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The face that sank the *Essex*: potential function of the spermaceti organ in aggression

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Summary

'Forehead to forehead I meet thee, this third time, Moby Dick!' [Ahab (Melville, 1851)]

Herman Melville's fictional portrayal of the sinking of the *Pequod* was inspired by instances in which large sperm whales sank whaling ships by ramming the ships with their heads. Observations of aggression in species of the four major clades of cetacean and the artiodactyl outgroup suggest that head-butting during male–male aggression is a basal behavior for cetaceans. We hypothesize that the ability of sperm whales to destroy stout wooden ships, 3–5 times their body mass, is a product of specialization for male–male aggression. Specifically, we suggest that the greatly enlarged and derived melon of sperm whales, the spermaceti organ, evolved as a battering ram to injure an opponent. To address this hypothesis, we examined the correlation between relative melon size and the level of sexual dimorphism in body size among cetaceans. We also modeled impacts between two equal-sized sperm whales to determine whether it is physically possible for the spermaceti organ to function as an effective battering ram. We found (i) that the evolution of relative melon size in cetaceans is positively correlated with the evolution of sexual dimorphism in body size and (ii) that the spermaceti organ of a charging sperm whale has enough momentum to seriously injure an opponent. These observations are consistent with the hypothesis that the spermaceti organ has evolved to be a weapon used in male–male aggression.

Key words: male–male aggression, sperm whale, cetacean, melon, Herman Melville, Moby Dick, *Essex*, *Ann Alexander*.

Introduction

In the 19th century, sperm whales (*Physeter macrocephalus* L.) were not only prized by whalers for the high-quality oil contained in their derived and greatly enlarged melon, known as the spermaceti organ, but were also feared by whalers because of their aggressive behavior. Herman Melville's (1851) fictional portrayal of the sinking of the *Pequod* was inspired by instances in which large sperm whales attacked, and in several cases sank, whaling ships by ramming the ships with their heads (Chase, 1821; Starbuck, 1878; Philbrick, 2000). Details of the sinking of two ships, the *Essex* and the *Ann Alexander*, are particularly well documented and relevant to this discussion. In both cases, the ships were solidly constructed and many times more massive than the attacking whale.

The attack on the *Essex* in 1821 is the first documented case of a sperm whale deliberately striking a ship (Chase, 1821). At the time, the *Essex* was approximately 20 years old and weighed approximately 238 tons (Philbrick, 2000). Its hull was composed almost entirely of white oak, one of the toughest and strongest woods available. Timbers 30 cm square in cross section made up the ribs of the ship. Over this were oak planks 10 cm thick covered by yellow pine more than 1 cm thick. This was covered and protected by a thick layer of copper that extended down from the waterline. The attack occurred while the crew was engaged in a hunt in which two sperm whales had already been harpooned (Chase, 1821). The first mate had been forced to return to the ship after his boat had been stove in by a harpooned whale and was in the process of repairing it when an approximately 26 m bull was observed 100 m from the ship, floating quietly, as if observing the ship. It suddenly dived and surfaced less than 30 m from the ship traveling at an estimated speed of 3 knots heading directly for the port side of the ship. The whale struck the ship, which shook 'as if she had struck a rock' (Chase, 1821). The whale then swam approximately 500 m leeward from the ship, where it acted as if it were 'distracted with rage and fury'. After several minutes of this display, it swam directly in front of the ship and then charged the ship again, this time with a speed near 6 knots. The whale struck the *Essex* directly beneath the cathead and completely stove in her bows. The *Essex* started sinking bow first, and capsized within 10 min on its port side.

The *Ann Alexander* was struck and sunk by a sperm whale in 1851 (Starbuck, 1878; Sawtell, 1962). Initially, the crew pursued the whale in rowing boats. After being harpooned, the

