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ARTICLE

Under pressure: Effects of instrumentation methods on fur seal pelt function

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Abstract

Tracking marine mammals with electronic devices enables researchers to better understand animal movements and at-sea behavior. For pinnipeds, instruments are typically glued to the animal’s hair, either directly to the pelage or via a fabric patch. These instruments are retrieved by cutting the pelage or cutting through the patch. The impact of these modifications to the pelage is presumed to be minimal and short-lived, but this has never been explicitly investigated. This study examined effects of instrument attachment on northern fur seal pelts. To assess thermal consequences of instrumentation, we determined thermal resistance of pelts in water for instruments glued directly to the pelage or with a neoprene base. For each attachment method, we measured the pelt unmodified, with instrument attached, and with instrument removed. Using a hyperbaric chamber, we measured the extent to which water could penetrate the pelt’s air layer during diving. Removing the tag by cutting the pelage reduced thermal function of the pelt in water and allowed more air to escape under pressure. In contrast, a neoprene patch better maintained the insulation in water and reduced air loss under pressure. Our results suggest the use of neoprene may reduce negative consequences of instrumentation in fur seals.

KEYWORDS

electronic instrumentation, hyperbaric pressure, marine mammal, pinniped, tagging, thermal conductivity, thermal resistance, thermoregulation

1 | INTRODUCTION

Much research effort has focused on understanding the ecology and behavior of marine mammal species (Johnson et al., 2009; Renouf, 1991; Shane et al., 1986). These efforts often include the attachment of electronic instruments (also called “tags”) to the animals to remotely sense their at-sea movements and diving behavior (e.g., Boehlert et al., 2001; Carter et al., 2016; Costa et al., 2010; Hart & Hyrenbach, 2009; Schreer et al., 2001; Williams et al., 2000), increasing our understanding of how these animals use the pelagic habitat in space and time (Cooke et al., 2004; Horning et al., 2019; Hussey et al., 2015; McIntyre, 2014). In addition, this technology allows us to utilize marine mammal movements for the measurement of oceanographic data (Boehlert et al., 2001; Boehme et al., 2009). However, it is important for researchers to consider how tag attachment affects the animals’ well-being (Horning et al., 2019; Walker et al., 2012). In particular, gluing instruments to the surface of animals has the potential to create long-term consequences that persist well beyond the length of the study (McMahon et al., 2011; Rosen et al., 2018; Walker et al., 2012). Studies of effects of instrumentation have primarily focused on the additional drag induced by the instrument itself (McMahon et al., 2008; Pavlov et al., 2007), which can lead to a decrease in swimming capability, altered behaviors, and/or an increase in energy required to swim and dive (Rosen et al., 2018; Skinner et al., 2012; van der Hoop et al., 2014). In an effort to reduce these possible effects, researchers are using fluid dynamics to develop smaller, high-performing instruments that minimize drag (McMahon et al., 2008; Pavlov et al., 2007). However, even relatively small, hydrodynamic instruments can affect behavior and energetics, particularly for smaller-bodied species like the northern fur seal (Rosen et al., 2018). Additionally, the effects of instrumentation have primarily been documented during the tracking period and do not consider the period after the instruments are removed (but see Field et al., 2012).

For most pinnipeds (e.g., seals, sea lions, and fur seals) electronic tags are glued with epoxy, either directly to the pelage or on an intermediate material that is then attached to the animal. Typically, the intermediate material, a neoprene patch or mesh fabric, is used to increase the attachment footprint to prolong instrument adhesion on short-haired pinnipeds (sea lions and phocid seals), whereas the longer pelage of fur seals enables researchers to glue instruments directly to the pelage with effective long-term adhesion. When the tags are retrieved for data collection, researchers either cut the top of the pelage to free the tag, or cut through the neoprene patch and leave the bottom layer of neoprene (or mesh fabric) attached to the animal. The effectiveness of the pelage as an insulator is dependent on its ability to maintain a layer of air trapped between the hairs (Kvadsheim & Aarseth, 2002). When the animal is submerged the air layer can become compromised, or in the case of short-haired pinnipeds completely replaced with water, and the insulative efficacy of the pelage may be reduced (Frisch et al., 1974; Kvadsheim et al., 2002; Scholander et al., 1950; Sharma & Liwanag, 2017). Furthermore, the hydrostatic pressure experienced at depth causes trapped air to escape from fur seal pelage during a dive (Liwanag, Berta, Costa, Abney, & Williams, 2012). Because fur seals rely exclusively on their pelage for insulation in water (Berta et al., 2006; Liwanag, Berta, Costa, Abney, & Williams, 2012; Liwanag, Berta, Costa, Budge, & Williams, 2012; Pabst et al., 1999), they are ideal study subjects for investigating the impacts of instrumentation on pelage function and recovery. Cutting the pelage for tag retrieval may allow water to penetrate to the skin, severely reducing the effectiveness of the insulating layer of pelage. Additionally, the presence of a neoprene patch glued to the pelage might affect the surrounding layer of pelage by introducing water in areas where epoxy has seeped into the pelage. These artifacts of instrumentation could affect the animals’ thermal insulation and therefore introduce metabolic costs.

