

# The ontogenetic changes in the thermal properties of blubber from Atlantic bottlenose dolphin *Tursiops truncatus*

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Accepted 23 February 2005

## Summary

In Atlantic bottlenose dolphins *Tursiops truncatus*, both the thickness and lipid content of blubber vary across ontogeny and across individuals of differing reproductive and nutritional status. This study investigates how these changes in blubber morphology and composition influence its thermal properties. Thermal conductivity ( $\text{W m}^{-1} \text{deg.}^{-1}$ , where deg. is  $^{\circ}\text{C}$ ) and thermal insulation ( $\text{m}^2 \text{deg. W}^{-1}$ ) of dolphin blubber were measured in individuals across an ontogenetic series (fetus through adult,  $N=36$ ), pregnant females ( $N=4$ ) and emaciated animals ( $N=5$ ). These thermal properties were determined by the simultaneous use of two common experimental approaches, the heat flux disc method and the standard material method. Thickness, lipid and water content were measured for each blubber sample. Thermal conductivity and insulation varied significantly across ontogeny. Blubber from fetuses through sub-adults was less conductive (range= $0.11\text{--}0.13\pm 0.02 \text{ W m}^{-1} \text{deg.}^{-1}$ ) than that of adults (mean= $0.18 \text{ W m}^{-1} \text{deg.}^{-1}$ ). The conductivity of blubber from pregnant females was similar to non-adult

categories, while that of emaciated animals was significantly higher ( $0.24 \pm 0.04 \text{ W m deg.}^{-1}$ ) than all other categories. Blubber from sub-adults and pregnant females had the highest insulation values while fetuses and emaciated animals had the lowest. In nutritionally dependant life history categories, changes in blubber's thermal insulation were characterized by stable blubber quality (i.e. conductivity) and increased blubber quantity (i.e. thickness). In nutritionally independent animals, blubber quantity remained stable while blubber quality varied. A final, unexpected observation was that heat flux measurements at the deep blubber surface were significantly higher than that at the superficial surface, a pattern not observed in control materials. This apparent ability to absorb heat, coupled with blubber's fatty acid composition, suggest that dolphin integument may function as a phase change material.

Key words: blubber, thermal conductivity, thermal conductance, lipid, ontogeny, dolphin, *Tursiops truncatus*, heat flux.

## Introduction

Blubber is the specialized hypodermis of cetaceans that streamlines the body, acts as a metabolic energy storage site, contributes to positive buoyancy, and provides insulation for the body core (e.g. Hamilton et al., 2004; Kipps et al., 2002; Koopman, 1998; Ling, 1974; McLellan et al., 2002; Pabst, 2000; Pabst et al., 1999a,b; Parry, 1949; Ryg et al., 1988; Worthy and Edwards, 1990). Several features of blubber, including adipocyte size, thickness and lipid content, vary significantly across ontogeny in Atlantic bottlenose dolphins *Tursiops truncatus* (Struntz et al., 2004). These morphological and compositional changes may result in differences in the insulative quality of blubber throughout development.

Insulation may be particularly important to neonatal bottlenose dolphins that are born into water, which is a fluid medium that conducts heat away from a body 25 times faster than air at the same temperature (Parry, 1949; Schmidt-

Nielsen, 1997; Scholander et al., 1950). Because a neonatal dolphin has a larger surface area to volume ratio than an adult, heat loss to the environment may be high (McLellan et al., 2002; Worthy and Edwards, 1990). Struntz et al. (2004) suggested that the blubber of neonatal dolphins may be specialized to provide enhanced insulation. To date, however, no study has measured changes in the thermal properties of blubber across an ontogenetic series.

Blubber's thermal properties have been measured across a phylogenetically diverse sample of cetaceans (Table 1). Thermal conductivity  $k$  ( $\text{W m}^{-1} \text{deg.}^{-1}$ ), a material property, is a quantitative measure of how well heat moves through a material (McNab, 2002; Schmidt-Nielsen, 1997) and is, thus, useful for comparing the insulative quality of blubber across species (Worthy and Edwards, 1990). Thermal conductance  $C$  ( $\text{W m}^{-2} \text{deg.}^{-1}$ ), which is dependent upon the material thickness, or quantity of blubber, provides an absolute value of heat

Table 1. Thermal conductivity  $k$  values for blubber from a variety of marine mammals and other substances

Species	$k$ (W m <sup>-1</sup> deg. <sup>-1</sup> ) (Reported mean)	Source	Method
Cetaceans			
<i>Balaenoptera acutorostrata</i>	0.20–0.28*	Kvadsheim et al., 1996	Standard material
<i>Balaenoptera acutorostrata</i>	0.18	Folkow and Blix, 1992	Hot plate
<i>Balaenoptera physalus</i>	0.21	Parry, 1949	Hot plate
<i>Delphinapterus leucas</i> (blubber)	0.102	Doidge, 1990	Heat flux plate
<i>Delphinapterus leucas</i> (epidermis)	0.249	Doidge, 1990	Heat flux plate
<i>Phocoena phocoena</i>	0.06	Yasui and Gaskin, 1986	Heat flux disc
<i>Phocoena phocoena</i>	0.1	Worthy and Edwards, 1990	Heat flux disc
<i>Stenella attenuata</i>	0.2	Worthy and Edwards, 1990	Heat flux disc
Pinnipeds			
<i>Mirounga leonina</i>	0.07	Bryden 1964, in Doidge, 1990	Unknown
<i>Phoca groenlandica</i>	0.18	Worthy, 1985	Heat flux disc
<i>Phoca groenlandica</i>	0.19	Kvadsheim et al., 1994	Standard material
<i>Phoca hispida</i>	0.2	Scholander et al., 1950	Hot plate
<i>Phoca vitulina</i>	0.18	Worthy, 1985	Heat flux disc
<i>Halichoerus grypus</i>	0.18	Worthy, 1985	Heat flux disc
Fatty acids			
Stearic acid (C18:0)	0.16	CRC 1967 in Doidge, 1990	Unknown
Palmitic acid (C16:0)	0.17	CRC 1967 in Doidge, 1990	Unknown
Oleic acid (C18:1)	0.23	CRC 1967 in Doidge, 1990	Unknown
Miscellaneous materials			
Air	0.024	Schmidt-Nielsen, 1997	Unknown
White pine wood	0.104	Liley, 1996	Unknown
Human fat	0.21	Hensel et al., 1973 in Doidge, 1990	Unknown
Lead	35	Schmidt-Nielsen, 1997	Unknown
Iron	80	Schmidt-Nielsen, 1997	Unknown

\*This range of values represent mean thermal conductivity across four body sites.

transfer across this thermal barrier. Conductivity can be calculated using the Fourier equation:

$$k = dQ / A(T_2 - T_1), \quad (1)$$

where  $d$  is the thickness of the blubber (m),  $Q$  is the rate of heat transfer (W),  $A$  is the surface area across which heat flows (m<sup>2</sup>), and  $(T_2 - T_1)$  is the temperature difference (°C) across the thickness of the blubber (Kreith, 1958; Kvadsheim et al., 1994; Parry, 1949; Schmidt-Nielsen, 1997; Scholander et al., 1950). Conductance can be calculated as:

$$C = H / (T_2 - T_1), \quad (2)$$

where  $H$  is heat flux (W m<sup>-2</sup>) (Kreith, 1958; Kvadsheim et al., 1994; Parry, 1949; Scholander et al., 1950; Worthy and Edwards, 1990). Another often reported value is thermal insulation  $R$  (m<sup>2</sup> deg. W<sup>-1</sup>), a measure of thermal resistance to heat flow, which is simply the inverse of thermal conductance.

