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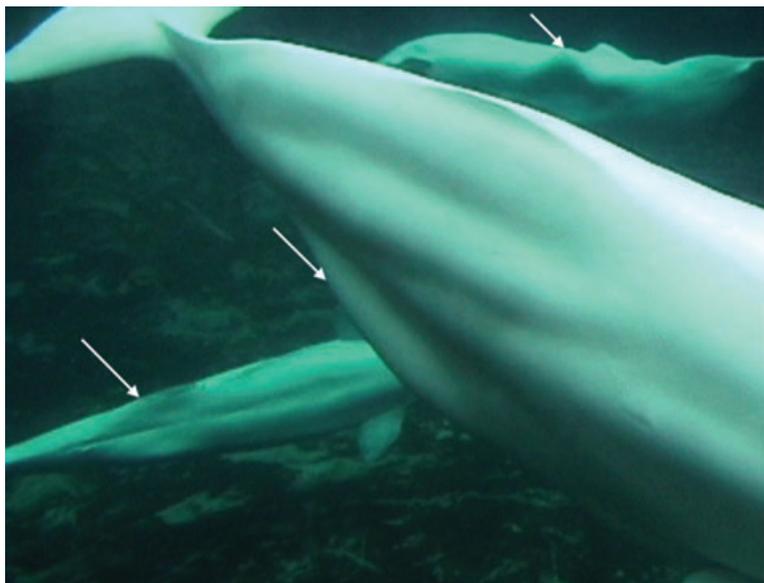
## Abdominal fat pads act as control surfaces in lieu of dorsal fins in the beluga (*Delphinapterus*)

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Almost all cetaceans have a dorsal fin, which acts as a surface to control attitude and prevent roll, yaw, and side-slip (Fish 2002, 2004). Among odontocetes, only right whale dolphins (*Lissodelphis*), the finless porpoise (*Neophocaena*), and both members of Monodontidae, the beluga or white whale (*Delphinapterus*) and narwhal (*Monodon*), lack a dorsal fin. Both *Delphinapterus* (whose generic name refers to its absence of a fin) and *Monodon* possess, like *Neophocaena*, an irregular, notched dorsal ridge running along the caudal portion of the back (Struthers 1895, Brodie 1989, Hay and Mansfield 1989), but the low (4–5 cm high) dorsal ridge of monodontids (also called a cuticular crest by Kleinenberg *et al.* 1964) appears insufficiently large to act as a suitable hydrodynamic control surface on these 4–5 m long odontocetes.

Based on kinematic analysis of locomotion in captive and wild beluga whales and dissection of abdominal musculature of *Delphinapterus*, we present a previously undescribed morphological feature that we believe allows belugas to enhance vertical stabilization and especially to control roll during turns and during swimming while in a partially rotated or wholly inverted position. This stabilization involves a pair of distinct fat (blubber) pads running longitudinally along the ventrolateral aspect of the abdomen, parallel to the dorsal ridge. These pads form large, elevated ridges that can be seen clearly (Fig. 1–3) in various views of *Delphinapterus*. The ventrolateral fat pads are in line with the pectoral flippers and extend from just caudal of the axilla to the level of the pelvic bones. The abdominal fat comprising the elevated ridges does not consist of discrete, paired bodies of isolated, encapsulated adipose tissue (as in the mandibular fat body of odontocetes). Rather, it involves a pair of unusually thick, longitudinal blubber deposits; it entails more than mere bulging of uniformly thick abdominal blubber. We contend that during some swimming maneuvers (inverted swimming, longitudinal rolls, and whole body turns), the fat pads formed by these markedly thickened blubber deposits are tensed and raised by abdominal muscles to form a pair of large, rounded erect structures (elevated 10–14 cm higher than the adjacent trunk and tailstock; 107–119 cm in length and 8–12 cm in width, averaging roughly 128 cm<sup>2</sup> in area), often including a focal bulging of the ridges near their caudal terminus which results in fin-like protuberances surrounding a crater-like, semicircular depression on the ventral surface of the animal (estimated at up to 16 cm deep; Fig. 3). Based on our qualitative and quantitative kinematic

