SKIN DENSITY AND ITS INFLUENCE ON BUOYANCY IN THE MANATEE (*TRICHECHUS MANATUS LATIROSTRIS*), HARBOR PORPOISE (*PHOCOENA PHOCOENA*), AND BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*)

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ABSTRACT

This study investigated how skin contributes to buoyancy control in the Florida manatee (*Trichechus manatus latirostris*), harbor porpoise (*Phocoena phocoena*), and bottlenose dolphin (*Tursiops truncatus*). Manatees are shallow divers and control their position in the water column hydrostatically. The two cetaceans are relatively deep divers that control their buoyancy hydrodynamically. Although the cetacean skin had been hypothesized to lower total body density (e.g., Dearolf *et al.* 2000, Nowacek *et al.* 2001), its buoyant force had

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not been calculated. The density of manatee skin, and its contribution to buoyancy, was unknown. Skin densities of 27 manatees, five harbor porpoises, and five bottlenose dolphins were measured volumetrically. Skin mass and density were used to calculate buoyant force. Harbor porpoise (952 kg/m$^3$) and bottlenose dolphin (969 kg/m$^3$) skins were less dense than seawater, and added 9 and 25 N of positive buoyant force, respectively, to total body buoyancy. By contrast, manatee skin (1,121 kg/m$^3$) contributed 56 N of negative buoyant force, which equaled 70% of the negative buoyant force of their dense, pachyosteosclerotic ribs. Calculation of buoyant forces of the skeleton, skin and lungs demonstrates that the manatee is positively buoyant at the surface and negatively buoyant at depths of less than 10 m.

Key words: manatee, bottlenose dolphin, harbor porpoise, buoyancy, density, energetics, hydrodynamic, hydrostatic, skin.

Buoyancy, a positive, vertical force exerted on an object by its surrounding fluid environment, is dependant upon the volume of the object, and the difference between the density of that object and the fluid being displaced:

\[ \text{Buoyant Force} = (\rho_f - \rho_o)V_sg \]

where $\rho_f$ = the density of the fluid, $\rho_o$ = the density of the object, $V_s$ = the volume of the object, and $g$ = acceleration due to gravity (9.8 m/sec$^2$). An object that is less dense than the surrounding fluid would displace less than its weight of that fluid and experience a net upward force. Such an object would be positively buoyant. An object that has displaced exactly its weight of fluid would be neutrally buoyant, and one that displaced more than its weight of fluid would experience a net downward force and, thus, be negatively buoyant.

Animals are composed of tissues with different densities, some of which vary with depth, and it is the composition of the body that will dictate at what depths they are positively, neutrally or negatively buoyant. For example, body compartments filled with air (1.3 kg/m$^3$) and lipids (900–920 kg/m$^3$), which are both less dense than fresh (1,000 kg/m$^3$) and seawater (1,026 kg/m$^3$) (Schmidt-Nielsen 1997), would contribute to an animal’s positive buoyancy. In contrast, body compartments containing significant amounts of dense materials, such as collagen (1,120 kg/m$^3$) and bone (1,900–2,000 kg/m$^3$) (Wainwright et al. 1982) would increase the total body density and, therefore, its negative buoyancy.

This study investigated the contribution of one body compartment, the skin, to total body density in three species of marine mammals, the Florida manatee (Trichechus manatus latirostris), the harbor porpoise (Phocoena phocoena), and the bottlenose dolphin (Tursiops truncatus). The Florida manatee has been described as "the most static of aquatic vertebrates" (Domning and de Buffrenil 1991). These placid herbivores, which inhabit shallow coastal waters, spend up to 75% of their time feeding on benthic sea grasses or simply resting on the seafloor (Hartman 1979, Reynolds and Odell 1991). They can also change their position in the water column without any obvious locomotor effort (Domning and de Buffrenil 1991, Rommel and Reynolds 2000). These ob-
servations suggest that the manatee can achieve negative or neutral buoyancy at shallow depths (i.e., <8 m) (Hartman 1979). Increasing the total body density of an animal decreases both the depth at which it becomes negatively buoyant and the energy required of it to descend (Lovvorn and Jones 1991, Beck et al. 2000).