Across cetacean species, blubber's thermal conductivity can vary by more than fourfold, from 0.06 W m<sup>-1</sup> deg.<sup>-1</sup> in harbor porpoises *Phocoena phocoena* to as high as 0.28 W m<sup>-1</sup> deg.<sup>-1</sup> in minke whales *Balaenoptera acutorostrata* (Table 1). These differences in blubber's quality as a conductive material are likely the result of differences in lipid and water content, which are highly variable among species. The lipid content of harbor

porpoise blubber can range between 76 and 88% (Worthy and Edwards, 1990), while that of minke whales can range between 42 and 96% lipid (Kvadsheim et al., 1996). Several studies have measured a significant inverse relationship between lipid content and conductivity as well as a strong positive relationship between conductivity and water content (Kvadsheim et al., 1996; Worthy and Edwards, 1990).

Blubber's thermal conductance, which is reliant upon both its conductive quality and quantity (i.e. thickness), also varies widely across species. For example, harbor porpoise blubber has a lower conductivity than that of a pan-tropical spotted dolphin *Stenella attenuata* (Table 1), and is twice as thick (1.50 cm and 0.77 cm, respectively; Worthy and Edwards, 1990). Spotted dolphin blubber thus has a conductance value four times greater than, or an insulative value one quarter of, harbor porpoise blubber.

In Atlantic bottlenose dolphins, blubber thickness and lipid content vary significantly throughout ontogeny. Blubber lipid content doubles between fetal (37%) and adult animals (68%) and mean blubber thickness increases over threefold between these life history categories (Struntz et al., 2004). These significant changes in quality and quantity suggest that changes in blubber's thermal properties across ontogeny may be equal to or greater than differences reported among species.

Multiple methods have been used to measure blubber's thermal conductivity and thermal conductance. Parry (1949) and Scholander et al. (1950) measured thermal conductivity by placing two pieces of blubber on either side of a hot plate and measuring the rate of energy (W) used to maintain the plate at a constant temperature. The surface area and thickness of the blubber sample, and the temperature differential between the hotplate and environment, were used to calculate thermal conductivity (Eq. 1). A more recent method of measuring thermal conductivity relies upon the use of heat flux discs. A heat flux disc is placed in series with, and usually between, a constant heat source and the blubber sample. Once steady state is achieved, Eq. 1 can be used to calculate conductivity (Doidge, 1990; Worthy and Edwards, 1990; Yasui and Gaskin, 1986). Kvadsheim et al. (1994) introduced a method to calculate conductivity that does not rely upon a direct measure of heat flux. Instead, this method uses a standard material, with a known thermal conductivity, aligned in series with a heat source and blubber sample. Once the system reaches steady state, the heat flow rate through each material must be equal (Kreith, 1958; Kvadsheim et al., 1994). The Fourier equation (Eq. 1) can then be used to calculate the thermal conductivity of blubber by setting equal the heat flow through the standard material and blubber sample. Each of these methods provides a minimum value of thermal conductivity and insulation, because they are measuring dead tissue (i.e. in the absence of convective heat transfer by blood flow) and are carried out in air, a less thermally conductive medium than water.

Each of these more recent methods has advantages and disadvantages. Heat flux discs are relatively affordable, convenient to use, and the results are directly comparable to many previous measurements of blubber's thermal properties (see Table 1). However, the placement of the disc on the surface of interest will cause a local increase in insulation, which may result in measured heat flux values that are lower than the actual values (Ducharme et al., 1990). This 'reactive error' varies with both the insulative quality of the material relative to that of the heat flux disc, and the insulative quality of the media overlying the disc (usually air or water; Ducharme et al., 1990; Frim and Ducharme, 1993). Reactive errors are

minimized when the disc's insulation is equal to or lower than that of the material being tested and when the experiments are conducted in air (Frim and Ducharme, 1993; Willis, 2003). The standard material method avoids these potential heat flux disc errors and, as reported by Kvadsheim et al. (1994), is accurate to within  $\pm 4.0\%$ . Because it is a relatively new technique, however, there are fewer studies that have measured blubber's thermal properties using this method. In the present study, both the heat flux disc and standard material methods were used simultaneously, permitting cross-calibration of these methods as well as an enhanced ability to compare results from previous studies.

The goals of this study were to (1) measure the thermal conductivity and thermal conductance of Atlantic bottlenose dolphin blubber across an ontogenetic series, (2) correlate these thermal conductivity and conductance values with measures of lipid and water content of blubber, and (3) compare the results of the heat flux disc and standard material methods to permit comparison with previous studies. Measurements were made across life history categories from fetus through adult. Pregnant females and emaciated adults were also included to investigate how blubber's thermal properties vary with the reproductive and nutritional status of the dolphin.

## Materials and methods

### *Specimens*

Blubber samples were acquired from 40 robust and 3 emaciated Atlantic bottlenose dolphins *Tursiops truncatus* Montagu 1821 that either stranded or were incidentally killed in fisheries in North Carolina and Virginia. The sample set also included one emaciated adult from Florida and one from New Jersey. Body condition was scored based upon a suite of characters defined in Cox et al. (1998). Twenty-four of the individuals used in this study were also investigated by Struntz et al. (2004). Only animals with a Smithsonian Institution Code of 1 (live stranded and died naturally or by euthanasia) or 2 (fresh dead; Geraci and Lounsbury, 1993) were used in this study. Seven life history categories were defined based upon a

Table 2. *Definitions of life history categories*

Life history category	Code	Defining characters
Fetus	1	Position <i>en utero</i> .
Neonate	2	Possessed four of the following six characters: presence of rostral hairs, floppy or folded dorsal fin, unhealed umbilicus, prominent fetal folds, floppy or folded dorsal keel, floppy or folded flukes.
Juvenile	3	Absence of neonatal characters and estimated to be less than 1 year of age based on total length ( $\leq 150$ cm).
Sub-adult	4	Absence of milk in the stomach, immature reproductive tissues, and total length ( $>150$ cm).
Adult	5	Mature reproductive tissues as indicated by obvious ovarian scars in females and the size of the testis and/or presence of sperm in males.
Pregnant female	6	Presence of a fetus.
Emaciated animal	7	Skeletal elements such as ribs, scapula, vertebral transverse processes, and/or skull prominently visible under blubber layer; atrophy of epaxial musculature and/or the nuchal fat pad.

Definitions are based on Dearolf et al. (2000) and Struntz et al. (2004).

suite of morphological characters described in Struntz et al. (2004) and Dearolf et al. (2000) (Table 2). These categories include fetus ( $N=7$ ), neonate ( $N=8$ ), juvenile ( $N=7$ ), sub-adult ( $N=8$ ), adult ( $N=6$ ), pregnant female ( $N=4$ ) and emaciated animals ( $N=5$ ).

Each animal was first weighed to the nearest kg (2000 kg capacity scale; Dillon, Brooklyn, NY, USA) and measured using a standard set of morphometrics (body and appendage lengths and body girths; see Norris, 1961). The carcass was then systematically dissected (McLellan et al., 2002) and full depth integumental samples, including epidermis, dermis and hypodermis (subsequently referred to as blubber samples), were taken from a dorsal, mid-thoracic site, just caudal to the pectoral flipper (Fig. 1). After removal, the blubber samples were notched at the dorso-cranial margin to maintain orientation and were then either vacuum sealed (Koch 1700, Kansas City, MO, USA) or wrapped in Saran wrap<sup>®</sup> and sealed in freezer bags to prevent desiccation. Samples were stored at  $-20^{\circ}\text{C}$  until analyzed. While these collection and storage methods may influence the thermal properties of blubber, they permitted standardized sample treatment within this study and comparison to previously published studies (see Table 1).

