

Fight or flight: antipredator strategies of baleen whales

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ABSTRACT

1. The significance of killer whale *Orcinus orca* predation on baleen whales (Mysticeti) has been a topic of considerable discussion and debate in recent years. Discourse has been constrained by poor understanding of predator-prey dynamics, including the relative vulnerability of different mysticete species and age classes to killer whales and how these prey animals avoid predation. Here we provide an overview and analysis of predatory interactions between killer whales and mysticetes, with an emphasis on patterns of antipredator responses.

2. Responses of baleen whales to predatory advances and attacks by killer whales appear to fall into two distinct categories, which we term the *fight* and *flight* strategies. The *fight* strategy consists of active physical defence, including self-defence by single individuals, defence of calves by their mothers and coordinated defence by groups of whales. It is documented for five mysticetes: southern right whale *Eubalaena australis*, North Atlantic right whale *Eubalaena glacialis*, bowhead whale *Balaena mysticetus*, humpback whale *Megaptera novaeangliae* and grey whale *Eschrichtius robustus*. The *flight* strategy consists of rapid (20–40 km/h) directional swimming away from killer whales and, if overtaken and attacked, individuals do little to defend themselves. This strategy is documented for six species in the genus *Balaenoptera*.

3. Many aspects of the life history, behaviour and morphology of mysticetes are consistent with their antipredator strategy, and we propose that evolution of these traits has been shaped by selection for reduced predation. *Fight* species tend to have robust body shapes and are slow but relatively manoeuvrable swimmers. They often calve or migrate in coastal areas where proximity to shallow water provides refuge and an advantage in defence. Most *fight* species have either callosities (rough and hardened patches of skin) or encrustations of barnacles on their bodies, which may serve (either primarily or secondarily) as weapons or armour for defence. *Flight* species have streamlined body shapes for high-speed swimming and they can sustain speeds necessary to outrun pursuing killer whales (>15–20 km/h). These species tend to favour pelagic habitats and calving grounds where prolonged escape sprints from killer whales are possible.

4. The rarity of observed successful attacks by killer whales on baleen whales, especially adults, may be an indication of the effectiveness of these antipredator strategies. Baleen whales likely offer low profitability to killer whales, relative to some other marine mammal prey. High-speed pursuit of *flight* species has a high energetic cost and a low probability of success while attacks on *fight* species can involve prolonged handling times and a risk of serious injury.

Keywords: cetacean, defence, killer whale, *Orcinus orca*, predation, predator avoidance

INTRODUCTION

Predation is one of the primary selective forces driving animal evolution, and many features of an organism's biology may represent adaptations to reduce the probability of detection and capture by predators. Predator-prey dynamics and their consequences can be considered at two different scales – those involving lethal interactions and the effects they have on an evolutionary scale, and those involving non-lethal interactions and the influences they have at an individual, group or ecological scale. Predation pressure as mediated through direct mortality is an important selective factor in the evolution of antipredator adaptations, such as protective armour, cryptic colouration and chemical defences, as well as life history traits, movement patterns, sociality, etc. (Edmunds, 1974; Stearns, 1976; Inman & Krebs, 1987; Sih, 1987; Lima & Dill, 1990; Lima, 1998; Abrams, 2000). Also significant, however, is predation pressure as mediated through the adaptive flexibility of prey behaviour in response to fluctuating risk of predation. Thus, the mere presence of predators can have a range of effects on a prey animal's habitat choice, activity schedules, etc., independent of actual predation (Sih, 1987; Lima & Dill, 1990; Lima, 1998; Preisser, Bolnick & Bernard, 2005).

Predator-prey interactions involving cetaceans tend to be difficult to observe and are thus poorly known, especially in comparison with interactions involving terrestrial predators and prey. Nevertheless, cetaceans can be subject to significant predation pressure and may show a variety of antipredator adaptations. For example, Norris & Dohl (1980) suggested that predation risk is the primary factor responsible for group living in many odontocetes (toothed cetaceans).

The principal predators of cetaceans are killer whales *Orcinus orca* and sharks. Both of these types of predator have wide distributions in the world's oceans and have been observed to prey on many different cetacean species (Jefferson, Stacey & Baird, 1991; Connor *et al.*, 2000; Heithaus, 2001; Weller, 2002). False killer whales *Pseudorca crassidens*, pygmy killer whales *Feresa attenuata* and short-finned pilot whales *Globicephala macrorhynchus* have also been implicated in predatory interactions among cetaceans although there is no evidence that predation by these species is common or widespread (Weller, 2002). Polar bears *Ursus maritimus* occasionally hunt belugas *Delphinapterus leucas* and narwhals *Monodon monoceros* in the Arctic (Weller, 2002).

