson, AZ 85713, USA). We also tested foam drogues used to house archival data loggers and tracking devices (Seminoff and Jones 2006) and National Geographic Crittercams (Marshall 1998; Heithaus et al. 2002; Seminoff et al. 2006). Placement of tags and various attachment techniques, i.e. harnesses (Eckert and Eckert 1986) and direct carapacial attachment (Lutcavage et al. 2002; Fossette et al. 2008; Lutcavage and Dodge 2008; Byrne et al. 2009), were also tested. All tags and testing configurations are listed in Tables 2 & 3 (below). The placements or tag codes described in Table 3 are shown visually in Figure 2 (below). All tags used were full scale from the manufacturer however the backpack harness and carapacial mount of Fossette et al. (2008) as well as the attached square and tear drop transmitters were scaled to fit the 74 cm SCL leatherback. The trials conducted on the adult leatherback used full-scale transmitters, harness and attachment materials (e.g., base plate).

TABLE 2
Tag codes and dimensions for all satellite, radio, sonic, and camera tags used in the study.

Tag	Tag code (1st-3rd characters)	Frontal area (m^2)	L x W x H (cm)
Wildlife Computers			
MK10-A(F)			
mold# 249A	WC1	0.0014	13.0 x 8.0 x 4.0
mold# 254A	WC2	0.0017	13.0 x 8.3 x 3.7
mold# 238A	WC3	0.0015	10.2 x 5.7 x 3.1
Splash			
mold# 224-00	WC4	0.0022	8.5 x 7.6 x 3.3
Spot 5			
mold# 244A	WC5	0.0011	7.1 x 5.4 x 2.4
mold# 181C	WC6	0.0006	4.8 x 4.2 x 1.4
mold# 206F	WC7	0.0008	7.2 x 3.4 x 2.5
Harness~	H__		
w/ bungy	HB_		
w/o bungy	HN_		
w/ square transmitter†	H_S	0.0008	5.7 x 2.0 x 4.0
w/ tear drop transmitter†	H_T	0.0006	11.9 x 1.8 x 4.0
w/ Kiwisat transmitter€	H_K	0.0040	22.9x8.3x5.1
w/o transmitter	H_N		
Fossette direct mount			
w/ square transmitter†	FDS	0.0008	5.7 x 2.0 x 4.0
w/ tear drop transmitter†	FDT	0.0006	11.9 x 1.8 x 4.0
w/ WC3 (see above)	FDW	0.0015	10.2 x 5.7 x 3.1
Telonics			
satellite A-1010B	TES	0.0027	12.3 x 6.0 x 2.8
radio MOD-400‡	TRL	0.0023	7.4 x 4.2 x 3.4
radio MOD-200‡	TRS	0.0021	5.7 x 2.0 x 3.6
TDR drogue*	DRO	0.0038	6.8 dia 30.5 L
Sonotronics			
sonic DT-97-L	SON	0.0003	1.8 dia 9.0 L
Crittercam (National Geographic)			
1st generationˆ	CR1		
2nd generationˆ	CR2		

~The underscores '_' represent place holders for the harness configurations.
†Frontal area and dimensions are of transmitter only not including the harness or direct plate mount, these tags were scaled for use on the juvenile leatherback.
€Sirtrack Kiwisat 101, ARGOS linked satellite tag, see Benson et al. 2007a for specifics.
‡The frontal area for the Telonics radio tags includes the area of the antennas (21.5 and 15 cm L by 0.07 cm diameter for TRS and TRL, respectively).
*Dimensions are given as diameter (dia) and length (L), see Seminoff et al. 2002 for specifics.
ˆContact National Geographic for details on frontal area and dimensions.

TABLE 3
The 4th and 5th characters of the 5 character tag codes referring to placement and orientation of tags on the turtles.

4th character		5th character	
Placement	Code	Direction	Code
front*	1	forward	F
1/4 back†	2	reverse	R
1/2 back†	3	with clay	C
valleyˆ	4		
head	5		
marginal‡	6		
marginal-2‡	7		

*Front placement is within 5 cm of the nuchal notch (scute).
†¼ and ½ back refer to placement one quarter and one half the length of the carapace from the nuchal notch (scute).
ˆThe valley placement was between 2nd and 3rd longitudinal ridge on the left side ½ back from nuchal notch.
‡Marginal and marginal-2 refer to placement on the marginal scutes at the widest point of carapace and half-way between the midline and marginal scutes, respectively.

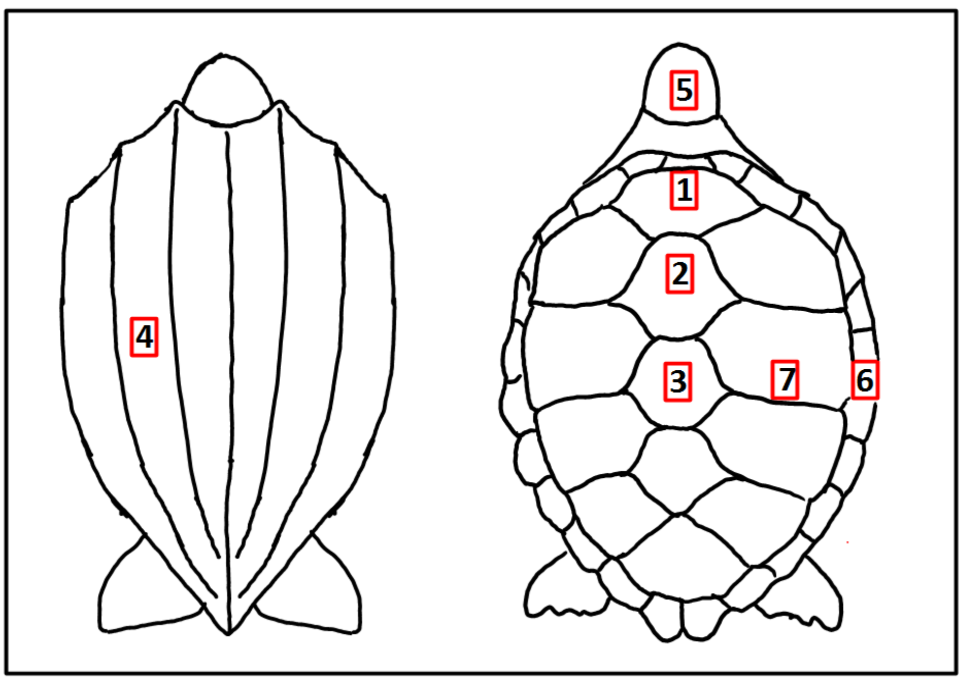

FIGURE 2
Schematic showing the placement of tags on the turtle cast carapace. Positions 1, 2, 3, 5, 6, and 7 are identical (proportionally) on all casts tested. Only position 4 is specific to the leatherback cast. See Table 3 for description of tag coding placement definition.

All tags were given a 5 character code where the first 3 characters refer to the tag (Table 2), the 4th refers to the placement of the tag on the cast, and the 5th character gives the direction of the tag relative to the turtle (Table 3). For instance, the tags were oriented as the manufacturer intended with the antenna generally towards the posterior of the turtle (forward, F) while R refers to turning the tag 180°, so it is reversed (Table 3; Figure 2).

As well as testing the various tags and tag positions listed in Tables 2, 3, and illustrated in Figure 2, we also tested the effects of double tagging and retrofitting existing tags to be tear drop shaped. For the double tagging trials we used rectangular blocks of wood that had frontal areas of 0.0014 m^2 and were 10 cm long. The blocks were of the length, width, height, and frontal area of typical tags (Table 2). The blocks were placed on the large green turtle cast both in parallel and in series (Figure 3, below). The increases in drag coefficient were compared with placing only one block on the cast and with the cast alone. To determine the effects of retrofitting existing tags, we used a flat bottomed wooden dowel of frontal area 0.0012 m^2 and 10 cm in length. The dowel was tested to determine the increase in drag it caused to the large green turtle cast, we then used clay (representing epoxy used in the field) to add a nose cone and tail keeping the frontal area equal but giving the tag a tear drop shape. The drag coefficient was then compared with the squared wooden dowel and with the cast alone.

Test Facility

The Boundary Layer Wind Tunnel (BLWT) at the Department of Mechanical Engineering, University of British Columbia, Canada, is an open-circuit wind tunnel 1.6 m high by 2.5 m wide by 23.6 m long and capable of 3 to 30 m s^{-1} wind speeds. The generated wind speeds are uniform across the test section except for a boundary layer near the tunnel walls (<5 cm). Differential pressure transducers mounted at the proximal end of the test section measured the dynamic air pressure (Q) in Pascals (Pa) during a test. The dynamic air pressure is related to wind speed using Bernoulli's equation,

Eq. 1) $$U=(2Q/\rho)^{1/2}$$

where U is velocity in m s^{-1} and ρ is air density (kg m^{-3}). A barometer and thermometer mounted on the wind tunnel provided values of atmospheric air pressure and air temperature. Air density in the wind tunnel was calculated using the ideal gas law $\rho=P/RdT$, where P is the barometric pressure, Rd is the gas constant for dry air, and T is the absolute air temperature (units, K).

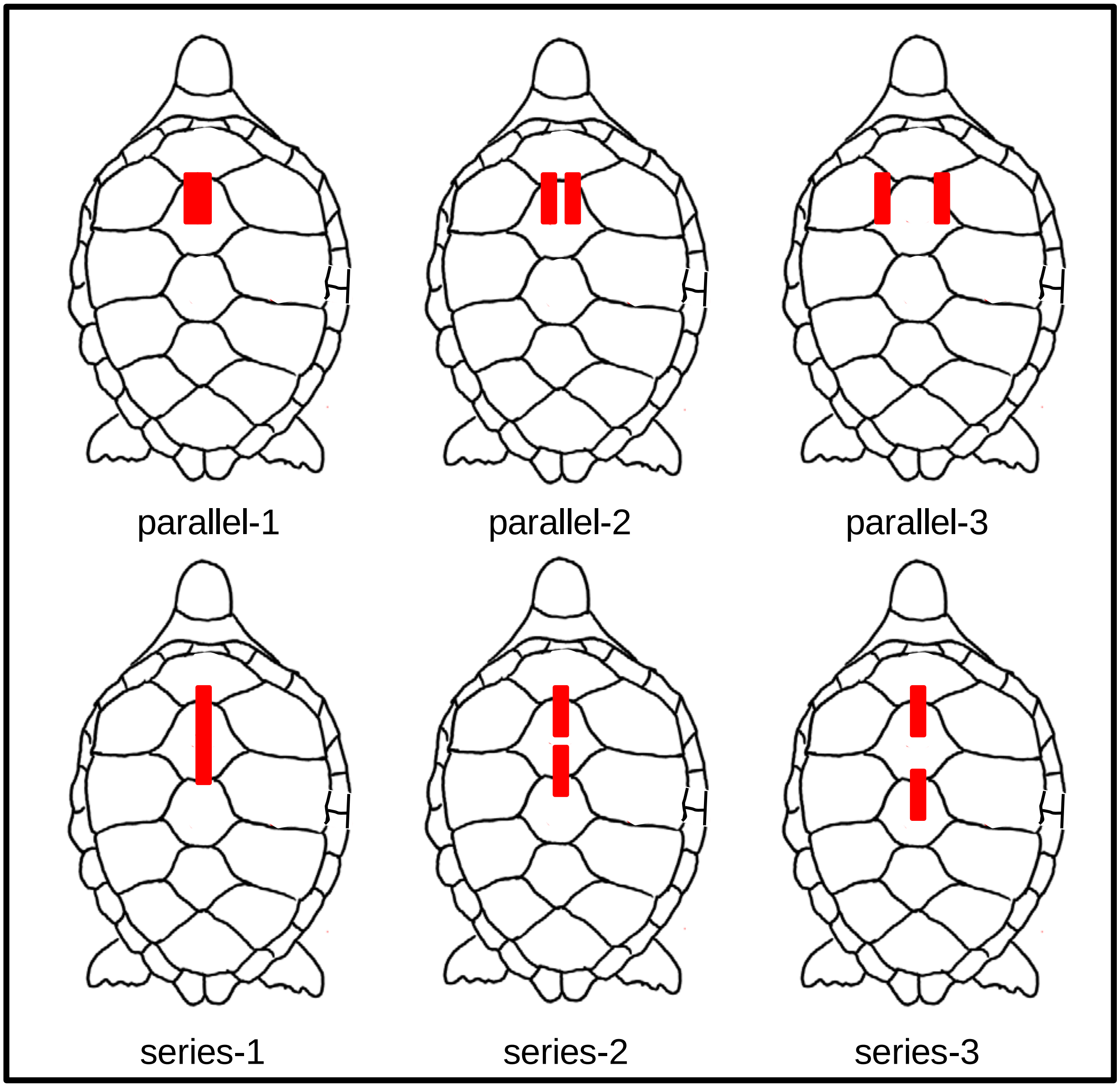

FIGURE 3
Schematic of tag placement for the double tagging trials. In parallel-1 and series-1 the two tags are touching. Parallel-2 and series-2 are one tag width apart while parallel-3 and series-3 are two tag widths apart.

