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FEATURE ARTICLE

Lethal entanglement in baleen whales

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ABSTRACT: Understanding the scenarios whereby fishing gear entanglement of large whales induces mortality is important for the development of mitigation strategies. Here we present a series of 21 cases involving 4 species of baleen whales in the NW Atlantic, describing the available sighting history, necropsy observations, and subsequent data analyses that enabled the compilation of the manners in which entanglement can be lethal. The single acute cause of entanglement mortality identified was drowning from entanglement involving multiple body parts, with the animal's inability to surface. More protracted causes of death included impaired foraging during entanglement, resulting in starvation after many months; systemic infection arising from open, unresolved entanglement wounds; and hemorrhage or debilitation due to severe gear-related damage to tissues. Serious gear-induced injury can include laceration of large vessels, occlusion of the nares, embedding of line in growing bone, and massive periosteal proliferation of new bone in an attempt to wall off constricting, encircling lines. These data show that baleen whale entanglement is not only a major issue for the conservation of some baleen whale populations, but is also a major concern for the welfare of each affected individual.

KEY WORDS: Baleen whales · Entanglement · Mortality · Cetacean · Strandings · Fishing gear · Necropsy · Northwestern Atlantic

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Location, recovery, beaching, necropsy and disposal of large dead whales pose unique challenges. However, examination of chronically entangled whale mortalities enables mitigation by modification of fishing gear and practices.

Photo: Cynthia Browning

INTRODUCTION

The rapid expansion of global fisheries since the turn of the last century has led to an increasingly large presence of fishing gear in baleen whale (mysticete) habitat (Myers & Worm 2003, Pauly 2009). Since many baleen whale populations inhabit and migrate across continental shelf waters, where >95% of fishing effort occurs, they are at serious risk of encountering and becoming entangled in gear (Pauly 2009). While many baleen whales are able to release

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themselves from fishing line or net, as evidenced by scarring patterns on many individuals (Knowlton et al. 2005), the outcome of entanglement can include long-term severe injury and mortality.

Worldwide, fatal entanglements are a source of non-natural mortality in baleen whale populations, many of which are at low levels of abundance due to intensive commercial whaling efforts during the past 2 centuries (Perrin et al. 1994, Clapham et al. 1999). Exacerbating this problem is the fact that entanglement mortality and its effects on population trends are likely greatly underestimated, due to underreporting by fishermen and a low probability of discovery and recovery at sea (Cole et al. 2006). Most balaenopterid carcasses (e.g. blue, Bryde's, fin, minke, and sei whales), regardless of body condition, initially sink upon death and then only refloat later if they bloat. In contrast, balaenid whales (e.g. right whales) and some humpback whales (family Balaenopteridae) that are in good body condition typically float. Some entangled right whale carcasses can be negatively buoyant due to emaciation at the time of death, after which point they may either bloat from decomposition and then resurface, or remain submerged (Moore et al. 2007).

In the western North Atlantic, entanglement mortality has slowed the recovery of some populations of baleen whales. The most severely affected species is the Critically Endangered North Atlantic right whale *Eubalaena glacialis* (NARW). Despite over 75 yr of legal protection, the NARW has an estimated population of between 400 and 450, making it one of the rarest baleen whale species in the world (Kraus et al. 2005, Josephson et al. 2009). A recent analysis of photo-identified NARWs found that >75% of the population had scars from a previous entanglement in fishing gear and that some of these animals had experienced as many as 6 separate entanglement events. Annual rates of entanglement are also on the rise (Knowlton et al. 2005). A minority of gear entanglements of NARWs resulted in mortality. Of the 50 reported deaths of this species between 1986 and 2002, there were 18 (6 confirmed and 12 presumed) cases of fatal gear entanglement (Moore et al. 2004, Kraus et al. 2005). Human-caused mortality of NARWs continues to be a serious problem (Caswell et al. 1999, Fujiwara & Caswell 2001).

In the Northwest Atlantic, entanglement in fishing gear is also a significant source of mortality for endangered humpback whales *Megaptera novaeangliae*. Five out of the 38 (16%) humpback whales that stranded in the mid-Atlantic to southeastern states of the USA between 1985 and 1992 had injuries consistent with entanglement (Wiley et al. 1995). In addition, 57% of humpback whales observed in the Gulf of Maine had entanglement scars on their caudal peduncle (Robbins & Mattila 2004). For stocks in some areas, such as the Gulf of Maine, entanglement mortality is slowing rates of recovery (Volgenau et al. 1995).

