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Marine Mammal Science

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ABSTRACT

This study's objective was to investigate mandibular fractures in 50 short-finned pilot whales, *Globicephala macrorhynchus,* from two mass strandings. Based on current

theories that this species is sexually dimorphic and polygynous, hypotheses were: (1) males should suffer more frequent or more substantial mandibular fractures than should females, and (2) fracture occurrence should increase with male reproductive maturity and potential correlates of maturity, such as age and length. Fractures were described and correlated with physical characteristics to infer possible explanations for injuries. Mandibular fractures were surprisingly common in males and females, being found in more than half of the animals examined (27/50, or 54% overall; 17/36 or 47% of females and 10/14 or 71% of males). Length was the only correlate of fracture presence; the proportion of animals showing evidence of fracture increased with length. These results offer some support to initial hypotheses, but there must be another set of consequences that contribute to mandibular fractures in females. A combination of intra- and interspecific interactions and life history characteristics may be responsible for fractures. Further research from a larger sample of this and other cetacean species are suggested to help elucidate both the causes and implications of mandibular fractures.

Of the two species of pilot whale, the long-finned pilot whale, *Globicephala melas,* is found in the higher latitudes of both hemispheres, while the short-finned pilot whale, *Globicephala macrorhynchus,* is found in equatorial to warm, temperate waters. Both species are subject to frequent mass strandings (Olson and Reilly 2002). Much is known about the biology and social structure of *G. melas* through examination of specimens obtained from drive fisheries and mass strandings (Sergeant 1962, Andersen 1993). In contrast, much less is known about populations of *G. macrorhynchus* in the northwestern Atlantic Ocean; these animals have been far less subject to mortality from directed or incidental fisheries takes (Caldwell *et al.* 1971). The National Museum of Natural History (Smithsonian Institution) in Washington, D.C., holds skeletal and other material from a total of 50 short-finned pilot whales that came ashore in two mass strandings in North and South Carolina in 1973. Preliminary observations revealed an unusually high frequency of mandibular fractures, all of which were determined to be antemortem given evidence of healing.

Intraspecific and interspecific interactions including play, competition, adult–juvenile interactions and predation, and anthropogenic factors such as entanglement and ship strikes could potentially result in trauma (Evans and Raga 1987, Cox *et al.* 1998, Patterson *et al.* 1998, Wells *et al.* 1999, Gulland *et al.* 2001, Dunn 2002, Cox *et al.* 2006, Campbell-Malone *et al.* 2008). Both species of pilot whale are sexually dimorphic, and polygyny is the presumed mating system (Reilly 1978, Andersen 1993, Carrier *et al.* 2002, Olson and Reilly 2002, Ralls and Mesnick 2002). There is some speculation that *G. macrorhynchus* males use their broad, flat heads as a protective cushion while ramming other males, but no behavioral data exist to support this theory. Intraspecific aggression in the form of head butting and tooth rakes has been observed in bottlenose dolphins (*Tursiops truncates*) (Parsons *et al.* 2003, Scott *et al.* 2005). In fact, males of many species of cetaceans, particularly those in which there is sexual dimorphism, engage in direct physical combat during intrasexual competition (Campagna 2002).

Accordingly, one could hypothesize that male pilot whales should suffer more frequent and more substantial mandibular fractures than should females. A second hypothesis follows: that the rate of fracture occurrence should increase with male

reproductive maturity and any potential correlates of maturity, such as age and length. The objective of this study was to investigate the occurrence, location, and characteristics of mandibular fracture in the two groups of mass-stranded short-finned pilot whales. Analyses of the occurrence and characteristics of fractures with regard to sex, age, reproductive maturity, and other life history characteristics of the animals concerned may provide insight into the possible behavioral, ecological, or other explanations for such fractures in these animals.

METHODS

Objectives

The goal of this study was to infer possible explanations for mandibular fractures in short-finned pilot whales from correlations between fracture presence and life history characteristics, notably sex, age, reproductive state, and total body length. To accomplish this goal, the age and reproductive state of the animals had to be determined. Then, data were collected on the occurrence and characteristics of fracture in the sample group. Characteristics of fracture that were described included location, complexity of fracture pattern, overall severity, and extent of healing.