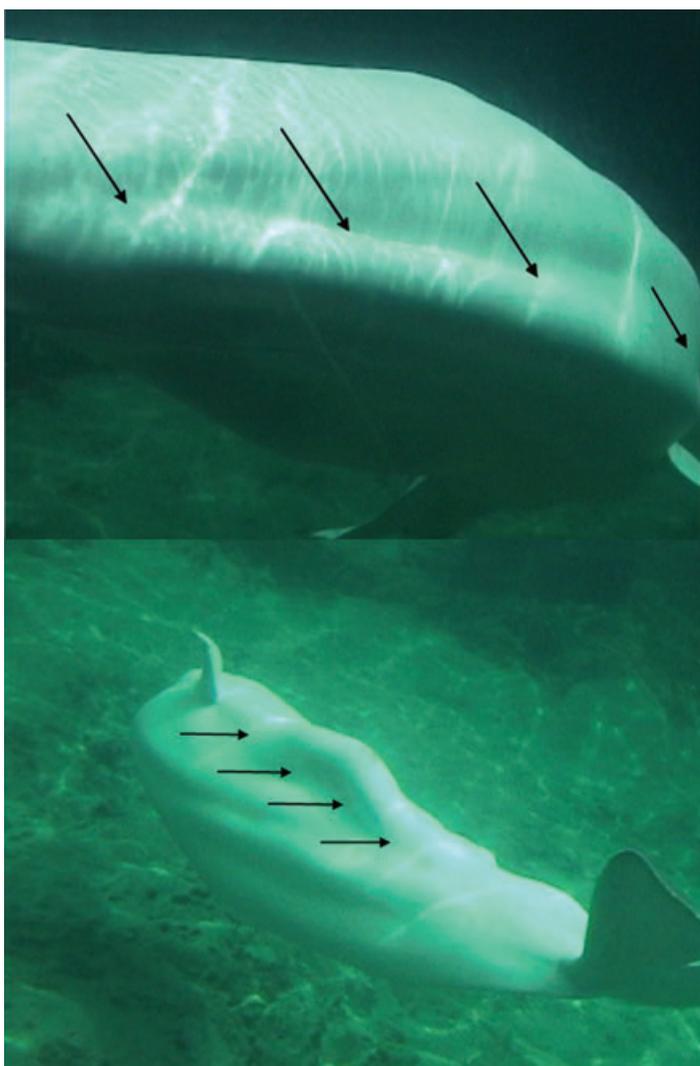
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*Figure 1.* Three views of the ventrolateral abdominal fat pads in captive *Delphinapterus*. The pads can be seen in lateral view (ventral to and in line with the dorsal ridge) in the animal in the foreground, in full ventral view in the lower left background, and inverted and fully distorted (with fin-like protuberances) as the whale in the upper right background swims upside down.

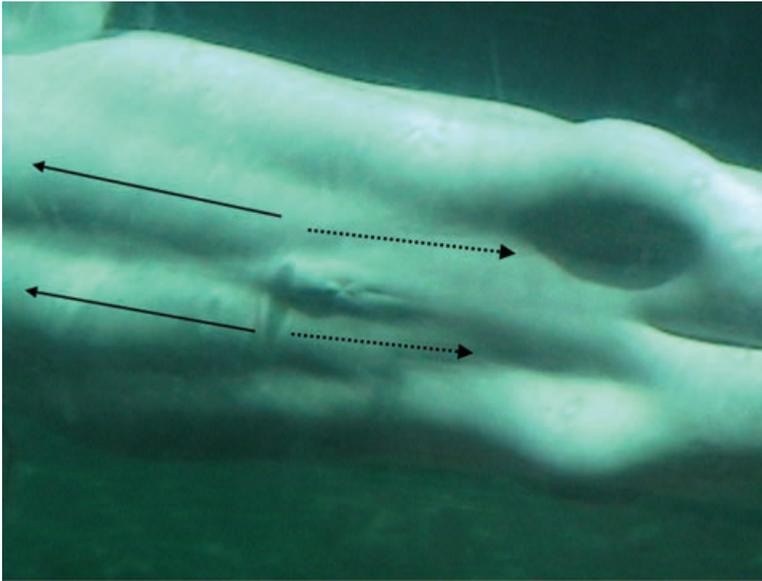
analysis, we suggest that these fat pads, when elevated, form a pair of prominent vertical stabilizers that (perhaps in conjunction with the dorsal ridge) enhance an animal's ability to control heading and limit roll.