Sting Balance

A sting balance system consisting of a bi-directional force balance and attached stand was used to measure drag and side forces (lift) on turtle casts. The horizontal arm (cantilever) of the sting balance attached to the casts from their wake therefore not disturbing the flow pattern around the cast (Figure 1). The stand was constructed using a steel pipe (to reduce vibrations) and consisted of a base plate (0.64 cm thick), a 1.12 m vertical support pipe (5.09 cm o.d., 2.55 cm i.d.), and a 0.82 m cantilever arm (3.65 cm o.d., 2.38 cm i.d.) with a tapered threaded end that was inserted into the posterior end of the casts. The cantilever arm was press-fitted into the support pipe which was welded to the base plate. The base plate was attached to the force balance using eight 1-cm diameter bolts. The vertical support pipe of the stand was shrouded by a 3" PVC pipe (schedule 80), which was attached to the floor of the wind tunnel. This shroud blocked the vertical support pipe from the wind and since the cantilever arm was in the wake of the cast model the measured force was due solely to the cast and not the attachment apparatus (Figure 1).

The forces exerted on the casts by the wind were transferred by the stand to a specially designed two-axis, air-bearing force balance mounted below the wind tunnel. The balance holds up to 2200 N of vertical load with a maximum measurable drag and side load of 70 N with accuracy better than 0.3% of full scale, independent of vertical load (Ostafichuk and Green 2002). The drag force was measured as the force parallel to the wind direction and the side force was perpendicular to the wind direction but still in the horizontal plane. The casts were mounted such that the dorsal/ventral axis of the turtle was horizontal and therefore the side force was equivalent to the lift. Data acquisition was performed using a computer outfitted with DasyLab software and a 16 channel digital interface board at a 1 kHz sampling rate through a 2 Hz low-pass digital filter (DasyLab and Daqboard model DBK16, IOtech, Inc., Ohio, U.S.A.). The system sampled at 1 kHz for 15 seconds and the standard deviation was calculated on the 15,000 point buffered data and used to determine the stability of the load cell readings. The mean of the collected load data were used plus/minus 1 standard deviation (s.d.).

Measuring Drag Force

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:

Eq. 2) $$F_D = \frac{1}{2} \rho C_D A U^2$$

where C_D (drag coefficient) is a unitless coefficient that describes the drag force that is characteristic of the blunt body. F_D can be changed to C_D by arranging equation 2 as follows:

Eq. 3) $$C_D = F_D / 0.5 \rho U^2 A$$

where $0.5\rho U^2$ is equal to the dynamic air pressure *Q (see equation 1).* C_D is independent of size but is a function of the fluid flow pattern around the object. The fluid flow around a body of length, L, can be predicted from the dimensionless Reynolds number,

Eq. 4) $$Re = LU/v$$

where v is the kinematic viscosity of the fluid ($m^2 s^{-1}$). *Re* greater than 5×10^5 represents turbulent flow around the object and the dependence of *Re* on C_D becomes weak in turbulent flow (Tritton 1988). Therefore, by measuring the C_D of an object in turbulent flow, it is possible to predict the F_D a similarly shaped object of any size would have when traveling at speed *U*. This is known as Reynold's similarity law (Hoerner 1965) or dynamic similitude (Kline 1986; Vogel 1994). Matching Reynold's numbers allows the calculation of air speeds that are representative of swimming speeds for wild turtles. The kinematic viscosity of sea water (v_{sw}) and air (v_a) are 1.004×10^{-6} and 1.56×10^{-5}, respectively, at 25 degrees Celsius.

Therefore matching Reynold's numbers (Eq. 4) for movement of the same object in sea water and air gives the following equation:

Eq. 5) $$(U_{sw}/v_{sw})v_a = U_a$$

Thus, air speeds of 8, 16, and 20 $m\ s^{-1}$ are equivalent to water speeds of 0.5, 1.0, and 1.3 $m\ s^{-1}$, respectively, which are typically employed by swimming turtles (Luschi et al. 1998; Eckert 2002; Fossette et al. 2008; Byrne et al. 2009).

To determine the energetic cost to the turtle from increased drag we use:

Eq. 6) $$P = F_D U$$

where *P* is power output ($j\ s^{-1}$). F_D is the thrust force the turtle must exert to move through the water or swim. Substituting equation 2 into 6, we get:

Eq. 7) $$P = \tfrac{1}{2} \rho C_D A U^3$$

As F_D increases, there is a proportional increase in the power output of the turtle in order to maintain velocity, simplified as:

Eq. 8) $$P = KU^3$$

where *K* is equal to ($\tfrac{1}{2} \rho C_D A$). If the turtle maintains power output in light of the increase in drag then a subsequent decrease in velocity will result described by:

Eq. 9) $$U = (P/K)^{1/3}$$

Measuring Flow Patterns

In addition to measuring the drag force and coefficients, the flow patterns around the casts and tags were also examined. For the leatherback, olive ridley, and large green turtle casts, several hundred short pieces (5-7.5 cm) of yarn were taped to the head, neck, carapace, and attached instrument being tested. The casts were then tested in the wind tunnel as detailed above with and without the various transmitters. The drag force was not recorded during flow pattern trials however, the trials were filmed and thus, the flow around the casts could be compared with the casts when tags were attached.

RESULTS

Drag and Lift Coefficients

The drag of the casts was determined at wind speeds ranging from 2 to 19.4 m s^{-1} and at -12 to +12 degrees (angle of attack) from the angle that produced the minimum drag coefficient for each cast (Figure 4A & B, below). The wind speeds were representative of Reynolds numbers of $1.9\text{-}5.3\text{x}10^5$ and $2.4\text{-}6.5\text{x}10^5$ for the green turtle casts (small and large), $2.9\text{-}8.0\text{x}10^5$ for the olive ridley cast, $3.5\text{-}9.7\text{x}10^5$ for the juvenile leatherback cast, and $1.9\text{x}10^5\text{-}1.8\text{x}10^6$ for the adult leatherback cast (calculated with Eq. 4). Between 6-8 m s^{-1} (equivalent to 0.38-0.51 m s^{-1} in sea water, Eq. 5), the drag coefficient became insensitive to further increases in velocity for all casts (Figure 4A), suggesting turbulent flow. Therefore, we used 16 m s^{-1} (to be sure we were above the laminar/turbulent flow transition) in all the figures and analyses. All drag data from the casts were normalized to the angle of attack (α) that gave the lowest C_D and this angle was referred to as angle 0 (Figure 4B). As can be seen in Figure 4B any deviations from $\alpha = 0$ lead to increases in C_D. This is due to the increased frontal area of the cast at angles other than 0. The exposed dorsal or ventral surface at angles other than 0 also increased the lift (Figure 5, below). The angles of attack for lift (Figure 5) are the corresponding angles used in Figure 4A for drag coefficient. At $\alpha = 0$ the lift coefficient was near 0 (Figure 5) and the drag coefficient was minimized (Figure 4B) therefore $\alpha = 0$ was used for all the figures and analyses of drag and lift effects.

The drag coefficient at $\alpha = 0$ and 16 m s^{-1} was 0.144, 0.126, 0.192, 0.137, and 0.174 for the green (small and large), olive ridley and leatherback (juvenile and adult) casts, respectively (Table 4, below). The olive ridley turtle had the highest drag coefficient, 10-53% higher than the green turtles and leatherbacks. The lift coefficient was 0.002, -0.009, -0.008, -0.002, and 0.019 for the green turtles (small and large), olive ridley and leatherback (juvenile and adult) casts, respectively (Table 5, below).

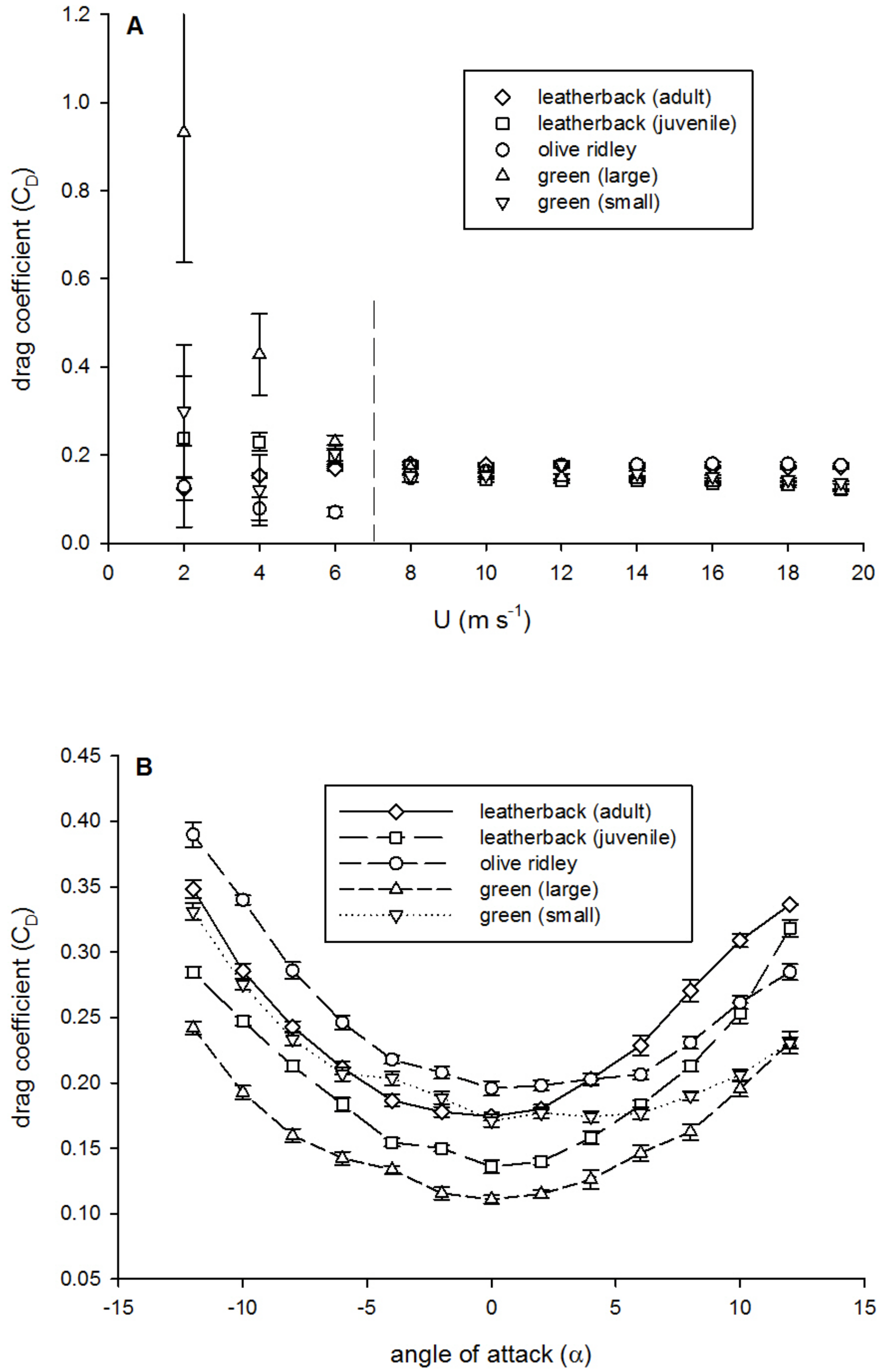

FIGURE 4A&B
Measured drag coefficient C_D versus velocity U (m s^{-1}) (A) and angle of attack (B) for all 5 casts used in wind tunnel experiments. The dotted line in A denotes the transition to turbulent flow for all casts. Error bars depict ± 1 standard deviation around the mean.

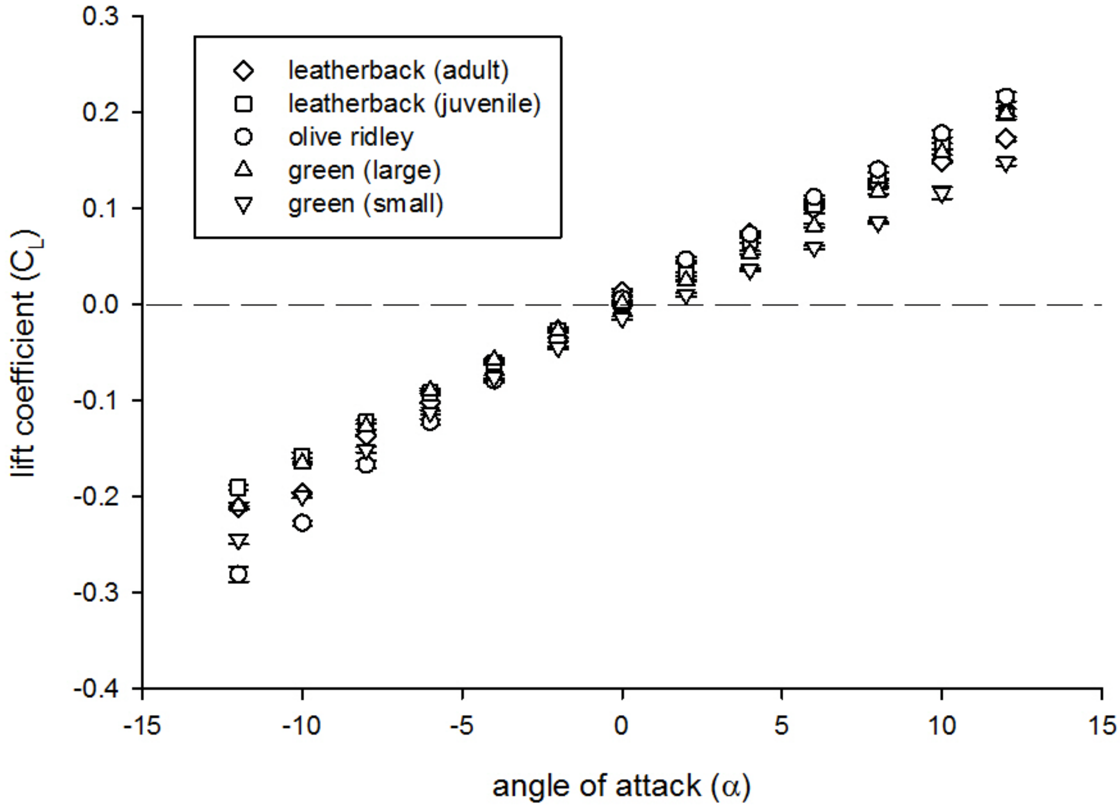

FIGURE 5
Measured lift coefficient C_L versus angle of attack for all 5 casts used in wind tunnel experiments. All measurements were performed at 16 m s^{-1} (Figure 4A). Error bars depict ± 1 standard deviation around the mean.