Stranding Data Collection

On 6 October 1973, 23 short-finned pilot whales stranded at Kiawah Island, South Carolina. The skulls and mandibles, including teeth, were collected from 22 of the 23 animals (16 females, 6 males). On 12 October 1973, 28 short-finned pilot whales stranded at Cape Lookout, North Carolina. The skulls and mandibles, including teeth, were collected from all 28 animals (20 females, 8 males). Stranding data were collected for all animals according to the standard procedures of the National Museum of Natural History, Smithsonian Institution (modified after Norris 1961).

Life History Characteristics

Animals were classified according to their total body lengths into one of four length groups: <300 cm, 300–350 cm, 350–400 cm, and >400 cm. These categories were not based on any life history characteristics, but were chosen so that a small number of distinct length groups could be used for statistical analysis.

Teeth were cut and stained according to the methods described in Perrin and Myrick (1980). Thin sections were mounted and viewed through polarized film on a Wild Heerbrugg M3 (Wild Heerbrugg, Heerbrugg, Switzerland) dissecting microscope at 16× magnification. Each animal was assigned an estimated age and a corresponding age group according to the following tooth factors: number of growth layer groups visible, whether irregular dentine deposition had occurred, and whether the pulp cavity was open or closed (Kasuya *et al.* 1988). Animals were classified into one of six age groups (in years): 1–3, 4–6, 7–9, 10–14, 15–19, and 20–30.

At the time of stranding, observations were made and measurements were taken that related to the reproductive and maturational states of the animals. The state of epiphyseal fusion of the midthoracic vertebrae was classified as open or closed, indicating physical maturity (Mackintosh and Wheeler 1929:447). For females, lactation and pregnancy at the time of stranding were recorded. For males, the weight

and dimensions (length × width) of both the right and left testes were measured wherever possible, and the presence of seminal fluids was examined. Reproductive organs were collected for 10 females and 3 males chosen arbitrarily.

Data from 36 females were collected: 16 from South Carolina and 20 from North Carolina. Females were classified according to their reproductive maturity as immature, mature, or unknown. Females were classified according to whether there was evidence of prior pregnancy (yes or no). Lactation or pregnancy at the time of stranding, or mature vascularization of the uterus in nonpregnant and nonlactating individuals were considered evidence that a female was or had previously been pregnant.

Data from 14 males were collected: 6 from South Carolina and 8 from North Carolina. Shortly after the stranding events occurred, testes of three of the males that had been collected were prepared histologically (8 μ sections, and stained with hematoxylin and eosin) and slides were examined using a Leitz Laborlux 12 (Leitz Group, Grand Rapids, MI) compound microscope at 63× magnification to score for the presence of spermatogonia or spermatocytes using Berg's stain (Berg 1963). Those three males were classified according to their reproductive maturity as immature, mature, or unknown. In addition, one large male (total length = 535 cm) with a left testis weight of 1.58 kg was classified as mature, and a 1-yr-old male was assumed to be immature. The remaining nine males were classified as having unknown reproductive maturity.

For statistical comparison, males were also assigned to groups according to testis size as represented by both testis weight and length. Males with individual testis weight ≤0.10 kg and length <15 cm were assigned to testis size group 1; those with individual testis weight = 0.11–0.19 kg and length 15–30 cm were assigned to testis size group 2; and those with individual testis weight ≥0.2 kg and length >30 cm were assigned to testis size group 3.

Examination of Fractures

Definition of fracture—A fracture is a partial or complete break in the continuity of a bone (Howorth 1959, Ortner 2003). For this study, all partial or complete breaks in the continuity of the mandible that were determined to be antemortem injuries were considered fractures. All but one of the fractures found in this study had begun callus formation and were therefore considered antemortem injuries. To permit comparisons across individuals, a number of assumptions were made regarding the etiology of the fractures. For example, it cannot be definitively determined postmortem whether a single area of intersecting fracture lines was the result of a single fracture incident or two separate injuries. Therefore, all fractures in this study were considered as single fracture events. Similarly, fractures on both the left and right mandible could have resulted from a single or multiple events. However, since it was impossible to determine for certain that injuries on both mandibles were sustained at the same time, all fractures on the left and right mandibles were considered separately from one another. All fractures were also considered to be traumatic in nature.

Visual examination of mandibles—All mandibles were examined visually and tactilely for evidence of fracture. Many fractures were visible as one or more lines or raised seams on the bone, either on the lingual or the labial side, or on both sides, of the mandible. All mandibles were examined and scored for fractures by four individuals.

