

Article type : Article

LRH: MARINE MAMMAL SCIENCE, VOL. **, NO. *, ****

RRH: ROSEN *ET AL.*: EFFECT OF TAGS ON NORTHERN FUR SEALS

Telemetry tags increase the costs of swimming in northern fur seals, *Callorhinus ursinus*

DAVID A. S. ROSEN,¹ Marine Mammal Research Unit, Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada; **CARLING G. GERLINSKY**, Department of Zoology, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada; **ANDREW W. TRITES**, Marine Mammal Research Unit, Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada.

ABSTRACT

Animal borne instruments have become a standard tool for collecting important data from marine mammals. However, few studies have examined whether placement of these data loggers affects the behavior and energetics of individual animals, potentially leading to biasing data. We measured the effect of two types of relatively small data loggers (<1% of animals' mass and front profile) on the swimming speeds and energy expenditure of four female northern fur seals (*Callorhinus ursinus*) while

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/mms.12460](https://doi.org/10.1111/mms.12460)

This article is protected by copyright. All rights reserved

swimming at depth. Swim speeds and rates of oxygen consumption were measured as the trained fur seals repeatedly swam an underwater circuit, with or without the tags. We found the placement of either tested tag significantly affected both the behavior and energetics of the fur seals in our study. Diving metabolic rate increased an average of 8.1%-12.3% (depending on tag type) and swim speed decreased an average of 3.0%-6.0% when wearing the tags. The combined changes in velocities and metabolic rates resulted in a 12.0%-19.0% increase in the total energy required by the fur seals to swim a set distance. The demonstrated effects of tags on behavior and energy expenditure may bias data sets from wild animals and potentially incur longer-term impacts on the studied animals.

Key words: northern fur seals, *Callorhinus ursinus*, telemetry, bioenergetics, biologging, diving, swimming, marine mammal.

Marine mammals are difficult to study through direct observation, given the time they spend at sea and below the water's surface. Animal-borne instruments—electronic packages equipped with a range of sensors that are attached directly to the animals, often referred to as data loggers—are a means of obtaining data without requiring direct observation by the researcher. With the rapid development of computing power and miniaturization, scientists have become increasingly dependent upon information gathered from external data loggers to study marine mammals (see review by McIntyre 2014). These data loggers (both biologgers and remote telemetry devices; Todd Jones *et al.* 2013) can sense and record numerous aspects of behavior, physiology, ecology, and bioenergetics of individual marine mammals (Hussey *et al.* 2015).

The use of electronic tagging technologies has permitted

scientists to make tremendous advances in scientific knowledge. In fact, this mode of data collection has become so prevalent that marine mammals have been increasingly used as platforms of opportunity to collect information on their external environment, including both biological and physical oceanographic data (e.g., Hooker and Boyd 2003, Fedak 2004, Roquet *et al.* 2013, Lawson *et al.* 2015).

One of the goals in biologging studies should be that placement of these tags has a minimal impact on the behavior, energetics, or well-being of the animal (Wilson and McMahon 2006). This is important for both ethical considerations, as well as to ensure that the resulting data accurately reflects "nontagged" conditions. However, only a handful of studies have directly or indirectly tested these assumptions, particularly for marine mammals (reviewed in McIntyre 2014). Yet, the method of attachment of devices to marine mammals—particularly pinnipeds—has remained relatively unchanged over the decades. For pinnipeds, tags are typically affixed to the external pelage via epoxy or physically attached to flippers (Fedak *et al.* 1983), while tags for cetaceans are affixed directly to the dermis (via subcutaneous anchors or suction cups). All of these methods can potentially affect the behavior, energetics, and hydrodynamics of targeted individuals (McConnell *et al.* 2010).

Furthermore, the total physical size of these data collection tags has not decreased as rapidly as improvements in component miniaturization might suggest, partly due to a parallel increase in the data collecting demands of the tags, as well as the associated power requirements (which have not benefitted from the same level of miniaturization as sensor and data storage components). As a result, scientists and engineers

are constantly faced with the problem of determining "how large" a tag can be without adversely affecting the data collection platform (*i.e.*, the individual animals). While the majority of what is known about some species has been gathered through electronic devices physically attached to their torso, surprisingly little is known about the potential effect that tag attachment has on the movements and energetics of individual animals.

The potential for animal-borne tags to affect the behavior and energetics of study animals is of concern with regard to interpreting data. For example, management decisions may be based upon flawed data. Also, changes in tag types could introduce bias that affects apparent historical trends or geographic comparisons. However, beyond these scientific considerations, there are larger concerns that tag placement may adversely impact the life history of the individual being studied, that often belong to threatened or endangered populations (Cooke 2008).

The effect of tag size on animals was originally focused on avian studies, an understandable concern given the obvious potential impediment of additional weight and cross-sectional profile on their flight capabilities. Early research suggested a target of a maximum load of 5% of body mass (Cochran 1980). Progress in miniaturization has permitted increasingly smaller tags to be deployed on avian species, but a similar trend for decreasing tag sizes for marine mammal studies has been less dramatic. This is due in part to a general feeling that the size of tags attached to marine mammals are a minor concern, given their comparatively large body size and the assumption that differences in buoyancy may be more of an impediment than mass.

However, tag size can also impact hydrodynamic profiles of the animal. Marine mammals evolved to be highly hydrodynamic (Fish 1994), and any change in body shape has the potential to dramatically impact swimming efficiency and costs to marine mammals, particularly given the higher density of water compared to air. While tag designs attempt to minimize potential hydrodynamic drag through complex simulation modeling during the design process, the actual effects of tag placement have also been directly measured on diving marine vertebrates (e.g., Hull 1997, Wilson *et al.* 2004, Todd Jones *et al.* 2013, Vandenabeele *et al.* 2015). Among marine mammals, this has focused almost entirely on cetaceans (Berga *et al.* 2014, Reisinger *et al.* 2014, van der Hoop *et al.* 2014, Gendron *et al.* 2015), with fewer studies examining the effects on pinnipeds (Blanchet *et al.* 2014, Maresh *et al.* 2015).

We measured the effect of animal-borne tags on the swimming energetics and behavior of a relatively small species of pinniped, the northern fur seal (*Callorhinus ursinus*). Specifically, we measured the rate of oxygen consumption and swimming speed of fur seals trained to swim a standard submerged course while outfitted with tags. The tested tags are models currently deployed in the field, and are considered relatively small: proportional to <1% of fur seal body mass and cross-sectional area. Our aim was to determine whether the presence of such tags could adversely bias the behavior or energetics of fur seals carrying biologging tags in the wild, and quantify their potential impact.

MATERIALS AND METHODS

Data were collected from 4 female adult northern fur seals (*Callorhinus ursinus*, Linnaeus) between 18 September and 6

November 2014. The fur seals were ~6 yr old and 21.9–34.1 kg at the start of the trials. The animals had been housed at the University of British Columbia's Marine Mammal Energetics and Nutrition Laboratory at the Vancouver Aquarium (Vancouver, Canada) since being obtained from the wild at 4 mo of age in October 2008. They were trained using positive reinforcement to be familiar with all experimental procedures and equipment.

The trials measured the rates of oxygen consumption and swimming speeds of the fur seals swimming five subsurface laps in a pool, with or without one of two types of commercial data logging tags (detailed below). The trials took place in a large square pool (Fig. 1). A floating respirometry dome (25 L) was placed at the surface of one corner of the pool. A fish delivery system, consisting of a PVC tube, sump pump, and control valve, was placed in the diagonal corner of the pool, at a depth of 3.2 m. The direct-line distance between where the animals exited the dome and where the fish was delivered near the bottom of the pool was 18.6 m, so that each "lap" had a total swimming distance of 37.2 m, requiring the fur seals to swim a total of 186 m for each trial.