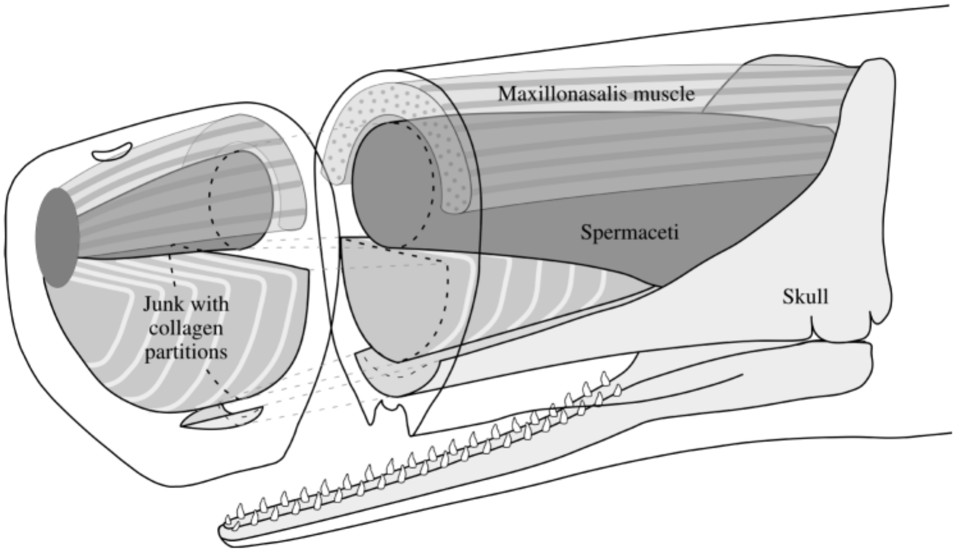

Fig. 1. Diagram of the anatomy of the head of the sperm whale *Physeter macrocephalus*. The relative size and position of the two oil-containing compartments of the spermaceti organ, the spermaceti and junk, are shown in relation to the skull. Modified from Clarke (1979).

whale attacked and destroyed two of the boats by crushing them in its jaws. The crew then returned to the ship in the single remaining boat and renewed the chase with the ship. The ship maintained the pursuit until the fleeing whale reversed its direction of travel, charged and rammed the bow of the ship with its snout. The impact did not damage the ship. While the crew debated the sensibility of continuing the pursuit, the whale attacked a second time and stove in the bow of the ship with a hole ‘just the size of the whale’s head’ (Sawtell, 1962). The ship sank in minutes. The whale was caught 5 months later by the crew of the *Rebecca Simms*, weak with infection caused by splinters and harpoons embedded in its flesh from the encounter with the *Ann Alexander* (Starbuck, 1878). This 5-month period demonstrates that long-term survival is possible after combat with a ship and presumably with another whale.

The anatomy of the head of sperm whales appears to have characterized the family Physeteridae since its inception in the Lower Miocene (Kellogg, 1928) and is unique among cetaceans (Fig. 1). Within the nose are two gargantuan oil-filled sacs that can constitute up to one-quarter of the body mass and extend one-third of the total length of the whale (Berzin, 1972; Clarke, 1978). The upper sac is termed the spermaceti sac because of the high-quality oil contained within it. This oil partially solidifies on contact with air, turning white and giving it a semen-like appearance. The case surrounding the spermaceti is made up of extremely tough, thick fibrous connective tissue, which lies below a strong tendinous-muscular layer. The lower sac, termed the junk, is filled with a denser oil and is organized into sections by transverse partitions of connective tissue. The junk is derived from the odontocete melon, whereas the affinity of the spermaceti sac is not known (Heyning and Mead, 1990). The posterior portion of the skull is curved like an amphitheater and holds the posterior end of the spermaceti sac. The maxilla, or upper jaw, forms a trough in which the junk sits. Both the spermaceti sac and the junk are triangular in shape when viewed in sagittal section. The spermaceti sits on top of the junk and is larger at the posterior end of the nose, while the junk is larger at the anterior end (Berzin, 1972; Clarke, 1978).

In large bulls, the spermaceti and junk are hypertrophied and can extend up to 1.5 m beyond the end of the maxilla (Berzin, 1972). It is this anterior extension of the spermaceti organ that sperm whales have been observed to use when striking ships (Chase, 1821; Starbuck, 1878; Sawtell, 1962). Although observations of males fighting are rare (Whitehead and Weilgart, 2000), the belief that the spermaceti organ functions as a weapon has been held by whalers who witnessed fights between males or who experienced attacks on their ships (Chase, 1821; Berzin, 1972). Similarly, observations of aggressive head-butting behavior by bottle-nosed whales led Gowans and Rendell (1999) to suggest that the enlarged melon of this species may be a specialization for male–male aggression. Nonetheless, previous attempts by biologists to explain the functional significance of the massive size and structural specialization of the spermaceti organ have focused on biosonar, acoustic sexual selection (Norris and Harvey, 1972; Cranford, 1999; Møhl, 2001), acoustic prey debilitation (Norris and Møhl, 1983) and buoyancy control (Clarke, 1978). Although the spermaceti organ may facilitate both sound production and buoyancy control, the successful attacks on 19th-century whaling ships led us to ask whether the spermaceti organ might also function as a weapon in male–male aggression.

To address this question, we performed two analyses. In the first analysis, we determined whether the relative size of the melon is correlated with the level of sexual dimorphism in body size among cetaceans. Relative weapon size is often correlated with the degree of polygyny and sexual dimorphism in body size (Clutton-Brock and Harvey, 1977; Parker, 1983; Andersson, 1994). The greatly enlarged melon, extreme sexual dimorphism in body size and polygynous mating system of sperm whales (Caldwell et al., 1966; Berzin, 1972; Whitehead and Weilgart, 2000) raise the possibility that a similar relationship might exist among cetaceans. Hence, if the melon is used as a weapon during male–male aggression in some species, we would expect the relative size of the melon to be positively correlated with sexual dimorphism in body size.