#### Lipid and water content

Lipid content was determined using procedures similar to those of Struntz et al. (2004). Briefly, an approximately 1 g full-depth blubber sample (excluding the epidermis) was weighed to the nearest 0.001 g, macerated and dried with approximately 30 g of sodium sulfate ( $\text{Na}_2\text{SO}_4$ ). The lipid was then extracted using an accelerated solvent extractor (Dionex, Salt Lake City, UT, USA). The excess solvent was evaporated (Turbo Vap II, Zymark, Hopkinton, MA, USA) and the extracted lipid was then reweighed to the nearest 0.001 g.

Water content was determined by excising an approximately 1 cm $\times$ 1 cm square through the depth of the sample and weighing it prior to and after freeze-drying (Labconco 4.5, Kansas City, MO, USA). Samples were weighed each day until the mass of the sample was stable ( $\pm 0.005$  g) for 2 consecutive days (total time=5 days).

#### Measurement of thermal properties

Blubber's thermal properties were measured using an experimental set-up that was similar to those of previous studies and that integrated both the standard material (Kvadsheim et al., 1994) and heat flux disc (e.g. Worthy and Edwards, 1990) methods. Tests were conducted in a dual

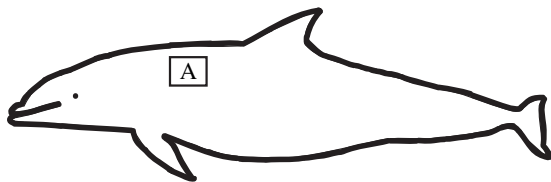


Fig. 1. A is the blubber sample site used for thermal measurements on an ontogenetic series of Atlantic bottlenose dolphins (*T. truncatus*).

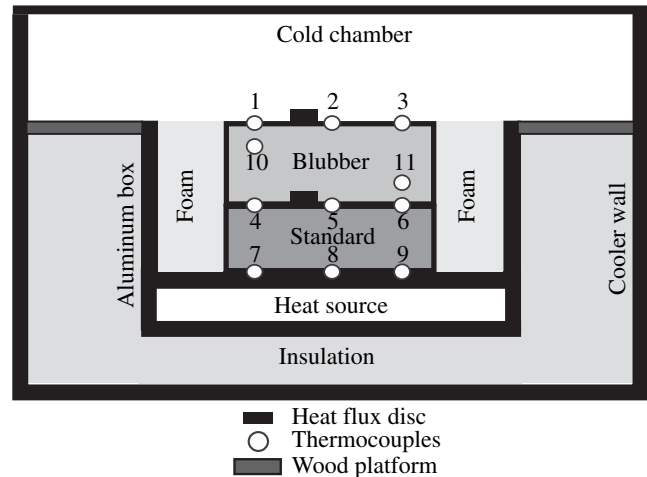


Fig. 2. Heat flux chamber showing placement of thermocouples and heat flux discs. Figure is not drawn to scale and the size of the thermocouples and heat flux discs are exaggerated for clarity.

compartment heat flux chamber (68 quart, Coleman Cooler, Albany, NY, USA) with a lower, highly insulated compartment, and an upper, chilled compartment, which were separated by a wood platform (Fig. 2). The heat source consisted of a two-part aluminum box. The lower portion was a sealed, hollow box into which heated water ( $35^{\circ}\text{C}$ ) from a water bath (RE-120 Lauda Ecoline, Brinkmann Instruments, Inc., Toronto, Ontario, Canada) was circulated to provide a constant heat source. The upper portion was an open platform upon which the standard material and blubber sample were placed. The insulated lower chamber ensured a constant water temperature and unidirectional heat flow through the standard material. The upper chamber was cooled with ice packs stacked upon the wood platform and cooled to between 16 and  $19^{\circ}\text{C}$ . This temperature was monitored with a thermocouple mounted 5 cm above the sample.

An elastomer (Plastisol vinyl, Carolina Biological Supply, Burlington, NC, USA) ( $k=0.109 \pm 0.01 \text{ W m}^{-1} \text{ deg}^{-1}$ ) was used as the standard material and was placed flush against the heated surface of the aluminum box. Depending upon the size of the available blubber sample, an approximately 4 cm $\times$ 4 cm to 15 cm $\times$ 15 cm blubber sample was used. The thickness of the blubber sample, including epidermis, dermis and hypodermis, was measured on each of its four sides (Absolute Digimatic calipers, Mitutoyo, Tylertown, MS, USA) and the mean of these values was used in thermal calculations. The blubber sample was placed in series, with the deep hypodermis in contact with the elastomer. The standard material and blubber were surrounded by insulating foam plates to ensure unidirectional heat flow through these materials (Fig. 2).

Temperatures were measured using copper-constantan (T-Type) thermocouples (Omega Engineering, Inc, Stamford, CT, USA) placed on the superficial surface of the epidermis (probes 1–3), between the blubber and the standard material (probes

4–6), and between the standard material and the surface of the heat source (probes 7–9; Fig. 2). The mean temperature of the three probes at each surface was used in the thermal calculations. In addition, to monitor temperature changes within the blubber, thermocouples 10 and 11 (Fig. 2) were placed at deep and superficial positions within the blubber sample.

Heat flux was measured directly using two heat flux discs [HA 13-18-19-P (C), Thermonetics Corp., San Diego, CA, USA]. One disc was placed on the superficial surface of the epidermis and the other was placed between the standard material and hypodermis (Fig. 2). The discs will be identified as the superficial and deep discs, respectively. The specific disc that was placed at the deep or superficial position was determined using a random schedule. To ensure complete contact between the superficial heat flux disc and the sample, thin strips of medical adhesive tape (Nexcare Advanced Holding Power, 3M, St Paul, MN, USA) were used to secure the disc. The tape was only in contact with the outer silicone edge of the disc and did not touch the thermopile surface. The superficial disc was visually inspected to ensure that it was flush against the epidermis.

All eleven thermocouples and the two heat flux discs were wired to a Fluke Hydra data logger (model 2625A, Fluke Inc., Everett, WA, USA) and the outputs in °C and mV, respectively, were recorded at 1 min intervals. These data were downloaded to a laptop computer for later analysis. The experiment was concluded once the heat flux values at the superficial and deep surfaces were stable ( $\pm 5 \text{ W m}^{-2}$ ) for 30 min (Fig. 3). Once steady state was achieved, temperature values measured at all positions varied only  $0.16 \pm 0.13^\circ\text{C}$  (mean  $\pm$  S.D.). Heat flux readings were converted into  $\text{W m}^{-2}$  using the calibration coefficient provided by the manufacturer.

The experimental set-up was calibrated using control materials (white pine wood, polystyrene foam; Dow Chemical, Midland, MI, USA) with known thermal conductivities. Additionally, experiments with the control materials were performed to determine if sample depth or surface area influenced thermal measurements.

### Statistics

For thermal conductivity, conductance and insulation values, an analysis of covariance (ANCOVA; SAS Inc., Cary, NC, USA;  $P=0.05$ ) was used with life history category and sample area as factors. Sample area was included to account for variation in the measurements that was a result of differences in the dimensions of the blubber sample. If significant differences were present, a Ryan's  $Q$ -test was used to determine which groups were different from one another. A one-way analysis of variance (ANOVA) ( $P=0.05$ ) was performed to determine if there were significant differences between life history categories in blubber thickness, lipid content, and water content. A Tukey–Kramer Honestly Significant Difference Test was used to identify significantly different groups.