Before the start of the experiment, a small Velcro patch (5.5 × 11.0 cm) was glued to the dorsal fur of the fur seals using a cyanoacrylate adhesive, just posterior to the shoulder blades (Fig. 2). The data loggers were temporarily attached during each individual trial (except for "no tag trials") under trainer control with a matching piece of Velcro permanently glued to the underside of the tag. The two tags that we used are commonly deployed on wild northern fur seals were supplied by Wildlife Computers (Redmond, WA): a Splash tag (Splash10-309A) and a slightly larger time depth recorder (TDR10-F238-F). The

TDR had an in-air mass of 234 g, a footprint of 105 × 56 mm and a frontal surface area of 16.8 cm², while the Splash tag had an in-air mass of 133 g, a footprint of 76 × 56 mm and a frontal surface area of 15.7 cm². Both tags had a 16 cm whip antennae and a minimal mounting strip to simulate the epoxy normally used to attach the tag that together increased their surface frontage by an additional 2.5 cm². Tag mass was proportional to <1% of fur seal body mass. Frontal surface area was also proportional to <1% of the animal, calculated from an average maximum girth of 80 cm with flippers positioned alongside their torso.

Our attachment method physically mimicked the usual process of tags permanently attached with epoxy, but allowed us to randomly assign experimental treatments to the Splash tag, TDR tag, or no tag conditions. It also allowed us to remove the data logger between testing sessions to avoid any damage from conspecifics between trials.

An individual fur seal only completed a maximum of one trial per day, which was conducted at the start of the day prior to the fur seals being fed. During the course of a single trial (and after suitable attachment of a tag, as determined by random assignment), the individual fur seal was first held in the respirometry dome for 3.5–4.5 min to allow measurement of a steady rate of oxygen consumption (see below for technical details). The animal was held in position behaviorally, and provided with minimal food reinforcement (maximum 5 × 20 g pieces of herring, *Clupea pallasii*). A submerged net cage with a "trapdoor" attached to the bottom of the dome assisted with this behavior, but did not act to physically restrain the individual.

After obtaining a baseline metabolic rate inside the dome, the fur seal was commanded by training staff to dive directly to

the diagonal bottom corner of the pool, where it received a reinforcement of a single herring (~100 g) at 3.2 m depth, before immediately returning to the respirometry dome. The animal paused briefly in the dome (maximum 10 s, sufficient to take ~3 breaths and receive a single 20 g piece of fish for reinforcement) before being sent on another dive. In total, the fur seal completed five consecutive circuits for each successful trial. After completing five dives, the fur seal remained in the dome for ~3.5-4.5 min, sufficient for rates of oxygen consumption and carbon dioxide production to return to pre-dive levels. Total food intake at the dome during an entire trial was limited to 500 g, about half of which was delivered during the final post-dive recovery phase.

A researcher recorded all of the times for entering and exiting the dome, and reaching the feeding tube using a multi-function electronic timer. This allowed calculation of the transit times between the dome and the feeding tube for each leg of each dive, as well as inter-dive intervals spent in the respirometry dome. Average swimming velocity (m/s) for each trial was calculated by dividing the total distance swum (186 m over five dives) by the total active swimming time between the respirometry dome and the feeding tube (*i.e.*, discounting inter-dive intervals in the dome).

Diving metabolic rate (DMR) was calculated from measured rates of oxygen consumption (expressed in mL O₂ min⁻¹) using standard flow through respirometry methods (Lighton 2008). Fresh air was drawn through the respirometry dome at a rate of 125 L/min by a Sable Systems Field Metabolic Pump, (Sable Systems; Las Vegas, NV). Subsamples of air from the excurrent airstream were dried through a canister of anhydrous CaSO₄, before the O₂

and CO₂ concentration were analyzed by the Sable Systems Field Metabolic System (P-Series). The resultant O₂ and CO₂ concentrations in the excurrent air were continuously recorded to a portable computer using Sable Systems' Expedata software. Changes in O₂ and CO₂ concentrations were compared in relation to baseline ambient air measurements at the start and end of each trial, which also allowed for correction from any system drift. The integrity of the entire system was checked using standard nitrogen dilution tests, and gases of known concentrations were also periodically used to calibrate the systems.

Instantaneous rates of oxygen depletion were calculated from measured changes in O₂ and CO₂ concentrations, using LabAnalystX software² and including the appropriate equations from Withers (1977) and compensation for humidity in the excurrent airstream. Estimated rates of O₂ consumption and CO₂ consumption during activities when the animal is breath-holding—such as diving metabolic rate (DMR)—are calculated from “excess” (greater than resting) rates of oxygen consumption observed during subsequent resting periods breathing in the respirometry dome. Hence, DMR was calculated as the increase in instantaneous VO₂ above baseline levels, divided by total submergence time (see fig. 3 in Rosen *et al.* 2017). This allowed us to calculate the VO₂ only during the submerged portion of the trial (discounting interdive intervals spent in the dome).

The cost of swimming a set distance was calculated by multiplying the DMR (rate of oxygen consumption) by the time to travel a given distance. We expressed this cost both as the total oxygen consumption over the entire five laps (DMR × dive time) and as the cost for traveling 1 m (DMR × dive time/186). Each fur seal completed 2–5 trials in a random order under each

of the tag conditions (Splash tag, TDR tag, and no tag); the number of trials for each treatment was equal within an animal. In reality, each fur seal undertook significantly more trials, including initial training dives (which also allowed them to become familiar with tag placement) and partial trials where testing criteria were not met (e.g., the animal surfaced between dives).

Statistics

All data were analyzed using R statistical software R.3.0.1 (R Core Team 2014). The statistical analysis used linear mixed-effects models (LME) from the *nlme* package (Pinheiro and Bates 2000) to examine whether "tag type" had an overall effect on swimming speed, diving metabolic rate, or total swimming cost. Body mass and tag type was a fixed effect (i.e., categorical factor) with three levels (TDR tag, Splash tag, no tag). LME models account for repeated measures among and within each animal (Zuur *et al.* 2009). Animal ID was included as a random effect for all analyses to account for repeated measures and allow inferences from the sample population to be extended. Separate models were run for each dependent variable of swimming speed, diving metabolic rate, and total swimming cost. Each model was compared to the simpler potential model (including the null model without any fixed factors) using a log likelihood ratio test (LRT) to determine whether inclusion of the fixed factor significantly improved the model (set as $\alpha = 0.05$). If tag type had an overall significant effect, Tukey *post hoc* tests with Bonferroni adjusted *P*-values were used to compare the means between multiple levels within significant fixed factors (*mvtnorm* and *multcomp* R libraries) to determine which tag conditions were significantly different from each other. All

values are reported as means \pm SE.

RESULTS

There was a high level of consistency in lap times (and calculated swimming speeds) within a trial for each fur seal. Overall, tag presence significantly affected swim speed (LRT = 7.20, $P = 0.027$). Specifically, swim speed was significantly reduced when wearing the larger TDR tag (1.98 ± 0.05 m/s; mean \pm SE) compared to wearing no tag (2.11 ± 0.06 m/s). As a result, dive time was greater for the fur seals to complete the circuit while carrying the TDR tag (94.5 ± 2.6 s) than when swimming without any tag (89.2 ± 2.7 s). The swimming speed (and hence dive time) while wearing the smaller Splash tag was intermediate (2.05 ± 0.04 m/s; 92.2 ± 2.3 s), and not significantly different than either the TDR or no tag conditions (Fig. 3A, Table 1).