Our kinematic analysis involved digitally recorded sequences (323 min of total footage recorded from 2005 to 2010) of nine captive adult belugas at three sites (the Georgia Aquarium in Atlanta, Georgia; Mystic Aquarium in Mystic, Connecticut; and Vancouver Aquarium in Vancouver, British Columbia), plus 36 min of videotaped sequences of an undetermined number of wild beluga whales observed off Point Lay and Point Barrow, Alaska. The captive belugas were recorded engaging in typical locomotion, resting, and other normal activities, alone and in groups of 2–4 animals (male and female), through clear viewing windows, and in some cases from above the surface of the water, almost always (>95% of sequences) during daylight hours when aquarium visitors were present. For some recordings a handheld camera (a Sony DCR-SX63 or JVC GR-D270U, with up to 60 $\times$  optical and 2,000 $\times$  digital zoom) was moved along with animals; for other recordings the camera was fixed to a tripod placed in front of the viewing window behind which animals swam, with a fixed or variable focal length to capture locomotor behaviors at different distances. Wild animals were recorded from the ice edge at distances of 3–30 m as they swam and surfaced in polynyas and leads in shorefast ice. Digital sequences (total  $n = 128$ , ranging from 3 s to 40 s for captive animals and  $n = 17$ , 2–29 s for wild belugas) were



*Figure 2.* Ventrolateral abdominal fat pads, with dorsal margin indicated by arrows: (top) lateral view, pads in relaxed position; (bottom) oblique lateral view, with fat pads extended, generating protuberances, on beluga rotated left 90°.

analyzed on a Dell Optiplex 745 or Dimension D10 computer using Kinovea 0.8.15 video chronometer and motion analysis software. Sequences were analyzed mainly for amounts of time spent in various postures (*e.g.*, rolls) and concomitant presence or absence of elevated fat pads (Fig. 4). Other kinematic variables include locomotor velocity, turning radius, turning and rolling rate, pitch, and roll angle, all tracked relative to observational references (fixed or on subject's body), and with playback at 10%–100% of original speed or frame-by-frame, synchronized to time coding.



*Figure 3.* Ventral view, showing funnel-like ventral concavity between abdominal fat pads fully extended to create fin-like protuberances. Note outlines of paired, contracted muscles, likely rectus abdominis to left, cranial to umbilicus, and pyrimidalis (dashed arrows) to right of umbilicus.

The software allowed for magnification, plane perspective, tracking of path distance, and velocity measurement. These were applied to whole animals and used to detect and measure elevation of the abdominal fat pads. Unless specified, all data include sequences of captive and wild animals analyzed together; ANOVAs and *t*-tests of kinematic data from captive *vs.* wild animals revealed no statistically significant differences.

Analysis (Fig. 4) revealed that the ventrolateral fat pads are not consistently present in footage of captive and wild animals; however, they are clearly apparent in 36.7% of all sequences showing normal forward locomotion (swimming in normal upright position, with dorsum of whale pointing toward water surface) and in 86.3% of all locomotor sequences in which the animal had rotated along its longitudinal axis. For sequences in which the animals were totally inverted during swimming (surprisingly common:  $n = 56$  or 44.2% of all swimming sequences of captive animals), with the ventral surface pointing upward ( $180^\circ$  roll), the ventrolateral fat pads were clearly visible in 96.1% of these sequences. The fat pads were frequently observed (89.1% of total sequences) in locomotion during which a whale made a “tight” turn, which we define as having a turning radius less than half the animal’s body length (turning radius measured directly from video sequence using known body length and/or external landmarks). Such turns were common (90.6% of all turns) when the whales were swimming in a laterally rolled position, and in all such cases the whale’s dorsum is on the “outside” of the turn (*i.e.*, ventral surface facing into turn). Most tight turns observed in captivity occurred along a barrier (a wall or window of an enclosure);