In the second analysis, we used a two-dimensional physical modeling program to simulate the impact of two sperm whales and asked whether it is physically possible for the spermaceti organ to function as a weapon. We assumed that, to be effective as an intraspecific weapon, the spermaceti organ would have to function simultaneously as a battering ram to injure the target whale and as a shock absorber to protect the brain and body of the attacking whale. Male–male aggression that results in injury or death is common among mammals (Geist, 1971; Berzin, 1972; Silverman and Dunbar, 1980; Clutton-Brock, 1982; Andersson, 1994; Wrangham and Peterson, 1996), and the potential for serious injury needs to be real for a male to achieve dominance (Darwin, 1871; Geist, 1971; Andersson, 1994). Because specific details of the structure of the spermaceti organ and the physical properties of the tissues that compose it are not known, our modeling was necessarily very simple and intended to answer two basic questions: (i) whether there is enough energy in the momentum of the spermaceti organ of a large swimming sperm whale to damage an equal-sized opponent and (ii) whether the shock absorption necessary to protect the attacking whale would dissipate the blow to the target whale and thereby render the spermaceti organ ineffective as a weapon. Thus, although the model was simple, it did have the potential to falsify the hypothesis that the spermaceti organ functions as a weapon in male–male aggression.

Materials and methods

Relative melon size and sexual dimorphism in body size

Among mammals, male weapons tend to be largest relative to body size in species that exhibit the greatest level of polygyny and the greatest level of sexual dimorphism in body size (Parker, 1983; Jarman, 1989; Andersson, 1994). Hence, to test the hypothesis that melons are used as weapons by some species, we looked for a correlation between relative melon size and the level of sexual dimorphism in body size in 21 species of cetacean (Table 1). To avoid a false correlation due to the influence of underlying phylogenetic relationships (i.e. the non-independence of the values associated with the species examined), we used a method known as analysis of independent contrasts (Felsenstein, 1985; Losos, 1990). Independent contrasts are derived by placing trait values for each taxon on a reliable phylogeny and then calculating the evolutionary change in the trait between sister taxa across the phylogeny (Fig. 2). The resulting contrast values, unlike the original values for each taxon, are statistically independent and normally distributed. The correlation between the independent contrasts for the two traits was then determined to examine the relationship between evolutionary change in relative melon size with evolutionary change in sexual dimorphism in body

Table 1. *Relative melon area (%) and body length sexual dimorphism (% difference) in the 21 species of cetacean used in the independent contrast analysis*

Taxa	Relative melon area	Body length sexual dimorphism	Reference
Eubalaena glacialis	0.2	–7	Whitehead and Payne (1981)
Kogia breviceps	13.1	6	Evans (1990)
Physeter macrocephalus	23.2	52	Connor et al. (2000)
Berardius bairdii	2.7	–3	Connor et al. (2000)
Hyperoodon ampullatus	4.2	9	Connor et al. (2000)
Mesoplodon ginkgodens	2.8	–4	Klinowska (1991)
Ziphius cavirostris	4.2	1	Connor et al. (2000)
Platanista gangetica	2.8	–10	Connor et al. (2000)
Lipotes vexillifer	1.8	–24	Connor et al. (2000)
Inia geoffrensis	2.3	11	Connor et al. (2000)
Pontoporia blainvillei	2.9	–6	Connor et al. (2000)
Delphinapterus leucas	5.3	15	Connor et al. (2000)
Monodon monoceros	5.1	18	Connor et al. (2000)
Phocoena phocoena	3.6	–8	Connor et al. (2000)
Phocoena spinipinnis	4.4	–3	Brownell and Clapham (1999)
Globicephala melas	7.0	25	Bernard and Reilly (1999)
Orcinus orca	2.7	16	Connor et al. (2000)
Pseudorca crassidens	7.1	20	Connor et al. (2000)
Tursiops truncatus	3.5	7	Connor et al. (2000)
Grampus griseus	3.3	5	Connor et al. (2000)
Lagenorhynchus obscurus	4.4	–1	Connor et al. (2000)

Body length sexual dimorphism is given as a percentage difference, positive values for species in which males are longer than females and negative values for species in which females are longer.

Relative melon area is the percentage of the lateral projected body area made up by the melon (see Fig. 3 and text).