The objectives of this study were to (1) investigate the physical and thermal consequences of electronic tag attachment and retrieval for the pelage of fur seals, and (2) determine the instrumentation method with the least unwanted effects on the pelage. We chose the northern fur seal (*Callorhinus ursinus*) as a model because this species relies on the densest pelage among fur seals for insulation (Liwanag, Berta, Costa, Abney, & Williams, 2012; Scheffer, 1964) and forages in high latitudes during the breeding season, where low water temperatures may lead to thermoregulatory challenges (Gentry & Holt, 1986; Kuhn, 2011; Liwanag, 2010). To assess the thermoregulatory consequences of instrumentation, we measured the thermal conductivity in water for (1) unmodified pelts, (2) pelts with a tag attached, and (3) pelts with a tag removed. We also placed pelts into a hyperbaric chamber to determine the extent to which water is able to penetrate the pelage when the animal is diving. We hypothesized that cutting the pelage would result in reduced pelt function during submergence as well as increased air loss under pressure, and that the use of neoprene for instrument attachment would help to mitigate these effects.

2 | METHODS

2.1 | Sample preparation

Pelt (pelage and skin) samples (*n* = 20) were collected postmortem from the dorsum of subadult northern fur seals during the annual subsistence harvest of the Aleut tribe of St. Paul Island, Alaska, in August 2013. All samples were stored in plastic food wrap and heavy-duty freezer bags to prevent desiccation, and were kept frozen (−20°C) until use. Samples were thawed at room temperature before use. Prior to analyses of pelt function, samples were cut into squares (approximately 13 cm × 13 cm) and any muscle or blubber tissue was removed, leaving samples with only pelage and skin layers. Before taking measurements, we cleaned the pelage using cold running water and restored the air layer to the pelage using a hairdryer on the cool setting (Liwanag, Berta, Costa, Abney, & Williams, 2012). Each sample was randomly assigned to a tag attachment treatment (see below), and measurements were first performed on the unmodified pelt before proceeding with tag attachment and removal.

2.2 | Instrument attachment and removal

We investigated two methods for attaching electronic instruments: gluing the instrument directly to the pelage (“direct method”) and by using a neoprene patch as a base that is attached to the pelage (“neoprene”). For the direct method, we mixed epoxy (Devcon 5-minute epoxy) and then applied it to the base of a research tag (Wildlife Computers HTR, approximately 5 cm × 7 cm). We placed the glued side of the tag firmly against the pelage of the sample and held it in place for at least 1 min for attachment. Tagged samples were stored at room temperature for a minimum of 3 hr to allow the epoxy to cure, prior to any measurements. Tags attached using the direct method were subsequently removed by cutting the top layer of hair, so the epoxy was no longer present in the remaining hair; typically, this resulted in the removal of all guard hairs, with a shortened layer of underhairs left behind.

For the neoprene method, we cut a patch of neoprene, slightly bigger than the tag dimensions, from wetsuits (~5 mm thick). We mixed epoxy and applied it to the base of the tag, and then attached the tag to the neoprene patch. We applied the remaining epoxy to the base of the neoprene and pressed the base of the neoprene firmly against the pelage of the sample for attachment. Tagged samples were stored at room temperature for a minimum of 3 hr to allow the epoxy to cure, prior to any measurements. Tags attached using the neoprene method were subsequently removed by cutting through the middle of the neoprene patch, such that a thinner piece of neoprene was left attached to the hair.