TABLE 4

Drag coefficients (C_D) for all the sea turtle casts and the various tags and tag configurations ± 1 standard deviation (s.d.). All measurements were performed at 16 m s^{-1} and at the angle of attack that gave minimal drag (Figures 4A & B). See tables 2 & 3 for details on the tag codes listed.

	Leatherback turtle (adult)	Leatherback turtle (juv.)	Olive ridley turtle	Olive ridley turtle (prone)	Green turtle (large)	Green turtle (small)
	C_D ± 1 s.d.	C_D ± 1 s.d.	C_D ± 1 s.d.	C_D ± 1 s.d.	C_D ± 1 s.d.	C_D ± 1 s.d.
CAST	0.174 ± 0.003	0.137 ± 0.004	0.192 ± 0.004	0.210 ± 0.005	0.126 ± 0.004	0.144 ± 0.004
DRO1F			0.264 ± 0.005	0.351 ± 0.010		
TES1F			0.222 ± 0.004		0.170 ± 0.007	0.187 ± 0.004
TES1C					0.175 ± 0.005	
TES2F			0.217 ± 0.004		0.170 ± 0.005	
TES3F			0.214 ± 0.006		0.174 ± 0.006	
TES1R			0.230 ± 0.004			
TRS1F			0.231 ± 0.004		0.174 ± 0.004	0.210 ± 0.004
TRS1R			0.240 ± 0.004			
TRL1F			0.227 ± 0.004		0.192 ± 0.004	
TRL1R			0.232 ± 0.004			
SON60			0.205 ± 0.004			
SON70			0.203 ± 0.004		0.130 ± 0.004	
TRL1F-SON70			0.222 ± 0.005			
TRL10-SON60					0.192 ± 0.004	
WC11F	0.177 ± 0.003	0.154 ± 0.003				
WC12F	0.175 ± 0.003	0.142 ± 0.004				
WC13F	0.175 ± 0.005	0.143 ± 0.003				
WC21F		0.153 ± 0.003				
WC22F		0.143 ± 0.004				
WC31F			0.212 ± 0.004		0.163 ± 0.004	
WC32F			0.213 ± 0.005		0.164 ± 0.004	
WC33F			0.201 ± 0.005		0.152 ± 0.006	
WC41F		0.155 ± 0.004				
WC42F		0.153 ± 0.004				
WC51F			0.202 ± 0.004		0.145 ± 0.003	0.167 ± 0.004
WC52F			0.203 ± 0.005		0.149 ± 0.003	
WC53F			0.202 ± 0.005		0.152 ± 0.008	
WC61F			0.208 ± 0.004		0.153 ± 0.004	
WC62F			0.216 ± 0.003		0.142 ± 0.004	
WC63F			0.200 ± 0.006		0.151 ± 0.006	
WC65F			0.207 ± 0.004		0.129 ± 0.005	
WC71F			0.194 ± 0.004		0.141 ± 0.004	0.174 ± 0.004
WC72F			0.204 ± 0.005		0.144 ± 0.003	
WC73F			0.197 ± 0.006		0.149 ± 0.006	
WC74F		0.136 ± 0.004				
WC75F			0.193 ± 0.004		0.144 ± 0.004	
CR11F				0.389 ± 0.011		
CR21F				0.442 ± 0.011		
HBN1F		0.244 ± 0.004				
HBS1F		0.279 ± 0.005				
HBT1F		0.249 ± 0.004				
HNN1F	0.334 ± 0.005	0.262 ± 0.003				
HNS1F		0.283 ± 0.004				
HNT1F		0.265 ± 0.004				
HBK1F	0.368 ± 0.009					
HNK1F	0.339 ± 0.008					
HNK2F	0.332 ± 0.005					
FDS1F	0.175 ± 0.005	0.196 ± 0.003				
FDS2F	0.179 ± 0.005	0.160 ± 0.003				
FDS3F	0.178 ± 0.003	0.159 ± 0.003				
FDT1F		0.164 ± 0.004				
FDT2F		0.145 ± 0.003				
FDT3F		0.152 ± 0.004				
FDW1F	0.175 ± 0.005					
FDW2F	0.179 ± 0.005					
FDW3F	0.178 ± 0.003					

TABLE 5

Lift coefficients (C_L) for all the sea turtle casts and the various tags and tag configurations ± 1 standard deviation (s.d.). All measurements were performed at 16 m s^{-1} (Figure 4A) and at the angle of attack that gave minimal drag and lift (Figures 4B, 5). Values in parentheses are negative. See tables 2 & 3 for details on the tag codes listed.

	Leatherback turtle (adult)	Leatherback turtle (juv.)	Olive ridley turtle	Green turtle (large)	Green turtle (small)
	C_L ± 1 s.d.	C_L ± 1 s.d.	C_L ± 1 s.d.	C_L ± 1 s.d.	C_L ± 1 s.d.
CAST	0.019 ± 0.004	(0.002) ± 0.003	(0.008) ± 0.004	(0.009) ± 0.001	0.002 ± 0.003
DRO1F			(0.012) ± 0.006		
TES1F			(0.013) ± 0.004	(0.009) ± 0.001	(0.001) ± 0.002
TES1C				(0.008) ± 0.001	
TES2F			(0.014) ± 0.004	(0.021) ± 0.001	
TES3F			0.001 ± 0.004	0.0001 ± 0.001	
TES1R			(0.011) ± 0.003		
TRS1F			(0.010) ± 0.004	(0.007) ± 0.001	0.002 ± 0.002
TRS1R			(0.010) ± 0.004		
TRL1F			(0.011) ± 0.003	(0.006) ± 0.001	
TRL1R			(0.010) ± 0.003		
SON60			(0.007) ± 0.003		
SON70			(0.008) ± 0.003	(0.007) ± 0.001	
TRL1F-SON70			(0.010) ± 0.004		
TRL10-SON60				(0.008) ± 0.001	
WC11F	0.039 ± 0.003	(0.004) ± 0.002			
WC12F	0.039 ± 0.002	(0.002) ± 0.001			
WC13F	0.039 ± 0.002	(0.003) ± 0.002			
WC21F		(0.003) ± 0.001			
WC22F		(0.003) ± 0.002			
WC31F			(0.012) ± 0.003	(0.010) ± 0.001	
WC32F			(0.012) ± 0.003	(0.011) ± 0.001	
WC33F			0.007 ± 0.004	(0.0003) ± 0.001	
WC41F		(0.001) ± 0.002			
WC42F		(0.003) ± 0.002			
WC51F			(0.012) ± 0.003	(0.010) ± 0.001	0.003 ± 0.003
WC52F			(0.010) ± 0.004	(0.010) ± 0.001	
WC53F			0.007 ± 0.004	0.0001 ± 0.0006	
WC61F			(0.010) ± 0.003	(0.006) ± 0.001	
WC62F			(0.010) ± 0.003	(0.007) ± 0.001	
WC63F			0.001 ± 0.003	(0.001) ± 0.001	
WC65F			(0.004) ± 0.004	(0.007) ± 0.001	
WC71F			(0.009) ± 0.004	(0.010) ± 0.001	0.003 ± 0.002
WC72F			(0.009) ± 0.003	(0.010) ± 0.001	
WC73F			0.001 ± 0.004	0.0001 ± 0.0006	
WC74F		(0.002) ± 0.002			
WC75F			(0.008) ± 0.003	(0.010) ± 0.001	
CR11F					
CR21F					
HBN1F		(0.009) ± 0.002			
HBS1F		(0.013) ± 0.002			
HBT1F		(0.012) ± 0.002			
HNN1F	(0.113) ± 0.005	(0.012) ± 0.002			
HNS1F		(0.013) ± 0.002			
HNT1F		(0.012) ± 0.002			
HBK1F	(0.088) ± 0.005				
HNK1F	(0.110) ± 0.003				
HNK2F	(0.071) ± 0.001				
FDS1F		(0.011) ± 0.003			
FDS2F		(0.009) ± 0.002			
FDS3F		(0.006) ± 0.002			
FDT1F		(0.006) ± 0.002			
FDT2F		(0.006) ± 0.001			
FDT3F		(0.004) ± 0.002			
FDW1F	0.037 ± 0.003				
FDW2F	0.038 ± 0.003				
FDW3F	0.036 ± 0.003				

Effect of Transmitters on the Measured Drag and Lift Coefficient

Leatherback turtle (adult).

The backpack harness caused an increase in drag coefficient of 91% to 112% depending on the configuration (Figure 6, below, Table 4). The harness was tested with and without a full scale Sirtrack Kiwisat 101 tag, with or without a bungee strap (see Eckert and Eckert 1986; Benson et al. 2007a), and with the tag and base plate in the 1 and 2 position (Table 3). Use of a bungee strap to secure the harness caused 17% greater increase in drag over the same harness configuration without a bungee strap. Moving the tag and base plate to the 2 position decreased the drag from the 1 position by 4.4% all else remaining the same.

The Fossette et al. (2008) direct carapacial mount with the Wildlife Computers MK 10-AF GPS satellite transmitter (FDW) caused a 1% to 3% increase in drag and the Wildlife Computers ridge-mount tag (WC1), mounted directly to the carapace, increased drag by 0.6% to 1.8% over the cast alone (Figure 6). For the harness, moving the tag and base plate to position 2 (Table 3) reduced the drag increase by 4.4% (from 95.2% to 90.8%, over the cast alone). Moving the Wildlife Computer tag to position 2 and 3 reduced the drag increase by 1% and 1.2%, respectively, over position 1. However for the Fossette et al. (2008) direct carapacial mount, there was no benefit from moving the tag posteriorly as the 2 position gave the highest drag measurement followed by the 3 and then 1 position.

We tested the backpack harness (HNN), Fossette et al. (2008) direct carapacial mount (FDW), and the Wildlife Computers ridge-mount tag (WC1) across a continuum of velocities, e.g., 2 – 19.4 m s^{-1}, in increments of ~2 m s^{-1}. The wind speeds tested were equivalent to velocities in sea water of 0.13 – 1.25 m s^{-1}. The backpack harness, without a transmitter or bungee strap caused an increase in drag of 173% at the lowest speed (0.13 m s^{-1}) and 94% at the highest speed (1.25 m s^{-1}) (Figure 7, below) relative to the cast alone. The Fossette et al. (2008) direct carapacial mount caused an increase in drag of 85.1% and 3.7%, while the Wildlife Computers ridge-mount tag caused an increase in drag of 63.3% and 1.1% at the lowest and highest speeds, respectively, compared with the cast alone. There was a marked drop in the added drag for all three telemetry packages from 0.13 m s^{-1} to 0.26 m s^{-1} (velocity in water), with a continued drop for the Fossette et al. (2008) direct carapacial mount and Wildlife Computers ridge-mount tag at 0.39 m s^{-1}. The harness dropped from 173% drag increase at 0.13 m s^{-1} to maintain between 80% to 100% drag increase from 0.26 to 1.25 m s^{-1}, whereas the direct carapacial mount and ridge-mount tag caused approximately 3% and 1% drag increases (respectively) from 0.51 – 1.25 m s^{-1}.

The Fossette et al. (2008) direct carapacial mount and the Wildlife Computers ridge-mount tag doubled the lift coefficient or lift force in all positions (Table 5), increasing the lift force from 3.2 N to 6.2 – 6.4 N for the cast alone (at 16 m s^{-1}). The drag force for the cast alone was 12.2 N (at 16 m s^{-1}). All of the configurations of the backpack harness changed the lift (negatively) by

4.7 to 6.9 times (Table 5), giving lift forces of -11.8 to -18.8 N (we use negative Newtons to denote the lift force is to the ventral side of the turtle cast) or -15 to -24 N in total change. For all harness configurations, the absolute lift force is close to or the same as the drag force, 15 – 24 N and 23 – 26 N, respectively. Whereas with the direct carapacial mount and ridge-mount tag, the lift force was maintained in the dorsal direction and was only 50% that of the drag force (increased from 25% on the cast alone).