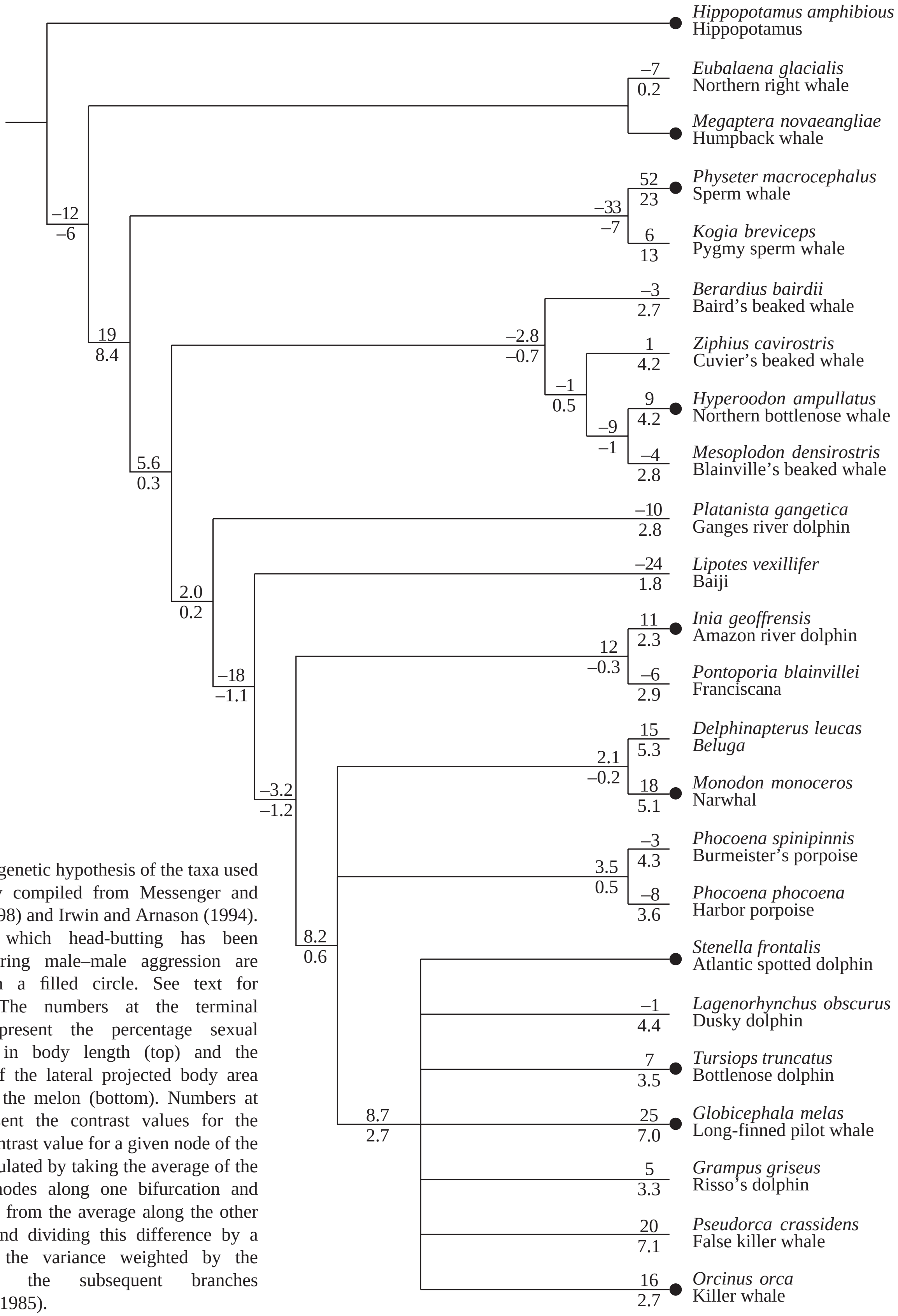

Fig. 2. Phylogenetic hypothesis of the taxa used in this study compiled from Messenger and McGuire (1998) and Irwin and Arnason (1994). Species in which head-butting has been observed during male–male aggression are marked with a filled circle. See text for references. The numbers at the terminal branches represent the percentage sexual dimorphism in body length (top) and the percentage of the lateral projected body area made up by the melon (bottom). Numbers at nodes represent the contrast values for the node. The contrast value for a given node of the tree was calculated by taking the average of the descendant nodes along one bifurcation and subtracting it from the average along the other bifurcation and dividing this difference by a measure of the variance weighted by the lengths of the subsequent branches (Felsenstein, 1985).

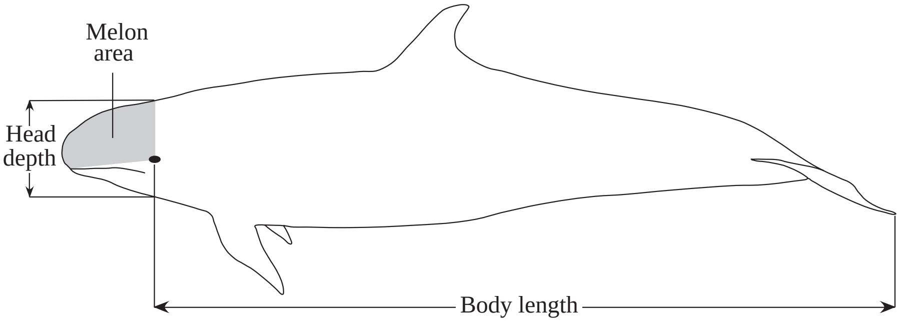

Fig. 3. Diagram of measurements taken to determine relative melon area. The shaded area is the lateral projected area of the melon. The index of body area is the head depth times the body length, measured from the eye to the tip of the flukes.

size. We used an independent contrast method that allows analysis using partially resolved phylogenies (Martins, 2001). The cetacean phylogeny used was the strict consensus tree of Messenger and McGuire (1998).

