

Levels and probable origin of predatory scarring on humpback whales (*Megaptera novaeangliae*) in east Australian waters

Patricia J. Naessig^{A,B} and Janet M. Lanyon^{A,C}

^ADepartment of Zoology and Entomology, School of Life Sciences, University of Queensland, Brisbane, Qld 4072, Australia.

^BPacific Whale Foundation, 101 North Kihei Road, Kihei, HI 96753, USA.

Present address: 2617 Clarkway Drive, Sioux Falls, SD 57105, USA.

Email: naessig@bigpond.com

^CTo whom the correspondence should be addressed. Email: jlanyon@zoology.uq.edu.au

Abstract. To investigate the incidence of non-lethal predation in Southern Hemisphere whales, more than 3400 fluke-identification photographs from resight histories of 1436 east Australian humpback whales were examined for evidence of predatory markings. Photographs were obtained from 1984 to 1996 at various locations along the east coast of Australia, from northern Queensland to southern New South Wales. Photographs were classified in terms of the level and type of scarring. The possible predator and whether the markings appeared fresh were also noted. In all, 17% of identified east Australian humpbacks possessed some form of predatory scarring, 57% of which was minor and 43% major. Almost all predatory scarring was consistent with that inflicted by killer whales. Only three whales demonstrated an increase in the level of predatory scarring after their first sightings. Two incidents of fresh scarring were recorded, and one fatal killer whale attack on a humpback whale calf was directly observed. The overall level of predatory scarring found in this study is comparable to those found in studies for Northern Hemisphere humpback whales. The low incidence of adult whales showing their first sign of predatory scarring after their initial sighting, and the small number possessing recent scarring, support the idea that east Australian humpback whales experience most predatory attacks early in life.

Introduction

Populations of humpback whales (*Megaptera novaeangliae*) in both the Northern and Southern Hemispheres assemble in warm waters for breeding and calving during winter months, and migrate to temperate or polar waters for feeding during summer months (Clapham 2002). Humpback whales found along the east coast of Australia migrate between their Antarctic feeding grounds and the breeding and calving grounds of the Great Barrier Reef and Polynesia (Chaloupka and Osmond 1999). The annual migration of these humpback whales along the eastern Australian seaboard made them the target of a major shore-based whaling industry that operated until the early 1960s. During this period, the east Australian humpback whale population dropped from an estimated 10000 whales in 1951 to as few as 200–500 animals (Chittleborough 1965; Bryden *et al.* 1990). Since the cessation of whaling, the east coast population has slowly recovered at a rate estimated at (arguably) 4–6% (Chaloupka *et al.* 1999) or as high as 11–12% per annum (Brown and Butterworth 1999; Paterson *et al.* 2001). Current extrinsic sources of mortality during

migration include net entanglement and predation (Corkeron and Connor 1999; Janetski and Paterson 2001).

The most commonly observed natural predators of humpback whales and other baleen whales are killer whales (*Orcinus orca*) (Jefferson *et al.* 1991). False killer whales (*Pseudorca crassidens*) (Palacios and Mate 1996) and a few species of large shark have also been recorded as attacking cetaceans at times (Long and Jones 1996). Predation affects mortality rates (Finley 1990), social behaviour (Connor 2000) and life-history strategies (Corkeron and Connor 1999; Connor and Corkeron 2001) of cetaceans. Corkeron and Connor (1999) hypothesise that baleen whales (including humpback whales) undertake extensive migrations from high-latitude feeding grounds to low-latitude breeding and calving grounds to avoid predation upon their newborn calves by common high-latitude predators such as killer whales.

Very little is known about the extent to which humpback whales and other baleen whales are exposed to predation (Clapham 2000). Jefferson *et al.* (1991) compiled records of fewer than 30 fatal killer whale attacks on humpback whales

around the world. Since that review, a few additional attacks on humpbacks by killer whales and other attackers have been observed (e.g. Florez-Gonzalez *et al.* 1994; Mazzuca *et al.* 1998; Visser 1999; Saulitis *et al.* 2000). These infrequent and opportunistic observations probably belie the number of predatory interactions and the total number of successful (lethal) predatory attacks that occur (Jefferson *et al.* 1991). Unless witnessed, a lethal attack would generally leave no trace (e.g. Hancock 1965; Paterson and Paterson 2001). Since direct observations of predation on baleen whales are relatively rare, the presence of non-lethal predatory scars has been used as an indicator of predatory interactions (Schevchenko 1975; Katona *et al.* 1980, 1988; Dolphin 1987; Kraus 1990). In the Northern Hemisphere, up to 23% of North Pacific humpback whales (Steiger and Calambokidis, personal communication) and 15–20% of identified Alaskan humpback whales (Dolphin 1987) show evidence of non-lethal predatory attacks.

This study examines the incidence and likely sources of non-lethal predatory scarring on Southern Hemisphere humpback whales along the eastern coastline of Australia from 1984 to 1996, and reports on one observed lethal attack. Whilst most other studies that document the incidence of scarring make assumptions regarding their origins, this paper attempts to document the relative frequencies of scars caused by multiple predators.