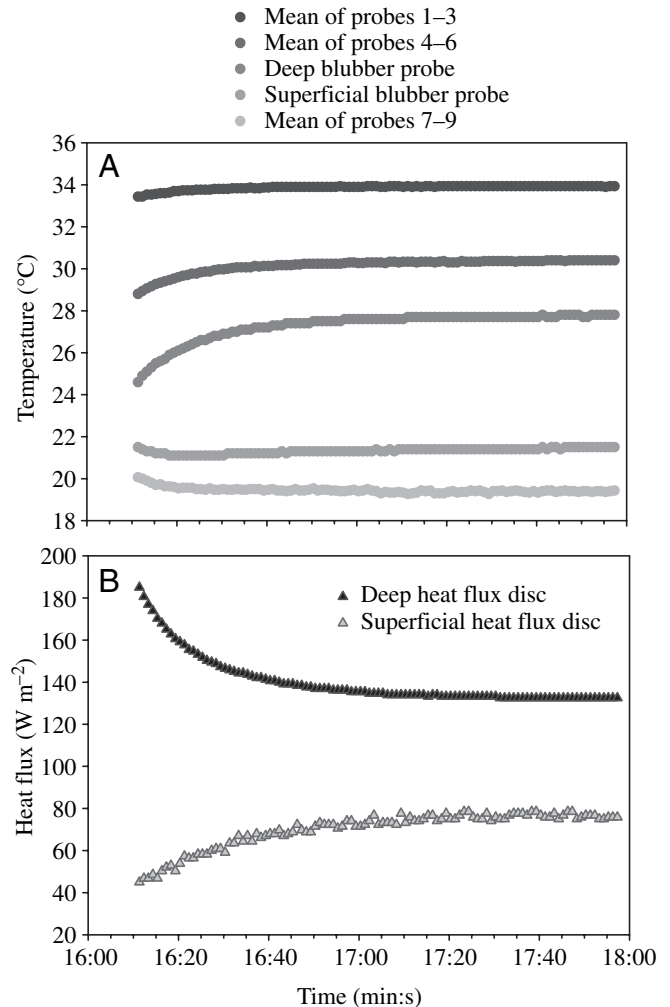


Fig. 3. (A) Example data trace of temperature measurements from one experiment. Probes 1–3 were placed at the interface between the heat source and the standard material, probes 4–6 were placed between the standard material and the deep blubber surface, and probes 7–9 were placed at the interface between the epidermis and air (see Fig. 2). (B) Example data trace of heat flux values from the deep and superficial heat flux discs from the same experiment. For both traces, only data from the final 30 min of the experiment were used in the thermal calculations.

## Results

### Morphology and composition

Blubber thickness steadily increased between fetal and adult life history categories, with maximal thickness reached in adult animals (Table 3). Fetal animals had significantly thinner blubber than all other life history categories ( $F=22.09$ ;  $P<0.001$ ), and within the fetal life history category, blubber thickness linearly increased with body length ( $r^2=0.74$ ;  $P=0.027$ ) (Fig. 4A). Blubber thicknesses of juveniles, sub-adults, adults, pregnant females and emaciated adults were not significantly different (Table 3). Mean blubber thickness of emaciated dolphins decreased by 26% compared to adults and was similar to the mean blubber thickness of neonatal and juvenile animals.

Table 3. Thermal data for blubber from each life history category in Atlantic bottlenose dolphins

	Fetus	Neonate	Juvenile	Sub-adult	Adult	Pregnant female	Emaciated adult
Blubber thickness <i>d</i> (cm)	0.49±0.001 <sup>c</sup>	1.23±0.002 <sup>b</sup>	1.61±0.001 <sup>a,b</sup>	2.0±0.003 <sup>a</sup>	2.13±0.004 <sup>a</sup>	2.05±0.004 <sup>a</sup>	1.57±0.003 <sup>a,b</sup>
Lipid mass/wet mass (%)	35.06±6.09 <sup>b,c</sup>	55.82±2.86 <sup>a,b</sup>	69.72±4.08 <sup>a</sup>	62.59±2.31 <sup>a</sup>	54.31±4.88 <sup>a,b</sup>	69.20±5.73 <sup>a</sup>	28.22±9.14 <sup>c</sup>
Water mass/wet mass (%)	50.3±3.52 <sup>a</sup>	33.06±1.97 <sup>b</sup>	29.9±0.96 <sup>b</sup>	30.16±2.35 <sup>b</sup>	32.78±1.08 <sup>b</sup>	31.66±1.57 <sup>b</sup>	59.34±6.63 <sup>a</sup>
Conductivity <i>k</i> (W m <sup>-1</sup> deg. <sup>-1</sup> )	0.12±0.01 <sup>c</sup>	0.13±0.01 <sup>c</sup>	0.12±0.01 <sup>c</sup>	0.11±0.01 <sup>c</sup>	0.18±0.02 <sup>b</sup>	0.12±0.01 <sup>c</sup>	0.24±0.04 <sup>a</sup>
Conductance <i>C</i> (W m <sup>-2</sup> deg. <sup>-1</sup> )	25.69±6.04 <sup>a</sup>	10.44±0.69 <sup>b,c</sup>	7.30±0.61 <sup>c,d</sup>	5.74±0.44 <sup>d</sup>	8.44±1.03 <sup>c,d</sup>	5.73±0.82 <sup>d</sup>	14.79±2.64 <sup>b</sup>
Insulation <i>R</i> (m <sup>2</sup> deg. W <sup>-1</sup> )	0.05±0.01 <sup>d</sup>	0.10±0.005 <sup>b,c,d</sup>	0.14±0.01 <sup>a,b</sup>	0.18±0.012 <sup>a</sup>	0.12±0.016 <sup>b,c</sup>	0.18±0.03 <sup>a</sup>	0.07±0.015 <sup>c,d</sup>

Values are means ± S.E.M.

For all measurements, life history categories with the same letter are not significantly different ( $P>0.05$ ).

Blubber lipid content increased linearly with body length in fetuses ( $r^2=0.65$ ;  $P=0.028$ ) and increased steadily from fetal through juvenile life history categories (Fig. 4B, Table 3). Although not a significant trend, lipid content declined between juvenile and adult life history categories. The blubber of pregnant females had a lipid content similar to that of juvenile animals, which represented an increase of 27% compared to adults. The blubber of emaciated adults contained significantly less lipid than all life history categories except fetuses (Table 3).

Across life history categories, blubber thickness was not a good predictor of lipid content (Fig. 5). Rather, the relationship between lipid content and blubber thickness displayed life history category-specific trends. In fetal and adult animals, lipid content increased linearly with blubber thickness ( $r^2=0.91$ ;  $P=0.0034$  and  $r^2=0.96$ ;  $P=0.0008$ , respectively). Although not a significant trend, blubber lipid content of sub-adults tended to increase with blubber thickness ( $r^2=0.54$ ;  $P=0.097$ ). Blubber thickness and lipid content were not correlated in neonatal, juvenile, or pregnant animals. There was no clear relationship between lipid content and blubber thickness in emaciated adults, however, both of these measures were highly reduced from adult values (Fig. 5, Table 3).

Water content was less variable across life history categories (Table 3). The blubber of fetuses and emaciated adults, which had significantly lower lipid contents, contained significantly more water than all other life history categories ( $F=14.84$ ;  $P<0.001$ ).