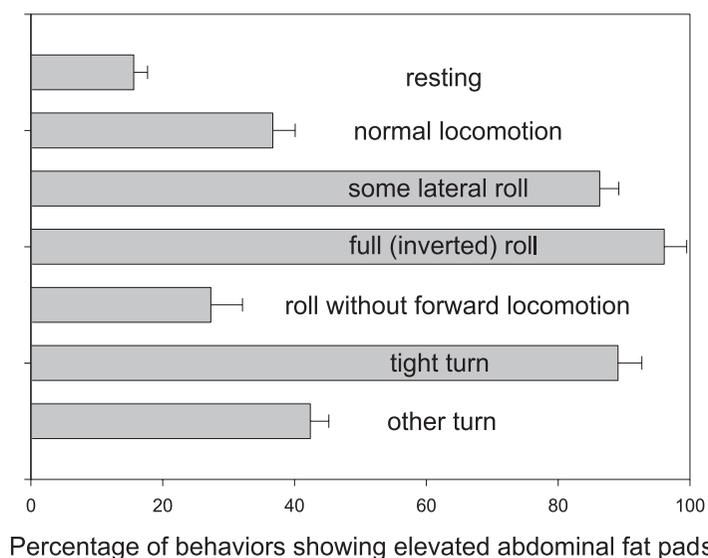


Figure 4. Results of the kinematic analysis of captive and wild belugas showing relation between abdominal fat pad elevation and different behavioral patterns and postures. Tight turns involve turning radius measured at less than one half body length.

they were seen only twice, at the ice edge, in wild animals. Elevation of the fat pads from their normal (nondeployed) condition was not found to have any significant correlation with turning velocity, turning radius, roll rate, or pitch.

The fat pads were visible but prominently elevated during only 15.6% of sequences when belugas were deemed “resting” (*i.e.*, not making forward progress; Fig. 4). During movements that involved obvious lateral rolls but no forward swimming, elevated fat pads were visible in 27.3% of sequences. Elevation of the paired ventrolateral pads could be sustained for long durations (in one extended sequence, for 9.5 min or 566 s). Elevated pads were visible during ascents, descents, and level swimming at all levels of the water column. Additional results of the kinematic analysis are that: (1) the pads are either clearly apparent (prominently elevated) or not, with no instances visible in videotaped sequences in which fat pads are partially elevated; (2) there are no sequences in which a fat pad is visible on only one side of the body (*i.e.*, one of the pair); (3) the presence or absence of the fat pads during locomotion is independent of a whale’s forward velocity (20–210 cm/s, with bursts to 365 cm/s), as measured by stationary landmarks in the pool or in front of the viewing window, controlling for the plane of the camera; (4) the presence or absence of fat pads is independent of the size or sex of a beluga; and (5) the fat pads were slightly more evident in captivity when more than one beluga was present in the enclosure ( $n = 95$ , or 74% of sequences, in which pads were visible) as opposed to alone ( $n = 33$ , or 26%), possibly due to the fact that these situations yielded interactions between animals that involved more swimming and turning than resting.

Table 1. Mean blubber thickness (cm) in adult specimens (excluding skin; all measurements taken post mortem; samples taken at genital slit, midway between umbilicus and anus).

Species	<i>n</i>	Lateral (mean $\pm$ SD)	Ventral (mean $\pm$ SD)
<i>Delphinapterus leucas</i>	30	4.71 $\pm$ 1.29	10.80 $\pm$ 1.93
<i>Monodon monoceros</i>	4	4.39 $\pm$ 1.86	6.17 $\pm$ 2.65
<i>Globicephala melas</i>	30	3.25 $\pm$ 0.41	3.36 $\pm$ 0.52
<i>Grampus griseus</i>	6	3.12 $\pm$ 0.35	3.62 $\pm$ 0.41
<i>Tursiops truncatus</i>	30	1.66 $\pm$ 0.24	1.58 $\pm$ 0.30
<i>Lagenorhynchus acutus</i>	30	1.74 $\pm$ 0.28	1.94 $\pm$ 0.33
<i>Delphinus delphis</i>	30	1.72 $\pm$ 0.33	1.85 $\pm$ 0.39
<i>Phocoena phocoena</i>	30	1.16 $\pm$ 0.28	1.19 $\pm$ 0.34