Materials and Methods

From 1984 to 1996, the Pacific Whale Foundation (PWF) collected identification photographs of ventral fluke (Katona and Whitehead 1981) and lateral body (Kaufman *et al.* 1987) pigmentation patterns for all humpback whales encountered at several locations along the east coast of Australia during both the northern and southern migrations (Fig. 1). The combined fluke and lateral body pigmentation photographs permitted identification of individual whales.

Observations were conducted from a small boat staffed by a photographer, an observer/driver and data recorder. Pods of whales were approached unobtrusively, and identification photographs taken whenever possible. For each pod encountered, the following data were recorded: date, time, location, group size and composition (e.g. calf, subadult, adult), sex (from photo-documentation of the genital area

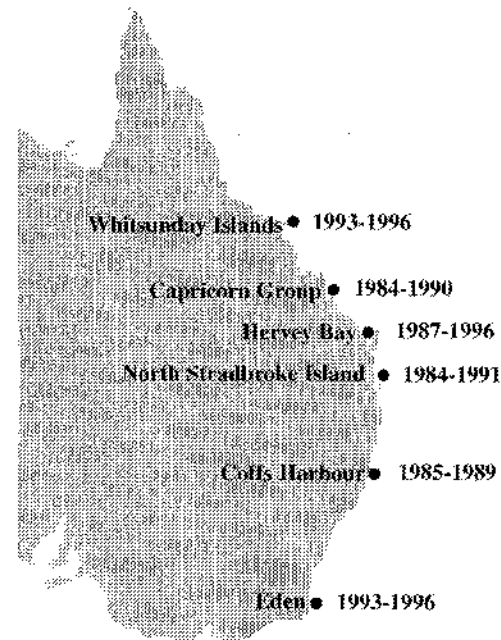


Fig. 1. Locations and dates of humpback whale photo-identifications compiled along the east coast of Australia.

and/or behaviour), behaviour, and sea surface temperature. Age class was based on body size and length of sighting history. Calves were always less than five months of age, i.e. observed in the neonatal period before the southward polar migration. Comparable research protocols were applied across all study areas and years (Kaufman *et al.* 1987, 1993; Chaloupka *et al.* 1999).

Individual whales identified by fluke and lateral body markings were catalogued for each season. A computerised frame-by-frame record of all photographs taken in the field and any associated data were maintained for each pod, and for each individual animal. The best fluke and lateral body images of each whale were compared within and across seasons to compile a resight history for each whale. This process resulted in an extensive catalogue containing over 3400 sightings of 1436 whales.

Identification photographs for each whale were examined for predatory scarring across their entire resight history (1–13 years). Whales were classified into categories of: 0 = no body scarring present,

Table 1. Characteristics of typical scar patterns from possible predators

Predator	Characteristics of scar patterns
Killer whale	Rake marks consistent with the dentition of killer whales comprise linear, parallel scars spaced 2.5–5.0 cm apart. The normal distance between scars is based upon the spacing of the 20–26 conical teeth found on the upper and lower jaw of the killer whale (10–12 teeth in a row, 40–54 total teeth in the skull) (George <i>et al.</i> 1994; Hooker 1998; Carwardine <i>et al.</i> 2000)
False killer whale	Rake marks consistent with the dentition of false killer whales comprise linear, parallel scars spaced ~1.0–2.5 cm apart. The normal distance between scars is based upon the spacing of the 14–24 pointed and curved teeth found on the upper and lower jaw of the false killer whale (7–12 teeth in a row, 28–48 total teeth in the skull) (Carwardine <i>et al.</i> 2000; Wursig <i>et al.</i> 2000)
Shark	Rake marks or bite patterns consistent with the dentition of sharks known to feed on larger cetaceans (e.g. great white sharks, tiger sharks, etc.) comprise wide parabolic or arc-shaped wounds with numerous penetrations, ragged edges and jagged serrations. The bite patterns can also take the form of deep oval continuous bites that cut completely through the tissue layer of the whale. The scar patterns are caused by numerous serrated teeth found in the upper and lower jaw of the shark (e.g. great white sharks have 12 or 13 teeth in a tooth row). Depending on the species, bite widths for possible predatory sharks range between 10 and 60 cm (George <i>et al.</i> 1994; Long and Jones 1996).