Diving metabolic rate (DMR) was not affected by body mass, as would be expected given the relatively consistent mass for each fur seal throughout the study (ANOVA, $P = 0.93$). There was a significant linear relationship between swim speed and DMR (ANOVA, $P = 0.028$), whereby DMR increased with swim speed (Fig. 4). Consistent with the effects observed on swim speed, tag type also affected DMR (LRT = 15.52, $P < 0.001$). DMR while wearing the Splash tag ($1,142.1 \pm 37.5$ mL O₂ min⁻¹) or the TDR tag ($1,186.4 \pm 42.9$ mL O₂ min⁻¹) was greater than when no tag was worn ($1,056.8 \pm 52.4$ mL O₂ min⁻¹; both $P < 0.001$), but did not differ significantly between tag types (Fig. 3B, Table 1). However, the best predictive model for DMR included both tag type and swim speed (LRT = 23.45, $P < 0.001$ vs. model with only one predictor).

The type of tag carried also significantly increased the total cost of swimming a given distance (LRT = 28.90, $P <$

0.001). Specifically, the total cost for swimming 1 m while wearing either a Splash tag ($9.35 \pm 0.20 \text{ mL O}_2 \text{ m}^{-1}$) or a TDR tag ($9.93 \pm 0.19 \text{ mL O}_2 \text{ m}^{-1}$) was greater than when wearing no tag ($8.35 \pm 0.34 \text{ mL O}_2 \text{ m}^{-1}$; both $P < 0.001$), with no statistical difference between the two tags ($P = 0.135$) (Fig. 3C, Table 1).

DISCUSSION

Data logging tags have become essential tools in the study of ecology, behavior, and physiology of marine mammals, providing insight that is not readily obtainable by other means. Most scientists take care to ensure the attachment or subsequent removal of data loggers do not cause physical pain or damage to individual animals (Walker *et al.* 2012). However, even apparently benign tags can cause changes in behavior or energy expenditure that can adversely affect individuals in both the short- and long-term. Despite the widespread use of this technology, surprisingly few studies have quantified the behavioral or energetic effects of tag attachment on marine mammals.

Short-term Effects on Energy Expenditure and Diving Behavior

In the short-term, the attachment of a data logger can alter behavior and/or energy expenditure. However, the two are not independent; for example, changes in gait can affect locomotory costs and changes in foraging patterns can affect energy expenditure and overall energy balance. The extent of any observed effects of attached devices may be proportional to physical aspects of the tag (*e.g.*, mass, cross-section, *etc.*) or may result solely from the presence of the device (*e.g.*, discomfort, coloration, *etc.*).

In our experimental study, the presence of either tested tag significantly affected both the behavior and energetics of

the fur seals, despite the fact that tag mass was <1% of body mass. Swim speed decreased an average of 3.0%–6.0% when wearing the tags and diving metabolic rate increased an average of 8.1%–12.3% (depending on tag type). These two parameters are intimately related, since changes in hydrodynamics and the associated costs of locomotion incurred from tag placement on a streamlined body effectively alter the cost of transport (COT) curve. The COT curve describes the curvilinear relationship between mass-specific velocity and energy expenditure and where this curve reaches a minimum defines the most optimal speed of swimming (see Williams 1999, Rosen and Trites 2002). While tag placement increases COT, it is not uniform across all velocities. This means that the net result is usually a “left shift” in the curve, effectively resulting in a decrease in the optimal swimming speed. This effect may be revealed as decreases in the animal’s preferred swimming velocity, as exhibited by the fur seals in our study.

Other species also demonstrate a strategy to minimize energy expenditure by decreasing swimming velocity while wearing tags. In African penguins (*Spheniscus demersus*), tag attachment decreased mean foraging speeds inversely with device cross-sectional size (3.4% vs. 4.9% of animal’s frontage; Wilson *et al.* 1986), and decreased dive descent rates in great cormorants (*Phalacrocorax carbo*) (Vandenabeele *et al.* 2015). Bottlenose dolphins (*Tursiops truncatus*) trained to swim a specific course were significantly (~11%) slower when wearing tags (DTAG2) (van der Hoop *et al.* 2014). This change was hypothesized to be a strategy to compensate for increased drag costs, with the result that the presence of tags did not significantly affect metabolic rates as measured during post task recovery phases.

Despite the significant decrease in mean swimming speed, the diving metabolic rate of the northern fur seals in our study was still greater with the tags than without. This demonstrates that behavioral changes can only partly offset changes in hydrodynamic drag. Further, while decreases in swimming speed are a strategy for minimizing the direct energetic costs associated with decreased hydrodynamics, there are potential negative consequences that may make such a tactic unfeasible, including decreased prey-capture abilities and group cohesiveness. For example, eels have been shown to maintain speed despite increased drag of telemetry tags during migration (Tudorache *et al.* 2014), indicating they willingly consume more energy to reach their spawning locations on time.

It is also important to note that the ultimate "goal" of locomotion is often to move across a specific distance. The total cost of swimming a set distance is a product of both swimming velocity and diving metabolic rate; hence, even in cases where tags result in a decrease swimming velocity and no increase in metabolic rate, total energy expended in swimming a given distance will be greater than when not wearing a tag. In our study, the combined changes in average swimming velocity and metabolic rate resulted in a 12.0%–19.0% increase in the total energy required by the fur seals to swim a set distance. These effects were surprising high, given the relatively small size of the tags. The potential impacts of tag attachment are of particular concern given that these same tags are routinely deployed on young northern fur seals in the wild (*e.g.*, Ragen *et al.* 1995; Sterling and Ream 2004; Baker 2007; Lea *et al.* 2009, 2010).

Determining Potential for Impacts

While the results of our study identified significant energetic and behavioral effects on northern fur seals, they are not a denunciation of the use of external data loggers. Instrumentation placed on northern fur seals have been invaluable in species conservation efforts by providing information about behavior, life history, critical habitat, energetics, foraging, and environmental effects that could not be obtained in any other fashion. Inevitably, researchers have a responsibility to balance the potential negative impacts of their research activities with the need to acquire valuable data, ideally through incorporating a decision framework (see McMahon *et al.* 2012). For biologging studies, this requires quantifying the potential impact of these devices on the animals being studied.

Unfortunately, few guidelines exist to inform decisions on tag size, configuration, or placement. Additionally, such information would likely be highly species-specific (Wilson and McMahon 2006). Guidelines of a maximum 3%-5% body mass are frequently cited (Cochran 1980, Kenward 2000), but the basis of these declarations is unclear. For marine mammals, the effect of tag placement on the individual's hydrodynamic profile is probably of greatest concern. It is widely acknowledged that the cost of locomotion in marine mammals is lower than their terrestrial counterparts (Williams *et al.* 2015), and is closely tied to their low hydrodynamic drag (Feldkamp 1987, Fish 2000). Hence, it is logical to assume that tags that increase hydrodynamic drag will increase rates of energy expenditure for actively swimming animals (Jones *et al.* 2013, van der Hoop *et al.* 2014). For example, the modeled effects of satellite tag placement on gray seals (*Halichoerus grypus*) revealed that the

hydrodynamic disruption resulted in an average 12% increase of the drag coefficient (Hazekamp *et al.* 2010).