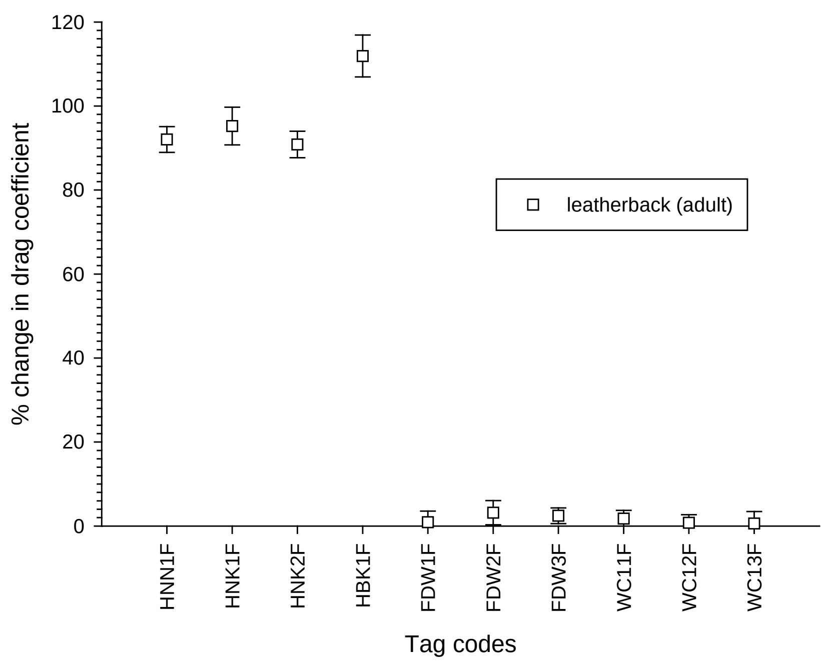

FIGURE 6
Percent change in drag coefficient when the various tags and tag configurations were added to the adult leatherback turtle cast. The y-axis was normalized to the baseline drag measurement of the cast without a transmitter therefore zero represents no increase in drag coefficient from the cast alone. All measurements were performed at 16 m s^{-1} and at the angle of attack that gave minimum drag (Figures 4A & B). See tables 2 & 3 for details on the tag codes listed on x-axis. Error bars depict ± 1 standard deviation around the mean.

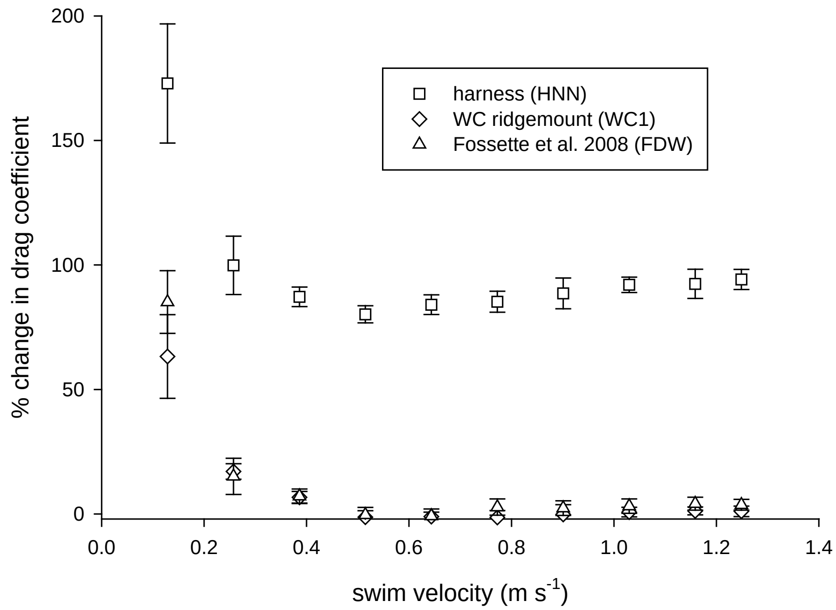

FIGURE 7
Percent change in drag coefficient when the various tags and tag configurations were added to the adult leatherback turtle cast over a range of swim velocities. The y-axis was normalized to the baseline drag measurement of the cast without a transmitter therefore zero represents no increase in drag coefficient from the cast alone. All measurements were performed over 0.13 to 1.25 m s^{-1} (equivalent swim speeds) and at the angle of attack that gave minimum drag (Figures 4A & B). See tables 2 & 3 for details on the tag codes listed on x-axis. Error bars depict ± 1 standard deviation around the mean.

Leatherback turtle (juvenile).

The backpack harness caused an increase in drag coefficient of 78% to 107% depending on the configuration (Figure 8, below, Table 4). The harness was tested with and without a bungee strap below and above the head (see Eckert and Eckert 1986; Benson et al. 2007a) and with or without a square and tear drop transmitter. Using a bungee strap to secure the harness, the drag was lowered by 7% compared with not using the bungee. Also, the tear drop transmitter caused a 12% reduction in drag compared with the square transmitter, however at a drag coefficient of 0.244 to 0.283 (Table 4) any configuration of the backpack harness caused a substantial increase in drag compared with the cast alone. In all of the backpack configurations, the transmitter and plate were in position 1 (see Table 3) or within 5 cm of the nuchal notch. All back pack trials on the juvenile leatherback were done with a scaled harness and transmitters.

The various configurations of the Fossette et al. (2008) direct carapacial mount caused an increase in drag coefficient of 6.4% to 43.3% compared with the cast alone (Figure 8). As with the harness the tear drop tag (modeled of the SirTrack Kiwisat satellite tag) gave a smaller increase in drag coefficient than the square transmitter. In all cases of tag attachment to the leatherback carapace, placement of tags ¼ of the way back on the carapace (placement position 2, see Table 3) gave the lowest increase in drag coefficient. As with the harness, the Fossette et al. (2008) direct carapacial mount and tags were scaled for the juvenile leatherback.

The Wildlife Computers (WC) satellite tags, in the various placement configurations, increased drag by 0 to 14% compared with the cast alone (Figure 8, Table 4). The ridge-mount (i.e., designed to attach directly to the longitudinal ridge) MK 10-A satellite transmitter (WC1 & WC2; see Table 2) increased drag by 12% in the front position, but when moved ¼ of the way back on the carapace the increase in drag was reduced to 4% over the cast alone. No further gains in drag reduction were found when the tags were moved halfway back on the carapace (midpoint of the carapace length). The WC Splash tags caused the greatest increase in drag coefficient (14%) while the WC Spot 5 tag placed in the valley between the 2^{nd} and 3^{rd} longitudinal ridge and ½ way along the carapace caused no detectable increase in drag coefficient. The Wildlife Computers tags placed on the juvenile leatherback were full scale.

All but one of the transmitters and attachment configurations caused negative lift (Table 5). The backpack harness caused negative lift (i.e., a downward force) of 6 to 9 times that of the cast alone. The direct carapacial mount of Fossette et al. (2008) negatively changed lift by 3 to 7 times while the WC tags in the various placements changed lift coefficient positively by 1.4 times for the splash tag and negatively by up to 3 times for all other tags and placements. The changes in lift coefficient however were negligible as the lift coefficient was nearly zero at $\alpha = 0$; the maximum lift force was 0.51 N whereas increases in the drag force were as great a 1.64 N.

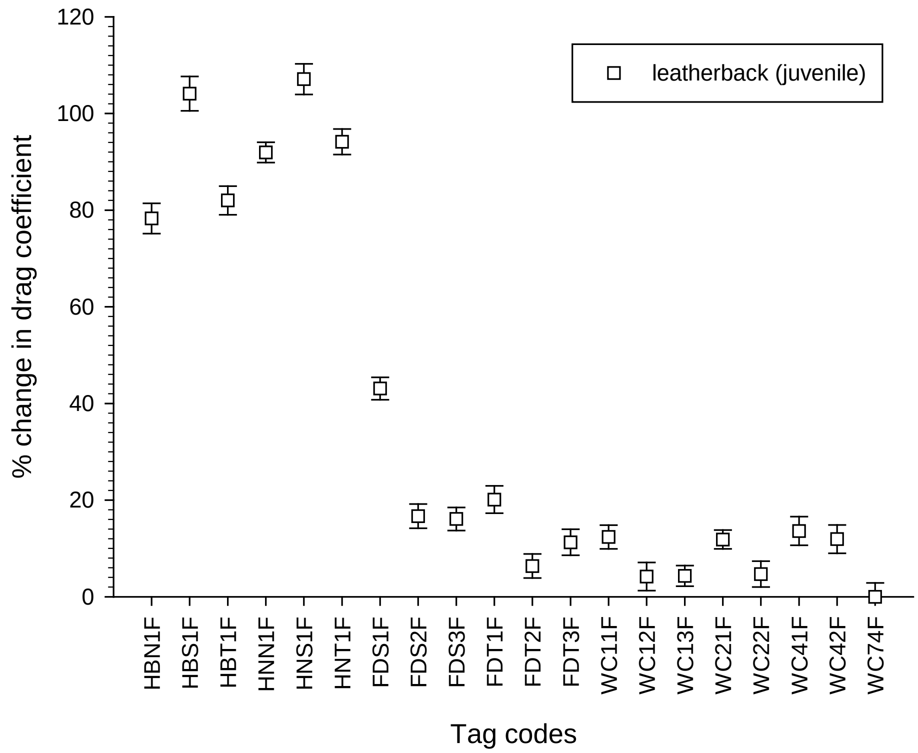

FIGURE 8
Percent change in drag coefficient when the various tags and tag configurations were added to the juvenile leatherback turtle cast. The y-axis was normalized to the baseline drag measurement of the cast without a transmitter therefore zero represents no increase in drag coefficient from the cast alone. All measurements were performed at 16 m s^{-1} and at the angle of attack that gave minimum drag (Figures 4A & B). See tables 2 & 3 for details on the tag codes listed on x-axis. Error bars depict ± 1 standard deviation around the mean.

Olive ridley turtle.

The TDR drogue increased drag by 37%, the Telonics satellite and VHF radio tags increased drag by 11% to 25%, the ultrasonic tags increased drag by 7%, and the WC satellite tags increased drag by 1% to 12% over the olive ridley cast alone (Figure 9A, below). There was a slight drop in the drag increase for the Telonics satellite tag (TES; Table 2) when the tag was placed in position 2 (¼ back on carapace; Table 3) however for all the WC tags, there was either no benefit or a slight increase in drag of 1% to 6% for tags placed in position 2 over position 1. All cases where the Telonics satellite and VHF radio tags were tested in both the forward and reverse position, the forward position resulted in 2% to 5% lesser drag increases than the reverse position. Ultrasonic tags (SON; Table 2) placed on or near the marginal scutes (positions 6 & 7; Table 3) increased drag by 7% over the cast alone. The combination of the ultrasonic and Telonics VHF radio tag did not have an additive effect; rather the total increase in drag coefficient was similar to the increase caused by the VHF radio tag alone. For the WC tags, the

GPS/satellite tag (MK 10-AF, WC3; see Table 2) gave the greatest increase in drag coefficient (1% to 6%), and no advantage was gained by moving the tags ¼ of the way back on the carapace. The smallest increases in drag coefficient (< 1%) were caused by the Spot 5 tag (WC7; Table 2) placed either in the front (1) or head position (5) (Table 3).

The TDR drogue (DRO; Table 2) and Crittercams (CR1, CR2; Table 2) increased drag by 67% to 111% over the cast alone when the olive ridley was placed in the prone position (Figure 9B, below). The cast had to be placed in the prone position to support the weight of the Crittercams. The second generation crittercam (CR2; Table 2) caused the largest drag coefficient measured (0.4423; Table 4) and the largest percent increase (111%) than any other configuration of the hardshell turtle casts (i.e., greens and olive ridley turtles).

The various tags and configurations changed lift negatively by up to 1.9 times with only the sonic tag (SON6F; Table 2 & 3) and the WC tag (WC65F; Tables 2 & 3) positively changing the lift coefficient by 1.15 to 2 times, respectively (Table 5). The decreases and increases in lift force were negligible at 0.23 N in comparison with the increases in drag force of up to 2.76 N. The total lift force was typically $1/5^{th}$ or less that of the drag force when the cast was instrumented and $1/6^{th}$ or less for the cast alone.