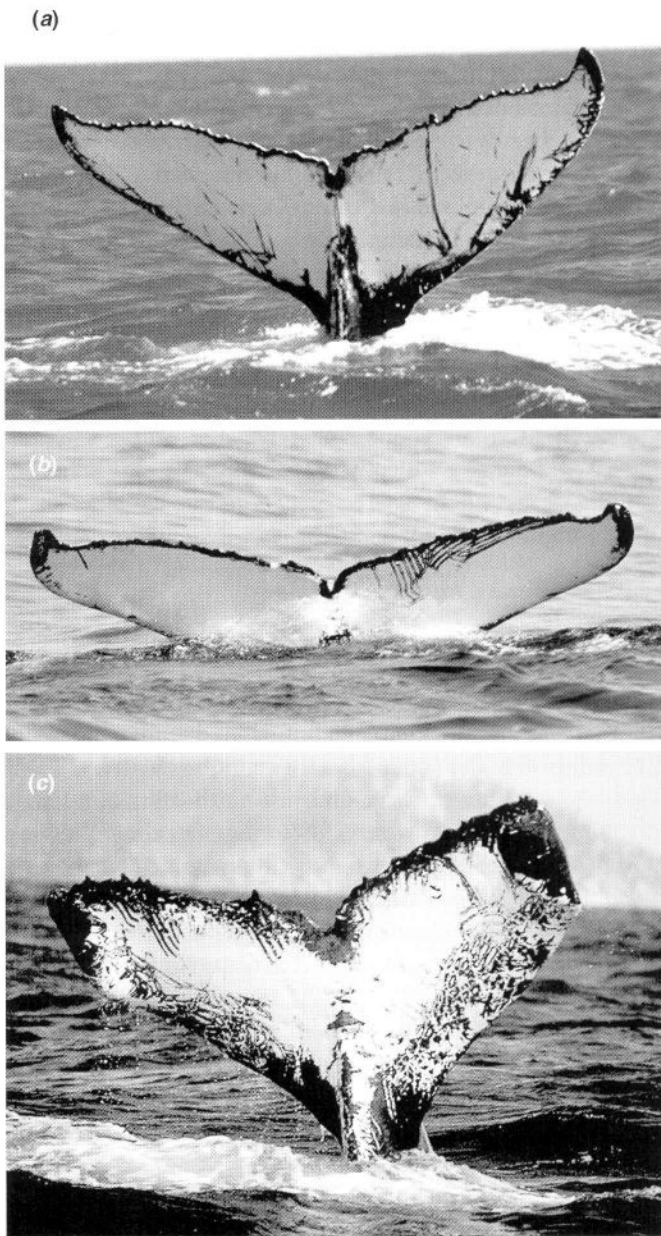


Fig. 2. Predatory scarring on humpback whales. (a) ‘Non-predatory scarring’, i.e. scarring on the tail flukes consistent with barnacle scratches and possible entanglement. (b) ‘Minor predatory scarring’, i.e. three sets of killer whale rake marks on upper right portion of fluke. (c) ‘Major predatory scarring’, i.e. extensive and overlapping killer whale rake marks on flukes and peduncle.

1 = non-predatory scarring (Fig. 2a), 2 = possible predatory scarring (origin unknown), 3 = minor predatory scarring (1–3 sets of rake marks) (Fig. 2b), 4 = major predatory scarring (4 or more sets of rake marks and/or a portion of the tail missing, resulting from repeated or sustained attack) (Fig. 2c). This classification scheme was similar to that adopted for analysis of scarring in North Pacific humpback whales (Steiger and Calambokidis, personal communication). Rake marks were defined as a set of at least three distinct parallel scars caused by the dentition of a predator (Table 1). Non-predatory scars included those attributable to barnacle scratches, net/rope entanglement, and collision with ships (after Kraus 1990). A classification of ‘possible

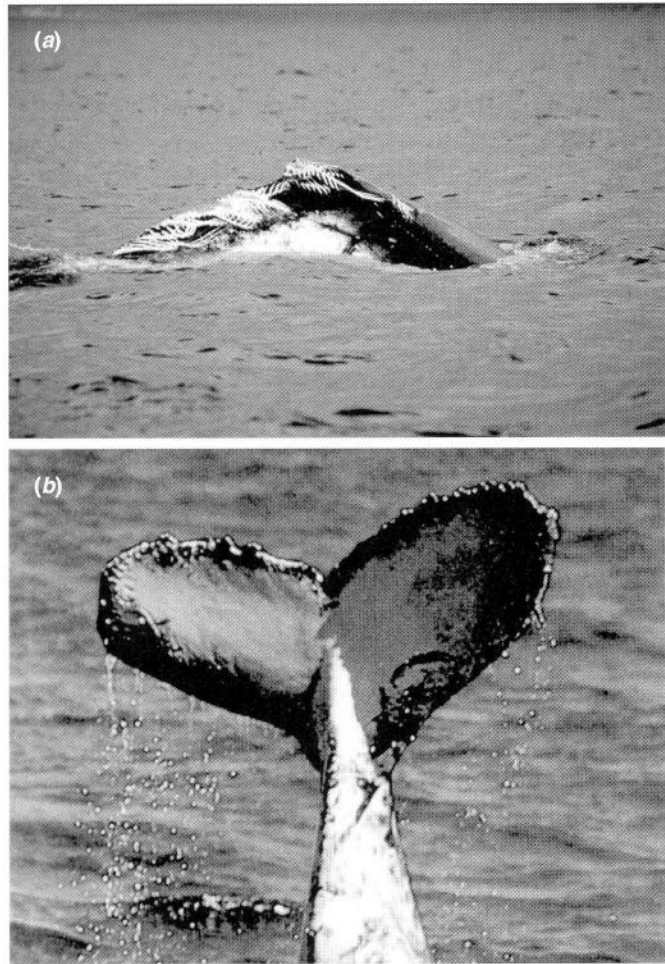


Fig. 3. Fresh predatory scarring on humpback whales. (a) Fresh exposed wounds and killer whale rakes along dorsal and lateral body. (b) Killer whale rakes along fluke edges.

predatory scarring’ was assigned to those whales with scars that were superficially similar to those caused by predators but did not fit the rake mark definition. If predatory scarring was present, the possible attacker involved (e.g. killer whale, false killer whale, shark) (Table 1) and whether the scarring was fresh (i.e. exposed raw flesh) (Fig. 3a) were documented. Any change in the level of predatory scarring over time was also documented. It should be noted that identification of the possible attacker was based on visual discrimination of scars only, since it was impossible to accurately measure the scar spacings on photographs without a scale.