Because the elevated fat pads can be seen in all beluga orientations except a pure dorsal view (and even then, whales often rotated or changed direction during swimming), they were clearly visible and easily noted. The marked semicircular ventral concavity at the caudal terminus of the paired fat pads, just cranial to the genital slit and medial to the fin-like protuberances (Fig. 3), is best seen in a ventral view, but was clearly visible in nearly half (46.1%) of all sequences in which a beluga was swimming and/or turning while rolled (from 0° to 180°) along its longitudinal axis. In such cases, the ventral concavity was present during the entire sequence; the concavity was most apparent during the turn, but this was not because it suddenly appeared during or prior to the turn—as long as the fat pads were prominently elevated in these sequences, the concavity was present. It may be that the more marked bulging of the fat pads (creating the distinct ventral depression) occurs during tight turns due to a dorsoventral compression of the trunk and tail stock and/or due to contraction of trunk and abdominal musculature. Although corrugations or wrinkles are frequently seen in beluga skin and blubber, the elevated fat pads we observed were consistently smooth in external appearance: no rippling, undulating, flexing or other movements were observed along these bulging, bulbous lines, which are taut but not inflexible and unyielding. This is not a deformable surface, and it is dynamic only in the sense that it is raised (elevated) or not.

The next portion of this study involved examination of anatomical specimens, with dissections of beluga whales and other odontocete species for comparative analysis (Table 1). Access to beluga carcasses captured for subsistence hunting (Frost and Suydam 2010) was graciously provided by Inupiat people of Point Lay and Point Barrow, Alaska (1992–2007). Thirty adult beluga specimens were examined for this study (13 male, 17 female), along with two juvenile female belugas and two (male and female) late term fetuses. Digital photographs and videotape sequences recorded these dissections, as sketches were made and measurements taken of blubber, abdominal musculature and other anatomical features, including the pelvic bones and adjacent structures, especially adipose and connective tissues. Three narwhals (one adult male, one adult female, and one late term female fetus) were also dissected, all near Pond Inlet, Nunavut. Comparative data for other adult specimens dissected for this study (all necropsy of stranded animals, at the New England Aquarium,