#### Comparison of standard material and heat flux methods

Both the standard material method and the heat flux method (using outputs of either the superficial or deep disc) yielded thermal conductivity values for the control materials that were similar to their commercially reported values. For polystyrene foam and white pine wood, thermal conductivity values, reported as mean ± standard error (S.E.M.), were determined to be  $0.033\pm 0.0014$  W m<sup>-1</sup> deg.<sup>-1</sup> (reported value

$0.03$  W m<sup>-1</sup> deg.<sup>-1</sup>; Dow Chemical Company) and  $0.11\pm 0.0025$  W m<sup>-1</sup> deg.<sup>-1</sup> (reported value  $0.104$  W m<sup>-1</sup> deg.<sup>-1</sup>, Liley, 1996), respectively. These values indicate a maximum error of 10% for conductivity values in the range of polystyrene foam, but error was minimized to 6% for materials with conductivity values similar to wood.

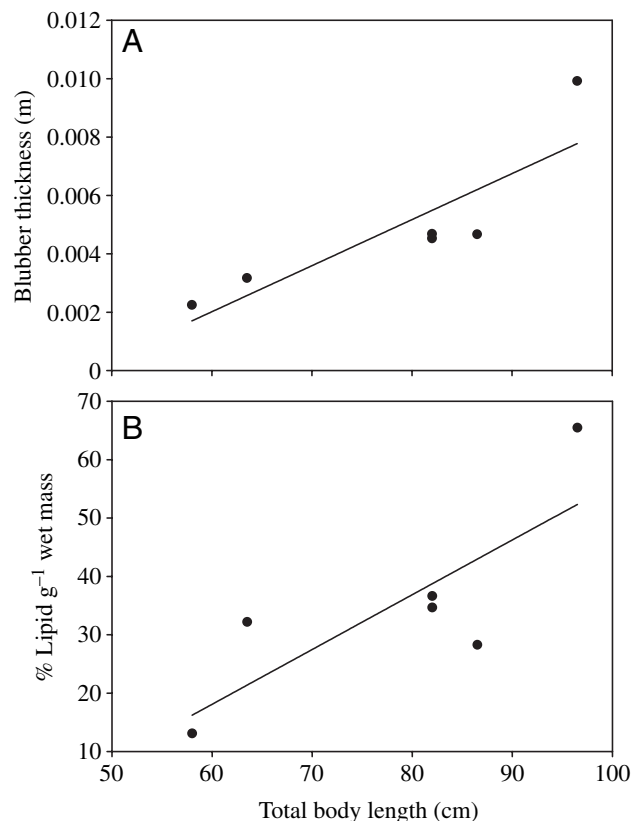


Fig. 4. Fetal blubber (A) thickness and (B) lipid content plotted against total body length in Atlantic bottlenose dolphins (*T. truncatus*).

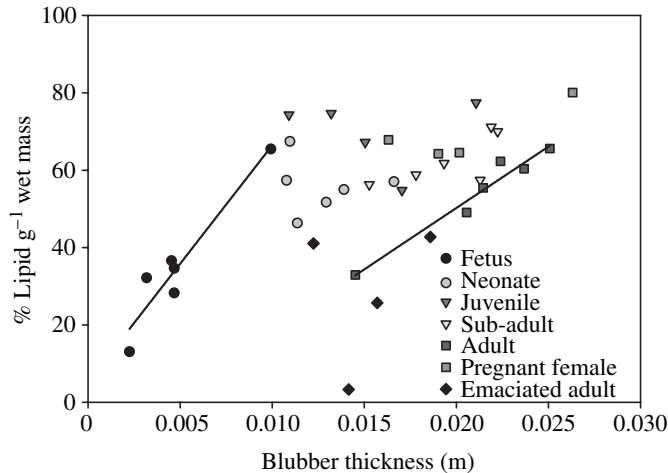


Fig. 5. Percent lipid content as a function of blubber depth in *T. truncatus*. Solid trend lines indicate life history categories where there was a significant linear relationship between lipid content and blubber thickness (fetus and adult). Trend lines are not shown for categories where there was not a significant relationship between lipid content and blubber thickness.

Blubber thermal conductivity values calculated with the standard material method and with the output of the superficial heat flux disc were similar ( $F=0.05$ ;  $P=0.81$ ) and yielded overall mean conductivity values that were within 2.0% of each other (Fig. 6A,B). The results of both of these methods though, were significantly different from the values obtained from the deep heat flux disc measurements ( $F=31.8$ ;  $P<0.001$ ) (Fig. 6C). On average, conductivity values of whole blubber calculated with the deep disc were 57% higher than those obtained with the other two methods. The differences between the deep and superficial heat flux measurements are described in more detail below.

For all subsequent analyses, the conductivity values obtained by the standard material method were used. The standard material method was chosen because recent studies (Kvadsheim et al., 1994, 1996) have extensively calibrated a similar system.

#### Thermal properties of blubber

Thermal conductivity of blubber remained similar in fetal through sub-adult life history categories but increased significantly in adult animals ( $F=6.93$ ;  $P<0.001$ ; Table 3; Fig. 6A). The conductivity of blubber from pregnant females was significantly less than that of adults while that of emaciated adults was significantly greater than all other life history categories (Table 3, Fig. 6A). There was a significant inverse relationship between thermal conductivity and lipid content ( $F=5.8$ ;  $P=0.021$ ) and a significant positive relationship between thermal conductivity and water content ( $F=4.83$ ;  $P=0.034$ ) (Fig. 7A,B).

The mean thermal insulation (inverse of conductance) between life history categories varied significantly ( $F=12.66$ ;  $P<0.001$ ; Table 3). Insulation increased from fetal through

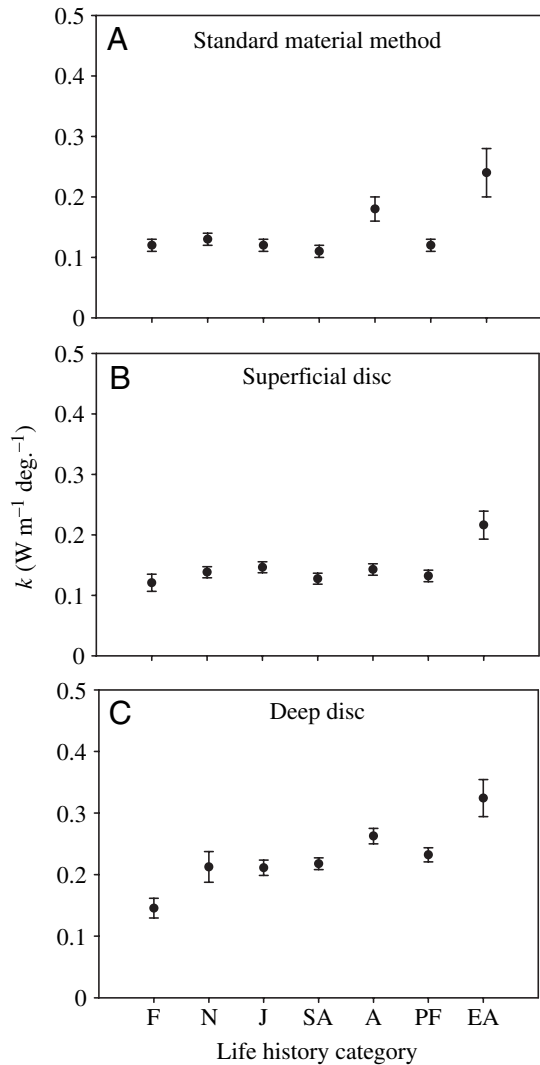


Fig. 6. Blubber thermal conductivity  $k$  values for *T. truncatus* calculated using (A) the standard material method, (B) heat flux values from the superficial disc, and (C) heat flux values from the deep disc. Life history categories are (F) fetus, (N) neonate, (J) juvenile, (SA) sub-adult, (A) adult, (PF) pregnant female and (EA) emaciated animals. Values represent mean  $\pm$  S.E.M. for each life history category.

sub-adult categories but declined in adult animals. Pregnant females had a significantly higher mean insulation value compared to fetuses, neonates, adults and emaciated adults. Emaciated animals had significantly less insulation than juveniles, sub-adults and pregnant females.