Results

Non-lethal predation

Of the 1436 east Australian humpback whales identified between 1984 and 1996, 17% (248 whales) displayed some form of predatory scarring. Of these scarred whales, 57% (141 whales) had ‘minor scarring’, and the other 43% (107 whales) had ‘major scarring’. Of these 248 scarred whales, the sex of the whale was known in 46 cases. Forty whales were identified as female (24 through close association with a calf, 16 by photo-documentation of genital area), and six as

male (two singers, four by sex identification). In all, 12.5% (31) of the scarred whales were juveniles (subadult or younger) when they were first identified, whilst the other 87.5% (217) were adults when they were first identified.

Almost all (98%) of the 248 whales that had been attacked possessed the distinctive parallel rake marks caused by killer whales (Table 1). Only six individuals had scar patterns consistent with other predators (Table 2). Four of these whales (E0097, E0147, E0379 and E1554) displayed the arc-shaped bite marks consistent with shark attack (Table 1), whilst two other animals (E0696 and E0757) showed parallel rake marks consistent with attack by false killer whales. In these cases, the distances between the scars of each rake set appeared to match the smaller intertooth spacing of a false killer whale more closely than that of a killer whale (Table 1).

When the fluke and lateral body identifications for every sighting of each individual whale were examined, only three whales (E0696, E0757 and E1554) showed an increase in the level of predatory scarring after their first sighting (Table 2). Animal E0696 lacked any predatory scarring when first identified as an adult in Hervey Bay, Queensland in 1989. When resighted in the Whitsunday Islands in 1994, she had one set of closely spaced parallel rake marks along the top edge of her fluke consistent with attack by a false killer whale. Similarly, animal E0757 had no rake marks when first observed in Hervey Bay in 1988, and then again in the Whitsunday Islands in 1994. At the next sighting in the Whitsundays in 1996, a set of parallel rake marks indicative of a false killer whale encounter was visible on the left tip of this whale's tail. Finally, whale E1554 was a newborn female calf without predatory scarring when originally photographed in Hervey Bay in September 1995. In the following year, she was observed as a yearling in the Whitsundays with

a semicircular bite pattern with jagged serrations on the upper right edge of her tail. This new scar pattern appeared to be the result of a shark attack.

In two instances, predatory scarring on a humpback whale was fresh. In July 1985, animal E0103 was first documented in the Capricorn-Bunker Group, Great Barrier Reef, as a subadult. E0103 possessed extensive scars and raw wounds covering its tail and peduncle area. The tips of this whale's fluke appeared to have been bitten away, leaving the tail with rounded edges (Fig. 3b). The spacing and appearance of parallel scars indicated that killer whales were the most likely attackers. Whale E0160 also exhibited fresh scarring when first photographed in July 1986 off Point Lookout, North Stradbroke Island, Queensland. This subadult possessed extensive killer whale rake marks along its tail. Although most of the scarring appeared to have healed, a small section of tail still had fresh, raw rake marks.

Lethal attack on a humpback whale calf

On 16 November 1998, a lethal attack on a humpback whale calf was observed by fishermen near Eden, southern New South Wales (Fig. 1). On the previous day, a group of seven killer whales comprising one adult male, one juvenile male, four adult females and a calf was observed by PWF researchers ~2 km offshore and just north of Twofold Bay, travelling in a south-easterly direction. On the following morning, a group of killer whales with the same composition was observed 3 km offshore from Green Cape Lighthouse, and 10 km south of the previous day's location. At 1030 hours, fishermen in the area reported observing this group of killer whales attacking a pod of humpback whales consisting of two adults and one calf. These witnesses stated that the killer whales attacked the tail of the calf. At one point, the

Table 2. Sighting histories for individual humpback whales with scarring from sharks or false killer whales

Note that only those sighting records in which scarring was first detected, and records immediately prior to the scarring event (if available) have been recorded here. ID#: individual identification number for each whale within the Pacific Whale Foundation Australia Fluke ID Catalogue. Sex: sex of whale (if known) for each sighting – FB: female by behaviour (mother); FS: female identified by sex shot. Loc.: location whale was photographed for each sighting – PL: Point Lookout, North Stradbroke Island; HB: Hervey Bay; ED: Eden; GB: Great Barrier Reef, Capricorn Group, WI: Whitsunday Islands. Day: day of each sighting. Mo: month of each sighting. Yr: year of each sighting. SF: social function of whale for each observation: AD: adult; SA: subadult; CA: calf; MO: mother; UK: unknown. Ad: no. of adults in pod for each sighting; SA: number of subadults in pod for each sighting. Ca: number of calves in pod for each sighting. Tot.: total number of whales in pod for each sighting. Scar obs.: whether predatory scarring was found on the whale photo-identification for each sighting Y: yes; N: no. Pred.: predator assigned as cause of scarring – SH: shark; FK: false killer whale