Hence, for aquatic organisms, the most critical physical feature of the tag is likely cross-sectional area (Ropert-Coudert *et al.* 2007), although position of placement and presence of antennae may also contribute to negative effects (Bannasch *et al.* 1994). As a result, tag design for marine mammals is primarily concerned with streamlining and minimizing frontage to diminish their overall impact. It is interesting to note the tags used in our study had a significant impact, despite the front profile of both of the tags being relatively low, accounting for <1% of the fur seals' minimum profile.

As part of the tag design process, recent efforts have focused on novel ways to model the potential impact of telemetry devices prior to manufacture and mass deployment (Pavlov *et al.* 2007, Hazekamp *et al.* 2010, Pavlov and Rashad 2012, Vandenabeele *et al.* 2015). Still, it is impossible to quantify the effect of data loggers without actual animal testing, particularly as individual animals can alter their swimming behavior or gait in response to tag attachment. Despite careful consideration of tag design to minimize disturbance, several studies have demonstrated negative effects on both drag, swim speed, dive depth, and maneuverability of aquatic animals (Culik *et al.* 1993, Hull 1997, Watson and Granger 1998, Geertsen *et al.* 2004, Wilson *et al.* 2004, Grusha and Patterson 2005, Tudorache *et al.* 2014, Vandenabeele *et al.* 2015).

Unfortunately, in many cases, it is inherently difficult to quantify the effect of tags on wild animals. Some studies (*e.g.*, Oliver *et al.* 1998) have tested for effects between different types of packages, but since instrumentation is usually required

to monitor the potentially affected behavior it is not possible to test for the effect of tag deployment *per se*. Comparisons to a "no tag" state are most easily determined in animals under controlled conditions, such as the current study. While our study only examined the effects of two tag types, future studies should utilize a range of tag sizes/types, so that guidelines could be developed to decrease the potential impact of field studies based on quantified behavioral and energetic effects.

Long-term Effects of Tag Placement

In addition to introducing data bias, the effects of tagging are a concern on the potential long-term impact on survival and reproductive success. Although our study concentrated on short-term effects of tags, we would be remiss if we did not note the potential long-term impacts. Such effects are generally thought to be more of a concern for smaller animals, although biotelemetry devices have been recorded to negatively impact behavior (Brooks *et al.* 2008) and survival (Swenson *et al.* 1999, Rasiulis *et al.* 2014) among large terrestrial mammals, although the trend is by no means universal. In addition, there is evidence that migratory species may be particularly susceptible to these potential effects as any effect of tags on the cost of transport would be magnified by the considerable distances they travel (Rasiulis *et al.* 2014). It must also be noted that there is some debate regarding whether animals can "adjust" to the presence of the tags, thereby mitigating the short-term effects of tag placement (such as those measured in this study) over the longer term.

The specific tags tested in our study are regularly deployed on a large range of animals in the field, and the effect of the tags is partly dependent on their size relative to

that of the study animal. Northern fur seals are relatively small (among marine mammals), and travel long distances during the nonbreeding season (Kenyon and Wilke 1953, Bigg 1990, Baker 2007). Lactating females also make extended foraging trips, the timing and success of which can greatly affect the condition and survival of their pups (DeLong and Antonelis 1991, Boltnev *et al.* 1998). Although we did not measure the long-term effects of tagging in our study, we did find that the tagged fur seals had to expend 12%-19% more energy than untagged seals to swim the same distance. This would translate into an even greater required increase in food energy intake given innate digestive inefficiencies (Diaz-Gomez *et al.* 2016). This calculation also assumes that they could accomplish the required tasks while reducing their swimming speed; if this were not possible (*e.g.*, during prey capture) the energetic consequences would be even higher. Thus, the costs of tag attachment to individual northern fur seals may be significant enough to disrupt their long-term energy balance and negatively impact critical life history parameters.

Some of the most robust long-term studies come from penguins, a similar group of aquatic vertebrates. For example, African penguins equipped with tags with a significant surface profile returned from unusually extended foraging trips in emaciated condition (Wilson *et al.* 1986). As noted by Todd Jones *et al.* (2013), the extra energy needed to overcome drag costs during locomotion could possibly deplete fat stores that were intended for reproduction, translating into reduced reproductive output of the tagged animal. In extreme cases, it may even impact survival. A recent long-term study with king penguins (*Aptenodytes patagonicus*) revealed that banding decreased

reproductive success by 39% and survival by 16%, significantly impacting population growth rates (Saraux *et al.* 2011).

A brief probe of the available literature on the potential longer-term impact of tagging on marine mammals is inconsistent—even within closely related group of animals. For example, McMahon *et al.* (2008) reported no adverse affects of tag attachment on adult southern elephant seals (*Mirounga leonina*), measured as either short-term (mass) or long-term (survival) effects. In contrast, Costa and Gentry (1986) found that female northern elephant seals (*Mirounga angustirostris*) expended 19% more energy on foraging trips when equipped with a TDR than when they were not, although the net effect of this difference (*e.g.*, maternal or pup mass changes) was not quantified. However, in a study of pregnant northern elephant seals, three seals carrying “large, nonstreamlined instrumentation” exhibited a 4-fold increase in the costs of locomotion, resulting in elevated overall rates of energy expenditure and only half the mass gain of study animals without such instrumentation (Maresh *et al.* 2015).

Among female Antarctic fur seals (*Arctocephalus gazella*), one study of the foraging and nursing patterns found no significant statistical differences in time at-sea or time ashore between individuals with and without TDRs, despite the fact that the at-sea hours of tagged females was on average 20% higher than nontagged females (Boyd *et al.* 1991). However, a subsequent study found female Antarctic fur seals carrying TDRs and radio transmitters had greater average foraging-trip and on-shore nursing durations than those carrying only TDRs (Walker and Boveng 1995). The authors suggested the 15% increase in foraging-trip durations was likely due to increased hydrodynamic

drag, and that the increased nursing-visit durations reflected a subsequent need for rest and recovery. The long-term impacts of instrumentation were further demonstrated in another study that reported both greater time at-sea and lower pup growth for pairs where mothers carried bulkier instruments (Blanchet *et al.* 2014).

Other Negative Effects of Tags

In addition to the direct change in hydrodynamics, tags can negatively affect individual animals in a number of less intuitive ways. This includes long-term irritation or infection of tag anchors that can potentially reduce reproductive success (Gendron *et al.* 2015, Norman *et al.* 2017) or heightened behavioral avoidance due to previous tagging events (Best *et al.* 2005, Tezanos-Pinto and Baker 2012, although see Reisinger *et al.* 2014). Secondary biological growth (*e.g.*, algae and barnacles) on the tag, the antennae, and even on the pelage can further disrupt their design hydrodynamics, particularly for tags deployed long-term (Hazekamp *et al.* 2010, Reisinger *et al.* 2010). Tag loss and associated pelage damage may also have a deleterious effect on thermoregulatory capabilities and associated costs of fur seals. Even the normal operation of tags may have unintended negative effects, as demonstrated by changes in behavior of juvenile northern elephant seals deployed with a pinging "sonar tag" (Lawson *et al.* 2015).

Conclusion

The results of our study indicate that the attachment of data logging tags can significantly affect both the short-term behavior and energy expenditure of female northern fur seals. Tag attachment increased diving metabolic rate, despite a simultaneous decrease in swimming speed to compensate for

changes in hydrodynamic drag coefficients. Together, this resulted in the fur seals expending an additional 12%–19% in energy to travel the same distance. This is likely to have a dramatic negative affect the energy budget of wild northern fur seals, given their pelagic, migratory, lifestyle.