X-Ray Examination of mandibles—All mandibles were x-rayed in lingual and labial views. The microfocus x-ray source was a PXS5–724EA Thermo Kevex X-Ray (Thermo Scientific, Scotts Valley, CA) source with CU017 controller (70 kV end window source, maximum current 0.1 mA, <20 μ focal spot, 34° cone of illumination, air cooled). The flat panel amorphous digital x-ray detector was a PaxScan 4030 (Varian Medical Systems, Inc., Palo Alto, CA) (28.2 × 40.6 cm pixel area; captures 7.1 million pixels, 12-bit image, 14.4 MB file size; 5–15 s to capture an image). FlashScan software, adapted for use on Windows 2000, was used for image capture. X-rays were saved in digital format and viewed with Adobe Photoshop 6.0 on a graphics workstation with a high resolution monitor (1.5 GHz, Pentium 4, 400 MHz system bus; 1 GB RDRAM; 73 GB SCSI hard drive). All mandibles were then reexamined visually and compared to x-rays to confirm the presence or absence of fractures, and to further clarify the location and patterns of fracture lines.

Classification of Fractures

Anatomical location—Mandibles of all 50 animals were examined, and fracture presence or absence was recorded. If present, fracture location on the left or right side was recorded. Each fracture was assessed as being visible and/or tactilely apparent on either the lingual, labial, or on both surfaces of the mandible.

To permit comparison across mandibles of very different size, the total length of the mandible was divided into equal thirds (caudal third, middle third, and rostral third) along the transverse body plane (see Fig. 1A). Similarly, the height of the mandible was divided into equal thirds (dorsal third, middle third, and ventral third) along the frontal body plane (see Fig. 1B). The location of each fracture was noted as being present in one or more of each third along the transverse or frontal body plane.

Rated fracture categories—Each fracture was rated in three categories: extent of healing of the fracture, complexity of the fracture pattern, and overall severity of fracture. Four of the authors rated all of the fractures in each category. The first author developed the protocols and rated each fracture three separate times to ensure her ratings were consistent. Before the other individuals rated the fractures, they were given protocols and examined broken mandibles of short-finned pilot whales in the National Museum of Natural History's collection that were not part of this study. These mandibles were rated according to the same protocols and labeled with their ratings. These procedures were undertaken to reduce interobserver and intraobserver error.

Spearman correlation coefficients and tests of proportions were calculated for the ratings made by the four scorers to ensure consistency. Because differences between

Figure 1. Division of short-finned pilot whale mandible into thirds in order to classify fractures by location. (A) The total length of the mandible was divided into a caudal third, middle third, and rostral third along the transverse body plane. (B) The height of the mandible was divided into a dorsal third, middle third, and ventral third along the frontal body plane.

the ratings by the scorers were insignificant, one set of ratings was then used in all further statistical analyses.

The extent to which a fracture had healed at the time of stranding was rated on a scale from 1 to 3, with 1 being a recent fracture and 3 being a well-healed fracture. Only one mandible showed evidence of a fracture that could have been sustained at the time of stranding; however, that break also could have occurred during the necropsy or preparation of the skeleton. Therefore, that "fracture" was not considered in this study. A fracture rated 1 was reunited slightly, but still an obviously recent fracture; some callus was present. A fracture rated 2 was reunited moderately with some callus tissue and remodeling visible; holes or other areas that were not yet reunited may have been present. Bone was smoothed to some extent and had begun to return to its normal contours, but the fracture site was still easily discernible. A fracture rated 3 was almost indiscernible; there was virtually no callus remaining and the bone closely resembled its normal contours. For example, there may be a slight callus remaining on the lingual surface, but the labial surface had normal contours.

The complexity of the fracture pattern was rated on a scale from 1 to 3. The complexity of fracture pattern was based on the number of fracture lines comprising the break, as well as the pattern, direction, and intersection of fracture lines. Any fracture resulting in multiple holes (areas of nonunion), depression, or displacement was considered more complex than fractures without these characters, regardless of the number of fracture lines. Crescentic fractures were not considered simple by nature because those observed were large, included several intersecting fracture lines, and were likely to have had considerable impact on the individual's ability to move the jaw due to their size and location. Therefore, a crescentic fracture could not have been classified as a 1, but only as a 2 or a 3. A fracture rated 1 was simple, with one or two fracture lines; fracture margins were clear, thin lines resulting from clean breaks; the pattern of fracture was easy to identify; fracture lines may have been straight or slightly curved, but were not crescentic. A fracture rated 2 was moderately complex, usually with two or three fracture lines; connections between fracture lines may not have been clear; fracture margins may have been broader or slightly less easy to identify. A fracture rated 3 was complex, usually with more than three fracture lines; the margins and pattern of fracture were extremely unclear.