The literature provides estimates of the degree of sexual dimorphism in body length for a number of cetacean species (Table 1). To estimate relative melon size, we measured the lateral projected area of the melon and an index of the postcranial lateral projected body area from high-quality illustrations (Carwardine, 2000) using a digitizing program (NIH Image). We defined the area of the melon as the area contained within a dorsoventral line between the top of the head and the eye, a line between the eye and the anterior tip of the upper jaw and a tracing of the front of the head from the tip of the upper jaw to the intersection with a line extending vertically from the eye. Our index of postcranial body area was the dorsoventral depth of the head at the eye multiplied by the body length from the eye to the caudal tip of the flukes (Fig. 3). We then divided the projected area of the melon by the index of the postcranial body area to yield a measure of relative melon size. 20 of the 21 species were analyzed in this way. Although large errors in relative melon size are possible because of the accuracy of the illustrations, we expected the errors to be both random relative to the level of sexual dimorphism in body size and small relative to the actual variation in relative melon size among species.

Although mysticetes do not posses a functional melon, they do have a fatty structure just anterior to the nasal passages that appears to be homologous to the melon of odontocetes (Heyning and Mead, 1990). Hence, we determined the relative size of the melon in *Eubalaena glacialis* from an illustration by Heyning and Mead (1990). In this case, we measured the area of the melon in the figure and then used the dorsoventral depth of the body at the eye to scale the figure to the illustration of *Eubalaena glacialis* in Carwardine (2000).

Modeling of head-butting

The impact of a sperm whale with a target whale of the same mass was simulated using a two-dimensional physical modeling program, Working Model 2D. The attacking whale had a total mass of 39 000 kg and consisted of a mass representing the spermaceti organ (20 % of body mass, 7800 kg) connected by a damper (spermaceti damper) to a mass representing the rest of the body (31 200 kg). The target whale consisted of a stationary mass of 78 000 kg (39 000 kg body mass plus the added mass of the attached water; we assumed an added mass coefficient of 1; Vogel, 1981) attached *via* a damper (tissue damper) to a much smaller 'bumper' mass (less than 1 % of body mass). The bumper mass and tissue damper modeled the shock absorption that would occur due to the tissues of the target whale. The attacking whale was given a velocity of $3\,\mathrm{m\,s^{-1}}$ (the estimated sum of the velocities of the whale and ship in the *Essex* incident; Chase, 1821) and directed so that the anterior end of spermaceti mass collided with the bumper of the target whale. Upon impact, the model calculated the instantaneous accelerations of the masses and the deformations of the dampers.

Because a head-on collision between two whales would result in the same damping values and, therefore, the same forces applied to the two whales, we modeled impacts in which the anterior end of the attacking whale's spermaceti organ struck the side of the head or body of the target whale. We assumed that this would result in greater damping in the target than in the attacking whale.

Hence, we assumed that a collision between two whales can be modeled as a series of masses and dampers that exert force in proportion to shortening velocity. The spermaceti organ clearly has mass that must be decelerated in a collision. Whether the tissues of the spermaceti organ respond with spring-like or damper-like properties is not known. It seems likely, however, that the mechanical behavior of the spermaceti organ in a collision will be a combination of spring and damper properties. To keep the model simple, however, we chose to model the two extremes. When the collision was modeled using springs only, an unrealistically wide range of values for spring constants was needed, suggesting that the shock-absorbing qualities of the spermaceti organ result more from dampening than elasticity. Furthermore, given that the mass of the spermaceti organ is composed primarily of a liquid (oil), it seems reasonable to assume that the spermaceti organ's initial absorption of the energy during impact would be due primarily to acceleration of the liquid (i.e. damping) rather than to deformation of elastic elements.