Levels of predation pressure on cetaceans appear to vary widely by species, population and region. In general, small cetaceans, such as dolphins and porpoises, are likely more vulnerable to predation than larger cetaceans. Certain populations of bottlenose dolphins *Tursiops* spp. experience high rates of predatory interactions with sharks, as indicated by evidence of wounding and scarring (see reviews by Connor *et al.*, 2000 and Heithaus, 2001). The risk of shark predation influences habitat use by bottlenose dolphins in western Australia (Heithaus & Dill, 2002) and Hawaiian spinner dolphins *Stenella longirostris* (Norris & Dohl, 1980; Norris *et al.*, 1994). Killer whales are important predators of small cetaceans (Jefferson *et al.*, 1991) and may, like sharks, influence patterns of habitat use (Srinivasan, Grant & Würsig, 2007). In temperate coastal waters of the north-eastern Pacific, Dall's porpoises *Phocoenoides dalli* and harbour porpoises *Phocoena phocoena* represent 25–50% of observed kills by mammal-hunting killer whales (Ford *et al.*, 1998; Saulitis *et al.*, 2000). Typical responses of small cetaceans to killer whale attacks are coalescence (grouping together), high-speed directional flight and rapid movement into shallow waters for refuge (Jefferson *et al.*, 1991; Ford & Ellis, 1999; Laidre, Heide-Jørgensen & Orr, 2006; JKBF, unpublished data).

The extent of predation pressure on large cetaceans – the mysticetes (baleen whales) and the sperm whale *Physeter macrocephalus* – and its role in shaping their life history, social organization and behaviour as well as the structure of marine ecosystems, is the subject of

ongoing discussion and debate (see review by Reeves, Berger & Clapham, 2006). Sharks seem not to pose a significant risk to large whales, though small calves of some species may be vulnerable to attacks occasionally (Weller, 2002; D. Mattila, pers. comm.). Killer whales, however, clearly prey on at least certain age classes of some species of large cetaceans. There is evidence that Antarctic minke whales *Balaenoptera bonaerensis* are important prey of killer whales (Yukov, Vinogradova & Medvedev, 1975; Budylenko, 1981; Berzin & Vladimirov, 1983), and numerous successful attacks on common minke whales *Balaenoptera acutorostrata* have been documented (Ford *et al.*, 2005). These two species are among the smallest mysticetes (Perrin & Brownell, 2002). There is also evidence that young calves of several large whale species are frequent targets of killer whale attacks. Gray whale *Eschrichtius robustus* calves migrating northward with their mothers from breeding lagoons in Baja California are hunted regularly in coastal California (Ternullo & Black, 2002). Scars characteristic of killer whale attacks are found on as many as 20–40% of individuals in some populations of humpback whales *Megaptera novaeangliae*, and evidence is strong that such scars are acquired when the animals are calves (Clapham, 2001; Naessig & Lanyon, 2004; Reeves *et al.*, 2006; Mehta *et al.*, 2007). Corkeron & Connor (1999) proposed that migrations of pregnant female baleen whales to low latitudes for calving are primarily a strategy to reduce killer whale predation on their newborn calves. Whitehead & Weilgart (2000) suggested that predation pressure is an important factor in promoting group living in sperm whales, since small calves would be highly vulnerable to killer whales and sharks if left alone at the surface during prolonged, deep foraging dives by their mothers.

Although killer whale predation on adult large cetaceans has been documented (Jefferson *et al.*, 1991), there is considerable uncertainty and a wide range of opinions in the literature regarding its significance. Jonsgård (1968a,b) contended that there was no proof that killer whales routinely take healthy adult baleen whales, and stated that it is probably difficult or impossible for them to do so under normal conditions. Similarly, Clapham & Mead (1999) maintained that there was ‘no good evidence that the humpback whale exists under continual threat from predators’. In contrast, Springer *et al.* (2003) proposed that large cetaceans are the preferred prey of killer whales in the North Pacific, and the depletion of this food source by industrial whaling forced killer whales to switch to smaller, less desirable marine mammal prey, causing a sequential collapse in populations of these alternative prey species. The Springer *et al.* hypothesis has been challenged on several grounds (DeMaster *et al.*, 2006; Trites *et al.*, 2007; Wade *et al.*, 2007), including the contention by some that ‘great whales have never been more than a rare item in the diets of killer whales’ (Mizroch & Rice, 2006). A different view was held by Pitman *et al.* (2001) who, after observing several attacks on groups of sperm whales, concluded that ‘killer whales, through their predatory habits, represent a much more important selective force in shaping life history traits of individual marine mammal species, and in structuring their communities, than has generally been acknowledged’. Reeves *et al.* (2006), in a review of historical and recent evidence for killer whale predation on large whales, reached a similar, though more measured, conclusion that ‘killer whales once played a role in structuring the behaviour and distribution of at least some populations of large cetaceans’.