The overall severity of each fracture was rated on a scale from 1 to 3, with 1 being mild and 3 being severe. The overall severity of each fracture was based on the complexity of fracture pattern, the size and length of fracture, orientation of fracture lines, and location on the mandible. For example, a vertical fracture that extends more than halfway through the height of the mandible at its caudal margin would be considered more severe than a short, horizontal crack in the pan bone that showed no displacement. See Figure 2 for images of some mandibular fractures from this study.

Statistical Analyses

All statistics were performed using SYSTAT 10.2 and Microsoft Excel. Procedures and details on Fisher's exact test (for analyses involving two groups) and on Chi-square tests (for analyses involving multiple groups) were taken from Hayek (1994) and Simpson *et al.* (1960). All tests were run at the 0.05 level of significance. Test used, observed probabilities and group sizes (n) are reported in results.
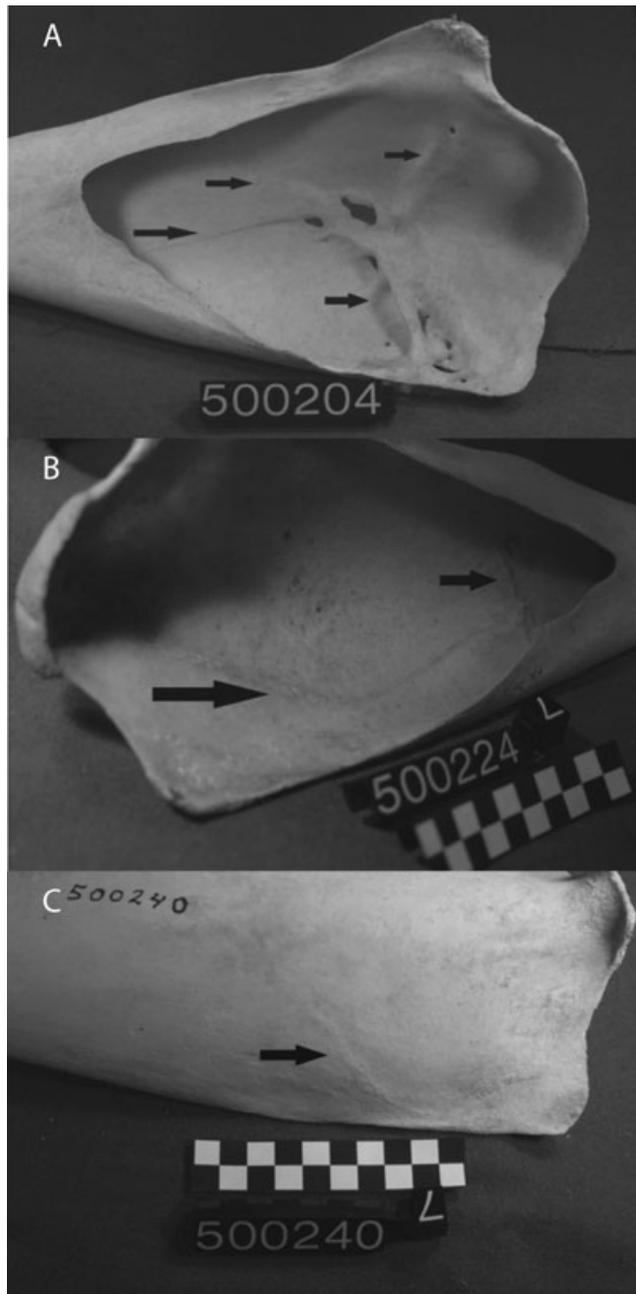
Figure 2. Mandibles of short-finned pilot whales: Fractures indicated by arrows. (A) A fracture rated 3 in complexity (complex); 3 in severity (severe); and 2 in healing (moderate healing evident). (B) A fracture rated 2 in complexity (moderately complex); 2 in severity (moderately severe); and 2 in healing (moderate healing evident). (C) A fracture rated 1 in complexity (simple); 1 in severity (mild); and 1 in healing (well healed).