Results

Relative melon size and sexual dimorphism in body size

The method of independent contrasts (Felsenstein, 1985) allows one to test for correlations in the evolutionary change

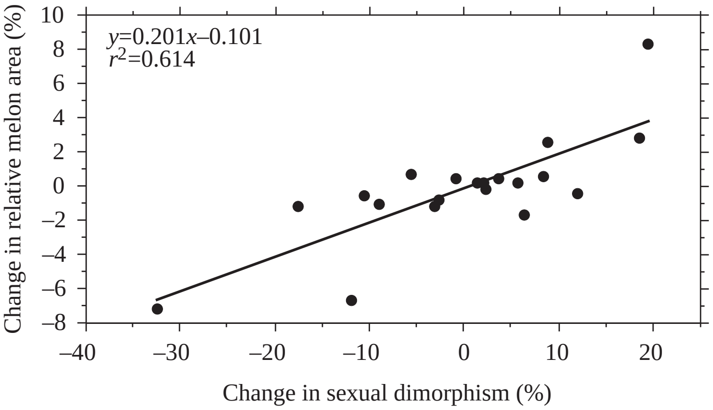

Fig. 4. Independent contrast analysis of evolutionary change in relative melon area and evolutionary change in sexual dimorphism in body length for 21 species of cetacean. Positive values on the y-axis represent the evolution of an increase in the lateral projected area of the melon relative to the lateral projected area of the rest of the body. Negative values on the y-axis represent the evolution of a decrease in the lateral projected relative area of the melon. Positive values on the x-axis represent the evolution of longer males relative to females and negative values represent the evolution of shorter males relative to females. This result shows that species that have evolved relatively larger males tend also to have evolved relatively larger melons.

of two characters within a monophyletic group. Our analysis yielded a strong positive correlation between the evolution of relative melon size and the evolution of sexual dimorphism in body length (r^2=0.61, P<0.0001, Fig. 4). Although the correlation was influenced by the species that represent the two extremes in relative melon size and sexual dimorphism in body size, the baleen and sperm whales, the relationship remained significant when these species were removed from the analysis. When the analysis was run without the baleen whale *Eubalaena glacialis*, the correlation coefficient increased slightly (r^2=0.63, P<0.0001). The sperm whales *Physeter macrocephalus* and *Kogia breviceps* had a larger influence, but the correlation remained significant when they were removed (r^2=0.31, P=0.015). When both the baleen and sperm whales were removed from the analysis, r^2 was 0.34 (P=0.014). Thus, species that have evolved to have relatively larger males tend also to have evolved relatively larger melons. In contrast, species that evolved towards relatively larger females tend to have evolved relatively smaller melons.

Modeling of head-butting

When springs were substituted for dampers in the model, we found that the stiffness of the tissue spring must be more than 19 times the stiffness of the spermaceti spring for the acceleration of the target whale to reach the same acceleration as the mass of the body of the attacking whale. For the acceleration of the target whale to reach twice the acceleration of the attacking whale, the ratio of spring stiffness must exceed 76. Corresponding ratios required for dampers (to achieve the same acceleration and twice the acceleration, respectively) are 1.15 and 8.30. Because the range of modulus of elasticity of the tissues and materials that would probably serve as the elastic elements in the two whales (collagen in the case of the spermaceti organ of the attacking whale and the bone of the skull of the target whale) is only 15-fold (Wainwright et al., 1976), modeling the spermaceti as masses and springs seemed inappropriate. Skin is an elastic tissue that would be involved in any collision, but its elastic modulus is relatively low, approximately three orders of magnitude less than that of tendon (Wainwright et al., 1978). Therefore, we assumed that the skin of the target whale would not serve as an important elastic element in the absorption of the energy of impact. Hence, further analysis used a model with dampers in the place of springs.

Given that we do not know the damping constant of a sperm whale's spermaceti organ or the damping constant of the various other parts of a sperm whale that might receive the impact of an attack, we examined the effects of different damping magnitudes and damping ratios (tissue damper/ spermaceti damper). The ratio of damping was varied systematically from 2 to 128, and the damping constants were varied within each damping ratio. The modeling yielded a line for each damping ratio when the resulting acceleration of the target whale was plotted against the resulting acceleration of the attacking whale's body (Fig. 5). The slope of the line was greater for higher damping ratios, but in all cases the peak acceleration of the target was greater than the peak acceleration of the attacking whale's body. Fig. 6 shows sample acceleration traces *versus* time for the target and attacking whale.

Discussion

Head-butting during aggressive behavior is common and widespread among cetaceans, suggesting that it may be a basal behavior for the group. Although data are not available for most species, head-butting has been observed in species in each of the four major cetacean lineages. Among the Mysticeti, male humpback whales (Baker and Herman, 1984) have been observed to ram each other with their heads during competition for females. Of the three species that constitute the Physeteroidea, sperm whales have been observed to use head-butting during male–male aggression (Berzin, 1972) and when attacking whaling boats and whaling ships (Chase, 1821; Starbuck, 1878; Sawtell, 1962). Among the Ziphioidea, male bottle-nosed whales have been observed to use their enlarged melon to ram competing males (Gowans and Rendell, 1999). Among the Delphinida, aggressive head-butting has been observed in Amazon river dolphins (Caldwell et al., 1989), narwhals (Silverman and Dunbar, 1980), long-finned pilot whales (Reilly and Shane, 1986), bottlenose dolphins (Ross and Wilson, 1996), spotted dolphins (Herzing and Johnson, 1997) and killer whales (Goley and Straley, 1994). Further, as noted by Gowans and Rendell (1999), in the artiodactyl lineage