By contrast, harbor porpoises and bottlenose dolphins are highly active cetaceans (reviewed in Read 1999, Wells and Scott 1999) that can dive to depths of 100–200 m (Westgate et al. 1995, Skrovan et al. 1999, Williams et al. 2000). Although empirical data do not yet exist for harbor porpoises, bottlenose dolphins become negatively buoyant only after they reach depths of approximately 70 m (Williams et al. 2000). Decreasing total body density increases the depth at which an animal will become negatively buoyant (Taylor 1994). It has been hypothesized that the lipid-rich skin of some cetaceans helps decrease their total body density (e.g., Webb et al. 1998, Pabst et al. 1999, Dearolf et al. 2000, Nowacek et al. 2001). The density of harbor porpoise skin, for example, is reported to be 980 kg/m³ (Parry 1949), suggesting that this body compartment contributes to a porpoise's positive buoyancy.

As any marine mammal descends, its total buoyancy decreases because hydrostatic pressure reduces lung volume. There will be a 50% reduction in buoyancy within the first 10 m of a dive, as the volume of gases in the lung is compressed to 50% of its volume at the surface (Taylor 1994). Interestingly, the increase in total body density that occurs within the first 10 m of a dive does not appear sufficient to achieve negative buoyancy in some deep-diving phocid seals and cetaceans (Skrovan et al. 1999, Williams et al. 2000). These marine mammals become negatively buoyant, as evidenced by free-gliding descents, at depths between 18 and 86 m (Williams et al. 2000), whereas, the manatee can become negatively buoyant at depths of only 3–4 m (Hartman 1979). Achieving negative buoyancy at such shallow depths requires that the manatee has a high total body density and a compensating large lung volume that would allow them to rest at the surface (Taylor 1994).

Manatees have large lungs, which they often fill with air prior to diving (Scholander and Irving 1941, Hartman 1979). To compensate for the manatee's large lung volume, Domning and de Buffrenil (1991) proposed that its dense, pachyosteosclerotic rib bones increase its total body density. To date, the skeleton of the manatee, specifically its dense ribs, is the only body compartment that has been identified as contributing to negative buoyancy. Manatees, though, possess a thick skin (Sokolov 1982) that is reinforced with densely woven collagen fibers and is nearly devoid of low-density lipids (Kipps, personal observation). Manatee skin therefore differs from the skins of deep-diving phocid seals and cetaceans, which contain a lipid-rich, blubber layer (e.g., Ling 1974, Sliper 1979, Pabst et al. 1999).

In this study the density of manatee skin was measured and its contribution to total body mass was calculated. These data permit the buoyant force attributable to the skin to be determined, and compared to that of the pachyosteosclerotic ribs, using data published by Domning and de Buffrenil (1991). Similar data for harbor porpoise and bottlenose dolphin, which possess
l lipid-rich skins, were collected to compare marine mammals that control their buoyancy hydrodynamically versus hydrostatically (Taylor 1994).

**Methods**

Twenty-seven fresh manatee carcasses were used in this study. Specimens were received at the Florida Marine Research Institute's Marine Mammal Pathobiology Laboratory in St. Petersburg, Florida. Five fresh harbor porpoise and bottlenose dolphin carcasses in robust body condition were provided by the Northeast and Southeast Regional Stranding Networks, the University of North Carolina at Wilmington's Marine Mammal Stranding Network, and the Grand Manan Whale and Seabird Research Station. Standard morphometrics and total body mass were recorded on all animals. Manatee total body mass was measured with a Dyna-Link Model 7200 (Measurement Systems International, Seattle, WA) digital hanging balance to the nearest 5 lb and then converted to kilograms. Cetacean total body mass was measured using a Dillon Dynalift 2,000-kg hanging scale (Dillon, Fairmont, MN) to the nearest 0.1 kg and organ mass on an OHAUS I-10 platform scale (Ohaus Corp., Florham Park, NJ) to the nearest gram.

On a subset of five manatees, the skin (defined here as the epidermis and the dermis) was carefully dissected free from the underlying tissue and weighed with a Mettler Toledo PM30 scale (Mettler Toledo, Greifensee, Switzerland) to the nearest gram. The fluke was included in the measurements, but the skin of the flippers, which is extremely difficult to remove from the underlying tissue, was not. The skins of the harbor porpoises and bottlenose dolphins (defined here as the epidermis, dermis, and the hypodermis commonly called "blubber") were carefully dissected free from the underlying muscle tissue and weighed using an OHAUS I-10 platform scale. The masses of the dorsal fin and fluke blades were included, but the mass of the skin of the flippers was not. One harbor porpoise, VMSM 991017, was missing its dorsal fin and flukes. We therefore took the mean mass of 10 dorsal fins and five flukes from harbor porpoises of similar body size (McLellan et al., in press) and added that mean mass to the total blubber mass for this animal.