ID#	Sex	Loc.	Day	Mo	Yr	SF	Ad	Sa	Ca	Tot.	Scar obs.	Pred.
E0097		GB	11	8	85	SA	2	0	0	2	Y	SH
E0147		PL	2	10	85	AD	4	0	0	4	Y	SH
E0379	FB	PL	20	10	87	MO	1	0	1	2	Y	SH
E0696		HB	5	9	89	AD	2	0	0	2	N	–
	FS	WI	3	8	94	AD	2	0	0	2	Y	FK
E0757		HB	30	9	88	AD					N	–
		WI	30	7	94	AD	2	0	0	2	N	–
		WI	29	7	96	AD	1	0	0	1	Y	FK
E1554		HB	17	9	95	CA	4	0	4	8	N	–
	FS	WI	25	6	96	SA	0	1	0	1	Y	SH

calf was positioned between the two adult whales. The calf was then observed diving below the surface for an extended period, and resurfacing between the two adults. At one stage the calf dived, but was not seen again. After watching the attack for ~30 min, these witnesses left the area. At 1230 hours, PWF researchers encountered the group of killer whales in the same area, diving and circling at the surface. About 100 m away from the killer whales, a 20 m by 40 m oily slick was evident at the water surface. In the middle of the slick, a piece of white-grey flesh was floating at the surface. This tissue comprised a 60 cm by 30 cm portion of a whale's lower jaw and ventral pleats with associated blubber. The pale pigmentation of the skin suggested that it came from a humpback whale calf. The tissue fragment also bore distinctive killer whale rake marks along its edges. The group of killer whales continued to dive and swim in circles; observations ceased 1 h later. During the time that the killer whales were observed by the researchers, no humpback whales were seen in the vicinity.

Discussion

Of the cast Australian humpback whales examined for this study, 17% exhibited non-lethal predatory scarring. This level of incidence falls within the range (14–23%) observed for humpback whales and other baleen whales around the world (Schevchenko 1975; Katona *et al.* 1980, 1988; Dolphin 1987; Finley 1990; Kraus 1990; George *et al.* 1994). In particular, this scarring rate is most similar to that found in Northern Hemisphere humpback whales: 14% of photographed humpback whales from the western North Atlantic (Katona *et al.* 1988) and 15–20% of identified Alaskan humpback whales bore killer whale tooth rake marks (Dolphin 1987). Also, 23% of photo-identified humpback whales in the feeding grounds off western USA show evidence of predatory attacks (Steiger and Calambokidis, personal communication).

A notable proportion of the scarred whales here (43%) had scarring that was indicative of sustained and/or repeated attack. Most of this scarring was restricted to the tail flukes, though this is possibly a function of the bias towards photography of this body region. This biting of flukes has been variously interpreted as an attempt to slow the whale down to increase the chance of a lethal attack (Jefferson *et al.* 1991), to snacking on 'energy-rich' whale flesh (Sih 1980; Whitehead and Glass 1985). If, however, killer whales focus their attacks on the heads of baleen whales (Silber *et al.* 1990), then we may have underestimated frequency of attack in this study.

In total, 98% of the scarring observed in this study was consistent with attack by either killer whales or false killer whales. The parallel scar patterns found on these humpback whales were similar to rake marks attributed to killer whales on other cetaceans (George *et al.* 1994; Long and Jones 1996; Visser 1999). This finding that killer whales probably

carry out most non-lethal attacks on this whale population agrees with assumptions made regarding the origin of scarring in other great whale populations (Schevchenko 1975; Dolphin 1987; Katona *et al.* 1988; Finley 1990; Kraus 1990; George *et al.* 1994). Further, most of the directly documented attacks upon humpbacks and other cetaceans have been by killer whales (Chittleborough 1953; Jefferson *et al.* 1991; Frost *et al.* 1992; Florez-Gonzalez *et al.* 1994; George and Suydam 1998; Visser 1999; Saulitis *et al.* 2000; Paterson and Paterson 2001).

Only two (1%) of the attacked humpback whales in the present study had scarring that could be directly attributable to false killer whales. This low level of attack by false killer whales is consistent with the relatively few predatory interactions recorded between false killer whales and large whales elsewhere (e.g. Palacios and Mate 1996; Mazzuca *et al.* 1998). The usual distribution of false killer whales, i.e. deep offshore tropical–subtropical waters (Carwardine *et al.* 2000), falls largely outside the usual migration paths for eastern Australian humpback whales. However, our methodology may have underestimated the true level of false killer whale attack: although the consistently wide spacing of rake marks suggests that killer whales rather than false killer whales were the probable aggressors here, it is possible that such wide spacings could result from ontogenetic growth of scars inflicted by false killer whales (George *et al.* 1994), especially if the attacks were perpetrated on humpback calves (see below).

Only four (2%) of the 248 scarred humpback whales in this study showed signs of shark attack. This concurs with the idea that large living cetaceans are not the primary food source for sharks (Long and Jones 1996; Mazzuca *et al.* 1998). Of the three humpbacks that acquired scarring through shark attack during this study, one was a yearling (second-year calf). If shark attacks on calves tend to have lethal rather than non-lethal outcomes, the frequency of attack may have been underestimated here. Certainly, humpback whale calves have been killed by sharks in eastern Australian waters (Paterson and Van Dyck 1991; Paterson *et al.* 1993).