The effects we observed occurred despite the relatively small size of the tags tested. In practice, scientists have deployed much larger devices on this species, and have often placed multiple devices on individual animals that will inevitably increase their impacts. Such concerns should be emphasized as innovations in tag design and usage press the boundaries of acceptable practice, including placement on flippers (Gauthier-Clerc *et al.* 2004) or head mounts (Harcourt and Davis 1997, Ydesen *et al.* 2014) that could affect animals substantially more than traditional back mounting.

While data logging instruments provide invaluable information about marine mammals and their environment, the potential impact of these devices cannot be discounted, and must be considered when designing ethical research programs. The consequences of instrumentation not only include short-term changes in behavior and energetics, but also potential critical biases in data sets and long-term impacts on life history traits.

ACKNOWLEDGMENTS

We thank the research and husbandry staff of the Marine Mammal Energetics and Nutrition Laboratory for their efforts. This work was accomplished through the cooperation and participation of the Vancouver Aquarium Marine Science Centre. All experimental protocols were approved by the Animal Care Committees of the Vancouver Aquarium and the University of

British Columbia (#A14-0330). This work was supported by funding provided to the North Pacific Universities Marine Mammal Research Consortium by the North Pacific Marine Science Foundation and the National Oceanic and Atmospheric Administration (grant number NA11NMF4390124); and the National Science and Engineering Research Council, Canada.

LITERATURE CITED

- Baker, J. D. 2007. Post-weaning migration of northern fur seal *Callorhinus ursinus* pups from the Pribilof Islands, Alaska. *Marine Ecology Progress Series* 341:243-255.
- Bannasch, R., R. P. Wilson and B. Culik. 1994. Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *Journal of Experimental Biology* 194:83-96.
- Berga, A. S., A. J. Wright, A. Galatius and S. Sveegaard. 2014. Do larger tag packages alter diving behavior in harbor porpoises? *Marine Mammal Science* 31:756-763.
- Best, P. B., D. Reeb, M. B. Rew, P. J. Palsbøll, C. Schaeff and A. Brandao. 2005. Biopsying southern right whales: Their reactions and effects on reproduction. *Journal of Wildlife Management* 69:1171-1180.
- Bigg, M. A. 1990. Migration of northern fur seals (*Callorhinus ursinus*) off western North America. Canadian Technical Report of Fisheries and Aquatic Sciences No. 1764. 63 pp.
- Blanchet, M.-A., C. Lydersen, M. Biuw, P. N. De Bruyn, G. Hofmeyr, B. A. Krafft and K. M. Kovacs. 2014. Instrumentation and handling effects on Antarctic fur seals (*Arctocephalus gazella*). *Polar Research* 33:21630.
- Boltnev, A. I., A. E. York and G. A. Antonelis. 1998. Northern fur seal young: Interrelationships among birth size, growth, and survival. *Canadian Journal of Zoology* 76:843-

854.

- Boyd, I. L., N. J. Lunn and T. Barton. 1991. Time budgets and foraging characteristics of lactating Antarctic fur seals. *Journal of Animal Ecology* 60:577-592.
- Brooks, C., C. Bonyongo and S. Harris. 2008. Effects of global positioning system collar weight on zebra behavior and location error. *Journal of Wildlife Management* 72:527-534.
- Cochran, W. 1980. Wildlife telemetry. *Wildlife management techniques manual* 4:507-520.
- Cooke, S. J. 2008. Biotelemetry and biologging in endangered species research and animal conservation: Relevance to regional, national, and IUCN Red List threat assessments. *Endangered Species Research* 4:165-185.
- Costa, D. P., and R. L. Gentry. 1986. Free-ranging energetics of northern fur seals. Pages 79-101 in R. L. Gentry and G. L. Kooyman, eds. *Fur seals: Maternal strategies on land and at sea*. Princeton University Press, Princeton, NJ.
- Culik, B., R. Wilson and R. Bannasch. 1993. Flipper-bands on penguins: What is the cost of a life-long commitment? *Marine Ecology Progress Series* 98:209-214.
- Delong, R. L., and G. A. Antonelis. 1991. Impact of the 1982-1983 El Niño on the northern fur seal population at San Miguel Island, California. Pages 75-83 in F. Trillmich and K. Ono, eds. *Pinnipeds and El Niño: Responses to environmental stress*. Springer-Verlag, Berlin, Germany.
- Diaz-Gomez, M., D. A. S. Rosen and A. W. Trites. 2016. Net energy gained by northern fur seals (*Callorhinus ursinus*) is impacted more by diet quality than by diet diversity. *Canadian Journal of Zoology* 94:123-135.
- Fedak, M. 2004. Marine animals as platforms for oceanographic

- sampling: A "win/win" situation for biology and operational oceanography. *Memoirs of National Institute of Polar Research* 58:133-147.
- Fedak, M. A., S. S. Anderson and M. G. Curry. 1983. Attachment of a radio tag to the fur of seals. *Journal of Zoology*, London 200:298-300.
- Feldkamp, S. D. 1987. Swimming in the California sea lion: Morphometrics, drag and energetics. *Journal of Experimental Biology* 131:117-135.
- Fish, F. E. 1994. Influence of hydrodynamic-design and propulsive mode on mammalian swimming energetics. *Australian Journal of Zoology* 42:79-101.
- Fish, F. E. 2000. Biomechanics and energetics in aquatic and semiaquatic mammals: Platypus to whale. *Physiological and Biochemical Zoology* 73:683-698.
- Gauthier-Clerc, M., J.-P. Gendner, C. Ribic, *et al.* 2004. Long-term effects of flipper bands on penguins. *Proceedings of the Royal Society of London B: Biological Sciences* 271:S423-S426.
- Geertsen, B. M., J. Teilmann, R. Kastelein, H. Vlemmix and L. A. Miller. 2004. Behaviour and physiological effects of transmitter attachments on a captive harbour porpoise (*Phocoena phocoena*). *Journal of Cetacean Research and Management* 6:139-146.
- Gendron, D., I. M. Serrano, A. U. De La Cruz, J. Calambokidis and B. Mate. 2015. Long-term individual sighting history database: An effective tool to monitor satellite tag effects on cetaceans. *Endangered Species Research* 26:235-241.
- Grusha, D. S., and M. R. Patterson. 2005. Quantification of drag

- and lift imposed by pop-up satellite archival tags and estimation of the metabolic cost to cownose rays (*Rhinoptera bonasus*). *Fishery Bulletin* 103:63-70.
- Harcourt, R., and L. Davis. 1997. The use of satellite telemetry to determine fur seal foraging areas. Pages 137-142 in M. Hindell and C. Kemper, eds. *Marine mammal research in the Southern Hemisphere. Volume 1. Status, ecology and medicine.* Surrey Beatty & Sons, Chipping Norton, U.K.
- Hazekamp, A. A., R. Mayer and N. Osinga. 2010. Flow simulation along a seal: The impact of an external device. *European Journal of Wildlife Research* 56:131-140.
- Hooker, S. K., and I. L. Boyd. 2003. Salinity sensors on seals: Use of marine predators to carry CTD data loggers. *Deep Sea Research Part I* 50:927-939.
- Hull, C. L. 1997. The effect of carrying devices on breeding Royal penguins. *Condor* 99:530-534.
- Hussey, N. E., S. T. Kessel, K. Aarestrup, et al. 2015. Aquatic animal telemetry: A panoramic window into the underwater world. *Science* 348:1255642.
- Jones, T. T., K. S. Van Houtan, B. L. Bostrom, et al. 2013. Calculating the ecological impacts of animal-borne instruments on aquatic organisms. *Methods in Ecology and Evolution* 4:1178-1186.
- Kenward, R. E. 2000. *A manual for wildlife radio tagging.* Academic Press, London, U.K.
- Kenyon, K. W., and F. Wilke. 1953. Migration of the northern fur seal, *Callorhinus ursinus*. *Journal of Mammalogy* 34:86-98.
- Lawson, G. L., L. A. Hückstädt, A. C. Lavery, et al. 2015. Development of an animal-borne "sonar tag" for quantifying prey availability: Test deployments on northern elephant