Baleen whales are unique compared to other, smaller cetaceans, in that entanglement mortality often results from chronic pathological processes, rather than drowning. During an encounter with fishing gear, baleen whales often have enough strength to break away from the lines and initially evade death. However, a portion of the gear may remain affixed to one or more body parts, commonly the mouth, flippers and caudal peduncle (Lien 1994, Johnson et al. 2007). The whale can become further entangled in this remaining gear, constricting body parts as the animal struggles to free itself or flexes and extends its body during swimming (Weinrich 1999).

Not only can entanglement directly impair locomotion and foraging ability, leading to starvation, but it can also cause debilitating injury to tissues through physical trauma, constriction, or immobilization (Knowlton et al. 2005, Moore et al. 2006). Serious and debilitating tissue damage caused by attached gear likely plays a major role in the pathogenesis of fatal chronic entanglement in baleen whales. Many of the chronic traumatic entanglement injuries are deep and extensive, penetrating through multiple tissue layers and involving several areas of the body. In a study of all existing necropsy reports for lethally entangled western NARWs for a 30 yr period (Moore et al. 2004), it was found that every whale had sustained gear-induced wounds that penetrated at least to the level of the dermis. In one case, fishing line had wrapped so tightly around the flippers that it had cut through all of the soft tissues, eventually embedding several centimeters into the bone. In another case, line had become anchored to both flippers and gradually excised a 1.5-m-wide section of blubber across the dorsum. Additionally, there have been 2 reported cases of entangled NARWs with severe constriction of the flippers, resulting in immobilization and disuse osteoporosis (Moore et al. 2006).

Gear-induced wounds can lead to death by impairing critical biological functions, becoming a source of hemorrhage, or providing a portal of entry for pathogens. Thirty years of longitudinal observations of NARWs (Knowlton & Kraus 2001) showed that serious (deeply penetrating or infected/necrotic) tissue damage associated with entanglement injuries was likely to be a predictor of mortality.

The progression to death due to entanglement, particularly when it involves severe gear-induced tissue damage, is likely to be slow and painful. Therefore, from a welfare perspective, lethal entanglements of baleen whales are, arguably, one of the worst forms of human-caused mortality in any wild animal. Moore et al. (2006) examined 6 cases of lethally entangled NARWs and found that the average time to death was 5.6 mo. However, some whales with potentially fatal entanglement injuries have survived considerably longer, up to 1.5 yr (Knowlton & Kraus 2001). This prolonged entanglement period is likely supported by the NARWs migratory habits, which are characterized by periods of extensive foraging in high-latitude waters in the summers, and periods of starvation lasting months for those that move to low-latitude waters in winter.

The progression of lethal entanglement in baleen whales and its associated clinical effects, such as chronic pain, have not been described or evaluated, except as part of a broader analysis of NARW mortality (Moore et al. 2004). The aims of the present study were to (1) analyze data collected between 1995 and 2009 from a series of Northwest Atlantic baleen whale mortalities involving acute or chronic entanglement in fishing gear and (2) summarize the pertinent gross and histopathology findings for these cases and compare these findings in order to gain a better understanding of the major factors contributing to entanglement lethality.

METHODS

Data for our analysis were obtained from 21 mortality reports for entangled baleen whales that stranded in Atlantic waters of the USA or Canada during the period from 1995 to 2009. Reports were provided by 4 different sources that maintain baleen whale stranding databases: The International Fund for Animal Welfare Marine Mammal Rescue and Research division (IFAW, formerly the Cape Cod Stranding Network); the North Atlantic Right Whale Consortium (NARWC) necropsy database, curated by the Woods Hole Oceanographic Institution; the University of North Carolina Wilmington (UNCW); and the Virginia Aquarium (VAQ). The extent of each post-mortem examination and report varied, depending on the condition and location of the carcass, the availability of necropsy equipment and experienced examiners, and the environmental conditions at the time of examination.

Life-history and carcass-quality data, when available, included sex, age or age class, total length (TL; straight distance from the tip of the snout to the fluke notch), total body weight, and a description of carcass quality. Age or age class was reported as either the minimum known age based on sighting histories archived in the NARWC sightings database maintained at the New England Aquarium, or estimated age based on published growth curves (Stevick 1999, Olsen & Sunde 2002, Moore et al. 2004). Total body weight was measured as described previously by Moore et al. (2004).