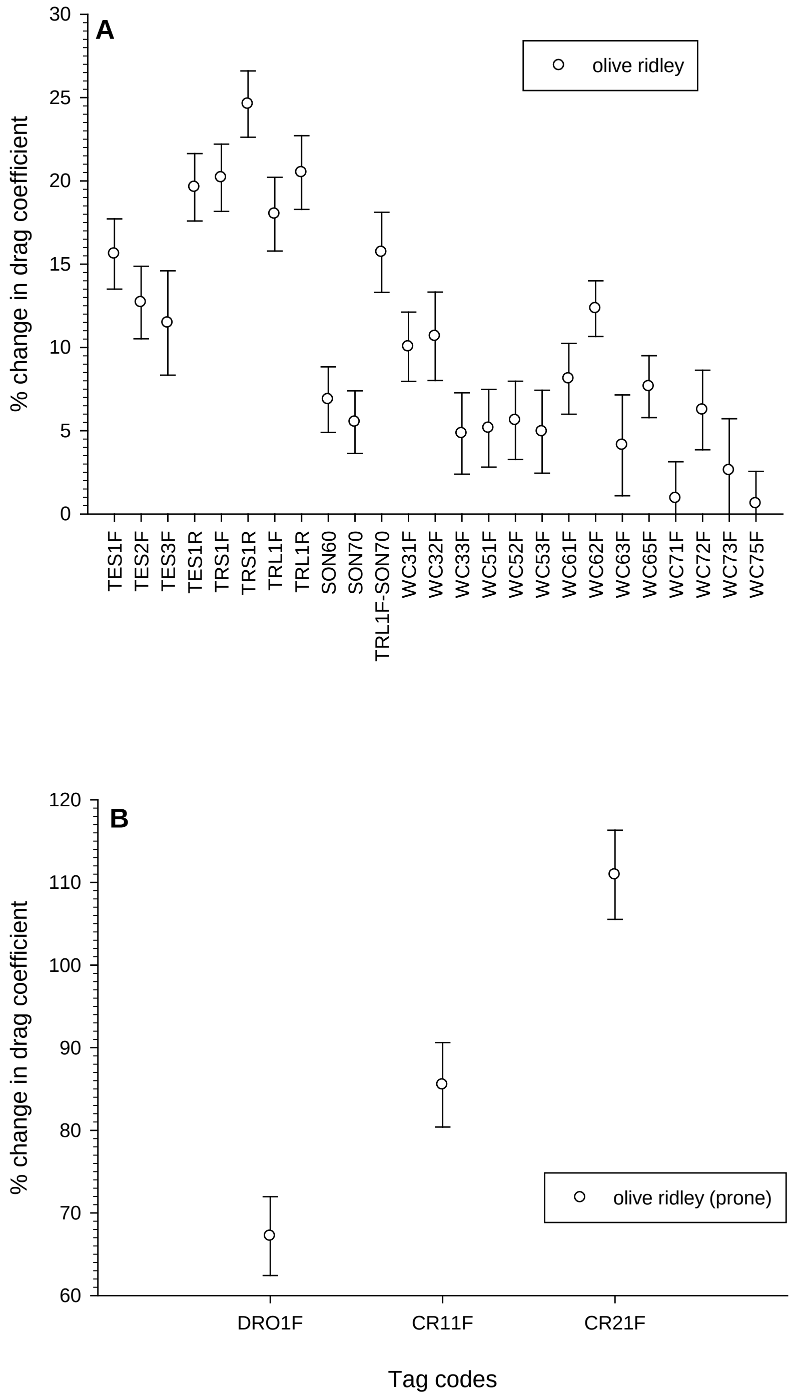

FIGURE 9A&B

Percent change in drag coefficient when the various tags and tag configurations were added to the olive ridley turtle cast. The y-axis was normalized to the baseline drag measurement of the cast without a transmitter therefore zero represents no increase in drag coefficient from the cast alone. All measurements were performed at 16 m s^{-1} and at the angle of attack that gave minimum drag (A) or with the longitudinal transect of the turtle in the prone position (B) (see Figures 4A & B). See tables 2 & 3 for details on the tag codes listed on x-axis. Error bars depict ± 1 standard deviation around the mean.

<u>Green turtle (large).</u>

The Telonics satellite tags increased the drag coefficient by 35% to 40% over the green turtle cast alone (Figure 10, below). There was no added benefit from moving the tag back to position 2 (Table 3). Clay was added around the satellite tag to replicate the use of epoxy and fiberglass resin to create a sloped ledge around the transmitter (TES1C; see Tables 2 & 3) like a saucer. This method is used in the field to protect tags from rocks, coral and other turtles (while possibly promoting flow this design increases the frontal area). The clay increased drag coefficient by an additional 5% over the satellite tag alone (Figure 10). The Telonics radio tags increased the drag coefficient by 38% to 53% with the larger tag having an additional 15% increase in drag over the smaller radio tag. The sonic tag (SON) in position 7 (Table 3) caused an increase in drag coefficient of 4% over the cast alone. When the sonic and radio tags were combined there was no additive effect with the total drag coefficient matching that of the radio tag alone (0.192; Table 4).

The WC satellite tags increased the drag coefficient by 3% to 31%. The MK 10-AF GPS/satellite tags increased drag the most at 29% and 31% for positions 1 and 2, respectively, (Table 3). The WC Spot 5 tags increased the drag coefficient by 3% to 22% with the head placement giving the smallest drag coefficient increase. In all cases, movement of tags to position 2 caused a 0 to 3% increase in drag except for the Spot 5 mold 181C (WC6; Table 2) which had a reduction of 9% in the increase in drag coefficient when placed in position 2 compared with 1.

The various tags and placements caused positive and negative changes in the lift coefficient, with only one exceeding 1.47 times that of the cast alone (Telonics satellite tag TES2F in the 2nd position which caused a 2.45 times positive change in lift; Table 5). The absolute change in the lift force caused by the transmitters was 0.35 N while maximum increase in drag force due to the transmitters was 0.56 N.

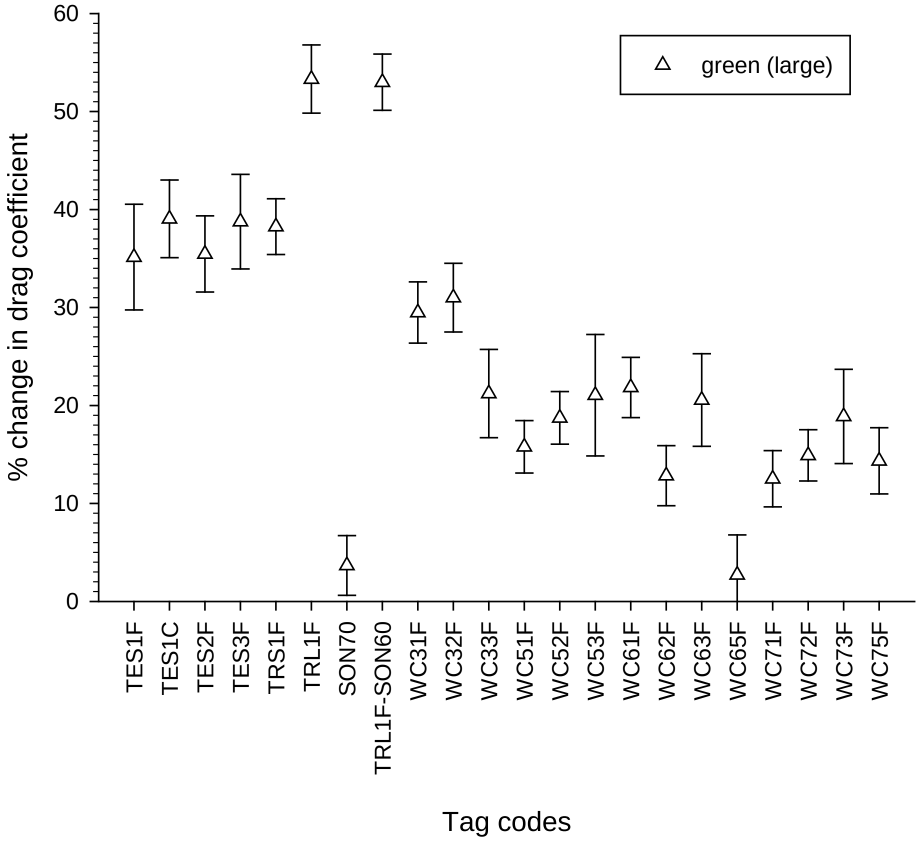

FIGURE 10
Percent change in drag coefficient when the various tags and tag configurations were added to the large green turtle cast. The y-axis was normalized to the baseline drag measurement of the cast without a transmitter therefore zero represents no increase in drag coefficient from the cast alone. All measurements were performed at 16 m s^{-1} and at the angle of attack that gave minimum drag (Figures 4A & B). See tables 2 & 3 for details on the tag codes listed on x-axis. Error bars depict ± 1 standard deviation around the mean.

<u>Green turtle (small).</u>

The Telonics satellite and VHF radio tags (TES1F & TRS1F; Tables 2 & 3) increased the drag coefficient of the small green turtle cast of 30% and 47%, respectively (Figure 11, below). The VHF radio tag had a 9% greater increase in drag coefficient for the small green turtle (40.5 cm SCL) compared with the large green turtle (49.5 cm SCL). WC Spot 5 satellite tags (WC5 & WC7; Table 2) increased the drag coefficient by 16% to 21% when placed in the front position (position 1; Table 3). There was a trend for greater increases in drag coefficient when the same transmitters were placed on smaller turtles. For instance, tags WC51F and WC71F (Tables 2 & 3) increased the drag coefficient 16% to 21% over the small green turtle cast but only increased the drag coefficient by 5% and 1% on the olive ridley cast (60.5 cm SCL) (Figures 9A & 11).

The Telonics satellite tag in the front position (TES1F; Tables 2 & 3) negatively changed the lift coefficient by 1.23 times while the WC satellite tag WC71F changed the lift coefficient positively by 1.4 times (Table 5). The maximum absolute change in lift force at 0.06 N was less than that of the drag force (0.49 N) from the various transmitters.

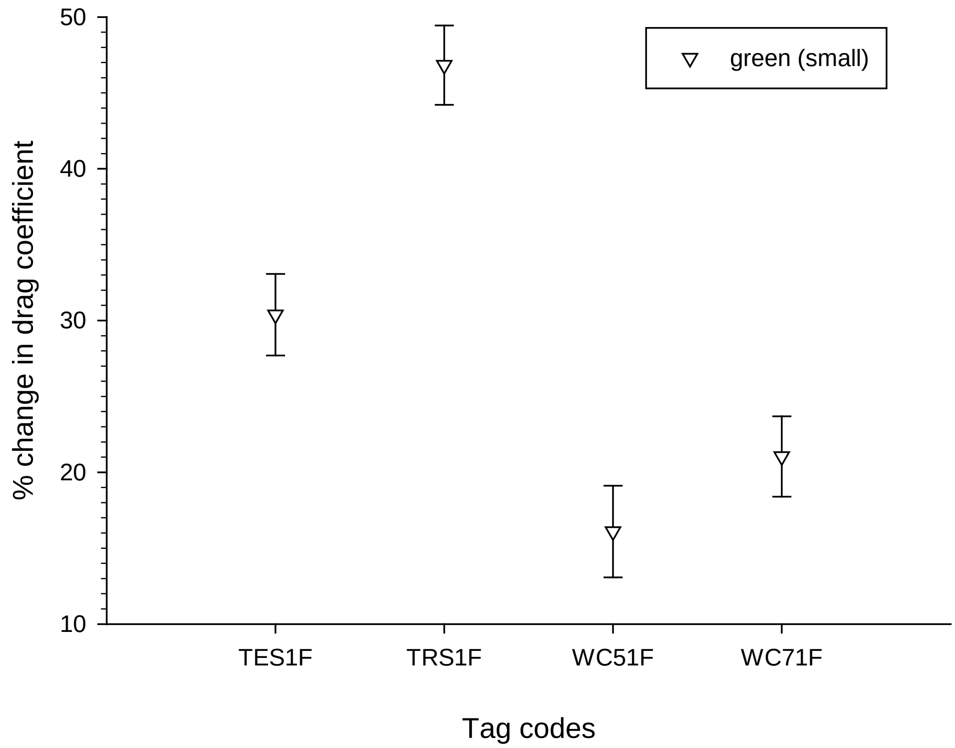

FIGURE 11
Percent change in drag coefficient when the various tags and tag configurations were added to the small green turtle cast. The y-axis was normalized to the baseline drag measurement of the cast without a transmitter therefore zero represents no increase in drag coefficient from the cast alone. All measurements were performed at 16 m s^{-1} and at the angle of attack that gave minimum drag (Figures 4A & B). See tables 2 & 3 for details on the tag codes listed on x-axis. Error bars depict ± 1 standard deviation around the mean.

Double tagging and retrofitting.

A rectangular wooden block representing the basic parameters of a satellite tag (see methods section, Tags and Tag Codes) was placed on the carapace of the large green turtle cast. When the "tag" was placed on the cast in the front position it increased the drag coefficient by 31.2% over the cast alone. A second block (of equal dimensions) was then placed on the cast both in parallel and in series (Figures 3) to determine if there was an effect of interference drag. When the two "tags" were placed in parallel-1 (touching) there was slightly more than a doubling of the increase in drag coefficient (from 31.2% to 69.4%) however when the tags were placed in parallel-2 and 3, the increase in drag coefficient more than doubled to 86.0% and 86.7%, respectively, over the cast alone (Figure 12, below). When placing the two "tags" in series-1 (Figure 3) there was a 3% increase in drag coefficient from a single tag only. Movement of the second tag to in series postion 2 and 3 increased drag by 54.0% and 48.5%, respectively, over the cast alone (Figure 12). All of the in series positions caused less drag then the parallel positions (Figure 12).

To determine the effect of retrofitting existing tags, we placed a flat bottomed wooden dowel on the large green turtle cast in position 1 and 2. The dowel caused an increase in drag coefficient of 34.5% and 29.2%, respectively, over the cast alone. We then fashioned the wooden dowel with a clay nose cone and clay tail (making the squared dowel, tear drop shaped but keeping the frontal area equal) and tested it in position 1 and 2. The increase in drag coefficient was 3.6% and 5.8% in positions 1 and 2, respectively, over the cast alone. Fashioning the tag into a tear drop shape caused an absolute reduction in drag of 30.9% and 23.4% in positions 1 and 2, respectively, or > 80% drag reduction with respect to the two tags themselves.