Much of the uncertainty about the importance of killer whale predation on large whales has been due to the scarcity of well-documented observations of attacks. Jefferson *et al.* (1991) reviewed published and unpublished accounts of killer whale attacks on marine mammals and listed over 100 incidents of predatory interaction between killer whales and large cetaceans. However, most of those accounts were second-hand, anecdotal and incomplete, and few provided details on the interaction or its outcome. As a result, the effectiveness

of the predatory tactics of killer whales and of the antipredator responses of their large cetacean prey could not be evaluated with any rigour. In other words, it has been difficult to assess when and how killer whales succeed in killing large cetaceans or to identify circumstances that lead to unsuccessful attacks. A better understanding of the dynamics of these predator-prey interactions would help answer the question often raised, implicitly or otherwise, in the debate over the importance of killer whales as predators of large whales (Jonsgård, 1968a,b; Clapham, 2001; Mizroch & Rice, 2006; Reeves *et al.*, 2006): if killer whales routinely prey on these animals, why are attacks not witnessed more often?

Since the review by Jefferson *et al.* (1991), a considerable number of additional predatory interactions between killer whales and large cetaceans have been observed and documented. Many of these accounts contain descriptions of incidents from start to conclusion, and include details on the behaviour of both predators and prey. Our goal in this article is to present a comparative analysis of the behavioural responses of baleen whales to predatory advances and attacks by killer whales, using these new accounts and some of the more detailed earlier incidents that were summarized by Jefferson *et al.* (1991). From this analysis, we describe two distinct patterns of antipredator responses by different baleen whale species, one involving high-speed swimming away from killer whales and no physical defence (the *flight* strategy), and the other involving physical defence and retreat to protective cover, but no prolonged high-speed flight (the *fight* strategy). We suggest that these divergent strategies and their associated behavioural and morphological adaptations are evidence that predation pressure from killer whales has played a role in the evolution of life history traits (encompassing behaviour, phenology and perhaps even morphology) in mysticetes.

ANTIPREDATOR RESPONSES OF BALEEN WHALES

We compiled and examined accounts of 84 predatory interactions in our review of responses to killer whales by baleen whales (Appendix). We considered interactions to be 'predatory' only if the behaviour of the predator indicated an intention to attack, or that of the prey indicated the perception of and response to a threat. Fifty-eight of the 84 interactions are from published sources, and 26 are based on unpublished accounts by colleagues and other experienced observers or come from personal observations. Numerous reported interactions were excluded because the description was insufficiently detailed or because we had no basis for an affirmative judgement concerning the observer's reliability. Also, we did not include those instances where killer whales and baleen whales were simply seen in close proximity with no suggestion of aggressiveness (cf. Dolphin, 1987; Jefferson *et al.*, 1991). Eleven species of baleen whales were involved, representing three mysticete families – Balaenidae, Eschrichtiidae and Balaenopteridae. Definitions of terms used in descriptions of behaviour of both killer whales and baleen whales involved in predatory interactions are provided in Table 1.

Balaenidae

Predatory interactions with killer whales have been described for four of the five currently recognized species of balaenids. Most involved southern right whales *Eubalaena australis* and bowhead whales *Balaena mysticetus*. A single account is available for the North Atlantic right whale *Eubalaena glacialis* (Appendix), and although a second-hand report exists of an attack on a North Pacific right whale *Eubalaena japonica*, no details of that attack are available (Gaskin, 1982). Predatory interactions with the pygmy right whale *Caperea marginata* do not appear to have been documented in the literature.