- seals. *Animal Biotelemetry* 3:1-16.
- Lea, M.-A., D. Johnson, R. Ream, J. Sterling, S. Melin and T. Gelatt. 2009. Extreme weather events influence dispersal of naive northern fur seals. *Biology Letters* 5:252-257.
- Lea, M. A., D. Johnson, S. Melin, R. Ream and T. Gelatt. 2010. Diving ontogeny and lunar responses in a highly migratory mammal, the northern fur seal *Callorhinus ursinus*. *Marine Ecology Progress Series* 419:233-247.
- Lighton, J. R. 2008. *Measuring metabolic rates: A manual for scientists*. Oxford University Press, Oxford, U.K.
- Maresh, J. L., T. Adachi, A. Takahashi, *et al.* 2015. Summing the strokes: Energy economy in northern elephant seals during large-scale foraging migrations. *Movement Ecology* 3:1-16.
- McConnell, B. J., M. Fedak, S. K. Hooker and T. Patterson. 2010. Telemetry. Pages 222-242 in I. L. Boyd, W. D. Bowen and S. J. Iverson, eds. *Marine mammal ecology and conservation: A handbook of techniques*. Oxford University Press, Oxford, U.K.
- McIntyre, T. 2014. Trends in tagging of marine mammals: A review of marine mammal biologging studies. *African Journal of Marine Science* 36:409-422.
- McMahon, C. R., I. C. Field, C. J. Bradshaw, G. C. White and M. A. Hindell. 2008. Tracking and data-logging devices attached to elephant seals do not affect individual mass gain or survival. *Journal of Experimental Marine Biology and Ecology* 360:71-77.
- McMahon, C. R., R. Harcourt, P. Bateson and M. A. Hindell. 2012. Animal welfare and decision making in wildlife research. *Biological Conservation* 153:254-256.
- Norman, S. A., K. R. Flynn, A. N. Zerbini, *et al.* 2017.

- Assessment of wound healing of tagged gray (*Eschrichtius robustus*) and blue (*Balaenoptera musculus*) whales in the eastern North Pacific using long-term series of photographs. *Marine Mammal Science* doi:10.1111/mms.12443.
- Oliver, G. W., P. A. Morris, P. H. Thorson and B. J. Le Boeuf. 1998. Homing behavior of juvenile northern elephant seals. *Marine Mammal Science* 14:245-256.
- Pavlov, V. V., and A. M. Rashad. 2012. A non-invasive dolphin telemetry tag: Computer design and numerical flow simulation. *Marine Mammal Science* 28:E16-E27.
- Pavlov, V., R. P. Wilson and K. Lucke. 2007. A new approach to tag design in dolphin telemetry: Computer simulations to minimise deleterious effects. *Deep Sea Research Part II* 54:404-414.
- Pinheiro, J. C., and D. M. Bates. 2000. Mixed effects models in S and S-PLUS. Springer-Verlag, New York, NY.
- Ragen, T. J., G. A. Antonelis and M. Kiyota. 1995. Early migration of northern fur seal pups from St. Paul Island, Alaska. *Journal of Mammalogy* 76:1137-1148.
- Rasiulis, A. L., M. Festa-Bianchet, S. Couturier and S. D. Côté. 2014. The effect of radio-collar weight on survival of migratory caribou. *Journal of Wildlife Management* 78:953-956.
- R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reisinger, R. R., T. McIntyre and M. N. Bester. 2010. Goose barnacles hitchhike on satellite-tracked southern elephant seals. *Polar Biology* 33:561-564.
- Reisinger, R. R., W. C. Oosthuizen, G. Péron, D. C. Toussaint,

- R. D. Andrews and P. N. De Bruyn. 2014. Satellite tagging and biopsy sampling of killer whales at subantarctic Marion Island: Effectiveness, immediate reactions and long-term responses. *PLOS ONE* 9:e111835.
- Robert-Coudert, Y., N. Knott, A. Chiaradia and A. Kato. 2007. How do different data logger sizes and attachment positions affect the diving behaviour of little penguins? *Deep Sea Research Part II* 54:415-423.
- Roquet, F., C. Wunsch, G. Forget, P. Heimbach, et al. 2013. Estimates of the Southern Ocean general circulation improved by animal-borne instruments. *Geophysical Research Letters* 40:6176-6180.
- Rosen, D. A. S., A. G. Hindle, C. Gerlinsky, E. Goundie, G. D. Hastie, B. L. Volpov and A. W. Trites. 2017. Physiological constraints and energetic costs of diving behaviour in marine mammals: A review of studies using trained Steller sea lions diving in the open ocean. *Journal of Comparative Physiology B* 187:29-50.
- Rosen, D. A. S., and A. W. Trites. 2002. Cost of transport in Steller sea lions, *Eumetopias jubatus*. *Marine Mammal Science* 18:513-524.
- Saroux, C., C. Le Bohec, J. M. Durant, et al. 2011. Reliability of flipper-banded penguins as indicators of climate change. *Nature* 469:203-206.
- Sterling, J. T., and R. R. Ream. 2004. At-sea behavior of juvenile male northern fur seals (*Callorhinus ursinus*). *Canadian Journal of Zoology* 82:1621-1637.
- Swenson, J. E., K. Wallin, G. Ericsson, G. Cederlund and F. Sandegren. 1999. Effects of ear-tagging with radiotransmitters on survival of moose calves. *Journal of*

- Wildlife Management 63:354-358.
- Tezanos-Pinto, G., and C. Baker. 2012. Short-term reactions and long-term responses of bottlenose dolphins (*Tursiops truncatus*) to remote biopsy sampling. *New Zealand Journal of Marine and Freshwater Research* 46:13-29.
- Todd Jones, T., K. S. Van Houtan, B. L. Bostrom, et al. 2013. Calculating the ecological impacts of animal-borne instruments on aquatic organisms. *Methods in Ecology and Evolution* 4:1178-1186.
- Tudorache, C., E. Burgerhout, S. Brittijn and G. van den Thillart. 2014. The effect of drag and attachment site of external tags on swimming eels: Experimental quantification and evaluation tool. *PLOS ONE* 9:e112280.
- van der Hoop, J. M., A. Fahlman, T. Hurst, J. Rocho-Levine, K. A. Shorter, V. Petrov and M. J. Moore. 2014. Bottlenose dolphins modify behavior to reduce metabolic effect of tag attachment. *Journal of Experimental Biology* 217:4229-4236.
- Vandenabeele, S. P., E. L. C. Shepard, D. Grémillet, P. J. Butler, G. R. Martin and R. P. Wilson. 2015. Are bio-telemetric devices a drag? Effects of external tags on the diving behaviour of great cormorants. *Marine Ecology Progress Series* 519:239-249.
- Walker, B. G., and P. L. Boveng. 1995. Effects of time-depth recorders on maternal foraging and attendance behavior of Antarctic fur seals (*Arctocephalus gazella*). *Canadian Journal of Zoology* 73:1538-1544.
- Walker, K. A., A. W. Trites, M. Haulena and D. M. Weary. 2012. A review of the effects of different marking and tagging techniques on marine mammals. *Wildlife Research* 39:15-30.
- Watson, K. P., and R. A. Granger. 1998. Hydrodynamic effect of a