RESULTS

Life History Characteristics

Of 50 animals examined, 4 (2 females and 2 males) were 1–3-yr old; 14 (11 females and 3 males) were 4–6-yr old; 7 (6 females and 1 male) were 7–9-yr old; 13 (5 females and 8 males) were 10–14-yr old; 5 (all females) were 15–19-yr old; and 7 (all females) were 20–30-yr old.

Of 36 females examined, 1 was classified as immature, 20 were mature, and there were insufficient data to determine a reproductive state for 15 animals. Of 14 males examined, 4 were classified as immature, 1 was mature, and there were insufficient data to determine reproductive state for 9 animals.

Presence of Fracture

Of 50 animals examined, 27 (54.0%) showed evidence of fracture. Seventeen of 36 females (47.2%) and 10 of 14 males (71.4%) showed evidence of fracture. There was no significant difference between the number of females and males with fractures (Fisher's exact test; $n = 50$, $P = 0.206$). Significantly more animals had a fracture on only one mandible (20 of 27 animals; 74.1%) than on both mandibles (7 of 27 animals; 25.9%) (Chi-square test; $n = 27$, $P = 0.012$). One of the animals (USNM 500232) had two separate fractures on the left mandible. A total of 35 separate fractures were classified in this study.

The number of animals showing evidence of fracture did not differ significantly by stranding location (North Carolina *vs.* South Carolina), between a single sex at either location, or between the females and males at the same location. Therefore, animals from both North Carolina and South Carolina strandings were combined for all further statistical analyses.

Fracture Location

Side of mandible—Of 35 total fractures, 20 (57.1%) were on the left mandible and 15 (42.9%) were on the right mandible. There was no significant difference between the number of fractures on the left and right mandibles (Chi-square; $n = 35$, $P = 0.398$). Of the 20 animals with a fracture on only one mandible, 12 (60.0%) were fractured on the left mandible and 8 (40.0%) were fractured on the right mandible. Significantly more fractures (Chi-square; $n = 35$, $P \leq 0.001$) could be seen on both the lingual and labial sides of the mandible (31 of 35, 88.6%) than could be seen only on the lingual side (4 of 35, 11.4%). None could be seen on only the labial side of the mandible.

Third of the mandible, divided along transverse and frontal body planes—Along the transverse body plane, all 35 fractures (100%) were located on the caudal third of the mandible; 20 fractures (57.1%) also extended onto the middle third of the mandible. None of the fractures extended to the rostral third of the mandible. Significantly more fractures (Chi-square; $n = 35$, $P \leq 0.001$) were located on the caudal third of the mandible than on either the middle or rostral third. Along the frontal body plane, 32 fractures (91.4%) were located on the ventral third of the mandible, 27 fractures (77.1%) were located on the middle third of the mandible, and 10 fractures (28.6%) were located on the dorsal third of the mandible. Significantly more fractures

Table 1. Number and percentage of total fractures for each of three-rated categories. (A) Extent of fracture healing was rated 1–3, with 1 being a recent fracture and 3 being a well-healed fracture. (B) Fracture pattern complexity was rated 1–3, with 1 being simple and 3 being complex. (C) Overall severity of fracture was rated 1–3, with 1 being mild and 3 being severe.

Rating	Number of fractures	% of fractures
(A) Extent of fracture healing		
1	1	2.9
2	18	51.4
3	16	45.7
(B) Fracture pattern complexity		
1	17	48.6
2	10	28.6
3	8	22.9
(C) Severity of fracture		
1	17	48.6
2	9	25.7
3	9	25.7

(Chi-square; $n = 35$, $P \leq 0.001$) were located on the ventral third of the mandible than on either the middle or dorsal third.

Fracture Description by Rated Fracture Categories

There were not significantly more fractures earning any one rating for fracture pattern complexity or overall severity. There were significantly more fractures rated 2 or 3 than rated 1 in extent of fracture healing (Chi-square test; $n = 35$, $P = 0.001$; Table 1).

Correlations of Fracture Characteristics

The presence and location of fracture—The percentage of animals with fracture(s) increased with increasing body length for all 50 animals (Chi-square test; $n = 50$, $P = 0.001$); for females only (Chi-square test; $n = 35$, $P = 0.009$); and for males only (Chi-square test; $n = 15$, $P = 0.049$; Fig. 3).The presence of fracture was not significantly correlated with sex (Fisher's exact test; $n = 50$, $P = 0.206$).

For all animals ($n = 50$), the presence of fracture was not significantly correlated with age (Chi-square test; $P = 0.340$), physical maturity (Fisher's exact test; $P = 1.000$), or reproductive maturity (Fisher's exact test; $P = 0.730$).