For all species, skin density measurements were determined volumetrically by first weighing an approximately 1-cm³ sample on a Mettler Toledo PB303 digital balance to the nearest milligram and then measuring its volume by the displacement of distilled water at room temperature when placed in a 20-ml volumetric cylinder. The volume was measured to the nearest tenth of a milliliter. The weight and volume for each sample was measured three times. Our precision, calculated as the percent difference between three density measurements of a single sample, was 6%.

Mid-thoracic skin density was measured from five harbor porpoises and five bottlenose dolphins (Fig. 1). For 27 manatees, skin density was measured at the dorsal umbilicus site, a position comparable to the mid-thoracic site, and compared to skin densities of the harbor porpoise and bottlenose dolphin. To determine whether manatee skin density varied in different locations, its den-
Figure 1. (A) Sample site for skin density measurements from harbor porpoise (*Phocoena phocoena*); 1 = mid-thoracic. (B) Sample site for skin density measurements from bottlenose dolphin (*Tursiops truncatus*); 1 = mid-thoracic. (C) Sample sites for skin density measurements from manatee (*Trichechus manatus latirostris*); 1 = dorsal umbilicus, 2 = lateral umbilicus, 3 = ventral umbilicus, 4 = dorsal anus, 5 = lateral anus, 6 = ventral anus. Figure adapted from Pabst *et al.* (1999) and Rommel and Reynolds (2000). Sample site 1 was used for comparison of skin densities among the three species.

Density was measured at two body positions, the umbilicus and anus (*n* = 6 animals). At each body position, skin samples were taken at three sites—dorsal, lateral, and ventral (Fig. 1). Each sample was subsampled three times, for a total of 18 skin density measurements per animal.

An unpaired, two-tailed *t*-test, assuming unequal variance, (Microsoft Excel 2000, Microsoft Corp.) was used to compare skin density measurements between male and female manatees and between manatees of differing length and weight. A Welch Modified two-sample *t*-test, assuming unequal variances
(S-PLUS 2000, Mathsoft Inc.) was used to compare density measurements among manatees, harbor porpoise, and bottlenose dolphins. A repeated measures ANOVA was used to compare skin densities among six body sites on the manatee (model used circumferential sites—dorsal, lateral, ventral—as repeated measure at each body position—umbilicus and anus—on each animal) (SAS Mixed Procedures System, SAS Institute, Inc). Measurements were considered significantly different at an alpha level of 0.05.

**Results**

At the site of the dorsal umbilicus, the skin densities of 27 manatees ranged from 1.058 to 1.189 kg/m² with a mean of 1.121 ± 42 (SD) (Table 1). Manatees ranged in length from 161 to 325 cm and in mass from 82 to 661 kg. There were no significant differences between the skin densities of male and female manatees ($t = 0.3074, P = 0.761$), nor manatees of differing mass ($t = 0.2690, P = 0.7907$) and length ($t = -0.2682, P = 0.7907$). A repeated measures ANOVA confirmed that there were no significant differences between skin densities across the six body sites chosen on the manatee (position: $F = 0.21, df = 1.5, P = 0.6656$; circumferential sites: $F = 2.60, df = 2.20, P = 0.995$) (Table 2). Mean skin density for the manatee (1,121 kg/m³) was significantly higher than those of both harbor porpoise (952 kg/m³) ($t = 7.4054, P = 0.0007$) and bottlenose dolphin (969 kg/m³) ($t = 6.1513, P = 0.0009$). There was no significant difference between the skin densities of harbor porpoises and bottlenose dolphins ($t = -1.5229, P = 0.1706$).