Whilst calves may be the most likely targets of sharks, they are not the sole targets. Two of the three whales in this study were not calves when they were attacked. It is possible that we have underestimated the incidence of shark attack on both adult and juvenile whales, particularly if sharks tend to attack parts of the body not examined in this study, e.g. urogenital and abdominal areas, dorsum, head and flanks (Long and Jones 1996). For example, a humpback whale calf carcass stranded on the shores of Fraser Island, Queensland, had an apparently lethal shark bite near its flipper (Paterson and Van Dyck 1991).

It is likely that predation pressures on humpback whales vary with latitude and water depth and thus across a migratory route. Large sharks that have been implicated as

possible predators on large whales are absent from polar waters (Corkeron and Connor 1999). Further, the humpback whale's preference for shallow nearshore habitats when moving through warmer waters may minimise predation by certain large pelagic sharks capable of attacking adult whales, including the great white shark (*Carcharodon carcharias*). On the other hand, shark attack on humpback whale calves has been recorded in inshore waters (Paterson and Van Dyck 1991; Paterson *et al.* 1993). In contrast, killer whales forage in inshore regions, ranging from tropical to polar waters (Carwardine *et al.* 2000), but are found in higher concentrations in colder high-latitude regions such as Antarctica (Mikhalev *et al.* 1981). Corkeron and Connor (1999) hypothesise that the extent and risk of predation by killer whales on baleen whale calves (including humpback whales) is potentially so great at these high latitudes that baleen whales will undergo extensive migrations to low-latitude waters to reduce this risk.

In almost every case where an east Australian humpback whale was documented with rake marks, these scar patterns were present at the first sighting of the animal. Only three (1%) scarred whales acquired predatory scarring after they were first observed, and in each case, a predator other than a killer whale was the cause of the scarring. The fact that most of the attacked whales were seen with scarring at their first sighting suggests that attacks occur very early in life (Chittleborough 1953; Corkeron and Connor 1999; Clapham 2000), possibly leading to substantial mortalities during early migrations.

The attack of a humpback whale calf off Eden, southern New South Wales, described here, and attacks elsewhere (Paterson and Paterson 2001) leave no doubt that killer whales kill humpback whale calves during their migration along the east coast of Australia. Since these predatory encounters are rarely observed (both in Australia and elsewhere), it is impossible to determine the frequency of lethal attacks. For the two cases of fresh non-lethal attacks on subadult (juvenile) humpback whales (one in the tropical Capricorn–Bunker Group of the Great Barrier Reef and the other off subtropical North Stradbroke Island, south-east Queensland) also reported here, the attackers involved were most likely killer whales. The areas involved are not outside the known distribution of killer whales, but are areas where killer whale sightings are not commonplace (Janetski and Paterson 2001). Killer whales have been observed in east Australian waters on several occasions during the northern and southern migration of humpback whales (Paterson 1987). It is possible that these killer whales are so-called 'transients' (Mikhalev *et al.* 1981), migrating in response to the movements of their marine mammal prey. However, the fact that only two animals were seen with fresh scarring suggests the possibility that most attacks by killer whales may occur away from the Australian coastline.

If calves are the main age-class of whale targeted by predators (Dolphin 1987; Connor 2000), then the number of calves included in any analysis would affect the estimated frequency of predation in a population. Humpback whale calves were under-represented in this study, which was conducted when first-year calves were less than five months old (Kaufman *et al.* 1993). In the first few months of life, calves tend to dive without lifting their flukes, and possess pigmentation patterns that change significantly over time (Carlson *et al.* 1990; Blackmer *et al.* 2000). These factors make obtaining good-quality photo-identifications of calves very difficult in the breeding and calving grounds and in adjacent locations along the migration route. In contrast, by the time calves reach the high-latitude feeding grounds of Antarctica, they have grown in size and strength, and display their fluke pigmentation patterns during more frequent fluke-up dives (Kaufman and Forestell 1986). However, they are also largely inaccessible to researchers at this stage. In contrast, photo-identification studies in the Northern Hemisphere are often conducted at feeding grounds so that calves are more proportionately represented (Katona *et al.* 1980, 1988; Dolphin 1987). For example, whilst only 12 of 1436 whales (1%) in this eastern Australian study were classified as calves at their first sighting, 33 calves (5% of 703 animals) were included in a California–Washington study (Steiger and Calambokidis, personal communication). Of these 33 calves, 18% had obvious rake marks on their flukes. On the other hand, none of the whales in this eastern Australian study had predatory scarring when they were first photographed as calves. The higher number of calves included in the California–Washington population may have contributed to the higher predatory scarring rate (23%) for that population. Further, Australian calves may exhibit a lower rate of scarring because they have not yet completed their first polar migration and are still at risk of predation. The overall estimate of 17% for the east Australian humpback population is likely to be an underestimate.

Acknowledgments

Thank you to all those who originally created and helped to curate the PWF Fluke ID Catalogue, especially Barb Largerquist, Mike Osmond and Carolyn Hogg. Thank you to Robin Baird, Sascha Hooker, Peter Klimley, Gretchen Steiger and John Calambokidis for graciously sharing their expertise regarding predatory scarring patterns. The Department of Zoology and Entomology at The University of Queensland supported this project. Two anonymous reviewers improved the manuscript.

References

- Blackmer, A. L., Anderson, S. K., and Weintich, M. T. (2000). Temporal variability in features used to photo-identify humpback whales (*Megaptera novaeangliae*). *Marine Mammal Science* 16, 338–354.