For all 27 animals showing evidence of fracture, whether one or both mandibles were fractured or whether there was a fracture on the left or right mandible was not significantly correlated with sex (Fisher's exact test; $P = 0.678$), age (Chi-square test; $P = 0.474$), physical maturity (Fisher's exact test; $P = 0.633$), length (Chi-square test; $P = 0.828$), or reproductive maturity (Fisher's exact test; $n = 22$, $P = 0.290$). Whether there was a fracture on the left or right mandible was not significantly correlated with sex (Fisher's exact test; $P = 1.000$), age (Chi-square test; $P = 0.642$), physical maturity (Fisher's exact test; $P = 1.000$), length (Chi-square test; $P = 0.432$), or reproductive maturity (Fisher's exact test; $n = 22$, $P = 0.432$).
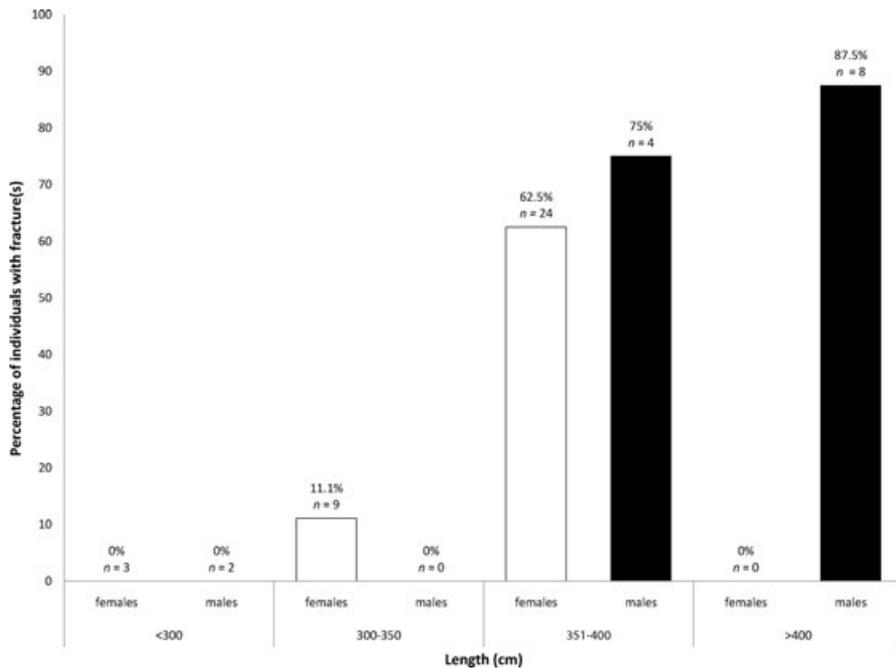
Figure 3. Number and percentage of female and male short-finned pilot whales with mandibular fracture(s) for each length group.

Fracture presence and characteristics were also not significantly correlated with life history characteristics for either females or males considered separately; statistical data are not reported for these individual groups because of the smaller sample size.

Rated fracture categories—For all 35 fractures, age was not significantly correlated with extent of fracture healing when comparing three age groups: 1–9 yr, 10–19 yr, and 20–30 yr (Chi-square test; $n = 35$, $P = 0.066$), but age was significantly correlated with extent of fracture healing when comparing two age groups: 1–9 yr and 20–30 yr (Chi-square test; $n = 35$, $P = 0.020$). Physical maturity was significantly correlated with extent of fracture healing (Chi-square test; $n = 35$, $P = 0.005$) and complexity of fracture pattern (Chi-square test; $n = 35$, $P = 0.006$). Length was significantly correlated with severity of fracture pattern (Chi-square test; $n = 35$, $P = 0.016$). Reproductive maturity was significantly correlated with extent of fracture healing (Chi-square test; $n = 35$, $P = 0.006$). Sex was not significantly correlated with any of the rated fracture categories (Chi-square test; $n = 27$, $P = 0.521$ (extent of fracture healing); $P = 0.835$ [complexity of fracture pattern]; $P = 0.993$ [severity of fracture]). Statistical data are not reported for rated fracture categories for either females or males considered separately due to small sample size.