The mortality reports used in our study were variably complete. Some or all of the following parameters were reported for each case: geographic position of the carcass upon discovery; carcass condition code at stranding; burden of cyamid whale lice (Crustacea: Amphipoda), scored subjectively as low, moderate, or high; duration of entanglement; involvement by a disentanglement group; number and types of body parts where gear was attached; amount of fishing lines or nets involved; depth of entanglement wounds; and presence of previous entanglement scars. Carcass condition code at stranding, which reflects the extent of carcass decomposition, was reported on a scale of 1 to 4, where 1 = live, 2 = fresh, 3 = moderate decomposition, and 4 = advanced decomposition (Geraci & Lounsbury 1993).

In order to describe the progression to death due to entanglement, we summarized major gross and histopathology findings, entanglement pattern, and reported cause of death, for each case. A suite of images of gross and/or microscopic lesions was compiled from the above-mentioned stranding databases to highlight important features involved in the pathogenesis of entanglement mortality. Cases were then compared in terms of sex, age, duration of entanglement, number and types of body parts entangled, and depth of gear-related tissue injury, in order to identify factors that likely contribute to lethality.

RESULTS

A total of 21 baleen whales (Table 1) were examined in our analysis, including 5 minke whales *Balaenoptera acutorostrata*, 1 Bryde's whale *B. brydei*, 7 North Atlantic right whales *Eubalaena glacialis*, and 8 humpback whales *Megaptera novaeangliae*. Complete post-mortem examinations were conducted on many of these animals: 8/21 were examined by partial or full necropsy with histopathology samples collected and analyzed; 8/21 were examined by partial or full necropsy only; and 5/21 were examined by external visual assessment only. Individual case

Table 1. Summary of life-history and body-condition data, as well as type of post-mortem examination performed (V: visual exam; N: necropsy; H: histopathology) and probable cause of death, for northwestern Atlantic large whale entanglement mortality cases between 1995 and 2009. CCSN: Cape Cod Stranding Network (now Marine Mammal Rescue Research, International Fund for Animal Welfare); UNCW: University of North Carolina Wilmington; NARWC: North Atlantic Right Whale Consortium; VAQ: Virginia Aquarium; TL: total length; –: no available data

Case	Field number(s)	Source	Sex	Age (yr)	TL (m)	Weight (kg)	Body condition	Exam. type	Probable cause of death
Balaenoptera acutorostrata									
1	CCSN 99-127/MH 99-638-Ba	CCSN	F	Juvenile	6.9	–	Emaciated	V	Could not be determined
2	CCSN 03-147-Ba	CCSN	F	Juvenile	4.5	–	Good	N, H	Impaired foraging and starvation
3	CCSN 04-175-Ba	CCSN	F	Adult	7.9	–	Not emaciated	N	Could not be determined
4	CCSN 07-194-Ba	CCSN	F	Juvenile	4.3	576	Severely emaciated	N, H	Systemic infection
5	CCSN 08-125-Ba	CCSN	F	Juvenile	4.7	907	Good	N	Asphyxia from drowning
Balaenoptera brydei									
6	WAM 587	UNCW	M	Adult	11.1	–	Severely emaciated	N, H	Impaired foraging and starvation
Eubalaena glacialis									
7	Eg 2366/MCZ 62052	NARWC	M	2.5	10.3	9 036	–	N	Impaired foraging and starvation
8	Eg 2030/CCSN 99-143	CCSN	F	Min. 10	13.5	15 382	Emaciated	N	Debilitating tissue damage
9	Eg 1238	NARWC	M	Min. 19	14.6	–	Not emaciated	N	Asphyxia from drowning
10	Eg 3107/MH 02-726	NARWC	F	1	11.0	–	Emaciated	N, H	Hemorrhage
11	Eg 2301/VAQS 2005-1008-Eg	NARWC	F	12	13.8	–	Emaciated	N, H	Hemorrhage
12	Eg NEFL-0603	NARWC	F	Calf	5.6	–	Good	N, H	Could not be determined
13	Dead Eg 052106	NARWC	F	3.5	11.3	–	–	V	Could not be determined
Megaptera novaeangliae									
14	CCSN 99-001/MH 99-403-Mn	CCSN	M	Juvenile	9.7	–	Good	N	Asphyxia from drowning
15	CCSN 00-079/MH 00-554-Mn	CCSN	M	Juvenile	8.4	–	Emaciated	V	Could not be determined
16	CCSN 00-126/MH 00-766-Mn	CCSN	-	Calf	6.4	–	–	V	Asphyxia from airway obstruction
17	SC 01-18-Mn	UNCW	M	Calf	7.9	–	Severely emaciated	N	Could not be determined
18	CCSN 02-255	CCSN	F	Calf	7.5	–	Good	N	Asphyxia from drowning
19	CCSN 03-145-Mn	CCSN	F	Juvenile	9.5	–	–	V	Could not be determined
20	MLC002	VAQ	M	Juvenile	9.4	–	Severely emaciated	N, H	Systemic infection
21	KLC033	VAQ	M	Juvenile	10.0	–	–	N, H	Could not be determined

material and images are available in the supplement at www.int-res.com/articles/suppl/d096p175_supp.pdf.