#### Differences in heat flux values across blubber thickness

For blubber samples, there was a substantial difference between heat flux values recorded by the deep and superficial heat flux discs. The deep disc consistently recorded higher values (mean of difference= $46.8 \text{ W m}^{-2}$ ; range= $9.9\text{--}87.2 \text{ W m}^{-2}$ ) than the superficial disc, and, thus, yielded thermal conductivity values that were higher than those reported for the other two methods (Fig. 6). This result is in

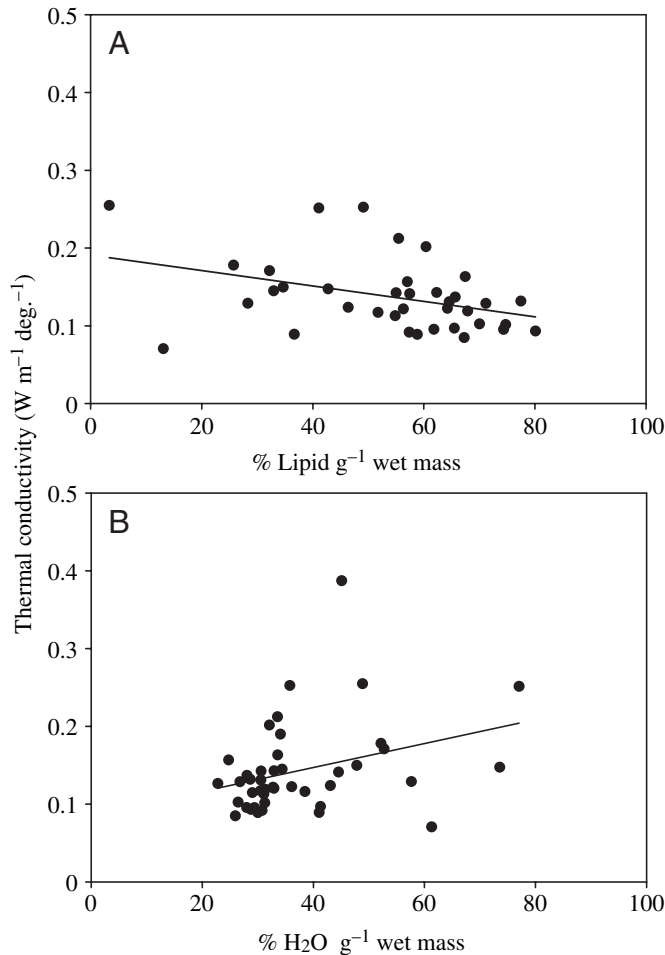


Fig. 7. (A) Blubber thermal conductivity calculated using the standard material method plotted against blubber lipid content and (B) water content in *T. truncatus*.

contrast to that for the control materials, polystyrene foam and white pine wood, where deep and superficial heat flux values were similar to each other. For the foam, the mean difference between the superficial and deep discs was 3.45 W m<sup>-2</sup> (range=3.5–6.2 W m<sup>-2</sup>) and for the wood, the mean was 10.25 W m<sup>-2</sup> (range=5.3–14.7 W m<sup>-2</sup>).

In blubber, sample thickness was significantly correlated with the difference in heat flux between the deep and superficial discs ( $F=11.91$ ;  $P=0.0014$ ) (Fig. 8). To determine if this difference was due simply to heat loss to the sides of the blubber sample, experiments using increasing layers of polystyrene foam or wood were performed. For these control materials, there was no pattern of increased heat loss with increased material depth (foam:  $F=0.85$ ;  $P=0.42$ ; wood:  $F=4.26$ ;  $P=0.28$ ) (Fig. 8). There was a weak, non-significant relationship between the surface area of the blubber sample and the heat flux difference ( $F=3.54$ ;  $P=0.067$ ). There was no relationship between the surface area of the foam sample and the difference in heat flux ( $F=5.8$ ;  $P=0.137$ ). Thus, in contrast to the control materials, there existed a substantial difference between the energy entering the deep surface of the blubber

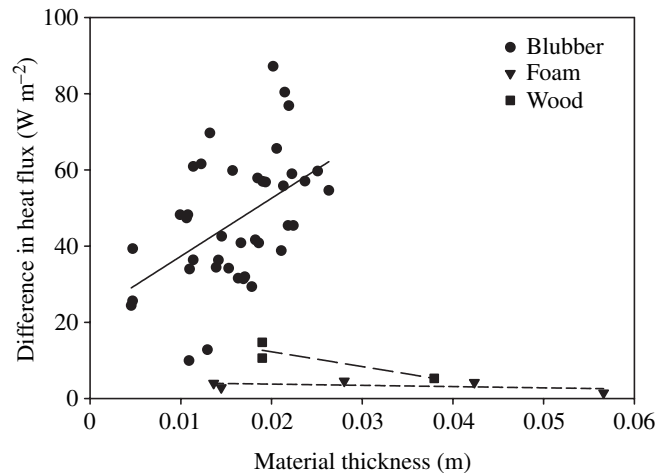


Fig. 8. The difference between the deep and superficial heat flux disc measurements plotted against the material thickness for *T. truncatus* blubber, foam and wood.

and that leaving the sample at its superficial surface per unit time. There was no relationship between the magnitude of this difference in heat flux and life history category ( $F=1.74$ ;  $P=0.14$ ), lipid content ( $F=1.49$ ;  $P=0.23$ ), or water content ( $F=0.06$ ;  $P=0.81$ ).

## Discussion

The goals of this study were to measure the thermal properties of blubber across an ontogenetic series of bottlenose dolphins and to correlate these properties with changes in blubber morphology and composition that occur across development. Specifically, it was hypothesized that neonatal dolphins may have blubber that is specialized to provide enhanced insulation compared to other life history categories. In addition, to permit comparison of these results with previously reported values, two distinct methods were used to measure blubber's thermal properties.

### *Blubber's quality, quantity, and thermal properties*

Fetal blubber underwent continuous growth throughout gestation, with both thickness and lipid content increasing rapidly. This growth pattern, similar to that observed by Struntz et al. (2004), prepares the animal for birth into water, a highly conductive medium. In contrast with pinnipeds, which are born on land, cetaceans must be fully capable of maintaining thermal homeostasis in water at the time of birth. Thus, blubber, their primary thermal barrier, must be of an appropriate thickness and quality to minimize heat loss.