Although not statistically significant aside from the data noted above, there was a trend toward fractures being more complex and severe with increasing age and physical maturity. Fractures also tended to show a greater extent of healing in physically immature *vs.* mature animals (Fig. 4).
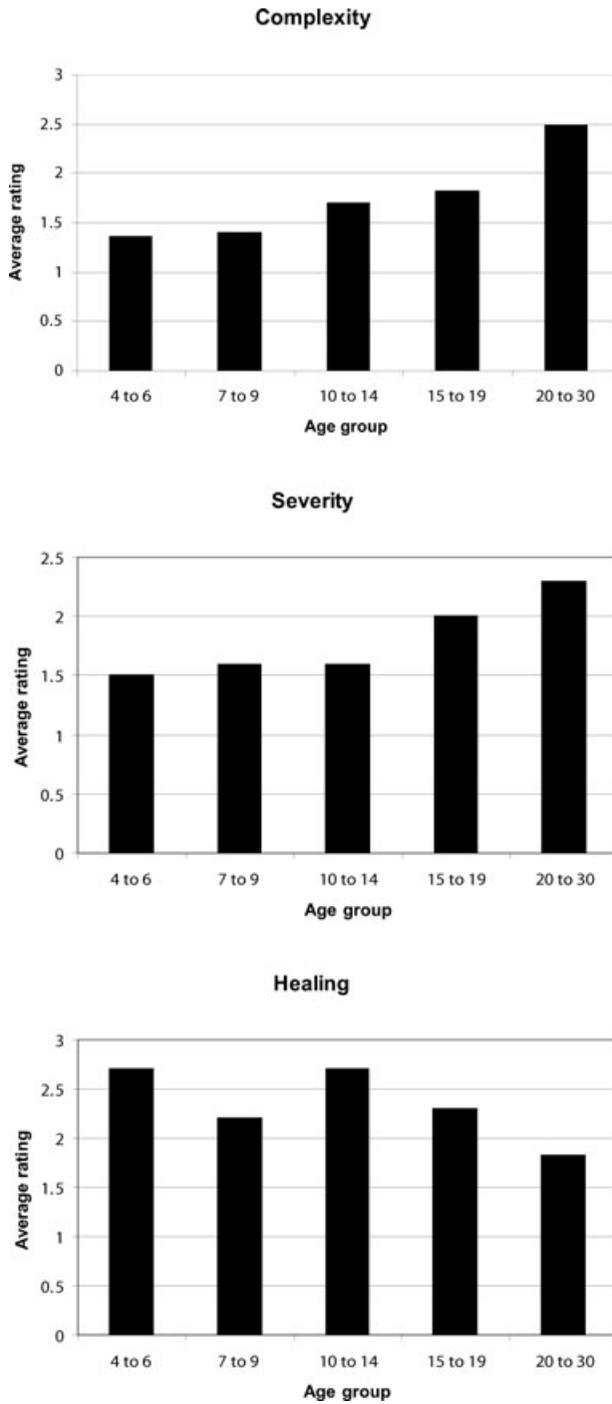
Complexity

Severity

Healing

Figure 4. Average ratings by age group for all fractures in short-finned pilot whale mandibular fractures rated for degrees of complexity, severity, and healing.

DISCUSSION

Fifty-four percent (27/50) of the short-finned pilot whales examined showed evidence of at least one mandibular fracture. This is a very high prevalence of location-specific fractures for a mammalian population. The distribution of fractures in wild populations has been studied mainly in primates (Lovell 1990:209). Lovell found the incidence of fractures in her sample of great apes (chimpanzees, gorillas, and orangutans) to be highest in the hands and feet (26%–27%), and second in ribs (4%–12%). She found no mandibular fractures in a total sample of 133 specimens. There is no study of which we know that provides comparable data in cetaceans. In addition, neither the presence of fracture nor location of fracture on the mandible was correlated with any life history parameters other than length. The proportion of animals showing evidence of fracture in each length grouping increased with length. As animals grow, they may change their behavior, take on a different social role, change their geographical location, or occupy a different ecological niche. In fact, total body length of short-finned pilot whales varies greatly and is not a good indicator of either age or reproductive state of individuals (Kasuya and Marsh 1984).

The initial hypothesis that male pilot whales should suffer more frequent and more substantial mandibular fractures than should females was supported by the high proportion of males showing evidence of fracture (71.4%). Male–male competition remains a plausible explanation for the observed mandibular fractures in male pilot whales. There has been no morphological evidence of rigorous male–male fighting in the short-finned pilot whale to date (Kasuya and Marsh 1984, Kasuya et al. 1993), but short-finned pilot whales in contrast to sperm whales do not show external scars from intra male fighting. It is thought that male pilot whales operate under a searching rather than harem strategy (Magnusson and Kasuya 1997). Interestingly, almost half (47.2%) of the females in this study also showed evidence of fracture. In light of these findings, other possible causes and implications of such fractures must be considered.