- satellite transmitter on a juvenile green turtle (*Chelonia mydas*). *Journal of Experimental Biology* 201:2497-2505.
- Williams, T. M. 1999. The evolution of cost efficient swimming in marine mammals: Limits to energetic optimization. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 354:193-201.
- Williams, T. M., L. A. Fuiman and R. W. Davis. 2015. Locomotion and the cost of hunting in large, stealthy marine carnivores. *Integrative and Comparative Biology* 55:673-682.
- Wilson, R. P., and C. R. McMahon. 2006. Measuring devices on wild animals: What constitutes acceptable practice? *Frontiers in Ecology and the Environment* 4:147-154.
- Wilson, R. P., W. S. Grant and D. C. Duffy. 1986. Recording devices on free-ranging marine animals: Does measurement affect foraging performance? *Ecology* 67:1091-1093.
- Wilson, R. P., J. M. Kreye, K. Lucke and H. Urquhart. 2004. Antennae on transmitters on penguins: Balancing energy budgets on the high wire. *Journal of Experimental Biology* 207:2649-2662.
- Withers, P. C. 1977. Measurement of VO_2 , VCO_2 , and evaporative water loss with a flow-through mask. *Journal of Applied Physiology* 42:120-123.
- Ydesen, K. S., D. M. Wisniewska, J. D. Hansen, K. Beedholm, M. Johnson and P. T. Madsen. 2014. What a jerk: Prey engulfment revealed by high-rate, super-cranial accelerometry on a harbour seal (*Phoca vitulina*). *Journal of Experimental Biology* 217:2239-2243.
- Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer Science+Business Media, New York, NY.

Received: 5 July 2017

Accepted: 28 September 2017

Figure 1. Schematic of experimental set-up. The northern fur seals repeatedly dove from a floating flow-through respirometry dome to the opposite bottom corner of the pool (where they received a fish reward) and back for each of the five segments of a trial. The total distance of each "lap" was approximately 37.2 m.

Figure 2. Tags used and tag attachment on the northern fur seals. The tags were affixed to the fur of the seals via a Velcro patch that allowed switching of tags for each trial (including "no tag" condition). The tags tested were a Wildlife Computers' (Redmond, WA) Splash tag (Splash10-309A; top) and a larger time depth recorder (TDR10-F238; bottom).

Figure 3. Differences in (top panel) average swimming speed, metabolic rate (middle panel), and swimming cost per meter (bottom panel) while either not wearing a tag, or wearing a Splash tag or a TDR tag. Box plots define the upper and lower quartile of the data from northern fur seals, transected by the median. Lines define the range of values that lie within $1.5 \times$ interquartile range. Letters above the bars indicate significantly different treatment means.

Figure 4. Relationship between average swim velocity and metabolic rate. Data points are for northern fur seals without a tag (boxes) or with a Splash tag (diamonds) or time depth recorder (circles). Second order polynomial curves are fit to the data for illustrative purposes.

¹ Corresponding author (e-mail: rosen@zoology.ubc.ca).

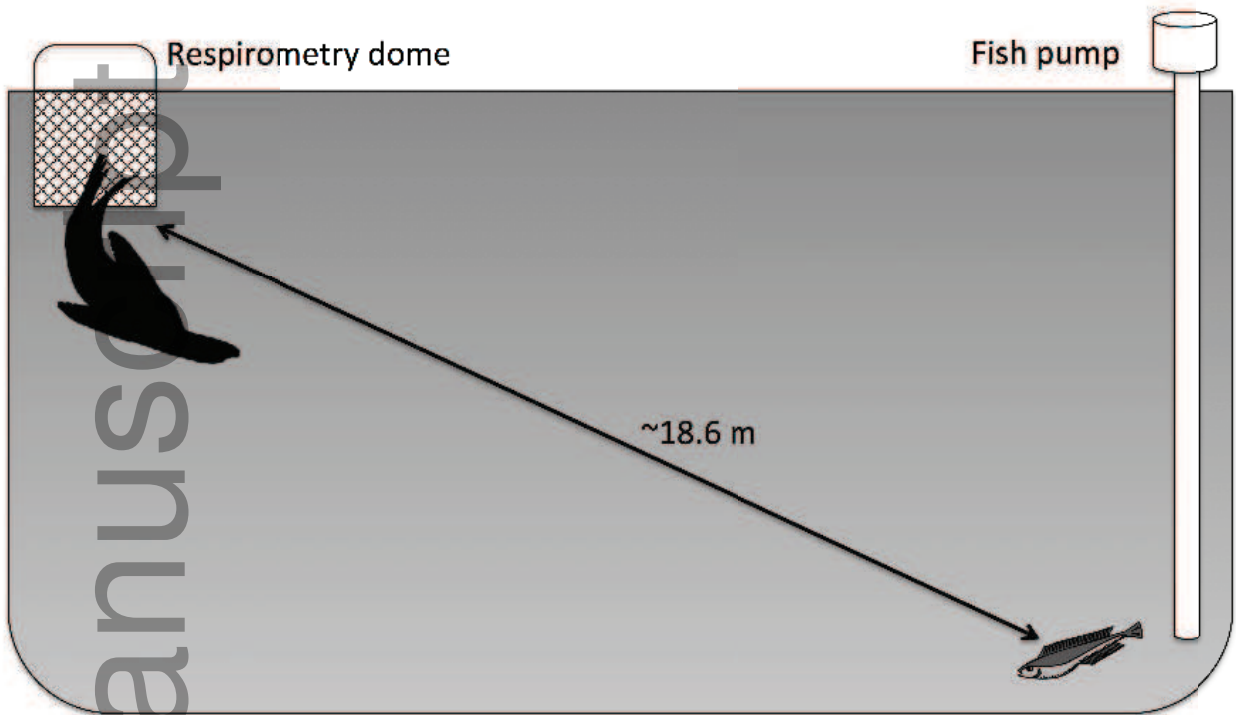
² Mark Chappell, Department of Biology, University of California

Riverside. Available at <http://warthog.ucr.edu/>.