2.3 | Measurements

To understand the effects of tag attachment and removal on the pelts, we measured thermal function and the effects of hydrostatic pressure. Each pelt sample was randomly assigned to an attachment treatment (direct method: *n* = 10; neoprene: *n* = 10). Within each treatment group (direct and neoprene), we measured each pelt sample under three conditions: (1) unmodified, with no tag attachment (“unmodified,” control); (2) with a tag attached to the pelt, either glued directly to the pelage (“tag on fur”) or via neoprene (“tag attached”); and (3) with the tag removed, either by cutting through the pelage to remove a direct tag (“cut fur”) or by cutting through the neoprene patch (“cut patch”).

2.3.1 | Thermal properties

To quantify insulative effectiveness (i.e., thermal resistance), we measured thermal conductivity for all treatment groups in air and in water using the standard material method (Kvadsheim et al., 1994; Liwanag, Berta, Costa, Abney, & Williams, 2012; Sharma & Liwanag, 2017). For all treatments, skin thickness, dry pelage thickness, and wet pelage thickness were measured to the nearest 0.01 mm with digital calipers (ABSOLUTE Digimatic Caliper Series 500; Mitutoyo America Corp., Aurora, IL) three times on the right, posterior, and left side of pelt samples.

For “cut fur” pelts (direct method, tag removed), differences in the height of the cut and uncut pelage were measured three times on the right, posterior, and left sides for both dry and wet samples. For “cut patch” pelts (neoprene method, tag removed), the thickness of the neoprene that remained attached to the pelage was measured three times on the right, posterior, and left sides. Averages of thickness measurements were used for subsequent calculations.

Thermal conductivity measurements were conducted in a heat flux chamber [162-quart (153 L) Igloo Marine ice chest; Igloo Commercial, Katy, TX] with a lower, highly insulated compartment and an upper, chilled compartment, as described in Pearson et al. (2014). The insulated compartment contained the heat source, a sealed aluminum box through which heated water (37°C) was circulated from a constant-temperature water bath (SD07R-20; PolyScience, Niles, IL). The upper chamber was cooled with ice packs to create a steady thermal gradient. An elastomer (Plastisol vinyl; Carolina Biological Supply, Burlington, NC) was used as the standard material ($k = 0.104 \pm 0.0023$ m^{-1} °C^{-1}) because both its conductivity and pliability are similar to blubber. The standard material was placed flush against the heat source, and the sample was placed in series with the standard so that the pelage was exposed to the cold part of the chamber. For measurements in water, water from an ice bath was carefully poured into the chamber to completely submerge the pelt, without allowing water to spill over the edges of the pelt (as in Sharma & Liwanag, 2017). The standard material and sample were surrounded by insulation to ensure unidirectional heat flow through the materials.

Temperatures were measured using copper constantan (Type T) thermocouples (Physitemp Instruments, Inc., Clifton, NJ), with three thermocouples placed between the surface of the heat source and the standard material, three thermocouples between the standard material and sample, and three thermocouples on top of the pelage. If the sample was tagged, the top three thermocouples were carefully placed on the pelage surrounding the tag. If the sample had a tag removed via the direct method (“cut fur”), three thermocouples were placed on the area of cut pelage and three additional thermocouples were placed on the surrounding, uncut pelage. If the sample had a tag removed with neoprene (“cut patch”), three thermocouples were placed on the remaining neoprene patch and three additional thermocouples were placed on the pelage immediately surrounding the neoprene patch. All thermocouples were wired to a Fluke Hydra data logger (model 2625A; Fluke Inc., Everett, WA), which recorded the outputs every 6 s onto a desktop computer. Trials lasted two hours to ensure that the apparatus reached steady state, and data were analyzed for the final 30 min of each trial.

Thermal conductivity was calculated across the pelt using the Fourier equation (Kreith, 1958): $H = k \times A \times \Delta T \times L^{-1}$, where H is heat transfer (in J s^{-1}), k is thermal conductivity (in W m^{-1} $^{o}C^{-1}$), A is the area (in m^2) through which the heat is moving, ΔT is the temperature differential (in ^{o}C) across the material, and L is the thickness of the material in meters. Assuming that heat transfer is equal across both the standard material and the sample, the equations for both materials can be set equal and solved for the thermal conductivity of the sample. To quantify insulative effectiveness, thermal resistance was calculated as: $R = L/k$, where R is thermal resistance (in m^2 ^{o}C W^{-1}), L is the thickness of the material (in meters), and k is the thermal conductivity (W m^{-1} $^{o}C^{-1}$).