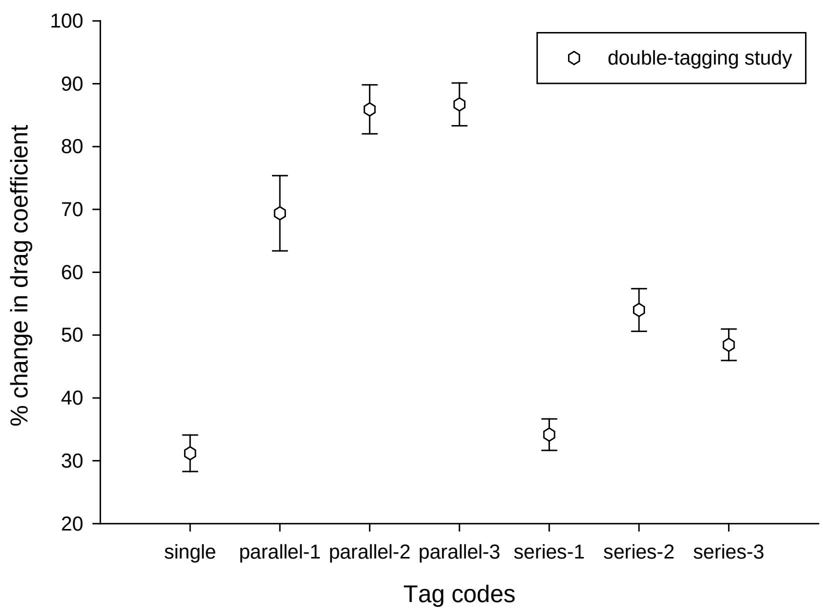

FIGURE 12
Percent change in drag coefficient from the cast alone when single or double tags (placed in parallel or series) were placed on the large green turtle cast. The y-axis was normalized to the baseline drag measurement of the cast without a transmitter therefore zero represents no increase in drag coefficient from the cast alone. All measurements were performed at 16 m s^{-1} and at the angle of attack that gave minimum drag (Figures 4A & B). See Figure 3 for details on the tag codes listed on x-axis. Error bars depict ± 1 standard deviation around the mean.

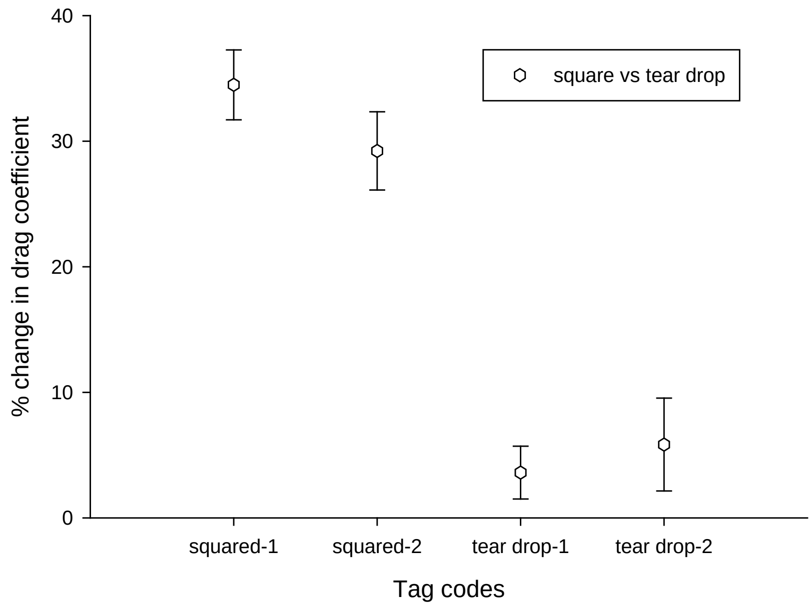

FIGURE 13
Percent change in drag coefficient from the cast alone when a squared or tear drop shaped tag (of equal frontal area) was placed on the large green turtle cast. The y-axis was normalized to the baseline drag measurement of the cast without a tag therefore zero represents no increase in drag coefficient from the cast alone. All measurements were performed at 16 m s^{-1} and at the angle of attack that gave minimum drag (Figures 4A & B). See methods section (Tags and Tag Codes) for details on the tag codes listed on x-axis. Error bars depict ± 1 standard deviation around the mean.

DISCUSSION

Summary of Pertinent Findings

The drag coefficient of the turtles casts in turbulent flow ranged from 0.126 to 0.192. The drag coefficients of common shapes in turbulent flow are 1.05 for a cube, 0.47 for a sphere, and 0.04 for a streamlined, teardrop shaped body (Hoerner 1965; Vogel 1994). Sea turtles are at the lower end of this spectrum, greater than what would be found for true streamlined bodies (such as the thunniform body of fish) but less than a spherical shape. However, to compare the drag coefficient of our sea turtle casts with other marine vertebrates, it is imperative that the characteristic area (*A*) from equation 2, in our case frontal area, is calculated the same way. For instance, in cetacean research it is common to use the wetted area or the total surface area of the body (Fish and Lauder 2006) or the volume of the animal (Bilo and Nachtigall 1980; Stelle et al. 2000). Several studies have used frontal area, the cross-sectional area when viewed from ahead, to report C_D for various marine vertebrates as we have done. For instance, Stelle et al. (2000) report C_D for stellar sea lions (*Eumetopias jubatus*) in the range of 0.08 to 0.13 and Lovvorn et al. (2001) report C_D for several species of diving birds (penguins Spheniscidae, puffins and auklet Alicidae, guillemot *Cepphus* sp., cormorant Phalacrocoracidae and eider Anatidae) ranging from 0.16 to 0.29 and, exceptionally, 0.07 for gentoo penguins, *Pygoscelis antarctica* (Bilo and Nachtigall 1980). Therefore, sea turtles have drag coefficients in the upper range of pinnipeds and at the lower range of diving birds.

Watson and Granger (1998) found a drag coefficient of 0.339 for a juvenile green turtle 47.8 cm in carapace length (CL) by mounting a cast of the turtle in a wind tunnel, and Prange (1976) determined the drag coefficient of a 27 cm CL green to be 0.430 (adapted from Figure 5), by mounting a frozen carcass in a water flume. These studies found green turtles to have drag coefficients 2 to 3 times greater than what we found in this study. In both Watson and Granger (1998) and Prange (1976) the attachment apparatus which held the turtles in the tunnel and flume, a mounting bracket and strut, were exposed to the oncoming fluid and added additional drag force on top of what the turtle created. Furthermore, the turtle used by Prange (1976) had its front flippers attached. In our study we used a back mounted sting balance and the support pipe (strut) was shrouded by 3" PVC pipe therefore only the drag of the casts was recorded and not that of the mounting materials.

Sea turtles, although armored with rigid shells and reptilian scales, have low drag coefficients and it is of no surprise that biotelemetry devices can cause considerable increases in drag. Wilson et al. (2004) found that the antenna of transmitters (10-20 cm in length and 0.1-0.4 cm in diameter) caused a 79 to 147% increase in drag force in Magellanic penguins (*Speniscus magellanicus*). The antennas on the radio tags, in this study, were 15 cm (L) x 0.7 cm (dia) and 21.5 cm (L) x 0.7 cm (dia) for the TRL and TRS tags, respectively. For these tags, the antennas make up nearly 43% to 67% of the frontal area of the tag. Furthermore, the antenna shape (cylindrical) has a large drag coefficient (1.2; Hoerner 1965; Vogel 1994). Bannasch et al. (1994) found that back-mounted biotelemetry devices of similar frontal area (0.002 m^2) as some of those we used increased drag by 15% to 100% compared with the drag of gentoo and chinstrap penguin (*Pygoscelis antarctica*) casts. A Telonics ST-6 satellite tag (frontal area 0.0025 m^2) increased the drag coefficient of a green turtle cast (47.8 cm CL) by 27% (Watson and Granger 1998). These findings corroborate our results of 0 to > 100% increases in drag (Figures 6-11) due to the various transmitters (Table 2) attached to sea turtle casts. The greatest increases in drag coefficient came from the backpack harness on the leatherback casts (78% to 112%), the TDR drogue (67%) and Crittercams (86% to 111%) on the olive ridley cast, and the Telonics VHF radio tags (47% to 53%) on the < 50 cm SCL green casts. The Fossette et al. (2008) direct mount also caused a high increase in drag coefficient (square transmitter 43% and tear drop transmitter 20%) when tested on the juvenile leatherback in the front position as used in their research. However, moving the direct mount ¼ of the way back on the carapace reduced the increase in drag to 17% and 6% for the square and tear drop transmitters, respectively. It is important to note that the Fossette et al. (2008) direct mount attached to the adult leatherback cast with a Wildlife Computers MK10-AF tag only caused a 1-3% increase in drag over the cast alone.

The WC tags generated the smallest increases in drag coefficient on all five turtle casts. The WC tags increased drag by 1% to 14%, depending on the tag, for the leatherback and olive ridley turtle casts (> 60 cm SCL). Regarding placement, tags placed behind the initial hump (position 2) in leatherback turtles consistently resulted in lower increases in drag (single exception FDW2F, Figure 6). For the green turtles (< 50 cm SCL), the WC tags caused the smallest increases in drag (13% to 30%) when attached to the carapace, however tag placement on the head (position 5) was necessary in order to reduce the drag increase to < 10%. It is important that researchers utilize the morphology of the individual turtles to help reduce drag, for instance placement of tags on the highest point (peak) of the carapace led to the greatest increases in drag coefficient therefore tag placement in position 1 was preferable for the hard-shell casts but placement in position 2 was better for the leatherback casts. Hard-shelled turtles had the peak of their carapace further back than the leatherbacks (proportionately) and therefore there was not a reduction in drag in position 2 but rather an increase.

The drag coefficient of an object stabilizes and becomes independent of velocity in turbulent flow or Reynolds numbers near or above $5x10^5$ (Hoerner 1965; Vogel 1994). As can be seen in Figure 4A, all of the casts attained turbulent flow between 6 to 8 m s^{-1}, the adult leatherback cast however reached turbulent flow much earlier (4 to 6 m s^{-1}). This is to be expected as the adult leatherback cast was 2 to 4 times longer than the other casts (Table 1). The Reynolds number equation (Eq. 4) suggests that the adult leatherback (147 cm SCL) should reach turbulent flow around 5.3 m s^{-1} (or 0.34 m s^{-1} in sea water) corroborating our findings of between 4 to 6 m s^{-1}. Due to the early shift to turbulent flow for the adult leatherback cast, we tested the cast with the three main biotelemetry packages (backpack harness, direct carapacial mount, and ridge-mount) across all known swim velocities, i.e. from 2 to 19.4 m s^{-1} in the wind tunnel (equivalent to swim speeds, matching Reynolds number, of 0.13 to 1.25 m s^{-1}). The most interesting finding was the extreme increases in drag at the slower speeds. For instance, the backpack harness caused an increase in drag of 173% at the slowest speed relative to the cast alone. The Fossette et al. (2008) direct carapacial mount and the Wildlife Computers ridge-mount tag caused an increase in drag of 85.1% and 63.3%, respectively, at the slowest speed. The increases were much larger than the increased drag caused by the biotelemetry packages at the faster speeds when the cast is estimated to be in turbulent flow (Figure 4A). The most probable reason is that the turtle body form was in laminar flow at the slower speeds. Placing harnesses and tags on the streamlined casts, however, disrupts the fluid flow causing a flow separation. As noted, there was a marked drop in the added drag for all three telemetry packages from 0.13 m s^{-1} to 0.26 m s^{-1} (velocity in water), compared to the cast alone, with a continued drop for the Fossette et al. (2008) direct carapacial mount and Wildlife Computers ridge-mount tag at 0.39 m s^{-1}. This reduction in the added drag was probably due to the cast reaching turbulent flow in the faster speeds, with a resultant reduction in the flow separation bubble caused by the harness. These data shed light that biotelemetry packages are disruptive to the turtles across their full range of swimming speeds, even more so (proportionately) at the slower swim speeds.

It was thought that biotelemetry packages would also increase the lift forces affecting the behavior and increasing the energetic costs of the animal to maintain swim speed and direction. However, the lift coefficients (C_L; Table 5) and subsequent lift forces were generally an order of magnitude less than drag force (with only a few exceptions), therefore, they do not incur a great cost to the animal in comparison with drag. Lift coefficient varied linearly with angle of attack (Figure 5) while drag varied nonlinearly (Figure 4B). There is a small plateau of ± 5° around $\alpha = 0$ where drag does not increase greatly with angle of attack, this most likely represents the range of angles for straight line swimming in turtles in the wild. Watson and Granger (1998) found the same plateau range with a juvenile green turtle cast. The drag coefficient versus α relationship for the leatherback casts was much steeper than for the hard shelled turtle casts (Figure 4B). This is due to the increased length to width (dorsoventral distance) ratio of the leatherback over the hard-shelled turtles (the leatherback morphology is closer to an airfoil or wing). The leatherback cast also had the greatest increases in lift forces. The leatherback body design (long, flat, and streamlined) makes it more sensitive to drag and lift perturbations from biotelemetry. For instance, the backpack harness with no bungy or transmitter caused an increase in drag of 11.25 N at 16 m s^{-1}, a 92% increase from 12.18 N for the cast alone. The same configuration of the harness increased lift force in the ventral plane by 21.34 N; giving a total drag and lift force of 23.43 N and -18.77 N on the cast, respectively. The resulting force vector needed to balance the drag and lift forces is 30.02 N in an anterior-dorsal direction (simply solved using the Pythagorean theorem). This suggests that for the turtle to overcome this added drag and lift force a 241% increase in its thrust force (power output) is required to maintain course and velocity.