Author Manuscript

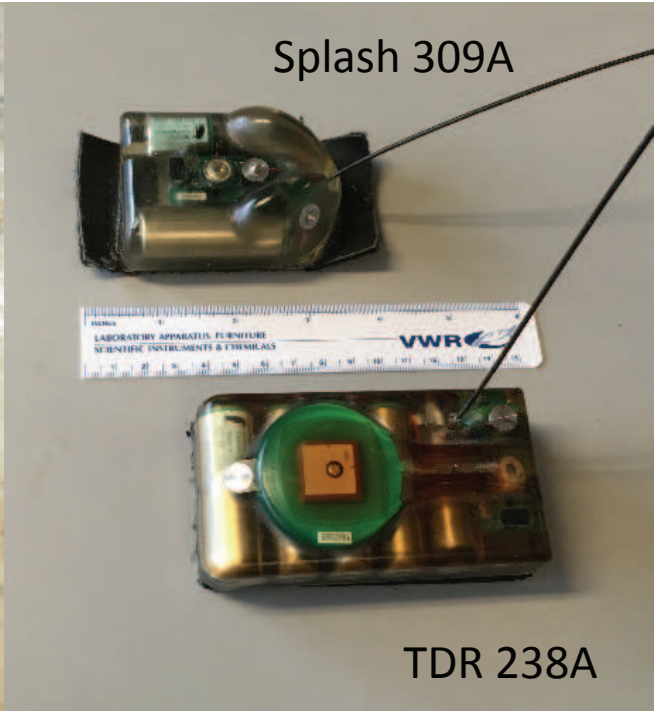
Table 1. Mean (and SE) from trials for each individual fur seal, for the no tag, smaller Splash tag, and large TDR tag trials. Data are presented for body mass (over all trials), dive time to complete five circuits (submerged time only, not including intervening surface times), average swim speed over the entire trial (calculated from submerged time over 186 m), diving metabolic rate (determined via gas respirometry), total cost of swimming the circuit (DMR × dive time) and cost to swim 1 meter (total cost/186 m).

	Tag	NFS08AN	NFS08AY	NFS08TI	NFS08TU	Overall
Body mass (kg)		26.7 (0.2)	22.4 (0.2)	33.5 (0.1)	28.1 (0.1)	
Dive time (s)	No tag	107.5 (6.4)	90.4 (3.0)	93.2 (4.0)	78.9 (1.6)	89.2 (2.7)
	Splash	106.7 (1.5)	91.2 (2.1)	97.2 (3.1)	83.4 (2.7)	92.2 (2.3)
	TDR	111.9 (2.7)	95.8 (4.0)	95.4 (2.8)	85.9 (2.2)	94.5 (2.6)
Swim speed (m/s)	No tag	1.74 (0.10)	2.06 (0.07)	2.01 (0.08)	2.36 (0.05)	2.11 (0.06)
	Splash	1.75 (0.02)	2.04 (0.05)	1.92 (0.06)	2.24 (0.07)	2.05 (0.04)
	TDR	1.66 (0.04)	1.95 (0.08)	1.95 (0.06)	2.17 (0.06)	1.98 (0.05)
DMR (mL O ₂ min ⁻¹)	No tag	839.0 (56.4)	900.2 (57.6)	1,080.1 (73.9)	1,214.3 (90.5)	1,056.8 (52.4)
	Splash	1,013.7 (20.9)	1,026.6 (31.8)	1,139.0 (51.1)	1,311.5 (45.7)	1,142.1 (37.5)
	TDR	992.3 (50.9)	1,036.8 (46.6)	1,228.5 (31.1)	1,350.1 (43.1)	1,186.4 (42.9)
Total cost (mL O ₂ min ⁻¹)	No tag	1509.5 (190.9)	1,356.9 (91.4)	1,671.8 (110.3)	1,597.1 (121.7)	1,552.3 (63.6)
	Splash	1,801.5 (11.7)	1,556.7 (18.3)	1,837.8 (51.1)	1,816.6 (49.2)	1,738.8 (37.1)
	TDR	1,848.4 (50.0)	1,646.6 (8.0)	1,949.9 (20.8)	1,925.8 (23.3)	1,847.5 (34.9)
Cost (mL O ₂ min ⁻¹) per m	No tag	8.12 (1.00)	7.30 (0.49)	9.00 (0.59)	8.59 (0.65)	8.35 (0.34)
	Splash	9.69 (0.06)	8.37 (0.10)	9.88 (0.27)	9.77 (0.26)	9.35 (0.20)



Author Manuscript

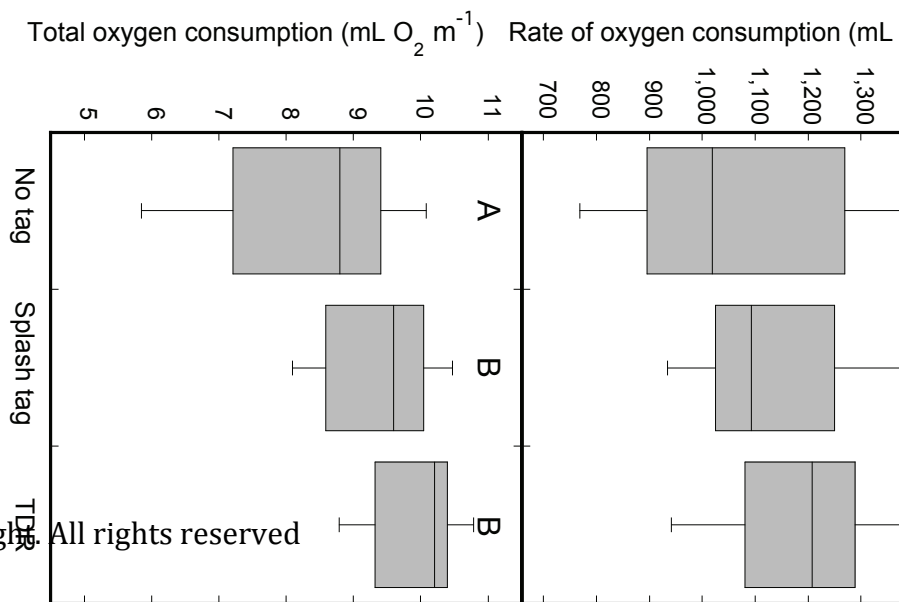
mms_12460_f1.eps



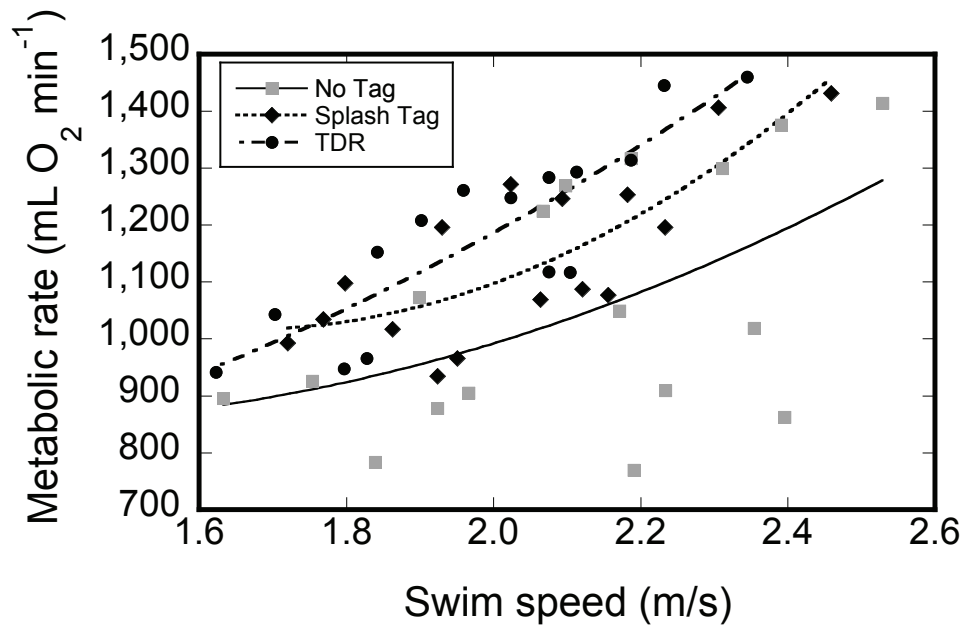
Author Manuscript

mms_12460_f2.eps

Author Manuscript



This article is protected by copyright. All rights reserved



mms_12460_f4.eps