Our sample consisted of 5 calves, 11 juveniles, and 5 adults. There were a slightly higher number of females than males (12 females, 8 males, and 1 of unknown sex) (Table 1 and the supplement for each case). Total length of these animals ranged from 4.3 to 14.6 m and averaged 9.0 m. Total body weight was reported for only 4 animals and ranged from 576 to 15 382 kg. Fifty-six percent (9/16) of whales of known body condition were reported to be either emaciated or severely emaciated, while 44 % (7/16) were reported to be either not emaciated or in good body condition (Table 1).

Baleen whale strandings occurred between Florida and Québec, Canada, although nearly half were concentrated along the Cape Cod peninsula in Massachusetts (Table 2). On average, the carcasses were moderately decomposed at the time of stranding (condition code = 3). Eight animals still had gear attached when their carcasses were found. In the other cases, the nature of the entanglement was inferred from line or net impressions and lacerations on the body (average number of lines = 3) (Table 2). The entanglements involved all body parts (i.e. mouth, head, blowhole, trunk, dorsal fin, flippers, peduncle, and flukes). However, the mouth was entangled in 67 % (14/ 21) of the cases, making it the most common attachment site for fishing gear. Other common sites of attachment were the peduncle and flippers, each present in 52 % (11/21) of cases.

The depth of gear-induced wounds ranged from 1.2 to 20 cm. In 7 of the whales, gear had penetrated at least into the blubber, and in 5 of these cases, gear had cut into the bone. Cyamid burden was reported for 3 cases in which there were

Table 2. Summary of stranding and entanglement data for northwestern Atlantic large whale mortality cases between 1995 and 2009. Code: body condition code (1 = live, ... 4 = advanced decomposition); –: no available data; max. depth: maximum depth of tissue penetration by fishing gear

Case	Stranding			Entanglement					Cyamid burden
	Date	Location	Code	Gear present	No. lines	Duration (d)	Body parts and tissue penetration: Type	Max. depth	
Balaenoptera acutorostrata									
1	Jun 16, 1999	Nauset Bch, Orleans, MA	4	N	–	–	Mouth, dorsal fin, peduncle	2 cm	–
2	Aug 10, 2003	Stage Hbr, Chatham, MA	3	N	–	–	Mouth, head, possibly flukes	–	–
3	Jul 19, 2004	Eastham, MA	3	N	–	–	Mouth, trunk, dorsal fin, peduncle, flukes	2 cm	–
4	Aug 5, 2007	Offshore near Cornhill Bch, MA	3	Y	1	–	Flippers, trunk, L fluke	4 cm	–
5	Jun 14, 2008	Nauset Bch, Orleans, MA	3	N	–	–	Mouth, head, blowhole, trunk, peduncle, L flipper	–	–
Balaenoptera brydei									
6	Mar 13, 2003	Carolina Beach, NC	2	Y	1	–	Mouth	–	–
Eubalanea glacialis									
7[a]	Jul 17, 1995	Second Bch, Middletown, RI	–	Y	7–9	323	Mouth, R flipper	7.6 cm	Moderate
8[b]	Oct 20, 1999	Offshore, near Cape May, NJ	4	Y	4	>126	Trunk, flippers	17.8 cm	Heavy
9[a]	Oct 29, 2001	Offshore near Magdalen Isl's, QB	4	Y	3–4	–	Mouth, flippers, peduncle, L fluke	–	Moderate
10[ab]	Oct 12, 2002	Low Bch, Nantucket, MA	3	N	1	28–268	Peduncle	19 cm	Heavy
11	Mar 3, 2005	Wreck Island, VA	–	Y	1	207–487	Mouth, blowhole, L flipper	–	Heavy
12	Jan 22, 2006	Offshore, near Jacksonville, FL	3	N	–	3–21	Peduncle	1.2 cm	Heavy
13	May 18, 2006	Offshore, near Block Isl, RI	–	N	–	–	Mouth, head, R flipper, peduncle	–	–
Megaptera novaeangliae									
14	Jan 12, 1999	Squibnocket Bch, Martha's Vd, MA	3	N	–	–	Mouth, peduncle	20 cm	–
15	May 12, 2000	First Encounter Bch, MA	4	N	–	–	Trunk	–	–
16	Oct 7, 2000	Sandy Neck Bch, MA	4	Y	1	–	Blowhole	–	–
17[c]	Apr 8, 2001	Myrtle Bch, SC	2	N	–	–	Peduncle	–	Heavy
18	Oct 1, 2001	Race Point Bch, P'town, MA	3	N	3	–	Mouth, flippers, trunk, peduncle	–	–
19	Jul 28, 2003	Georges Bank	3	N	–	–	Mouth, head, flippers	–	–
20[a]	Dec 21, 2007	Offshore near Ocean Sands, NC	3	Y	1	–	Mouth, flippers, trunk, peduncle, dorsal fin, L fluke	–	–
21[a]	Feb 16, 2009	Nags Head, NC	3	N	–	–	Mouth, head, flippers, trunk	3.5 cm	–
Mean					Mean = 3				