There may be multiple explanations for mandibular fractures in females. Intraspecific interactions such as intraspecific play or aggression by adults toward juveniles, defensive behavior of mothers toward male pilot whales in the presence of juveniles, or female competition for mates could theoretically result in fracture (Campagna 2002, Parsons et al. 2003, Scott et al. 2005). Interspecific interactions in mixed-species schools or encounters, or defensive behavior toward sharks or killer whales may also lead to fractures (Connor and Smolker 1990, Shelden et al. 1995, Ross and Wilson 1996, Weller et al. 1996, Mann and Barnett 1999, Mann and Tyack 2000). No patterns of fracture occurrence were found in this study suggesting intra- or interspecific interactions as a primary cause of mandibular fractures in pilot whales, but they may have lead to a small number of the fractures observed.

Other explanations for mandibular fractures in pilot whales may be based upon life history characteristics as well as behavior. The observed pattern of fractures was not consistent with wounds sustained by cetaceans from ship strikes, harpoon or gunshot wounds, or other anthropogenic factors (Haley and Read 1993, Philo et al. 1993, Gulland et al. 2001). Some short-finned pilot whales bear scars on the lips that are consistent with hook injuries from entanglement, and this species is known to interact with long-line fisheries off North Carolina. The data records for the animals in this case series do not allow a consideration of whether soft tissue scars commensurate with this source of trauma were present. Therefore fisheries interaction

should be considered a potential cause of the observed mandibular trauma. Changes in the mechanical structure of bone such as osteoporosis, osteomalacia, or past history of disease or fracture could also affect the propensity of a bone to fracture (Cullinane and Einhorn 2002, Garnero and Delmas 2002, Ortner 2003). The source of the study specimens should also be considered. Because these specimens had mass-stranded, there may be other factors affecting their health or behavior that could have lead to prior strandings. They also had to survive their fractures, since all fractures were healed to some extent. In fact, there was only one fracture rated as obviously recent while a vast majority were rated as being moderately to extensively healed. Therefore, the occurrence of fractures in the population will be influenced both by an individual's capacity for injury and survival of that injury.

A clue as to the source of these fractures may be provided in their location on the mandible itself. All 35 fractures occurred in the caudal third of the mandible (divided transversely), with 20 of those fractures extending into the middle third as well. No fractures were found in the rostral third of the mandible. The caudal mandible is most likely more vulnerable to fractures due to its thinness and less compact structure compared to the rostral portion of the mandible. However, the ventral third of the mandible (divided along the frontal plane) was the location of significantly more fractures than either the middle or dorsal thirds. It is possible that the source of the traumatic injuries is focused on these caudal, ventral portions of the mandible, or that the impact of the injury is transmitted primarily to that region.

One of the most interesting results of this study was that there were so few correlations of fracture characteristics with any morphological or life history characteristics. The small sample size, especially of males, and paucity of data on mandibular fractures in other cetacean species precludes differentiating the aforementioned potential causes of fracture. However, further research on mandibular fractures and characteristics of the force necessary to cause such fractures may help to isolate one or more causes of mandibular fractures in this species.

A broader survey of the incidence and characteristics of mandibular fractures in short-finned pilot whales could help to elucidate the causes of fracture. Comparative data from other sexually dimorphic and socially similar cetacean species may help rule out some explanations and increase the likelihood of others, as would comparison with nonpolygynous or less social species. Incorporating genetic relatedness among members of groups could provide further insight as to the causes and implications of fractures. Such a high occurrence of mandibular fractures in this or other species could have implications for individuals and possibly the species because of the role of the mandible in eating and sound reception. At minimum, quick evaluation and basic data collection on evidence of mandibular fractures at stranding events could be valuable to current understanding of trauma and behavior in cetaceans.

Conclusions

Based on the correlation between body length and fracture presence, male–male competition remains the most likely—but not necessarily the only—explanation for mandibular fractures in males. The causes of the prevalent mandibular fractures in females are not known. Relatively little is known about trauma and behavior in cetaceans, and the high prevalence of fractures and associated results of this study warrant a closer look at fractures in these and other species.

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