2.3.2 | Effects of hydrostatic pressure

To examine the effects of different electronic instrumentation methods on the functioning of pelts when under pressure, we conducted simulated dives with unmodified pelts (n = 19) and pelts with the tag removed: cut pelage (n = 10) or cut neoprene patch (n = 9), with each pelt serving as its own control (i.e., the same pelt was measured unmodified and after tag removal). We used a custom-made Plexiglas clamp, approximately 12.5 cm × 12.5

cm, with inner dimensions of 8 cm × 8 cm × 5 cm, to secure pelt samples for submergence in water (Figure 1). The bottom piece of the clamp was solid Plexiglas, and the top piece had an open center to hold water on top of the pelt (Figure 1). For the pelt samples to fit the clamp, we used hollow metal rods and a metal guide matching the clamp’s bolt locations and dimensions to pierce holes (approximately 0.7 cm in diameter) through the pelage and skin of the sample in eight peripheral locations (approximately 4.75 cm apart on each side). We then clamped the pelt sample between the two Plexiglas pieces and secured it with wingnuts to ensure a waterproof seal (Figure 1). To measure changes in water height, we secured a plastic ruler vertically to the inner part of the clamp, with the base of the ruler aligned with the top of the pelt, using an “A” clamp (Figure 1); this allowed us to use the ruler to measure the height of the water sitting on top of the pelt. We then submerged the area of the pelt (64 cm^2) in the center of the clamp by carefully pouring cold water onto the sample. We recorded the initial water level in relation to the ruler with the setup on the lab bench, before moving the setup into the hyperbaric chamber.

We placed the clamp with the submerged pelt into a hyperbaric chamber with a viewing window (Global MFG test chamber DC-300C). Once the clamp with the pelt was placed into the chamber, we recorded the water level before the chamber door was closed and again after the door was closed. We simulated dives to 120 m (nearing the maximum chamber capacity and within the range of northern fur seal dive depths; Kuhn, 2011), and water levels were recorded at pressure changes equivalent to 10 m increments on the dive descent (increasing pressure) and the dive ascent (decreasing pressure). Due to the design of the chamber, pressure changes during descent took about 10 s per 10 m increment, and pressure changes during ascent took about 30 s per 10 m increment. Visual observations of bubbles released from the pelt and the depths at which they occurred were noted. After the simulated dive, the water level was recorded at 0 m in the chamber and again on the lab bench. Any reduction in the water level was attributed to loss of air from the pelt during the dive. To determine if there was any air remaining in the pelt, we moved a blunt probe through the pelage to forcibly remove the air. We considered all air removed once there were no more bubbles produced when the probe was moved through the pelage. The final water level, after air removal, was then measured on the bench, and any further reduction in water level was used to determine the amount of air that was still trapped in the pelage after the dive was completed.

2.4 | Statistical analyses

Thermal resistance was compared using a full factorial general linear model, followed by the Tukey HSD test. The model included tagging method (direct or neoprene), pelt condition (unmodified, tag attached, or tag removed), and substrate (air or water) as main effects, along with all possible interactions, and sample ID as a random effect. The amount of air trapped in pelts during submergence at atmospheric pressure and the amount of air remaining trapped after a dive were compared among unmodified pelts (control), pelts with the pelage cut, and pelts with a cut neoprene patch using a nested ANOVA, with pelt condition nested within tagging method and sample ID as a random effect, followed by the Tukey HSD test. All statistical analyses were performed with JMP Pro 12 (SAS Institute Inc., Cary, NC). Where unspecified, $p < .05$ was considered statistically significant.