[a]These animals were reported to have scars from a previous entanglement event
[b]These animals were partially or fully disentangled by a disentanglement group
[c]This animal also had propeller wounds

deep bone-penetrating entanglement injuries, and was found to be heavy in all instances. A diagnosis of probable cause of death was reached in 13 of the cases. Each diagnosis fell into 1 of 5 major categories: asphyxia due to drowning or airway obstruction (n = 5), starvation due to impaired foraging (n = 3), systemic infection (n = 2), severe hemorrhage (n = 2), or debilitating tissue damage (n = 1) (Table 1). In the remainder of the cases, a specific cause of death could not be determined, but entanglement was identified as a major factor.

DISCUSSION

Acute drowning

Drowning due to entanglement was the probable cause of death in 4 whales and was the only acute cause of mortality identified in our study. Three of the 4 individuals that drowned were either calves or juveniles, suggesting that young age may predispose whales to drowning. The greater vulnerability of younger age classes is likely most attributable to their smaller size. Evidence from previous studies suggests that there may be a threshold size above which individuals have gained enough body mass and strength to either drag the gear to the surface or tear free of the line. An analysis of data from 576 humpback whales *Megaptera novaeangliae* reported entangled in inshore fisheries off Newfoundland and Labrador (Lien 1994) found that most of the whales that drowned were juveniles (<11 m TL). Similarly, all but one of the whales in our study that succumbed to drowning were <10 m TL. The exception to this size limit was Case 9, a 14.6 m right whale *Eubalaena glacialis*. However, this whale was extensively entangled in >200 m of a 2.2 cm diameter line. Thus, drowning is possible at any body size if the extent, weight, and strength of the entangling gear are sufficient.

Another factor that may increase the risk of drowning in gear is the number of body parts affected by entanglement. In our study, nearly all of the whales that drowned had gear fixed to 5 or more body parts. As more of the body becomes wrapped in fishing gear, the amount of line reduces the probability that enough of the gear will part to release the whale. Additionally, mobility would be expected to become increasingly restricted, diminishing the likelihood of escape. In fact, one of the whales that drowned had one of the worst entanglement scenarios among all 21 cases, with line wrapped 12 times around its body from head to tail, forming a crisscross pattern along its back and pinioning its flippers tightly to its sides (Fig. 1).

Impaired foraging and starvation

Impaired foraging and starvation was another major cause of mortality in entangled baleen whales and was identified as the probable cause of death in 3 individuals. Not surprisingly, we found that the deterioration of health due to compromised foraging can be extremely protracted. For example, a NARW gradually starved to death over the course of a 320 d period, which was the longest confirmed entanglement duration reported in our sample. Furthermore, 1 Bryde's whale *Balaenoptera brydei* (Case 6) was so severely emaciated when it died that the outlines of its ribs and scapulae were very evident through the blubber, suggesting long-term starvation.