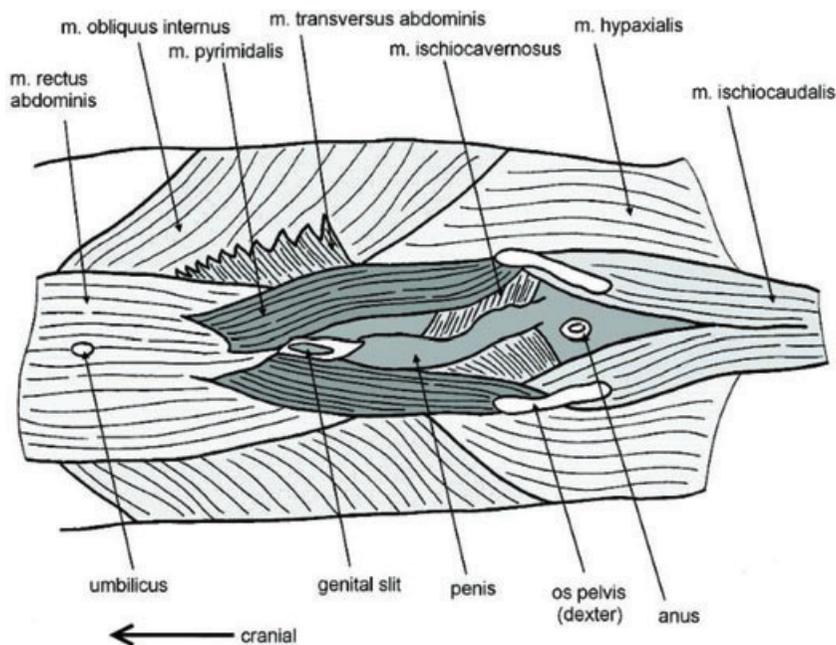


Figure 5. Schematic illustration (ventral view) of superficial dissection of caudal abdominal and trunk musculature of an adult beluga, *Delphinapterus leucas*, showing the paired pyramidalis abdominis muscles which originate on the pelvic bones and insert onto the superficial surface of the rectus sheath and *via* terminal tendons along the linea alba ventral and medial to rectus abdominis muscle fibers. Note that the deep transversus abdominis is partially reflected over the internal oblique.

Boston, Massachusetts, from 1989 to 2004) include six species (Table 1): the long-finned pilot whale (*Globicephala melas*), Risso's dolphin (*Grampus griseus*), bottlenose dolphin (*Tursiops truncatus*), common dolphin (*Delphinus delphis*), Atlantic white-sided dolphin (*Lagenorhynchus acutus*), and harbor porpoise (*Phocoena phocoena*).

Dissections and manipulation indicate that elevation of the fat pads in *Delphinapterus* is a consequence of the contraction of ventral abdominal muscles (Fig. 5) that tense the abdomen and its overlying blubber, and especially of muscles that attach to the pelvis, creating the bulbous, "erected" folds. Although various abdominal muscles likely contribute to this action (Cotten *et al.* 2008), and the rectus abdominis is the largest such muscle (measured by cross-sectional area and total length of excursion), we believe that the paired pyramidalis abdominis muscles of the lower abdomen (Evans and Christensen 1979, Schaller *et al.* 2007) is an especially important contributor. The pyramidalis (also known as the pyramidalis, NAV 2005) is not consistently seen in all odontocetes; it is rarely described in myological accounts of cetaceans. Of the dissections conducted for this study, we found a distinct, well defined pyramidalis abdominis muscle in all specimens of *Delphinapterus* and *Monodon*, and in a majority of specimens of *Grampus* and *G. melas*. An unequivocal

pyrimidalis muscle was observed in 1 of 10 *Tursiops* specimens, 2 of 10 *L. acutus* specimens, and in no other specimens dissected for this study.

In *Delphinapterus*, the pyrimidalis abdominis (Fig. 5) originates on the cranial end of the pelvic bone and inserts on the linea alba (a fibrous structure composed mostly of collagen running down the abdominal midline) at its ventral, caudal border, approximately midway between the pelvic bones and umbilicus (Howell 1930a); its fibers resemble a caudal continuation or head of the rectus abdominis, but the pyrimidalis has separate, shorter fibers with a discrete epimysial sheath. The pyrimidalis is dorsoventrally flattened, approximately 22 cm in mean length in adults ( $n = 30$ ,  $SD = 1.4$ ) and 7 cm in mean width ( $n = 30$ ,  $SD = 0.6$ ), with a cross-sectional area (mid-belly) of roughly  $36.7 \text{ cm}^2$  ( $n = 10$ ,  $SD = 3.5$ ). The caudal portion of the rectus abdominis sheath splits (near its origin on the pelvis) and encloses the pyrimidalis muscles. Few fibers of either the pyrimidalis or rectus abdominis attach to the overlying blubber. The prime motion of both the pyrimidalis and rectus abdominis is to tense (stiffen) the abdominal wall and draw the pelvic bones ventrally and cranially. Because the cetacean os pelvis is a single, rod-like element not fused to the vertebral column, contraction of this musculature causes the abdomen to shorten and the skin and blubber to tighten, elevating the paired ventrolateral fat pads of the abdominal blubber. Although we performed no histological analysis, the dense, vascularized layer of hypodermis in these paired structures appeared (upon gross anatomical examination) indistinguishable from adjacent blubber apart from its greater thickness. The hypodermal fat in the pads feels, to the touch, the same as other blubber, with similar pliability, and qualitatively appears to behave similarly when deformed in both tension and compression, though it is somewhat looser than surrounding blubber due to its greater thickness and abundance of fascia ventral to the pads (just beneath the skin). There is no notable innervation (though a nerve which may be the iliohypogastric nerve was often seen; Schaller *et al.* 2007), nor any subcutaneous muscle fibers in the prominent fat pads, which average roughly 130 cm long, 12 cm wide, and 12 cm high in a full-grown adult.