- Brown, M. R., and Butterworth, D. S. (1999). Estimating abundance of Southern Hemisphere humpback whales. *International Whaling Commission Document SC/51/CWWS* 35, 1–15.
- Bryden, M. M., Kirkwood, G. P., and Slade, R. W. (1990). Humpback whales, Area V. An increase in numbers off Australia's east coast. In 'Antarctic Ecosystems: Ecological Change and Conservation. (Eds K. R. Kerry and G. Hempel.) pp. 271–277. (Springer-Verlag: Berlin.)
- Carlson, C. A., Mayo, C. A., and Whitehead, H. (1990). Changes in the ventral fluke pattern of the humpback whale, and its effect on matching; evaluation of its significance to photo-identification research. In 'Individual Recognition of Cetaceans: Use of Photo-identification and Other Techniques to Estimate Population Parameters'. (Eds P. S. Hammond, S. A. Mizroch and G. P. Donovan.) pp. 105–112. (IWC: Cambridge, UK.)
- Carwardine, M., Evans, P., and Weinrich, M. (2000). 'Whales, Dolphins and Porpoises.' (Dorling Kindersley: London.)
- Chaloupka, M. Y., and Osmond, M. G. (1999). Spatial and seasonal distribution of humpback whales in the Great Barrier Reef region. In 'Life in the Slow Lane: Ecology and Conservation of Long-lived Marine Animals'. (Ed. J. A. Musick.) pp. 90–107. (American Fisheries Society: Washington, DC.)
- Chaloupka, M. Y., Osmond, M. G., and Kaufman, G. D. (1999). Estimating seasonal abundance trends and survival rates of humpback whales in Hervey Bay (east coast Australia). *Marine Ecology Progress Series* 184, 291–301.
- Chittleborough, R. G. (1953). Aerial observations on the humpback whale *Megaptera nodosa* (Bonaterre), with notes on other species. *Australian Journal of Marine and Freshwater Research* 4, 219–226.
- Chittleborough, R. G. (1965). Dynamics of two populations of the humpback whale *Megaptera novaeangliae* (Borowski). *Australian Journal of Marine and Freshwater Research* 16, 33–128.
- Clapham, P. J. (2000). The humpback whale: seasonal feeding and breeding in a baleen whale. In 'Cetacean Societies: Field Studies of Dolphins and Whales'. (Eds J. Mann, R. Connor, P. Tyack and H. Whitehead.) pp. 173–196. (University of Chicago Press: Chicago, IL.)
- Clapham, P. J. (2002). Humpback whale. In 'Encyclopedia of Marine Mammals'. (Eds W. F. Perrin, B. Würsig and J. G. M. Thewissen.) pp. 589–592. (Academic Press: California.)
- Connor, R. C. (2000). Group living in whales and dolphins. In 'Cetacean Societies: Field Studies of Dolphins and Whales'. (Eds J. Mann, R. Connor, P. Tyack and H. Whitehead.) pp. 199–218. (University of Chicago Press: Chicago, IL.)
- Connor, R. C., and Corkeron, P. J. (2001). Predation past and present: killer whales and baleen whale migration. *Marine Mammal Science* 17, 436–439.
- Corkeron, P. J., and Connor, R. C. (1999). Why do baleen whales migrate? *Marine Mammal Science* 15, 1228–1245.
- Dolphin, W. F. (1987). Observations of humpback whale, *Megaptera novaeangliae* – killer whale, *Orcinus orca*, interactions in Alaska: comparisons with terrestrial predator–prey relationships. *Canadian Field Naturalist* 101, 70–75.
- Finley, K. J. (1990). Isabella Bay, Baffin Island: an important historical and present-day concentration area for the endangered bowhead whale (*Balaena mysticetus*) of the Eastern Canadian Arctic. *Arctic* 43, 137–152.
- Florez-Gonzalez, L., Capella, J. J., and Rosenbaum, H. C. (1994). Attack of killer whales (*Orcinus orca*) on humpback whales (*Megaptera novaeangliae*) on a South American Pacific breeding ground. *Marine Mammal Science* 10, 218–222.
- Frost, K. J., Russel, R. B., and Lowry, L. F. (1992). Killer whales, *Orcinus orca*, in the southeastern Bering Sea: recent sightings and predation on other marine mammals. *Marine Mammal Science* 8, 110–119.
- George, J. C., and Suydam, R. (1998). Observations of killer whale (*Orcinus orca*) predation in the northeastern Chukchi and western Beaufort Seas. *Marine Mammal Science* 14, 330–331.
- George, J. C., Philo, L. M., Hazard, K., Withrow, D., Carroll, G. M., and Suydam, R. (1994). Frequency of killer whale attacks and ship collisions based on scarring on bowhead whales of the Bering–Chukchi–Beaufort Seas stock. *Arctic* 47, 247–255.
- Hancock, D. (1965). Killer whales kill and eat a minke whale. *Journal of Mammalogy* 46, 341–342.
- Hooker, S. K. (1998). Extensive scarring observed on female or juvenile male sperm whales off the Galapagos Islands. *Mammalia* 62, 134–139.
- Janetski, H. A., and Paterson, R. A. (2001). Aspects of humpback whale, *Megaptera novaeangliae*, calf mortality in Queensland. *Memoirs of the Queensland Museum* 47, 431–435.
- Jefferson, T. A., Stacey, P. J., and Baird, R. W. (1991). A review of killer whale interactions with other marine mammals: predation to co-existence. *Mammal Review* 21, 151–180.
- Katona, S. K., and Whitehead, H. (1981). Identifying humpback whales using their natural markings. *Polar Record* 20, 439–444.
- Katona, S. K., Harcourt, P. M., Perkins, J. S., and Kraus, S. D. (1980). 'Humpback Whales: A Catalogue of Individuals Identified in the western North Atlantic Ocean by Means of Fluke Photographs.' (College of the Atlantic: Bar Harbor, ME.)
- Katona, S. K., Beard, J. A., Girton, P. E., and Wenzel, F. (1988). Killer whales (*Orcinus orca*) from the Bay of Fundy to the Equator, including the Gulf of Mexico. *Rit Fiskideildar* 11, 205–224.
- Kaufman, G. D., and Forestell, P. H. (1986). 'Hawaii's Humpback Whales.' (Island Heritage Press: Honolulu, HI.)
- Kaufman, G. D., Smultea, M., and Forestell, P. H. (1987). Use of lateral body pigmentation patterns for photographic identification of East Australian (Area V) humpback whales. *Cetus* 7, 5–13.
- Kaufman, G. D., Lagerquist, B. A., Forestell, P. H., and Osmond, M. (1993). Humpback whales of Australia: a catalogue of individual whales identified by fluke photographs. Queensland Department of Environment and Heritage, Brisbane.
- Kraus, S. D. (1990). Rates and potential causes of mortality in North Atlantic Right Whales (*Eubalaena glacialis*). *Marine Mammal Science* 6, 278–291.
- Long, D. J., and Jones, R. F. (1996). White shark predation and scavenging on cetaceans in the eastern North Pacific Ocean. In 'Great White Sharks – The Biology of *Carcharodon carcharias*'. (Eds A. P. Klimley and D. G. Ainley.) pp. 293–307. (Academic Press: San Diego, CA.)
- Mazucca, L., Atkinson, S., and Nitta, E. (1998). Deaths and entanglements of humpback whales, *Megaptera novaeangliae*, in the main Hawaiian islands, 1972–1996. *Pacific Science* 52, 1–13.
- Mikhalev, Y. A., Ivashin, M. V., Savusin, V. P., and Zelenaya, F. E. (1981). The distribution and biology of killer whales in the Southern Hemisphere. *Reports of the International Whaling Commission* 31, 551–566.
- Palacios, D. M., and Mate, B. R. (1996). Attack by false killer whales (*Pseudorca crassidens*) on sperm whales (*Physeter macrocephalus*) in the Galapagos Islands. *Marine Mammal Science* 12, 582–587.
- Paterson, R. A. (1987). Recovery in the east Australian humpback whale stock. *Australian Fisheries* 47, 32–36.
- Paterson, R. A., and Paterson, P. (2001). A presumed killer whale (*Orcinus orca*) attack on humpback whales (*Megaptera novaeangliae*) at Point Lookout, Queensland. *Memoirs of the Queensland Museum* 47, 436.
- Paterson, R. A., and Van Dyck, S. M. (1991). Studies of two humpback whales, *Megaptera novaeangliae*, stranded at Fraser Island, Queensland. *Memoirs of the Queensland Museum* 30, 343–351.
- Paterson, R. A., Quayle, C. J., and Van Dyck, S. M. (1993). A humpback whale calf and two subadult dense-beaked whales