While there was evidence in 1 case that impaired locomotion contributed to starvation, direct disruption of feeding mechanics by gear was likely the primary reason why starvation occurred, as all 3 whales had severe entanglement of the mouth. The Bryde's

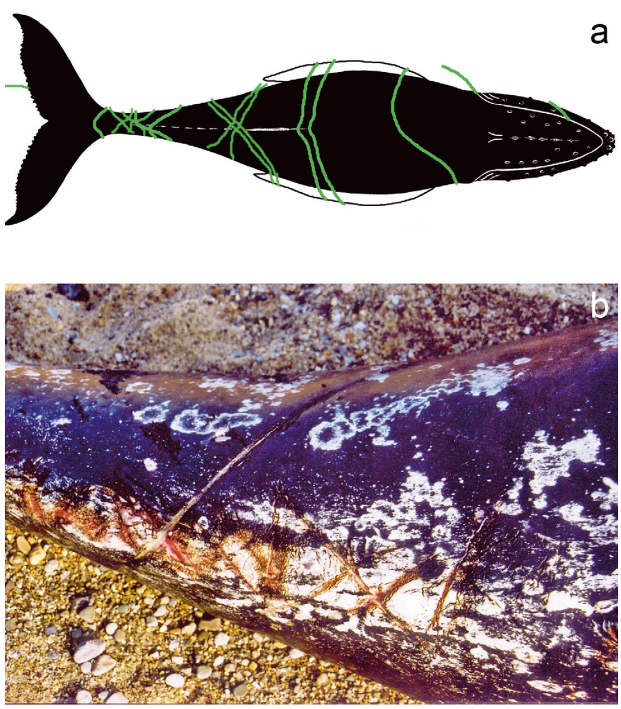

Fig. 1. *Megaptera novaeangliae.* Case 18: (a) Sketch of the entanglement that drowned a humpback whale (drawing by Scott Landry, Provincetown Center for Coastal Studies). (b) Multiple line impressions across the caudal peduncle

whale (Case 6), had lines stretched tightly across its oral cavity, deeply embedded in the bones of the roof of the mouth (Fig. 2). One minke whale *Balaenoptera acutorostrata* (Case 2) had a large amount of net wrapped around its mandible, passing through the oral cavity and over the distal rostrum.

In baleen whales, foraging is likely greatly disrupted by gear in or around the mouth, given the complexities of the filter-feeding apparatus. Although all mysticetes have many long, hair-fringed baleen plates suspended from the maxilla, each of the baleen whale families has evolved numerous morphological and functional adaptations of the mouth that greatly enhance their feeding ability (Pivorunas 1979, Werth 2004). For example, in balaenid whales (e.g. right whales), the ability of the jaw to rotate laterally during feeding leads to the formation of hydrostatic forces that not only suck water out of the mouth's interior through the baleen, but also reduce bow wave formation, allowing the whale to approach prey in stealth (Lambertsen et al. 2005). These negative pressures generated could also suck line deeply into the oral cavity.

In balaenopterids (e.g. humpback, minke, Bryde's whales) successful feeding is highly dependent on the whale's ability to engulf enormous volumes of prey-laden water (>60 m^3) that is later filtered by the baleen (Pivorunas 1979). To facilitate engulfment, the whales have loose joints in the mandible that allow the lower jaw to drop almost 90°; a long, greatly distensible ventral cavity (cavum ventrale) beneath the mouth, throat, and thorax to increase the oral capacity; and a flaccid, pouch-like tongue that distends the ventral cavity by filling with water (Lambertsen 1983).

Fig. 2. *Balaenoptera brydei*. Case 6: Bryde's whale with impaired feeding. Line under great tension ran across and embedded in the mouth, penetrating the midline bones of the rostrum. It was concluded that this animal died from debilitation and impaired foraging leading to starvation due to chronic entanglement. Photo: Marine Mammal Stranding Program, University of North Carolina Wilmington

A considerable impairment of feeding mechanics due to entanglement has been documented in an adult minke whale *Balaenoptera acutorostrata* (Kot et al. 2009). The whale had a single, circumferential line laceration around the throat, and, although gear no longer remained on the animal, ventral cavity distention was still significantly reduced. Compared to 5 uninjured minke whales, the injured animal distended its ventral cavity 25% less. This whale also displayed nearly continuous bouts of foraging, likely in an attempt to compensate for impaired feeding ability due to its entanglement injury.

In an entanglement of the mouth, the negative effects on feeding mechanics may be further compounded by disruption of another critical adaptation, the hydrostatic oral seal, which is thought to form when upper and lower lips are in complete apposition. The seal allows for negative pressure generation in the oral cavity and, in turn, passive elevation of the lower jaw (Lambertsen & Hintz 2004). If fishing gear were to compromise this seal, the high energetic costs associated with actively keeping the mouth closed during swimming would eventually lead to starvation and death (Lambertsen et al. 2005).