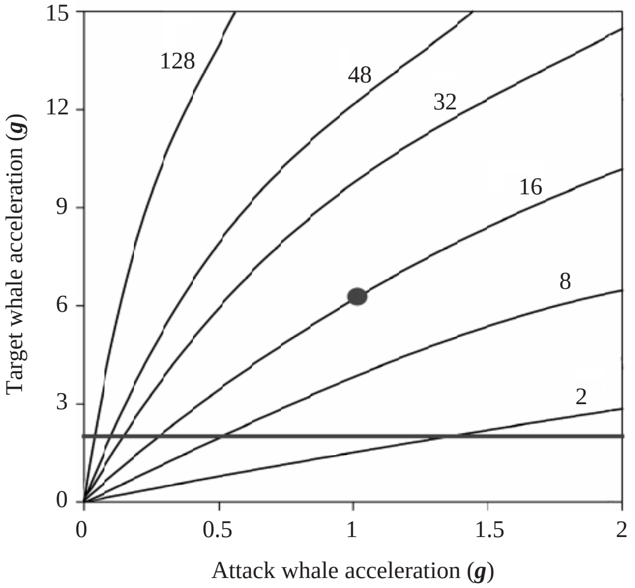

Fig. 5. Graph of the modeled peak accelerations of the target and attack whales during a collision at $3\,\mathrm{m\,s^{-1}}$ for different ratios of damping constants. Each line extending from the origin illustrates the accelerations that the model produced for a given ratio of damping constants for the tissue and spermaceti dampers. The number beside each line is the ratio of the tissue damping constant of the target whale to the spermaceti damping constant of the attacking whale. The magnitude of damping increases as the lines extend from the origin. As the ratio becomes larger, the accelerations experienced by the target whale become larger relative to the accelerations of the attacking whale. Twice the acceleration due to gravity ($2\boldsymbol{g}=19.6\,\mathrm{m\,s^{-2}}$) is the estimated acceleration above which fatal injury is likely to occur for a vertebrate the size of the modeled whales (Farlow et al., 2000). Hence, the area above the horizontal line represents accelerations that would probably injure the target whale and but not the attacking whale. The filled circle on the line for a damper constant ratio of 16 represents the damping constants used for the sample acceleration traces shown in Fig. 6.

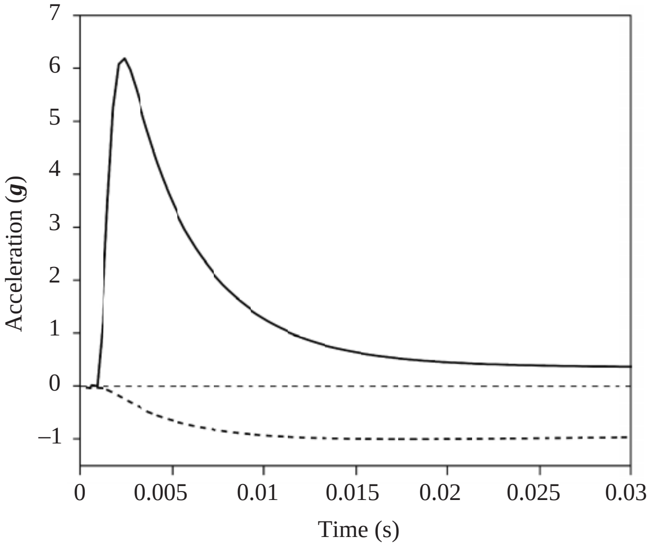

Fig. 6. Sample acceleration traces from the model of a collision of two 39 000 kg sperm whales. The acceleration experienced by the target whale is shown with the solid line and the acceleration experienced by the attacking whale is shown by the dashed line. In this case, the ratio of the damping constants was 16 ($2\,040\,480\,\mathrm{N\,s\,m^{-1}}$ for the tissue damper and $127\,530\,\mathrm{N\,s\,m^{-1}}$ for the spermaceti damper).

from which cetaceans are thought to be derived, head-butting is used during male–male aggression by many species. Specifically, competing males of the closest outgroup to cetaceans, *Hippopotamus* (Irwin and Arnason, 1994), employ head-to-head, open-mouth charges and impacts, followed by head-to-head pushing contests (Kingdon, 1979). Although the lack of observational data on most cetacean species makes a phylogenetic analysis impossible, the presence of aggressive head-butting in species of all four major lineages of cetaceans, and in the outgroup to cetaceans, suggests to us that some form of aggressive head-butting is a basal behavior in cetaceans. Hence, cranial specializations that enhance the effectiveness of head-butting may be present in some species of cetacean.