- recently stranded in southern Queensland. *Memoirs of the Queensland Museum* **33**, 291–297.
- Paterson, R. A., Paterson, P., and Cato, D. H. (2001). Status of humpback whales, *Megaptera novaeangliae*, in east Australia at the end of the 20th century. *Memoirs of the Queensland Museum* **47**, 579–586.
- Saulitis, E., Matkin, C., Barrett-Lennard, L., Heise, K., and Ellis, G. (2000). Foraging strategies of sympatric killer whale (*Orcinus orca*) populations in Prince William Sound, Alaska. *Marine Mammal Science* **16**, 94–109.
- Schevchenko, V. I. (1975). The nature of the inter-relationships between killer whales and other cetaceans. *Morskiye Mlekopitayuschchiye* **2**, 173–174.
- Sih, A. (1980). Optimal foraging: partial consumption of prey. *American Naturalist* **116**, 281–290. doi:10.1086/283626
- Silber, G. K., Newcomer, M. W., and Perez-Cortez, M. H. (1990). Killer whales (*Orcinus orca*) attack and kill a Bryde's whale (*Balaenoptera edeni*). *Canadian Journal of Zoology* **68**, 1603–1606.
- Visser, I. N. (1999). A summary of interactions between orca (*Orcinus orca*) and other cetaceans in New Zealand waters. *New Zealand Natural Sciences* **24**, 101–112.
- Whitehead, H., and Glass, C. (1985). Orcas (killer whales) attack humpback whales. *Journal of Mammalogy* **66**, 183–185.
- Wursig, B., Jefferson, T. A., and Schmidly, D. J. (2000). 'The Marine Mammals of the Gulf of Mexico.' (Texas A&M University Press: College Station, TX.)

Manuscript received 24 June 2002; accepted 16 September 2003