3 | RESULTS

There was a significant interaction between tagging method and pelt condition for thermal resistance ($F = 7.00$, $p = .0002$; Table 1), as well as a significant decrease in thermal resistance for pelts in water compared to air ($F = 24.1$, $p < .0001$), as would be expected from the physics. In particular, there was a significant reduction in thermal resistance for pelts with cut pelage (i.e., after a directly glued tag had been removed) in water, both at the fur in the middle of the region where the pelage had been cut for tag removal and at the uncut pelage surrounding the tag removal site, compared to most other treatment groups (Figure 2). Interestingly, the thermal resistance in water was not significantly reduced in the middle of the cut pelage relative to that of the control pelt in water; but the thermal resistance in water at the adjacent, uncut region was significantly reduced relative to the control pelt in water (Figure 2). However, the thermal resistance in water at the surrounding, uncut pelage after tag removal was not significantly different between attachment methods. Thermal resistance in air at the cut neoprene patch after tag removal was significantly higher compared to the pelage surrounding a cut neoprene patch, the intact pelage surrounding the area of cut pelage where a direct tag was removed, or the cut pelage in the middle of a direct tag removal site (Figure 2).

We observed air bubbling out of the pelage in all pelts during the ascent of simulated dives (i.e., as pressure was decreasing); the average depth at which this occurred was 56 m for unmodified pelts, 69 m for cut pelage samples, and 42 m for cut neoprene samples. Air escaped most readily from the pelts with cut pelage, almost exclusively from the cut region with only underfur present. The total amount of air trapped in the pelage of unmodified pelts during submergence at atmospheric pressure was significantly higher than the amount of air trapped in pelts with cut pelage (*F* = 41.34, *p* < .0001; Table 2), and pelts with cut neoprene trapped an intermediate amount of air that was not found to be significantly different from the amount of air trapped in unmodified pelts (Figure 3). Additionally, the amount of air that remained trapped in the pelage after a dive was significantly higher for unmodified pelts and pelts with a cut neoprene patch compared to pelts with cut pelage (*F* = 6.54, *p* = .0070; Table 2, Figure 3). On average, pelts with cut pelage allowed a greater proportion of the trapped air to escape compared with pelts with cut neoprene (Table 2), though this was not found to be statistically significant.

4 | DISCUSSION

The use of electronic tags has greatly expanded our understanding of movements and underwater behavior of marine species, as well as provided detailed information about the marine environment in which they live. As researchers strive to use the best techniques possible to limit unintended impacts of studies with electronic tags, it is necessary to identify the potential short-term (during attachment) and long-term (after attachment) consequences of this work. Previous work suggests that there are few long-term impacts on survival or mass gain, particularly for phocid species (Field et al., 2012; McMahon et al., 2008). In this study, we provide evidence that supports our hypothesis of negative thermal consequences for fur seals associated with the direct method of tag attachment when the instrument is removed, consequences that become particularly evident when the animal is submerged (Figure 2). Additionally, our results show reduced thermal resistance for cut pelage in still water at atmospheric pressure; the increase in thermal conductivity associated with convective forces during swimming and diving, along with increased hydrostatic pressure during diving, would only serve to further reduce thermal resistance in pelts with cut pelage (Fish, 2000). Reduction in thermal insulation at sea can result in long-term energetic costs associated with thermoregulation (Liwanag, 2010; Rosen & Trites, 2014), which would be incurred after instrument removal. These negative consequences can be mitigated by using a neoprene patch for instrument attachment, as the neoprene patch that remains after instrument removal prevents the pelage from being cut and maintains a similar level of thermal resistance to an unmodified pelt, both in air and in water. Although the method of using a neoprene patch and/or mesh fabric was originally devised to increase the footprint and prolong instrument adhesion on short-haired pinnipeds (Fedak et al., 1983; Jeffries et al., 1993), we suggest that researchers should use neoprene for attaching instrument to fur seals as well, to remove the need to cut the pelage.

Maintaining thermal insulation in water is critical for pinnipeds because heat loss in water occurs 25 times faster than in air (Dejours, 1987). Mammalian fur functions as an insulator by maintaining a layer of still air between the animal’s skin and the surrounding environment (Ling, 1970). Under water, this air layer becomes especially important because heat loss increases three-fold when water is able to penetrate the pelage (Kuhn & Meyer 2009; McEwan et al., 1974; Williams, 1986; Williams et al., 1988). During a dive, the air layer trapped in the pelt of fur seals becomes compressed as the animal descends; some of the air bubbles out during the ascent as the surrounding pressure decreases and the hairs lift (Liwanag, Berta, Costa, Abney, & Williams, 2012). For fur seals in particular, the loss of air from the pelt represents a loss of insulation, which can result in increased thermoregulatory costs (Liwanag, 2010; Rosen & Trites, 2014). In addition, a loss of air would reduce buoyancy, potentially increasing the energetic and biochemical costs of swimming and diving, especially during the ascending phase of a dive (Fish et al., 2002). To compensate, the animals would likely need to perform increased grooming behaviors to restore air to the pelage (Liwanag, 2010). Not only did cutting the pelage for instrument removal prevent the pelt from trapping as much air, but it also allowed almost all of the air to escape under hydrostatic pressure (Table 2, Figure 3). In contrast, the neoprene patch trapped an air layer that appeared to be similar to what remained in an unmodified pelt, thus avoiding the potential for air loss introduced by cutting the pelage.