The skin of the harbor porpoise constituted significantly more of its total body mass (27%–36%) than the skins of either the manatee (16%–24%) ($P = 0.001$) or bottlenose dolphin (15%–27%) ($P = 0.004$) (Table 3). The density and mass of the skin were used to calculate skin volume and buoyant force in seawater. The skin of the manatee, dependent on an individual’s total body mass, contributes 5–91 N of negative buoyant force, whereas the skins of harbor porpoise and bottlenose dolphin add 5–13 N and 5–36 N of positive buoyant force, respectively (Table 3). To determine the buoyant contribution of manatee skin compared to that of the skeleton and pachyosteosclerotic ribs, an individual in this study (MNW 9824) was compared to one of a similar body size as described by Domning and de Buffrenil (1991) (Table 4). In this hybrid manatee, derived using data from both individuals, the skin contributed 17% to the total body mass, while the dry mass of the entire skeleton, contributed only 8%, and the ribs alone 4%. The skin contributed 61 N of negative buoyant force, while the pachyosteosclerotic ribs contributed 88 N and the entire skeleton 166 N of negative buoyant force. The buoyant force calculated for the entire skeleton is potentially an overestimate. The density of the manatee ribs, which are denser than other bones, was used to calculate the buoyant force of the entire skeleton because that was the only density measurement available in Domning and de Buffrenil (1991).
Table 1. Mean (± SD) length, mass, and skin density of all specimens used in this study. Skin densities of twenty-seven manatees were measured at site of dorsal umbilicus; skin densities of five harbor porpoises and five bottlenose dolphins were measured at dorsal, mid-thoracic site.

<table>
<thead>
<tr>
<th>Species</th>
<th>Trichechus manatus latirostris</th>
<th>Phocoena phocoena</th>
<th>Tursiops truncatus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex</td>
<td>Female</td>
<td>Male</td>
<td>Combined</td>
</tr>
<tr>
<td>Total length (cm)</td>
<td>244 ± 188</td>
<td>259 ± 37</td>
<td>253 ± 45</td>
</tr>
<tr>
<td>Total mass (kg)</td>
<td>323 ± 54</td>
<td>355 ± 154</td>
<td>341 ± 167</td>
</tr>
<tr>
<td>Skin density (kg/m³)</td>
<td>1,124 ± 44</td>
<td>1,119 ± 42</td>
<td>1,121 ± 42</td>
</tr>
<tr>
<td>Animal ID #</td>
<td>Dorsal umbilicus</td>
<td>Lateral umbilicus</td>
<td>Ventral umbilicus</td>
</tr>
<tr>
<td>------------</td>
<td>-----------------</td>
<td>------------------</td>
<td>------------------</td>
</tr>
<tr>
<td>MSW 0007</td>
<td>1.116</td>
<td>1.061</td>
<td>1.093</td>
</tr>
<tr>
<td>MSE 0014</td>
<td>1.189</td>
<td>1.101</td>
<td>1.073</td>
</tr>
<tr>
<td>MEC 0028</td>
<td>1.149</td>
<td>1.123</td>
<td>1.079</td>
</tr>
<tr>
<td>MSW 0030</td>
<td>1.070</td>
<td>1.116</td>
<td>1.063</td>
</tr>
<tr>
<td>MSW 0055</td>
<td>1.071</td>
<td>1.084</td>
<td>1.078</td>
</tr>
<tr>
<td>Mean ± SD</td>
<td>1.130 ± 3</td>
<td>1.086 ± 19</td>
<td>1.084 ± 19</td>
</tr>
</tbody>
</table>

Table 2. Density (kg/m³) of manatee skin as function of body position.
Table 3. Skin buoyant force for manatee, harbor porpoise, and bottlenose dolphin.

<table>
<thead>
<tr>
<th></th>
<th><em>Trichechus manatus</em></th>
<th><em>Phocoena phocoena</em></th>
<th><em>Tursiops truncatus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Total body mass (kg)</td>
<td>296 ± 160</td>
<td>37 ± 11</td>
<td>205 ± 74</td>
</tr>
<tr>
<td>Skin mass (kg)</td>
<td>53 ± 24</td>
<td>11 ± 2</td>
<td>41 ± 13</td>
</tr>
<tr>
<td>Skin as % total body mass</td>
<td>19 ± 3</td>
<td>31 ± 4</td>
<td>21 ± 4</td>
</tr>
<tr>
<td>Skin density (kg/m³)</td>
<td>1.145 ± 60</td>
<td>952 ± 19</td>
<td>969 ± 25</td>
</tr>
<tr>
<td>Skin volume (m³)</td>
<td>0.046 ± 0.02</td>
<td>0.0117 ± 0.002</td>
<td>0.0420 ± 0.014</td>
</tr>
<tr>
<td>Skin buoyant force (N)</td>
<td>−56 ± 34</td>
<td>9 ± 3</td>
<td>25 ± 12</td>
</tr>
</tbody>
</table>