In light of our findings and the presence of such complex feeding adaptations in baleen whales, we suggest that oral entanglement may pose one of the greatest threats to survival in entangled baleen whales. Not only did oral entanglement occur in 64% of all lethally entangled whales that we examined, but it directly led to the demise of at least 3 animals, due to impaired foraging and possibly loss of function of the hydrostatic seal. Gear in or around the mouth would almost certainly lead to some degree of nutritional stress, leaving animals in a more vulnerable state of health and, thus, increasing the risk of mortality. The survival of Critically Endangered NARWs may be more severely threatened by mouth entanglement, as this species is particularly prone to contacting gear with its mouth (Johnson et al. 2005), given that it tends to swim open-mouthed for long periods when feeding. Attempts to remove gear attached to the mouth by human disentanglement teams have proved to be very challenging, since the head is the least accessible area on the whale's body. However, Moore et al. (2010) describe a technique to sedate whales at sea in order to facilitate removal of gear from the mouth in baleen whales.

Systemic infection

Disseminated infection was diagnosed as the primary cause of death in 2 fatally entangled whales. Gross and histopathology findings suggest that disease was initiated by laceration and subsequent infection of the skin during entanglement. Gear-induced wounds in both animals were relatively superficial (none penetrated past the blubber), but covered a large surface area. For instance, one minke whale (Case 4) had a gaping cut (up to 7 cm wide), which exposed the blubber and encircled most of the body's diameter (Fig. 3). In addition, it had multitudinous line lacerations on the flippers and left fluke. In both of the whales, post-mortem examination revealed that bacteria had proliferated in the lacerations. Given that the wounds were relatively superficial, they likely did not cause severe debilitation initially. However, the gear lacerations left a large area unprotected by epithelium, promoting bacterial colonization and the entry of pathogens into the body.

The progression to death due to systemic infection was characterized by the gradual weakening of immune defenses and the development of multiple secondary infections. For example, in addition to having bacterial infections of its gear lacerations, Case 4 developed severe necrosuppurative bronchopneumonia that most likely led to bacterial embolization of the brain. Histological analysis of gear lacerations in the 2 animals that died from systemic infection indicated that the time course of disease ranged from weeks to months.

Fig. 3. *Balaenoptera acutorostrata*. Case 4: Minke whale with septicemia, following a line-induced necrotic laceration around two-thirds the girth anterior to the left flipper. Internally the animal had severe necrosuppurative bronchopneumonia and bacterial emboli in the brain, as well as liver and blubber atrophy

Chronic stress resulting from entanglement may have contributed to the development of systemic infection in the whales we examined. Entanglement in fishing gear is sufficiently stressful to cause both a behavioral and physiological stress response in baleen whales. A humpback whale entangled in gill net showed considerable signs of distress, including long bouts of continuous tail thrashing, vigorous head shaking, and repeated distress calls (Weinrich 1999). Fecal glucocorticoid measurements in free-ranging NARWs showed that the hormone levels in a severely entangled whale were dramatically elevated (4 to 5 times above baseline) (Hunt et al. 2006). As cetaceans are sensitive to the immune-compromising effects of glucocorticoids, they would be more susceptible to acquiring infectious disease under conditions of chronic stress (St. Aubin & Dierauf 2001). Long-term stress from being chronically wrapped in gear may explain why the 2 whales that we examined were unable to fight off the initial insult of infected gear lacerations, most likely leading to their demise.

Hemorrhage or debilitation from severe tissue damage

In 3 of the whales that we examined, fishing gear caused massive traumatic tissue damage that resulted in either fatal hemorrhage or debilitation. The compressive and constrictive forces exerted by the entangling lines were so extreme that they caused some of the worst traumatic gear-induced injuries in baleen whales ever reported in the published literature. In 1 NARW (Case 8), line stretched between both flippers flensed a 1.5 m wide section of blubber from the back, revealing underlying muscle, as well as both scapula bones (Fig. 4). In addition, it incised through all of the soft tissues at the leading edge of the flipper and embedded deeply into the bone, causing fatal debilitation. In another animal (Case 11), sink and float lines, extending from the mouth to the left flipper insertion, carved a 6 cm wide, 42 cm long furrow across the blowhole, as well as a 60 cm wide notch in the left humerus, resulting in severe hemorrhage and death (Fig. 5). In the third

Fig. 4. *Eubalaena glacialis*. Case 8: Debilitating tissue damage in a North Atlantic right whale. Lines under marked tension were wrapped around each flipper insertion and across the dorsum and ventrum from flipper to flipper, incising down to the skeletal muscle on the back. The lines then moved caudally, flensing a large section of blubber. Photo: Lisa Conger

animal (Case 10), lobster gear constricted the caudal peduncle and cut 19 cm into the soft tissue, severing 2 large superficial ventral arteries, which were presumed to be the site of fatal blood loss.