Fig. 9 illustrates how blubber's thickness, lipid content, conductivity, and insulation values varied across life history categories. Between fetal and juvenile life history categories, both lipid content and blubber thickness increased. Blubber's thermal conductivity, which is independent of thickness, remained stable between these life history categories. In contrast, thermal insulation, a measure of both blubber quality



Table 4. Calculated mass-specific metabolic rates for neonatal and adult bottlenose dolphins

	Neonates	Adults
Body mass (kg)	18.23±11.4	194.35±13.92
Insulation $R$ ( $m^2 \text{ deg. } W^{-1}$ )	0.10±0.01	0.12±0.01
Surface area ( $m^2$ )*	0.308±0.13	1.759±0.16
Surface area/volume	27.48±1.27	12.48±1.92
Mass-specific metabolic rate ( $l \text{ O}_2 \text{ h}^{-1} \text{ kg}^{-1}$ )	0.301±0.017	0.111±0.02
Predicted Kleiber mass-specific metabolic rate ( $l \text{ O}_2 \text{ h}^{-1} \text{ kg}^{-1}$ )	0.331±0.01	0.182±0.005

Values are means  $\pm$  S.E.M.

\*Surface area and volume were estimated by modeling the trunk (nuchal crest to anus) as a cylinder and the tailstock (anus to fluke insertion) as a truncated cone. The head and appendages were excluded from these calculations.

(i.e. conductivity) and quantity (i.e. thickness), increased threefold. The results suggest that neonatal blubber is not specialized to provide enhanced insulation, but rather that fetal, neonatal and juvenile life history categories represent a period of continual blubber growth – blubber's thermal conductivity remains static but its thermal insulation increases as a result of increased blubber quantity.

The juvenile life history category represented a transitional period in blubber's development, in which lipid content peaked and blubber thickness values were similar to those of adults. Between juvenile and adult life history categories, blubber lipid content decreased steadily and adult blubber had a significantly higher conductivity than all non-emaciated categories. The insulation of adult blubber was also significantly less than that of sub-adults, due to a decrease in blubber quality, rather than quantity. Thus, two distinct patterns describe ontogenetic changes in the thermal properties of blubber. Dolphins that were either completely or partially dependent on their mother's milk increased blubber *quantity* but maintained similar blubber *quality*. Dolphins that were nutritionally independent maintained relatively stable blubber *quantity*, and rather varied the *quality* of the blubber layer.

Interestingly, the blubber of neonatal and juvenile animals had the same insulation value as that of adult dolphins. This result suggests that the mass-specific metabolic rates of these young animals could be higher than those of adult dolphins to compensate for the relatively higher rates of heat loss resulting from their larger surface area to volume ratios. Across mammalian species, mass-specific metabolic rates scale to body mass<sup>-0.25</sup> (Kleiber, 1961) and young animals are known to have relatively higher mass-specific metabolic rates compared to adult animals of the same species (reviewed in Lavigne et al., 1986). To estimate the relative metabolic rates of neonatal and adult dolphins in this study, the heat flux value ( $W \text{ m}^{-2}$ , from the superficial disc) for each dolphin was

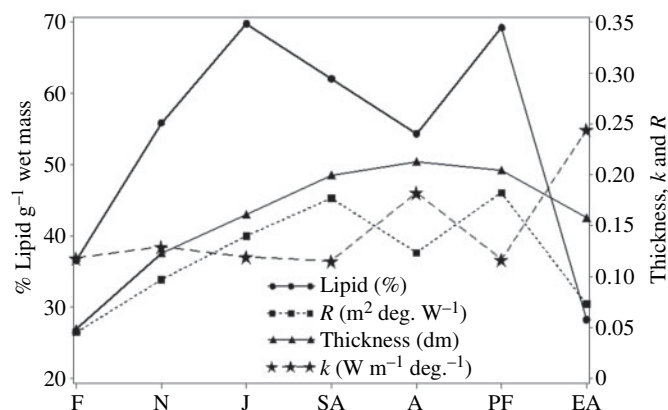


Fig. 9. Blubber thickness, lipid content, thermal conductivity  $k$  and insulation values  $R$  for *T. truncatus* plotted against life history category. Life stages as in Fig. 6.

multiplied by the surface area ( $m^2$ ) of the dolphin (see Table 4 for methods of estimating surface area). The resulting metabolic rate was then divided by the mass of the animal to obtain a mass-specific metabolic rate.

The results of these calculations indicate that the mass-specific metabolic rate of neonatal bottlenose dolphins is approximately three times higher than that of adult dolphins. This result is consistent with experimentally derived values for newborn harbor seals *Phoca vitulina* (Miller and Irving, 1975), and pups of California sea lions *Zalophus californianus* (Thompson et al., 1987) and northern fur seals *Callorhinus ursinus* (Donohue et al., 2000), which ranged between 2.4 and 4 times higher than mass-specific metabolic rates predicted by Kleiber (1961) for adults of similar body mass. Noren (2002) also found that northern elephant seal *Mirounga angustirostris* pups had metabolic rates 0.9–1.6 times those predicted by Kleiber (1961) for adult animals.

The estimated mass-specific metabolic rate for neonates in this study, though, is 9% lower, and the adult value 38% lower, than those values predicted by Kleiber (1961). The calculated adult metabolic rate is also considerably lower than the resting metabolic rate for this species ( $0.392 \pm 0.01 l \text{ O}_2 \text{ h}^{-1} \text{ kg}^{-1}$ ; measured by Williams, 1999). There are multiple reasons why the mass-specific metabolic rates measured in this study may be low. First, only the post-cranial body surface area was calculated – the appendages and head were excluded. Second, blubber thickness is not uniform across the cetacean body (e.g. Doidge, 1990; Koopman, 1998), and because these calculations were made with heat flux values at one body site, errors associated with differences in blubber thickness are likely to occur. Finally, the calculated metabolic rates in this study used heat flux values that were measured in air and on inert tissue in the absence of blood flow. These calculated metabolic rates do, however, illustrate the relative differences in the cost of endothermy in animals of varying body size as well as represent an estimated minimum metabolic rate for bottlenose dolphins.

The thermal properties of blubber were also influenced by

morphological and compositional differences associated with changing reproductive and nutritional status. Blubber from pregnant females had lipid contents similar to juveniles, and blubber thicknesses that were similar to adults, which resulted in an overall insulation value that was higher than that of adults. Blubber layers of sub-adult and pregnant females had the highest insulation values of any life history category, suggesting that these categories may represent a maximal insulation value for bottlenose dolphins.

Emaciation profoundly impacted blubber's thermal properties. The insulation value of emaciated blubber was substantially lower than that of adults. With a low blubber insulation value, emaciated animals likely experience relatively higher rates of heat loss to the environment compared to non-emaciated adults, and their metabolic rates may, thus, be higher. In the emaciated state, blubber's dual roles of providing insulation and storing metabolic energy are in direct opposition. Fasting marine mammals rely upon both lipid and protein catabolism (e.g. Noren et al., 2003; Worthy and Lavigne, 1987), but as lipid is depleted for utilization as energy, the thermal insulation of the blubber layer is compromised and, therefore, the rate of heat loss to the environment is increased. The metabolic rate of the animal may increase to compensate for the increased heat loss and in turn, more lipid is depleted to meet the increased demand. In this way, the potential for a positive feed-back loop exists and declining nutritional and health status is potentially accelerated by the opposing thermal and metabolic demands on the blubber.

Across life history categories, blubber thickness was generally not a good predictor of lipid content. For a given blubber thickness, lipid content could vary by more than 50%. In an extreme example, emaciated individuals, WAM 533 and WAM 591, had similar blubber thicknesses; however, their blubber lipid content was 41% and 3.3%, respectively. Reducing the thickness of this tissue may be detrimental to blubber's other functions such as streamlining the body. Interestingly, in the life history categories where lipid content was highly reduced (fetuses and emaciated animals), water content was significantly higher. The replacement of lipid with water may be a potential mechanism for maintaining the structural integrity of the tissue despite fluctuations in its lipid content. However, increasing the water content of blubber may compromise its thermal integrity because blubber's thermal conductivity was positively related to its water content and inversely related to its lipid content.