True described the beluga's blubber distribution in 1910:

"Beginning opposite the anterior end of the dorsal fin, the body, seen from above, assumed a form resembling a pillar consisting of three attached columns, laid horizontally. It was made up of a median dorsal rounded ridge, with a similar rounded mass below it on either side." However, True (1910) did not speculate on the potential functional significance of these structures. Extensive review of publications on beluga whale morphology yields no prior mention of this morphological feature, aside from reference to abnormally thick blubber (to 25 cm) "on the venter near the milk and anal glands" by Kleinenberg *et al.* (1964) in their book-length monograph on *Delphinapterus*. Although Reeves *et al.* (2002) noted that in belugas "the belly and sides may be lumpy, with folds and creases of fat," the fixed anatomical distribution of the adipose pads as revealed by necropsy and their characteristic position during swimming (Fig. 1–3) reveals a highly uniform rather than variable arrangement. The presence of elevated abdominal ridges in deceased specimens indicates that they can appear without need for muscular contraction by the abdominal musculature if the animal is laid out properly (lying on its side); their presence in animals hauled out im-

mediately after death indicates that elevation is not due to post mortem contraction and stiffening of the pyramidalis and rectus abdominis muscles or other structures. However, we contend that muscular contraction plays a role in the appearance of these pads *in vivo*. Further, the presence of the ventrolateral fat pads in wild belugas demonstrates that these are not an artifact resulting from obesity in captivity.

Based upon our kinematic and morphological investigation, and especially the finding that these structures are not uniformly present but become visible during nearly all locomotion in which an animal adopts a rotated or fully inverted body position, we suggest that they act as vertical stabilizers. Our novel hypothesis is that in the absence of a dorsal fin, the paired ventrolateral fat pads of *Delphinapterus* offer a previously undescribed surface to control roll. An alternative hypothesis is that rolling is common in *Delphinapterus*, and is especially manifested in inverted (upside down) swimming, precisely because this species has no vertical stabilization due to its lack of a dorsal fin. However, our data show that rolling in belugas is in fact not uncontrolled; whales clearly were able to maintain attitude (without roll, pitch, or yaw) for long distances and durations during locomotion, even during sharp and wide turns and changes in depth. Whales in which the fat pads were raised (elevated) were still observed to continue rolling (rotating along the longitudinal body axis), but most often (>70% of sequences analyzed) did not do so. Further, the presence of elevated ventrolateral fat pads during almost all (90% of) rolls and tight turns, coupled with their rarity during periods of rest, lends credence to our functional inference, which is in turn bolstered by evidence from our comparative anatomical survey. We do not dare surmise the functional significance, if any, of the crater-like, semicircular depression at the caudal terminus of the fat pads; this may be a mere artifact of the stiffened abdominal musculature and blubber, although it is possible that it somehow controls hydrodynamic flow over the body, particularly during high speed swimming (infrequently observed in this species). When this depression appears, the caudal portion of the adjacent pads are elevated to such a degree and at such an angle as to present protuberant structures (Fig. 3, plus Fig. 1 upper right and Fig. 2 lower) that may act similarly to fins. We propose, based on the shape and timing of appearance of these fin-like features, that they, like the fat pads generally, have functional significance as attitudinal control surfaces.

Our preliminary investigation of the abdominal musculature and adipose distribution in *Monodon* suggests that this sister species may possess a similar system of paired ventrolateral abdominal fat pads that are elevated during inverted and other locomotion for attitudinal control. However, the pilot necropsy data we have gathered indicates that although the abdominal musculature is similar in both monodontid species, in accord with reported findings of Howell (1930*a, b*, 1935) and Watson and Young (1880), the ventrolateral abdominal blubber of the narwhal is not distributed as thickly nor in the pronounced, track-like pads as in *Delphinapterus*. Although both monodontids share a similar external form, and both possess thick hypodermal layers (Table 1), the narwhal exhibits fewer blubber folds and less loose skin and fat. The blubber and associated subcutaneous adipose layers of adult belugas (Table 1) is nearly 5 cm (excluding the epidermis) on the lateral surface, but is much thicker (mean 11 cm) on the ventral surface of the abdomen, where the paired fat

pads lie. The narwhals we examined had a similarly thick layer of lateral blubber (over 4 cm thick, second only to belugas in our comparative study) and thicker (>6 cm) ventral blubber, but without an unequivocal pattern of paired pads. In other odontocetes surveyed there was no significant difference between lateral and ventral blubber thickness (Table 1).