Several studies have recently raised the question of the ethics of turtle-borne telemetry (Wilson and McMahon 2006, Godley et al. 2008; Sherill-Mix and James 2008). Furthermore, Fossette et al. (2008) and Byrne et al. (2009) examined differences in performance of leatherback turtles outfitted with satellite transmitters attached using a harness (Eckert and Eckert 1986) and direct carapace attachment by drilling through the dorsal longitudinal ridge (first suggested by Lutcavage et al. 2002). Fossette et al. (2008) found that leatherback turtles with harness attachments swam 16% slower than leatherbacks with direct attachment while Byrne et al. (2009) found harnessed turtles swam 28% slower than with direct attachment (the direct attachment and harness methods varied between the two papers). It is impossible, however, to determine absolute performance effects from the harness and direct attachments in the wild as the turtles may have altered behavior as well as power output to overcome an increased drag. The sole paper to date quantifying the drag caused by turtle-borne telemetry is Watson and Granger (1998) determining that a satellite transmitter (Telonics ST-6) directly attached to the carapace of a juvenile green turtle (*Chelonia mydas*) (47.8 cm SCL, 11.65 kg), with fiberglass, increased drag as much as 27%, or conversely decreased velocity by 11% if thrust force was maintained (see equation 9 for this relationship). The increase in drag is similar to what we recorded for Telonics satellite tags on juvenile greens. The reduction in velocity reported by Fossette et al. (2008) and Byrne et al. (2009) correspond with the velocity decreases that we calculated would occur due to the measured increase in drag on the leatherback casts. For instance, a 16% reduction in velocity (Fossette et al. 2008), would require a 70% increase in the drag force if power output was maintained. We recorded drag increases of 1-40% for the Fossette et al. (2008) direct mount and 80% to > 100% increases for the harness, the difference in drag force we measured for the two attachment methods corresponds to the difference in velocity measured in the field for the respective attachment methods (Fossette et al. 2008).

Why Drag Increases

The drag forces on an object are made up of three elements, 1) form drag also called pressure drag, 2) skin-friction and 3) interference drag (Hoerner 1965). Briefly, form drag is due to the energy needed to part the molecules such that the object can move through the medium, skin friction is due to the surface dragging molecules along with the object, and interference drag is due to the creation of vortices from fluid flow around sharp angles on the object. Form drag is generally the dominant component of the drag forces on a blunt or bluff body while skin-friction plays a larger role as a body becomes longer. For instance, an object or body such as a snake would have a low form drag and large skin-friction. Form drag is determined primarily from the size and shape of an object, the larger the cross-sectional area of an object the greater the form drag (Hoerner 1965). Streamlining an object and lowering the profile will reduce the frontal area and consequently the form drag. Skin-friction is caused by the added energy needed to drag the fluid trapped in the boundary layer around an object (Hoerner 1965). The larger the boundary layer around an object and the longer the object the more fluid is dragged behind it and this leads to a larger skin friction. Turtles have profiles much like an airfoil; the boundary layer at the front of the airfoil (or turtle) is usually laminar in flow and is thin. This layer becomes turbulent, however, and therefore thicker towards the rear (Vogel 1994). To reduce skin-friction, the object should maintain an airfoil shape, have a proper aspect ratio, have a reduced cross-sectional area, and minimize the turbulent boundary layer as much as possible. Interference drag is created when two surfaces meet at sharp angles (~ 90°), because the fluid flow around the objects form vortices (Hoerner 1965). Interference drag can also be caused by closely spaced parallel surfaces. The vortices and resulting low pressure area behind the object increase the drag force. All three of the components listed above work in concert to increase the drag force of an object moving through a fluid, are all incorporated in the drag force equation (see equation 2), and increase with the square of the velocity of the object.

Biotelemetry packages could increase all the components of the drag force on a turtle. Any tag placed on a turtle increases the frontal area and therefore the form drag. Telemetry tags can create vortices and increase the interference drag. Transmitters such as the Telonics satellite tag (TES, see Table 2) have sharp edges and meet the carapace of the turtle at 90° angles. The plate that is used to fix a transmitter to the backpack harness (Eckert and Eckert 1986) and the Fossette et al. (2008) direct mount may act as a parallel surface with the carapace therefore potentially creating vortices and increasing interference drag. Skin-friction is increased from the tags protruding from or increasing the boundary layer area around the turtle. Tags placed close to the anterior of the carapace disrupt the thin laminar flow along the leading edge of the airfoil (profile of turtle) causing flow separation. The backpack harness for leatherbacks created some of the largest drag increases (78% to 173%; Figures 6, 7, 8) which is due to the disruption of flow over the surface with the front bands (the tubes going over the shoulders of the turtle) acting as leading edge spoilers (separating flow and increasing skin-friction by dragging along excess molecules) and possibly disrupting high pressure flow along the plastron (induced drag) similar to an airplane wing (Hoener 1965; Vogel 1994).

For the leatherback, olive ridley, and large green turtle casts several hundred short pieces (5-7.5 cm) of yarn were taped to the head, neck, and carapace. The casts were then tested in the wind tunnel as detailed above with and without the various transmitters (yarn was also placed on the transmitters). In all cases the transmitters caused a disturbance in the flow pattern over the casts immediately behind the transmitters, the flow pattern from the transmitters expanded like a ship's wake. The backpack harness, which caused > 80% drag increase, created flow disruption starting at the leading edge of the cast. The TDR drogue and NG Crittercams (DRO, CR1, CR2; see Table 2) caused 67% to 110% increase in drag force and disrupted the flow patterns from lateral edge to lateral edge of the carapace, furthermore, these tags had the greatest frontal areas leading to large form drag and were the longest tags at > 30 cm contributing to increased skin-friction drag. In all of the above instances the drag force can be decreased by reducing the frontal area of the tags, making the tags more streamlined, and by avoiding any space between the tags and the carapace.

Migratory Energetics

The most important effect of transmitters on turtles may be the increased energy expenditure of the turtle from carrying the transmitter. This is based on the concept that the balance of energy expenditure with energy intake determines survival of the animal (Wilson and McMahon 2006). Along with survival, attached transmitters may in turn affect life-history traits, the timing of migratory events, and reproductive output of the animal.

Benson et al. (2007a) recently documented the first trans-Pacific migration of a leatherback turtle. Several turtles were outfitted at a nesting beach in Papua New Guinea with satellite tags attached via backpack harnesses (Eckert and Eckert 1986). One particular turtle was outfitted on July 22nd, 2003 and arrived in the northeastern Pacific foraging grounds in late August 2004, nearly 400 days later. The straight-line distance from the nesting site to the foraging grounds is greater than 10,000 km. Travel rates calculated from the distance traveled and time of arrival suggest the turtle was moving at a minimum of 0.36 m s^{-1}, as the dive profiles and three dimensional movement of the turtle is not known the swim speed cannot be determined. However, as travel rate is determined from the shortest distance between two points and as the time sequence remains the same, any vertical or horizontal movement of the turtle would lead to greater swim speeds. Therefore calculated travels rates represent the minimum velocity of the turtle. Data from the other outfitted turtles suggest they may travel as fast as 0.83 m s^{-1}; this range of travel rates is within the calculated modal swim speeds for adult leatherbacks (0.56 to 0.84 m s^{-1}; Eckert 2002). Furthermore, these travel rates and known swim speeds (Eckert 2002) combined with the average carapace length of the turtles (162 cm) equate to Reynolds numbers of $5.8x10^5$ to $1.3x10^6$. These Reynolds numbers are within the range we tested on the leatherback casts and are representative of turbulent flow around the turtle.

Measurements indicate that the backpack harness increased the drag force by 92% over the adult leatherback cast alone at speeds representative of turbulent flow. This would equate to an increase in 92% of the power output of a swimming turtle, if velocity is maintained, or a 20% drop in the velocity of the turtle if the power output is not increased (equation 8 and 9). For the turtle migrating across the North Pacific (Benson et al. 2007a) a 20% reduction in velocity would equate to the turtle showing up at the foraging grounds nearly 80 days behind schedule. The temperate water foraging grounds off of the western coast of the United States are typically used from August through October (Benson et al. 2007b). Therefore, a turtle arriving 80 days late could miss the entire foraging season and have to provide the energy of 80 more days of swimming. However, as the turtle described in Benson et al. (2007a) arrived at the foraging site in late August (presumably on time), the turtle must have increased its power output to maintain the migratory schedule and arrived at the appropriate time but at a 92% greater energetic cost. As the trek across the North Pacific took the turtle ≈ 400 days, this suggests that the turtle spent upwards of 192% of its yearly energy budget generally allocated to migration. Furthermore, if the induced drag from lift is calculated in, the turtle would have to increase its power output by 241% (using 341% of its yearly migratory budget) or realize a 34% reduction in velocity, all else being equal.

What happens if a turtle has an increase of 5%, 10%, 50%, or even 100% in energy expenditure? It has been postulated that animals could offset the energetic cost by eating more (Wilson et al. 2004) but many turtles fast during migration or feed on prey items with patchy distributions. Wilson et al. (2004) found that penguins feeding on anchovies encounter prey every 30 minutes and then have a couple dives on the prey before they disperse. They found that penguins with devices attached are only 1/5 as efficient at foraging as birds without transmitters. If animals have to spend more time foraging to make up for carrying a transmitter they are doing so again at greater costs, the extra time foraging and the extra energy required while swimming and attaining food due to the transmitter all equate to dwindling returns for the effort. Therefore animals may not be able to offset the cost simply by eating more. A leatherback arriving at a foraging site having spent an extra 92% of its energy reserves (fat stores) may have to spend an extra year or more at the foraging grounds, or the turtle may simply have less energy to allocate to reproduction in the next nesting season, either way leads to the lowering of the reproductive output of the animal. Also turtles may incur a greater risk of commercial fisheries interactions due to increased foraging time in both the amount of time spent foraging daily and the extra day-years spent at the foraging sites.

Scaling Drag Force

We can determine the increased drag forces the tags used in this study would have on turtles of any size by scaling the drag forces relative to the turtles' surface area. The Reynolds similarity law and dynamic similitude state that the drag force of any sized object can be predicted from the unitless drag coefficient as long as the objects maintain similar shape and they are tested at equivalent Reynolds numbers for the medium representing turbulent flow around the objects (Hoerner 1965; Kline 1986; Vogel 1994). Therefore in order to scale the drag coefficient/forces measured using the casts, from the juvenile stage through to adult turtles, the frontal area (*A*) of the turtle is needed. The frontal area can be determined by the following equation. Mass scales as length^3 and area scales as length^2. Therefore frontal area (*A*) scales with mass, *M*, as:

Eq. 10) $$A = aM^{2/3}$$

where *a* is the proportionality constant. Combining Eq. 10 and Eq. 2 gives a drag force of a turtle with mass, *M*, as:

Eq. 11) $$F_M = QC_D aM^{2/3}$$

The drag of the transmitter alone is equal to the difference between the turtle with and without a transmitter,

Eq. 12) $$F_{tag} = F_{tag,\ turtle} - F_{turtle}$$

Therefore the drag of a turtle with mass, *M*, equals F_M (Eq. 11) and the drag of the same turtle with a transmitter attached is given by (Eq. 11 + 12):

Eq. 13) $$F_{M,\ tag} = F_M + F_{tag}$$

Using the equations above, it is possible to determine the increase in drag the transmitters from Table 2 would cause on any sized turtle.

The WC1 tag (Table 2) caused a 12% increase in drag in position 1 and a 4% increase in drag in position 2 on the juvenile leatherback cast (Figure 8). However, we calculate for a nesting leatherback turtle of 408 kg (Georges and Fossette 2006), the WC1 tag would cause a 2.8% and 1% increase in drag in position 1 and 2, respectively. We measured drag increases of 1.8% and 1% for the WC1 tag on the adult leatherback cast (Figure 6), thus validating the scaling relationship above.

For the olive ridley cast, the WC3 and WC5 tags caused a 10% and 5% increase in drag coefficient in position 1, respectively, and there was no benefit from moving the tags to position 2. For an average size adult olive ridley turtle weighing 50 kg (Spotila 2004) the same tags in position 1 would cause a 6.7% and 3.5% increase in drag, respectively. The WC3, WC5 and WC7 tags in position 1 caused a 29%, 16% and 13% increase in drag on the larger green turtle cast. These same tags on an adult green turtle (166 kg; Hays et al. 2002) would cause an increase in drag of 5.3%, 2.8%, and 2.3%, respectively.

Recommendations for Tagging Turtles

When instrumenting turtles with biotelemetry packages, the goal should be to minimize the added drag effects (form drag and induced drag). Of all the tags that we tested, the one with the least drag (0%) was tag WC740 when it was placed in the valley of the leatherback ridges, ½ way back on the carapace (Figure 8). Whereas several tags (13) caused < 10% increase in drag force, the majority of the tags increased drag by 10% to 30%, with 7 tags (and attachment methods) causing even greater drag (up to 173%).

Researchers will not have available the means to test the additional drag force directly when purchasing tags or outfitting turtles in the field. Therefore the following recommendations will help reduce drag force.