Discussion

Taylor (1994) described two extreme methods by which marine tetrapods control their buoyancy—hydrostatic and hydrodynamic. Animals that use hydrostatic mechanisms rely primarily upon their body density to control their position in the water column and are generally slow swimmers and shallow divers. These animals tend to have large lung volumes and heavy bones that maximize their air volume and total body density, respectively (Taylor 1994). Buoyancy regulation in these animals depends upon pressure changes that occur within the first 10 m of depth and the consequent density changes that occur within their large, air-filled lungs. These animals can achieve neutral or negative buoyancy at relatively shallow depths. In contrast, animals that control their position in the water column hydrodynamically, by exerting thrust forces on the fluid surrounding their bodies (Alexander 1990, Taylor 1994), tend to be rapid swimmers and deep divers. These animals tend to have small lungs, light bones, and lipid-rich tissues that minimize their lung volume and total body density. These animals are less influenced by changes in density in their relatively small lungs with changes in depth and, thus, have a greater depth at which they reach neutral or negative buoyancy. Most recent studies on buoyancy control mechanisms in marine mammals have focused on phocid seals and cetaceans that use hydrodynamic methods for controlling their position in the water column (Webb et al. 1998, Skrovan et al. 1999, Beck et al. 2000, Williams et al. 2000).

The skins of both harbor porpoise (mean = 952 kg/m³) and bottlenose dolphin (mean = 969 kg/m³) investigated in this study, were indeed less dense than both fresh and seawater and contribute 5–13 N and 5–36 N of positive buoyant force, respectively. Skrovan et al. (1999) found that the net buoyant force for a 177-kg bottlenose dolphin near the surface was +24.3 N. The results of this study suggest that for an animal of similar size (205 kg), over 86% of the net buoyant force of the bottlenose dolphin may be attributable to their lipid-rich skin.

The influence of a lipid-rich skin on diving behavior has recently been demonstrated for two species of phocid seals. Webb et al. (1998) discovered that northern elephant seals (*Mirounga angustirostris*), with naturally or artificially enhanced buoyancy, descended at slower rates than less-buoyant seals,
<table>
<thead>
<tr>
<th>Body compartment</th>
<th>Animal ID#</th>
<th>Total body mass (kg)</th>
<th>Compartment mass (kg)</th>
<th>% of total body mass</th>
<th>Density (kg/m³)</th>
<th>Volume (m³)</th>
<th>Buoyant force (N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>pachyosteosclerotic ribs</td>
<td>527.901a</td>
<td>454</td>
<td>18.4</td>
<td>4</td>
<td>2.020</td>
<td>0.009</td>
<td>-88</td>
</tr>
<tr>
<td>skeleton</td>
<td>527.901a</td>
<td>454</td>
<td>34.9</td>
<td>8</td>
<td>2.020b</td>
<td>0.017</td>
<td>-166</td>
</tr>
<tr>
<td>skin</td>
<td>MNW 9824</td>
<td>446</td>
<td>76.2</td>
<td>17</td>
<td>1.121c</td>
<td>0.066</td>
<td>-61</td>
</tr>
</tbody>
</table>

a Data from single animal studied in Domning and de Buffrenil (1991) where body size was comparable to individual used in this study.

b Density of ribs used for entire skeleton.

c Skin density was mean for all individuals used in this study.
especially during the passive drift portions of their dives. During lean periods, adult gray seals (*Halichoerus grypus*) are 48% less buoyant, and descend at significantly greater rates than during more robust periods (Beck *et al.* 2000). Clearly, these changes in lipid stores, which affect diving behavior, are doing so by changing an animal's total body density.

To overcome positive buoyancy, many cetaceans and phocids must actively swim to depths at which they become negatively buoyant (but see, for example, Beck *et al.* 2000). Bottlenose dolphins, elephant seals, and Weddell seals (*Leptonychotes weddellii*) become negatively buoyant at depths greater than 70 m, at which point they begin gliding (Williams *et al.* 2000). Gliding occurs when the negative buoyant forces are greater than or equal to the drag forces on the body (Skrovan *et al.* 1999, Williams *et al.* 2000). Gliding increases the depth and duration that can be achieved by deep-diving marine mammals by reducing their metabolic energy consumption (Williams *et al.* 2000). For example, the energy saved by gliding increased a Weddell seal's dive time by 38%, which increased its foraging time at depth.