Progression to death due to severe tissue damage

The degree of traumatic injury inflicted by gear is most likely dependent on the extent and duration of entanglement. When gear is attached to >1 body part, it becomes more tightly cinched as the animal flexes and extends to propel itself through the water. As time passes, it cuts more deeply into tissues (Moore et al. 2007). Based on sighting histories, the 3 whales that died from gear-induced tissue damage were entangled for extremely long periods of time, on average, at least 6 mo. One whale may even have been entangled for as long as 1.3 yr before it died from its entanglement wounds. Currently, modern fishing gear, such as monofilament, traplon, and polypropylene rope, is designed to maximize strength and durability (McKenna 2006), jeopardizing the safety of whales that encounter it. Fishing gear modifications are the most widely advocated approach for reducing entanglement mortality (Johnson et al. 2005, 2007). Modifications, such as designing fishing line with increased elasticity so that it stretches when the animal flexes, with weak segments that break under marked tension, or with more rapid biodegradability, may reduce the likelihood of severe entanglement trauma and mortality in baleen whales (Johnson et al. 2007, Winn et al. 2008).

We found that the degree of cyamid infestation may be a useful indicator of the severity of gear-related injuries in baleen whales. Cyamids live exclusively on cetaceans, feeding primarily or exclusively on epidermal cells (Schell et al. 2000). Since they are unable to survive once detached from their host, they tend to aggregate focally on areas of the skin surface where water flow is reduced, such as the blowhole, skin folds, lip margins, and callosities (i.e. patches of thickened epidermis) (Rowntree 1996). However, in some chronically debilitated animals, which are unable to maintain normal swimming speeds, cyamids have been found to increase in abundance and, in some cases, occupy most of the body surface (Osmond & Kaufman 1998, Pettis et al. 2004). For this reason, cyamid burden could be used to visually assess overall health in baleen whales (Pettis et al. 2004). Although cyamid burden was not reported for the majority of cases in our study, it was highly elevated in the 3 chronically entangled whales that sustained massive traumatic injuries from fishing line. Not only did cyamids cover most of the whales' skin surface, but they also concentrated in very high densities within the shelter of deep entanglement lacerations.

Fig. 5. *Eubalaena glacialis*. Case 11: Line impression resulting from chronic occlusion of the left nares of a North Atlantic right whale. Line embedded in multiple twists around the left baleen plates, exited the right mouth, crossed over the blowhole, and then wound tightly around the left flipper inducing a major periosteal proliferation around the radius and ulna. Photo: Virginia Aquarium Stranding Program

Deep gear-related tissue injuries in baleen whales are a major concern, not only because they cause mortality, but also because they likely are accompanied by chronic pain and, therefore, may jeopardize the welfare of individual animals. In our study, severe constriction of 1 or more limbs by fishing line occurred in all 3 whales that died from gear-induced tissue damage. The appendages of fin whales are supplied by an extensive neurovascular plexus, of a size and structure which suggests that pain sensation in whales is likely comparable to that in humans (Ogden et al. 1981). Thus, the clinical effects of limb constriction injuries would be expected to cause intense and persistent pain in baleen whales.

Furthermore, long-term circumferential limb constriction in humans (e.g. when a cast is applied too tightly) results in an extremely painful condition called compartment syndrome (Janzing 2007, Singh et al. 2008). The syndrome occurs due to reduced venous outflow and subsequent elevation of tissue pressure within the constricted limb. If pressure is not relieved, ischemia and necrosis of muscle and nerve fibers ensues, causing the disorder's hallmark symptom of intense, unrelenting, deep pain that is unresponsive to analgesia (Kampa & Fairbank 2005, Janzing 2007). According to our data, entangled whales with severe limb wraps may thus endure extreme pain for very protracted periods of time, ranging from months to over a year.

CONCLUSIONS

There is an increasing concern in the scientific literature about the welfare implications of baleen whale entanglements (Moore et al. 2006, 2007). However, entanglement reduction strategies have continued to focus solely on the impact of entanglement on species survival, while overlooking the issue of animal welfare (Moore et al. 2006). The present study highlights the urgency and importance, not only of reducing the risk of serious gear-related trauma, but also of addressing the potential suffering of baleen whales entangled in fishing gear.

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