<u>Frontal area.</u>

The frontal area of a tag increases the overall frontal area of the turtle, which directly increases the drag force of the turtle when moving through water. Therefore, minimizing the frontal area of tags will help to reduce the increase in drag force. In all cases, the tag with the largest frontal area (when shape was similar) caused a greater increase in drag when placed on the same cast and in the same position. For example, tags TES, WC3 and WC5 have frontal areas 0.003, 0.002 and 0.001 (m^2), respectively, and the three tags have a square or nearly rectangular front. When placed on the olive ridley cast in position 1, the tags increased drag by 15%, 10% and 5%, respectively. When these same three tags were placed on the large green turtle cast in position 1, they caused 35%, 29% and 16% increase in drag. When tags TES and WC5 were placed on the small green turtle they caused 30% and 16% increase in drag. To reduce drag force we recommend that tags have minimal frontal area. The frontal area recommendations include the area of the antenna as the antenna can increase the overall frontal area of a tag by a 100% or more, e.g. Telonics VHF radio tags (Table 2).

Attachment materials.

The build-up of materials (e.g., epoxy, elastomer, and base plates) either under or over the tag causes an increase in profile and thus the frontal area. Therefore it is important that these materials are minimized. Maintaining a low profile for the tags will help to keep frontal area to a minimum and also not disrupt the boundary layer around the animal. When clay was added to replicate the use of epoxy to seat and armor the tags (i.e., placing clay around the tag like a saucer thus increasing the frontal area) it increased the drag force by 14% over the tag alone (Figure 10).

Shape.

Along with the frontal area, the overall shape of the tag can decrease the additional drag force it will cause. For the leatherback turtle, the use of the teardrop shaped tag caused 13% to 22% less drag than the square tag depending on the configuration of the backpack harness and by 10% to 23% depending on the position of the Fossette et al. (2008) direct mount. It is important to note, however, that the square transmitter had a slightly larger frontal area than the teardrop tag. Tags WC6 and WC7 were placed on the olive ridley in positions 1 and 2. The tags have similar frontal areas but WC6 is a square tag with edges and WC7 is teardrop shaped. Tag WC6 caused an increase in drag of 8% and 12% in positions 1 and 2 whereas WC7, the teardrop shaped tag, caused an increase in drag of 1% and 6%. When the same two tags were placed on the large green in position 1 tag WC6 increased drag by 22% while tag WC7 increased drag by 13%. We recommend that tags placed on turtles should have a tear drop shape to minimize drag and have a low profile to minimally disrupt the boundary layer.

Furthermore, when tear drop shaped tags are not available or if researchers have existing squared tags the drag force can be greatly reduced by adding a nose cone and tail with epoxy or fiberglass. We were able to reduce the increased drag force by > 80% when we affixed a clay nose cone and tail to a squared tag (Figure 13), frontal area remaining equal.

Size (or species) of turtle.

The size and species (length, mass, and frontal area) of the turtle should be considered when applying tags. For example, the olive ridley turtle had a greater frontal area and was longer and wider than the large green turtle. Nearly all the same tags in the same positions were used on both the olive ridley and large green turtle cast and in most cases the induced drag force was ~ 50% less on the olive ridley. The small green turtle was tested with several of the same tags and in all cases the drag was ≥ 50% more than on the olive ridley and similar to or greater than when placed on the large green turtle cast. For example tag WC710 increased drag by 21%, 13% and 1% for the small green, large green and olive ridley turtles, respectively. The WC1 tag when placed on the adult leatherback cast caused 1.8%, 0.8%, and 0.6% drag increase in positions 1, 2, and 3 compared with 12%, 4.2%, and 4.3% for the juvenile leatherback. For juvenile turtles of (< 50 cm SCL) tag size and/or length of deployment need to be well considered.

Tag placement.

Placement of the tag in relation to the morphology of the turtle carapace is important. The drag force caused by a tag can be further reduced by avoiding the peak of the carapace. Unfortunately, this is where satellite tags are generally placed to ensure uplink to the satellite. The leatherback casts used in this study had the initial hump of the carapace in the first quarter (measured as total length from nuchal notch to posterior end of the carapace). Therefore, tags placed in position 1 were at the peak of the carapace. When looking at Figures 6, 7, and 8, it can be seen that placing tags in position 2 (25% back on the carapace) decreased the drag force caused by the tag. For example, when the Fossette et al. (2008) direct mount (FDS and FDT) and tags WC1 and WC2 were placed in position 2 there was greater than a 50% reduction in the additional drag force on the juvenile cast. The adult cast had an absolute reduction in the drag force caused by the transmitters of 1% and 1.2% by moving tags to position 2 and 3, respectively. However for the olive ridley and green turtle casts, the initial hump of the turtle was further back on the carapace (> 25% from the nuchal scute). Therefore there was no benefit from placing tags in position 2 or in some cases there was an increase in the drag force over position 1. Placing tags at the peak of the carapace while aiding in satellite uplinks causes the greatest increase in total frontal area possibly exposing the tag to the greatest fluid flow rate. Therefore it is our recommendation that researchers avoid placing tags at the highest peak but rather place tags slightly anteriorly or posteriorly to the peak where uplinks will be maintained and the salt water switch (Watson and Granger 1998) will still be exposed to the air when the turtle breathes but the increase in total frontal area will be minimized as well as exposure to the oncoming fluid flow rate. This will lead to an acceptable compromise between ensuring satellite transmissions and minimizing the drag force.

Double tagging.

There is substantial interest in understanding the probability of post-hooking mortality of sea turtles that have been returned to sea after interactions with longline gear. One method to estimate post-release mortality has been to release the turtle with a satellite tag to determine movements and potential mortality through tag transmissions. However, such methods are flawed given that a tag can cease to transmit for a number of reasons, not simply a turtle's mortality. In order to resolve some of the issues between tag failure and mortality, researchers have sought to place multiple tags on turtles. As such, NOAA has received requests for permits proposing to double tag turtles. It is not known however, what will be the added drag associated with double tags, simply an additive effect or will there be an interaction effect of the tags known as interference drag.

In order to address the possible additional constraints placed on a turtle with double tags, we evaluated the drag associated with the large green turtle cast with and without tags in various configurations. Two tags were created out of wood blocks similar in size to tags currently used in field studies (See methods section, Tags and tag codes). The blocks were arranged in parallel and in series (Figure 3). There was an interaction effect or interference drag when two tags were placed on the turtle carapace (Figure 12). Two tags side by side (parallel) separated by 1 or 2 tag widths caused greater than double the drag of a single tag alone. Placing the tags parallel but touching caused only a doubling of the drag. Placing the two tags one behind the other (in series) did not increase the drag over a single tag alone. However as the separation between the tags grew there was a slight interaction effect (N.B. as the space between the tags becomes large enough they probably would not interact and the drag would be equivalent to two tags). Therefore we recommend when possible that multiple tags are placed on turtles in series and as close as possible. The only complicating factor would be the potential for the tag transmissions to interfere with each other. Transmission interference testing is outside the scope of this study but should be further discussed with tag manufacturers before conducting double tagging experiments.

<u>Research and development.</u>

Research and development should focus on uncoupling the tag body, antenna, and salt water switch allowing placement of a small antenna and switch near the head or upper carapace of the turtle while placing the body of the transmitter near the posterior of the turtle where the boundary layer is thicker and turbulent thus causing smaller drag increases. It is vital that research and development for biotelemetry continue and commercial companies and scientists alike strive to reduce the drag induced by transmitters not only bettering the data gathered from biotelemetry devices but ensuring the continued welfare of the animals studied. Schroeder and Balazs (2000) met with Telonics, Inc. in the late 1990s to develop a prototype of the ST-14 satellite tag that would encase an internal helix antenna and be more streamlined. The concept was meant to prevent damage and shearing of the antenna when the turtles (greens) were in foraging areas (i.e., rocky, coral reef habitat). The prototype tags continued to transmit after the standard tags had stopped however the internal antenna gave low-quality uplinks which did not allow location data. Therefore they concluded that the existing external antenna model was still the preferred option. Nevertheless, experimental approaches such as this are to be encouraged if we are to move biotelemetry research forward in regards to data quality and animal welfare.

<u>Special considerations.</u>

Leatherback turtles –

Leatherback sea turtles have a smooth carapace covered in a rubbery skin. Traditional methods of tag attachment (i.e., epoxy and fiberglass) simply do not work or have very low retention time. Therefore, Eckert and Eckert (1986) developed a backpack harness that could carry transmitters on leatherbacks and had retention times > 1 year. This backpack design gave researchers the first look into the ecology of leatherbacks determining internesting movements (Eckert et al. 1989, 2006), swim speeds (Eckert 2002), dive patterns (Eckert et al. 1986; Keinath and Musick 1993; Eckert et al. 1996), and oceanic movement patterns (Hughes et al. 1998; Hays et al. 2004; Eckert 2006; Benson et al. 2007a). While the harness was ingenious in its design, and allowed the first look into leatherback ecology, behavior, and physiology, the increased drag caused by the harness (Figures 6,7, and 8) prevents us from recommending its continued use in its current form. Tags WC1 and WC2 were created from the encouragement of researchers working with leatherbacks. These tags were designed to mount directly to the longitudinal ridge of the leatherback offering greatly decreased frontal area and a low profile. Our data suggest that these tags placed in the various positions caused a 4-12% increase in drag on our juvenile cast and a 0.6-1.8% increase on our adult leatherback cast. Therefore, with respect to drag forces, it is our recommendation that the use of the ridge-mount tags directly attached to the longitudinal ridge be pursued. However, the use of direct attachment should be scrutinized with respect to health issues associated with drilling into the ridge (Lutcavage et al. 2002; Fossette et al. 2008; Byrne et al. 2009), such as risks of infection, pain and/or discomfort to the turtle, and potential further damage if the tag pulls through the ridge due to the drag force of the fluid flow across the carapace. These questions will have to be answered in field situations where the application of a direct mount can be viewed within weeks, months, and years after initial attachment. Byrne et al. (2009) have recently addressed some of these issues, when direct mount tags were placed on a nesting female during internesting events, there was no sign of infection after 1 month. If after further investigations this attachment technique is believed to have minimal negative effects on the well-being of the turtle, then it is our recommendation their use be pursued in future leatherback turtle tagging efforts.

Turtle cameras –

Turtle-borne cameras have been used in both hard-shelled and leatherback sea turtles. The cameras (National Geographic Crittercams or homemade versions) are attached by epoxy and fiberglass as well as suction cups. These camera systems can place considerable drag on the outfitted turtles, up to 86-111% (Figure 9B). However it is important to note the NG Crittercams are usually deployed for 1-3 days and automatically pop-off the turtle. The energetic cost to a turtle (assuming it increases power output due to increased drag costs) carrying a NG Crittercam for 3 days is only an increase of 0.82% of its yearly energy budget. Alternatively, carrying a NG Crittercam tag for a year will increase the yearly energy budget proportionally to the increase in drag force the tag causes (86-110%), which would be unacceptable. While large increases in drag force may disrupt the turtles' (short term) daily energy budget if these tags are carried for < 5 days the long-term effects are negligible. Therefore we recommend that special considerations be made for the time scale and questions being asked when placing tags that cause considerable drag on turtles.

Migration versus residence –
Further considerations must be made based on the activity of the turtles. The VHF radio tags (TRS and TRL) caused increases in drag force of 18% to 53% (Figures 9A, 10, and 11). However if these tags are to be used for small scale local movements and home range assessment (vanDam and Diez 1998; Seminoff et al. 2002; Makowski et al. 2006) then special consideration should be made due to the fact that the diel activity of these animals is not dominated by migration. Therefore the energetic cost to the turtle is far less than for a migrating turtle where the energetic cost of locomotion dominates the energy budget of the animal. Therefore we recommend that the guideline of allowable tag size, shape, and placement be relaxed when researchers study small scale local movements and home range of turtles.

On the other hand, loggerheads and olive ridleys migrating westward in the North Pacific swim largely against prevailing currents (Nichols et al. 2000; Polovina et al. 2004) and when swimming eastward with the currents they are still active often maintaining swimming speeds two times or more than that of the water current. Even within the various eddies and meanders from the main currents, where turtles can often spend several months, loggerheads maintain active swimming patterns (Polovina et al. 2006). Migrations of leatherback turtles from nesting beaches in the Atlantic and Pacific show that they move across, against, and with currents remaining active throughout (Godley et al. 2008). For instance, Benson et al. (2007a) tracked five adult leatherback turtles heading east from the western Pacific, three of the turtles associated with the westward flowing North Equatorial Current while the other two turtles showed marked decreases in crossing time and were associated with the eastward flowing Equatorial Counter Current. Therefore, it is imperative that for migrating turtles (hard-shell and leatherback) that the drag induced by telemetry devices is minimized and the recommendations given are adhered to as closely as possible.

<u>Summary of recommendations.</u>

- The frontal area of the tags should be reduced and the tags should have a low profile,
- the tags should have a tear drop shape,
- the antenna length and diameter should be minimized,
- the tags should not be placed at the peak height of the carapace, and
- adhesives should be minimized and use of base plates or building up of material avoided.
- Special considerations should be made for 1) researching the effects of direct attachment to leatherbacks, 2) tags that have large increases in drag upwards of 50% or more but are

not intended for extended deployments (i.e. 1-3 day deployments, etc.) and 3) the movement of the turtle, i.e. migration versus small scale home range, should be considered and allowances made for turtle research where locomotion does not dominate diel activity.

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