#### *Phylogenetic and methodological comparisons of blubber's thermal properties*

The ontogenetic changes in blubber's thermal properties observed in this study are nearly as great as those observed across a broad range of cetaceans (Table 1; note that both sample size and range of life history categories for many of these species were limited). For all non-adult bottlenose dolphins, blubber thermal conductivity values were similar to that of harbor porpoise and beluga whale *Delphinapterus*

*leucus* blubber. Thus, relatively small bodied, young dolphins possessed blubber of the same thermal quality as northern temperate to polar species. In contrast, conductivity of adult bottlenose dolphin blubber was more similar to that of large baleen whales and tropical delphinids (Table 1). However, direct comparisons of absolute thermal conductivity values may be complicated by differences in experimental methods.

This study simultaneously utilized two common methods of determining the thermal conductivity of blubber. The standard material method (Kvadsheim et al., 1994) relies upon the physical principle that under steady state conditions, the rate of heat flow through materials placed in series will be equivalent (Kreith, 1958). The use of a heat flux disc permits the direct measure of the rate of energy entering or leaving a given material (e.g. Worthy and Edwards, 1990). In this study the thermal conductivity values calculated using the standard material method and the heat flux values from the superficial disc yielded values that were very similar. In contrast, conductivity values calculated using heat flux values from the deep disc were more than 50% higher. In most previous studies that have used the heat flux method, the disc has been placed deep to the blubber (Worthy, 1991; Worthy and Edwards, 1990; Yasui and Gaskin, 1986). Thus, comparisons between values obtained with deep heat flux measurements and those obtained by either the standard material method or superficial heat flux values, must be made with caution. A discussion of the potential explanation for this pattern is presented here.

The observed difference in the rate of energy entering and leaving the surfaces of the integument, which was significantly correlated with sample thickness, may be attributable to several factors. First, heat loss to the sides of the blubber could cause a reduction in heat flux measured at the skin surface. The results of calibrations with foam and wood, however, suggest that changing the thickness of the sample did not affect the difference between superficial and deep heat flux values in these control materials. Second, the reactive error (Ducharme et al., 1990) of the superficial heat flux disc may reduce the heat flux value at this surface. However, as discussed previously, this error is expected to be low because the ratio between the insulative quality of the tissue and disc is low ( $R_{\text{blubber}}/R_{\text{heat flux disc}}$  ranged between 6.02 and 21.7; Frim and Ducharme, 1993). The maximum reactive error can be calculated using the correction factors provided by Frim and Ducharme (1993) and a maximum heat flux value (in this study maximum heat flux=142.7 W m<sup>-2</sup>). The maximum error attributable to reactive error in this study was calculated as 8 W m<sup>-2</sup>. Because the difference between the deep and superficial heat flux measurements could be as high as 87.2 W m<sup>-2</sup> and was usually near 50 W m<sup>-2</sup>, it is unlikely that the observed difference in heat flux values is the result of this source of experimental error. Instead, the difference in heat flux may be indicative of a previously undescribed property of the integument – its capacity to store heat. We hypothesize that this function may be attributable to its ability to undergo temperature dependent phase change.

Phase change materials are defined as latent thermal storage

materials that use chemical bonds to store and release heat (Suppes et al., 2003). These materials are currently being investigated for use in residential and commercial buildings as a means of increasing energy efficiency (Nikolic et al., 2002; Sari, 2003; Sari and Kaygusuz, 2001; Sari et al., 2003; Suppes et al., 2003). For a phase change material to efficiently store and release heat, four requirements must be met (Nikolic et al., 2002; Sari, 2003; Sari and Kaygusuz, 2001; Sari et al., 2003; Suppes et al., 2003) First, the melting point of the material must be in an appropriate temperature range for the desired application (e.g. near room temperature for building materials). Second, the material must have a relatively large latent heat plateau (i.e. the range of temperatures over which a material will change phase), to maximize the amount of heat that may be stored. Third, the material must not stratify in the liquid phase, which would result in an inability to properly solidify when the environmental temperature is reduced. Finally, an intermittent heat load must be present to deliver and absorb heat from the material.

There is substantial evidence to support the classification of the integument, and specifically the blubber layer, as a phase change material. First, many of the fatty acids found in blubber are classified as phase change materials and have melting points in the range of mammalian body temperatures (Sari, 2003; Sari and Kaygusuz, 2001; Sari et al., 2003; Suppes et al., 2003). Suppes et al. (2003) classified palmitic (C16:0), steric (18:0), oleic (C18:1), linoleic (C18:2), linolenic (C18:3) and arachidic (C20:0) fatty acids as excellent phase change materials. All of these fatty acids have been identified in cetacean blubber (Koopman et al., 1996). Mixtures of these fatty acids yield phase change materials with melting points between 29° and 38°C (Suppes et al., 2003), which include the range of mammalian body temperatures. Second, these fatty acids also satisfy the requirement that the material has a relatively large latent heat plateau, with latent heat values generally greater than 180 J g<sup>-1</sup> (Suppes et al., 2003). Third, their stratification in blubber may be prevented by their containment in adipocytes as well as the highly structured nature of adipocytes in the blubber tissue. Finally, cetaceans are known to have fine vascular control to their appendages and to the periphery of their body (Elsner et al., 1974; Kvadsheim and Folkow, 1997; Ling, 1974; Meagher et al., 2002; Pabst et al., 1999b; Scholander and Schevill, 1955). Intermittent heat loads could be applied to the blubber through shunting of warm blood to the blubber layer, followed by periods of vasoconstriction. Future studies are needed to fully characterize blubber's potential phase change properties as well as investigate the possible functions that may be associated with such a property.

### Conclusion

Blubber's thermal properties were influenced by morphological and compositional changes that occurred across ontogeny, and in individuals of differing reproductive and nutritional status. In nutritionally dependant life history categories, changes in blubber's thermal properties were

characterized by stable blubber quality and increased blubber quantity. In nutritionally independent animals, blubber quantity remained stable while blubber quality varied. The ontogenetic differences in thermal conductivity and thermal insulation were as large as those reported across temperate to tropical cetacean species. This study also demonstrated that thermal conductivity values determined by the standard material method and by a heat flux disc placed deep to the blubber can differ markedly. Thus, caution should be used when comparing absolute conductivity values of blubber across studies. Finally, blubber's fatty acid composition, coupled with the differences in heat flux values measured at the deep and superficial surfaces of the sample under steady state conditions, suggest that dolphin blubber may be a phase change material. The functional consequences of this previously undescribed feature of the dolphin's integument warrant further study.

We thank the Virginia Marine Science Museum, the National Marine Fisheries Service Beaufort Lab, and the UNCW Marine Mammal Stranding Program for access to specimens, and Dr John Kucklick at the National Institute for Standards and Technology in Charleston, SC for assistance with the lipid analysis. We also thank D. J. Struntz, Sue Barco, Mark Swingle, Erin Meagher, Michelle Barbieri, Ari Friedlaender, Cally Harper, Anne Harrell and Bill and Bob Dobo for their assistance. This manuscript was improved by comments from Drs Steven Kinsey, Robert Roer, Terrie Williams, and two anonymous reviewers. Specimens used in this study were collected under a National Marine Fisheries Service Letter of Authorization and UNCW IACUC permits (#2001-001 and 2003-013). This work was supported with funding from a NOAA Prescott Stranding Grant and a Sigma Xi Grants-in-Aid of Research.

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