To achieve similar energy savings while foraging, manatees must become neutrally or negatively buoyant at shallow depths, usually less than 3–4 m (Hartman 1979). In contrast to the skins of the marine mammals previously discussed, manatee skin is nearly devoid of lipid (Kipps, personal observation). Its mean density is 1,121 kg/m³ in the dorsal umbilicus region, which is greater than both fresh and seawater. Due to its large contribution to total body mass, the skin contributes between 5 and 91 N of negative buoyant force (Fig. 2).

How does the manatee skin's contribution to negative buoyancy compare to that of its dense, pachyosteosclerotic ribs? The manatee skin accounted for a larger percentage of the total body mass (17%) than the dry skeleton (including the ribs) (8%) and the ribs alone (4%) (skeletal data from Domning and de Buffrenil 1991). Because of its lower density, though, the skin contributes less negative buoyant force (−62 N) than the dense pachyosteosclerotic ribs (−89 N) and the entire skeleton (−166 N).

The manatee skin, together with its entire skeleton, accounts for a total of
Table 5. Buoyant force attributable to fully inflated lungs of manatee. Lung volume data from Bergey and Baier (1987). The air density used in this study was 1.3 kg/m$^3$ (Schmidt-Nielsen 1997).

| Animal ID # | Sex | Total body mass (kg) | Lung volume at surface (m$^3$) | Buoyant force (N) | Lung volume at 10 m$^3$ | Buoyant force at 10 m
<table>
<thead>
<tr>
<th></th>
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</thead>
<tbody>
<tr>
<td>No. 2</td>
<td>F</td>
<td>14</td>
<td>0.00166</td>
<td>17</td>
<td>0.00083</td>
<td>8</td>
</tr>
<tr>
<td>No. 3</td>
<td>F</td>
<td>266</td>
<td>0.0237</td>
<td>238</td>
<td>0.01185</td>
<td>119</td>
</tr>
<tr>
<td>No. 4</td>
<td>F</td>
<td>174</td>
<td>0.00747</td>
<td>75</td>
<td>0.003735</td>
<td>38</td>
</tr>
<tr>
<td>No. 5</td>
<td>M</td>
<td>297</td>
<td>0.0231</td>
<td>232</td>
<td>0.01155</td>
<td>116</td>
</tr>
<tr>
<td>No. 6</td>
<td>M</td>
<td>628$^a$</td>
<td>0.0402</td>
<td>404</td>
<td>0.0201</td>
<td>202</td>
</tr>
</tbody>
</table>

$^a$ Calculated from total body length following Odell et al. (1981).

$^b$ Calculated from the equation $V_D = V_s (1 + 0.1 h)$ where $V_D =$ volume at depth, $V_s =$ volume at surface and $h =$ depth in meters in Skrovan et al. (1999).

228 N of negative buoyant force. The positive buoyant force of the lungs must be able to compensate for the sinking forces of these body compartments. The buoyant force of manatee lungs was calculated using lung volume data from Bergey and Baier (1987). The lungs of a manatee (of a similar body size to the animals used when calculating the buoyant force of the skeleton and skin) add between 232 and 404 N of positive buoyancy (Table 5). The positive buoyancy of the lungs is, thus, sufficient to stabilize the manatee at the surface, but at 10 m the buoyant force of the lungs will decrease by half (116–202 N). For a manatee with an intermediate lung buoyancy of 318 N, the lung volume will need to decrease by approximately 30% to overcome the 228 N of negative buoyancy from the skin and skeleton. This hypothetical manatee will, thus, be negatively buoyant at 4 m when considering the lungs, skin, and skeleton alone. These calculations were performed using the density of seawater; in freshwater, manatees would become negatively buoyant at even shallower depths. These measurements do not account for the additional negative buoyancy of the muscle, most organs, and gut contents, but conversely, the positive buoyant forces of the subcutaneous fat deposits and the gaseous intestine are not included.

These results suggest that the skins of both the harbor porpoise and bottlenose dolphin contribute to their positive buoyancy. In contrast, manatee skin contributes 70% as much negative buoyant force as their pachyosteo-sclerotic ribs, a morphological feature that has been identified as an adaptation to increase total body density (Dorning and de Buffrenil 1991). To the best of our knowledge, this is the first report of the skin of a marine mammal contributing to negative buoyancy.

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LITERATURE CITED


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