Our laboratory-based assessment represents a conservative estimate of the effects of tag attachment and removal on fur seal pelage. In this experiment, we were able to carefully remove tags attached using the direct method, ensuring that a short layer of underfur remained on the tag removal site. In the field, without the luxury of a controlled setting, a greater amount of hair may be removed from the animal during this process, creating an even larger thermal liability. Researchers often work the epoxy into the fur during tag attachment, which would necessitate the removal of more hair upon tag retrieval. Additionally, in an effort to prolong tag attachment, researchers may use mesh as an attachment base to snag onto the hairs, requiring more hair to be cut upon retrieval (Field et al., 2012; Horning et al., 2019). In some cases, researchers are unable to retrieve the tags at all, and the tags remain attached to the animal until the pelage is molted. It is generally thought that the cut pelage will be fully restored, or the neoprene/fabric patch shed during the molt, but research on phocids has shown there can be damage to the pelt or underlying follicles (Field et al., 2012), and this has never been explicitly investigated for fur seals. In fact, for many species we know very little regarding the time it takes for the hair to fully regrow after being modified by tagging efforts (Walker et al., 2012). Future research should investigate the timing of molting and pelage regrowth following instrument retrieval for fur seals, to fully understand the long-term consequences imposed upon these animals.

As the technology has advanced, the footprint associated with an individual tag has become smaller (Horning et al., 2019). The 35 cm^2 tag tested in our study represents approximately 0.6% of the furred surface area for an adult female northern fur seal and 0.2% of the furred surface area for an adult male northern fur seal (Scheffer, 1962). However, studies may also deploy multiple tags on the same animal (e.g., Fowler et al., 2006; Robinson et al., 2012), which would increase the relative impact. In addition, a small breach in the pelage that allows water to penetrate and/or air to escape during swimming and diving will likely introduce energetic and/or behavioral costs, however small, which can accumulate over time (Kuhn, 2011; Liwanag, 2010). Because we do not know how long it takes for the pelage to be fully restored, there are potential long-term impacts that have yet to be quantified.

Overall, our results indicate that researchers should consider altering the traditional methodology for instrument attachment on fur seals, to reduce unintended effects. This study shows that the use of neoprene for instrument attachment on fur seals can help to mitigate some of the negative consequences associated with instrument retrieval, including reduced thermal function and increased loss of air from the pelage. Although the use of neoprene is not necessary to maintain adhesion of the instrument, it is a minor and relatively inexpensive modification that will likely benefit the animals in the long term.

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TABLE 1 General linear model results for thermal resistance (m^2 °C W^{-1}) of northern fur seal pelts according to tagging method (direct or neoprene), pelt condition (unmodified, tagged, or modified), and substrate (air or water).

Fixed effect	***F***	***p***
Tagging Method	7.508	.0135
Pelt Condition	9.999	<.0001
Substrate	**24.098**	**<.0001**
Tagging Method * Pelt Condition	**6.998**	**.0002**
Tagging Method * Substrate	3.186	.0767
Pelt Condition * Substrate	1.823	.1463
Tagging Method * Pelt Condition * Substrate	1.463	.2278

Note: Sample ID was included as a random effect. Significant variables not complicated by a significant higher order interaction are shown in bold.

TABLE 2 Mean (± SEM) amount of air trapped in the fur and lost during simulated dives for northern fur seal pelts that were unmodified (control) and pelts that had a glued instrument removed by cutting the fur (direct method, *n* = 10) or by cutting through a neoprene patch (*n* = 9). Amount of air was measured as the height of water displaced (mm). Each pelt served as its own unmodified control.