Inverted and otherwise rolled swimming was frequently seen in juvenile belugas, captive and wild, but only data from adults was included in our kinematic analysis. Limited examination of fetal beluga specimens indicates that abdominal fat pads may be present at this stage but are not as conspicuous as in juveniles and adults. In beluga fetuses, ventral abdominal blubber ( $\bar{\theta} = 3.35$  cm,  $SD = 0.60$ ,  $n = 2$ ) is only slightly thicker than general body blubber deposits ( $\bar{\theta} = 2.92$  cm,  $SD = 0.88$ ,  $n = 2$ ). We also found that the dorsal ridge is more conspicuous and narrow and slightly but not significantly higher in *Delphinapterus* than *Monodon*; it is split in belugas by transverse notches into a series of small bumps, giving it a serrated appearance (Brodie 1989). Kleinenberg *et al.* (1964) noted that the dorsal ridge's prominence varies widely in beluga populations.

Precise control of orientation is essential in species that navigate and forage in a complex three-dimensional environment, especially when swimming—as is the case in *Delphinapterus*—in varied habitats ranging from shallow river deltas and estuaries to deep water under an ice sheet that limits movement and breathing. Foraging in such habitats could be enhanced by a partially rolled or wholly inverted posture, which might cause echolocation waves to be beamed more toward food resources and away from a shallow bottom or ice surface, potentially minimizing interfering return echoes. Heptner (1930) suggested that the lack of a dorsal fin in monodontids (as in the only finless mysticetes, the bowhead and right whales, *Balaena* and *Eubalaena*) relates to the presence of ice in their habitat, although this does not explain why subtropical and temperate odontocetes (*e.g.*, *Neophocaena* and *Lissodelphis*) lack a fin or why other species that inhabit icy water (*e.g.*, *Orcinus*) have large dorsal fins. Brodie (1989) asserted that belugas are frequently observed (*via* aerial observers) to swim in an inverted position, as was very commonly seen in captive subjects of our study. DTAG data published by Dietz *et al.* (2007) indicate that free-ranging narwhals swim in an inverted posture 80% of the time they are submerged. We contend that the ability of belugas and possibly narwhals to roll along the body axis during forward locomotion as well as during sharp turns, readily evident in both species, relates to their lack of a dorsal fin and apparently corresponding presence of ventrolateral fat pads. According to Sleptsov (1952), longitudinal ridges or keels might take the place of a dorsal fin, providing stability in odontocetes that lack a fin. (However, DTAG telemetry [Madsen *et al.* 2005] indicates that foraging beaked whales frequently rotate during dives, and all ziphiids possess a dorsal fin.) We postulate that the paired ventrolateral fat pads of *Delphinapterus* (and likely to a much lesser extent in *Monodon*) serve the same control purpose but, unlike a dorsal fin, can be manipulated *via* muscular contraction for variable deployment, and that this is a morphological feature unique to Monodontidae. The absence of a dorsal fin might also limit heat loss in these cold-water odontocetes. Further study should be done to assess the role of the paired ventrolateral fat pads in locomotor control. In their study of finless

porpoise (*Neophocaena*) abdominal myology, Tajima *et al.* (2004) argued that muscles attached to the pelvis likely played a key role in cetacean evolution by contributing to dorsolateral undulation that replaced pelvic limb motion in locomotion. The kinematics and morphology of other finless odontocetes (*e.g.*, *Lissodelphis*) might be examined for similar features that could potentially serve as compensatory adaptations to control roll and yaw.

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