One possible clue as to whether some species use their melon as a weapon is the degree to which relative melon size is correlated with the level of sexual dimorphism in body size. Among species of mammals, the level of polygyny is strongly correlated both with the extent to which males are larger in body size than females and with relative size of weapons (Clutton-Brock and Harvey, 1977; Parker, 1983; Andersson, 1994). In the artiodactyl family Cervidae, male weapons are largest relative to body size in species with the highest level of polygyny (Clutton-Brock et al., 1980). Most significantly, in the Cervidae and Bovidae, as well as in the marsupial family Macropodidae, male weapons tend to be largest relative to body size in species that exhibit the greatest sexual dimorphism in body size (Jarman, 1983). Hence, our finding that the evolution of relative melon size is positively correlated with the evolution of sexual dimorphism in body size suggests that some species of odontocetes may use their melons as weapons in contests for access to females.

Our simple modeling of the accelerations involved in head-butting behavior by two sperm whales has the potential to falsify the hypothesis that the spermaceti organ is a weapon used in male–male aggression. If the spermaceti organ functions as a weapon, males must be able to use it to injure an opponent (Geist, 1971; Andersson, 1994). In all cases, our modeling showed that the peak acceleration of the target whale was greater than the peak acceleration of the attacking whale's brain and body. But are the predicted accelerations physiologically relevant? The acceleration at which injury occurs is known to decrease as body size increases (Diamond, 1989; Farlow et al., 1995). Scaling relationships based on records of injuries sustained by humans in car crashes (Alexander, 1996; Farlow et al., 2000) suggest that twice the acceleration due to gravity ($2\boldsymbol{g}=19.6\,\mathrm{m\,s^{-2}}$) is the acceleration at which a 39 000 kg vertebrate would suffer fatal injury. The portion of Fig. 5 above the horizontal line ($2\boldsymbol{g}$ on the *y*-axis) represents accelerations above injury threshold for the target

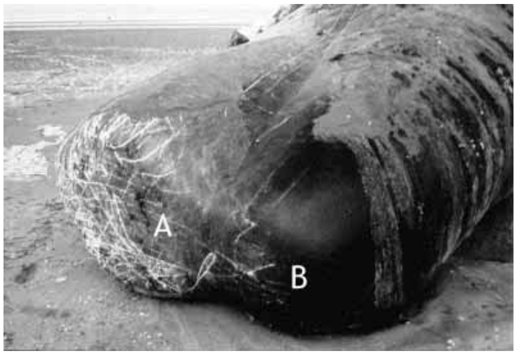

Fig. 7. Frontal view of a stranded bull sperm whale showing the location of scars on the anterior aspect of the spermaceti organ. The bull is lying on its left side. The relative size and shape of the two major compartments of the organ can be distinguished: (A) junk and (B) spermaceti. Note the 'battering-ram'-like appearance of the junk compartment and that the scars are largely restricted to the junk. The scars probably result from tooth-raking during male–male aggression as has been suggested by Best (1979) and Kato (1984). The scars are usually concentrated on the anterior end of the junk, suggesting that tooth-raking occurs during head-butting. If the scars were the result of jaw-to-jaw wrestling matches, which have been observed to occur between male sperm whales (Berzin, 1972), we would have expected them to be concentrated at the angle of the mouth. Reprinted with permission from Møhl (2001).

whale and below injury threshold for the attacking whale's body. These results suggest that the momentum of the spermaceti organ of a large swimming sperm whale could seriously injure a stationary opponent of similar body mass. Further, and most importantly, the level of damping necessary to protect the attacking whale from injury would not necessarily diminish the effectiveness of the system as a weapon.

To conclude, we raise several additional observations that are consistent with the weapon hypothesis. First, the spermaceti organ is considerably larger relative to body size in males than in females (Cranford, 1999). Weapons used in male–male aggression often exhibit sexual dimorphism in size (Andersson, 1994). Second, although not all cetaceans have fused cervical vertebrae, the posterior six cervical vertebrae form a fused mass in sperm whales (De Smet, 1972). This would presumably facilitate the transfer of the energy of impact from the head to the body and would reduce the chances of spinal compression injury. In addition, the skin on the anterior end of the spermaceti organ (i.e. impact surface) is unusually thick and tough (Chase, 1821; Berzin, 1972), and in large males it is often covered extensively with scars (Best, 1979; Kato, 1984). The scars tend to be concentrated on the ventral portion of the spermaceti organ, known as the junk (Fig. 7). The junk is reinforced with collagenous partitions and is directly in line with the cervical vertebrae (Berzin, 1972; Clarke, 1978). These observations, combined with the results of our study, suggest that the spermaceti organ does function as a weapon in male–male aggression. Although the spermaceti organ probably serves a variety of functions, possibly including vocal communication, echolocation, acoustic prey debilitation (Norris and Harvey, 1972; Norris and Møhl, 1983; Cranford, 1999) and buoyancy control (Clarke, 1978), we suggest that its great size and structural specialization may represent the result of selection for use as a battering ram.

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