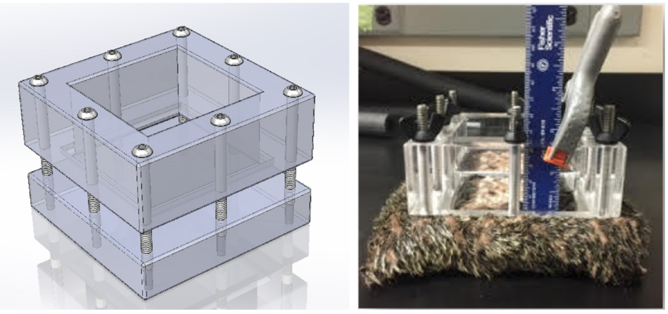
Tagging method	**Pelt condition**	**Total air trapped when submerged (mm)**	**Air lost during dive (mm)**	**Air trapped after dive (mm)**	**Proportion air lost during dive (%)**
Direct method	Unmodified	3.90 ± 0.36^{A}	1.75 ± 0.26	2.15 ± 0.27^{A}	47.7 ± 4.6
	Cut fur	1.35 ± 0.16^{B}	1.20 ± 0.15	0.15 ± 0.08^{B}	72.7 ± 7.9
Neoprene	Unmodified	4.22 ± 0.44^{A}	1.72 ± 0.26	2.50 ± 0.36^{A}	51.0 ± 7.5
	Cut neoprene	2.39 ± 0.77^{AB}	0.72 ± 0.30	1.67 ± 0.57^{A}	53.2 ± 3.4

Note: Different superscript letters represent statistically significant differences among means within a response variable.

FIGURE 1 Left: Diagram showing both pieces of the Plexiglas clamp [outer dimensions 12.5 cm × 12.5 cm × 5 cm; inner dimensions (upper piece only) 8 cm × 8 cm × 5 cm] with eight bolt locations. The pelt was secured between the two Plexiglas pieces, with bolts running through the pelt. For testing air loss in the hyperbaric chamber, water was poured into the inner area of the upper piece to submerge the pelt. Right: Side view of Plexiglas clamp, showing fur seal pelt sample secured between Plexiglas pieces with bolts and wingnuts, with a ruler (secured with an A clamp) used to measure changes in water level during simulated dives.

FIGURE 2 Thermal resistance (m^2 °C W^{-1}; mean ± *SEM*) of northern fur seal pelts, by treatment and condition, in air (white bars) and in water (black bars). With the direct method, the tag was glued directly to the pelage (tag on fur), and the pelage was later cut to remove the tag (cut fur). With the neoprene method, the tag was glued to a piece of neoprene, which was then glued to the pelage (tag attached); the neoprene was cut to remove the tag, leaving a neoprene patch behind (cut patch). Adjacent fur refers to the intact pelage surrounding the cut fur (direct method) or the pelage surrounding the cut neoprene patch (neoprene method). Different letters above the bars indicate statistically significant differences among means.

FIGURE 3 Amount of air trapped in the pelage and lost during simulated dives for northern fur seal pelts, measured as the height of water displaced (mm), under three conditions: unmodified (control), with a tag removed by cutting the pelage under the tag (cut fur, *n* = 10), and with a tag removed by cutting neoprene and leaving the neoprene patch on the pelage (neoprene, *n* = 9). Full height of each bar indicates the mean total height of the air layer trapped in the pelage prior to a 120 m simulated dive. Gray bars represent the mean amount of air lost during the ascent of a 120 m simulated dive. Black bars represent the mean amount of air remaining in the pelage after a 120 m simulated dive.



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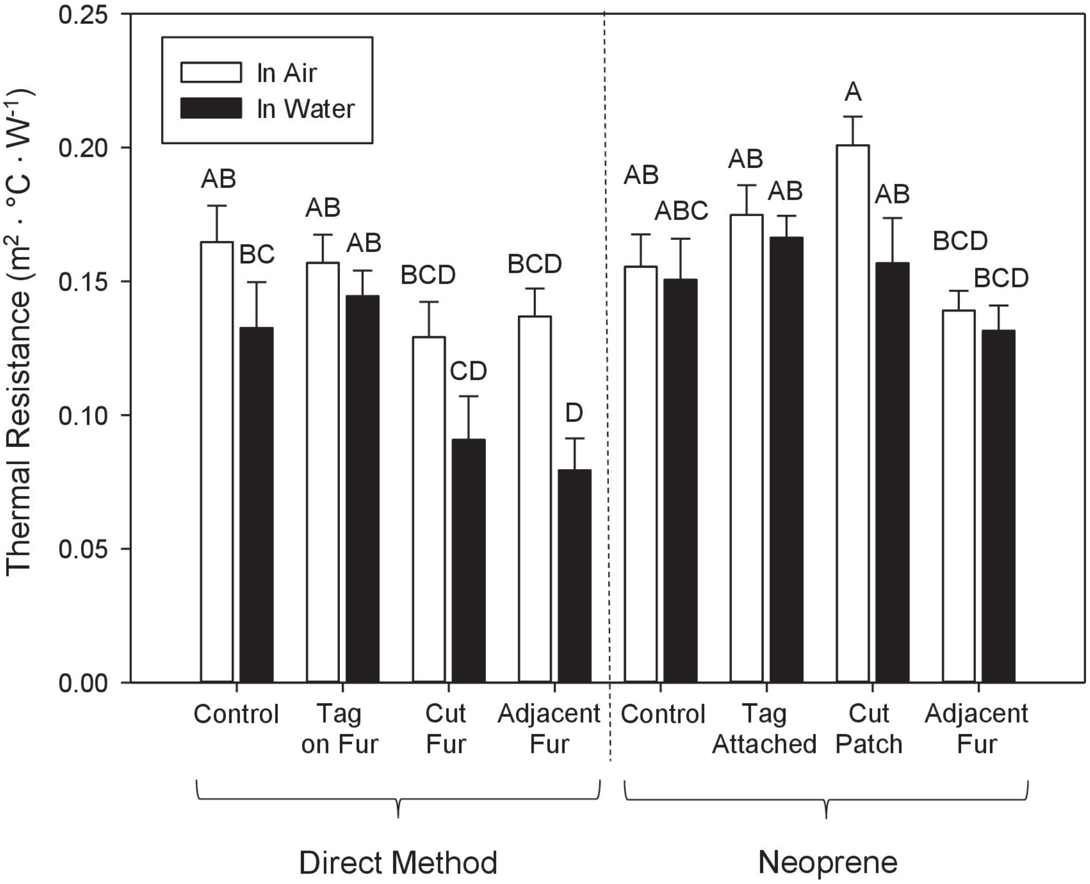

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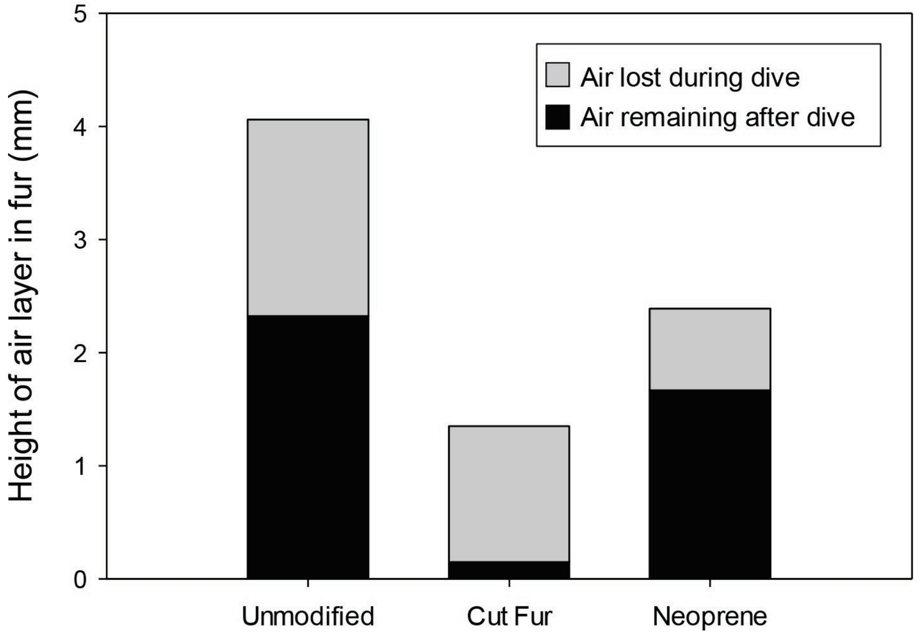

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