Table 1. Terminology used to describe killer whale – baleen whale interactions in text and in Appendix

Term	Definition
Approach	Swimming towards a baleen whale, with or without indication of predatory intent
Chase	Pursuit of a fleeing baleen whale
Harass	Swimming closely around and under, or rushing towards, a baleen whale, but no evidence of physical contact
Attack	Predatory interaction with a baleen whale that involves physical contact
Avoid	Movement away from approaching killer whales, but not at high speed
Flee/flight	High-speed swimming away from killer whales
Hide	Movement of baleen whale into cover for refuge (e.g. kelp bed, shallow water, sea ice)
Strand	Movement of baleen whale into shallow water resulting in contact with beach
Group	Formation of a tight group when baleen whales are approached, harassed or attacked by killer whales
Defend	Physical self-defence or defence of calf

Southern right whale

All 13 predatory interactions involving killer whales and southern right whales were described from the latter's nearshore calving and nursing grounds in Argentina and South Africa (Appendix). Of these, seven were harassments and six were attacks. Most interactions involved multiple right whales (range 2–8), though lone individuals were the focus in four attacks. In each case, the response of groups of right whales harassed or attacked by killer whales was to join tightly together and roll, turn and thrash their tail flukes and flippers at the water's surface, creating considerable splashing and white water. Individuals frequently slashed their tails towards the killer whales. A calf was present in five of the nine groups harassed or attacked, and these were positioned between adult whales or swam tightly alongside the mother. On two occasions, groups of whales formed a 'rosette' with tails out and heads towards the centre; a calf present in one of these groups was repeatedly pushed towards the centre by an adult. Once surrounded by killer whales, the right whales made little forward progress, but thrashed their flukes and flippers vigorously. During two interactions, a killer whale was struck by a right whale's tail flukes. A lone juvenile under attack appeared to attempt to strike the killer whales with its head. Right whales being harassed or attacked often attempted to retreat into shallow waters. During two interactions, a pair of adult right whales approached whales that were being harassed, and joined into a defensive formation. In one instance, an adult right whale left a defensive group and charged towards the killer whales, then returned.

North Atlantic right whale

The single predatory interaction involving North Atlantic right whales *Eubalaena glacialis* involved harassment of four adults by 10–11 killer whales off Cape Cod, Massachusetts. The response of the right whales was typical of those described for southern right whales – they formed a tight defensive group and thrashed with flukes and flippers as the killer whales circled and dove under them (Fig. 1).

Bowhead whale

The six predatory interactions involving bowhead whales *Balaena mysticetus* summarized in the Appendix have features in common with harassments or attacks on right whales. Tight grouping with splashing, and movement into shallow water or ice cracks, appear typical. In



Fig. 1. Four North Atlantic right whales in defensive group being harassed by 10–11 killer whales, off Cape Cod, New England, 21 July 2005. Photo by T. Voorheis.

one early second-hand account (Eschricht, 1866), a bowhead was reported to strike a killer whale with its tail, possibly killing it.

Eschrichtiidae

The family Eschrichtiidae consists of a single living species, the grey whale *Eschrichtius robustus*. Fourteen of the 15 predatory interactions described for grey whales in the Appendix involved groups of grey whales, eight of which were mothers with young calves. One interaction involved a single adult-sized grey whale. Grey whales responded to harassing or attacking killer whales by grouping tightly together and, in cases where the coast was within a few kilometres, swimming towards shore in an apparent attempt to gain protective cover in shallow water, sometimes in the line of breaking surf or in kelp beds. Grey whale mothers with calves were frequently reported to roll over while attempting to hold their calves on their ventral side at the surface. Mothers also defended their calves by slashing their tail flukes towards the killer whales or by vigorous spinning and turning at the surface, creating considerable splashing. During one interaction, a grey whale mother and calf being circled by harassing killer whales slowly moved 5 km shoreward over a 3-hour period, at which point the killer whales aborted their attack. During three interactions, it was noted that grey whales adopted a distinctive style of respiration during their retreat to shallow water, where individuals exhaled underwater and exposed their blowholes above the surface just high enough to inhale. An early account of killer whales attacking a grey whale in Korea (Andrews, 1914) described the grey whale as rolling over onto its back at the surface and lying motionless.

Balaenopteridae

Predatory interactions with killer whales have been documented for six balaenopterids: humpback whale, common minke whale, Antarctic minke whale, Bryde's whale *Balaenoptera edenilbrydei*,¹ sei whale *B. borealis*, fin whale *B. physalus* and blue whale *B. musculus*.

¹The systematics and taxonomy of Bryde's whales are unresolved, so it is impossible to be certain, in a given instance, which of the two (or more) species in this group is meant.

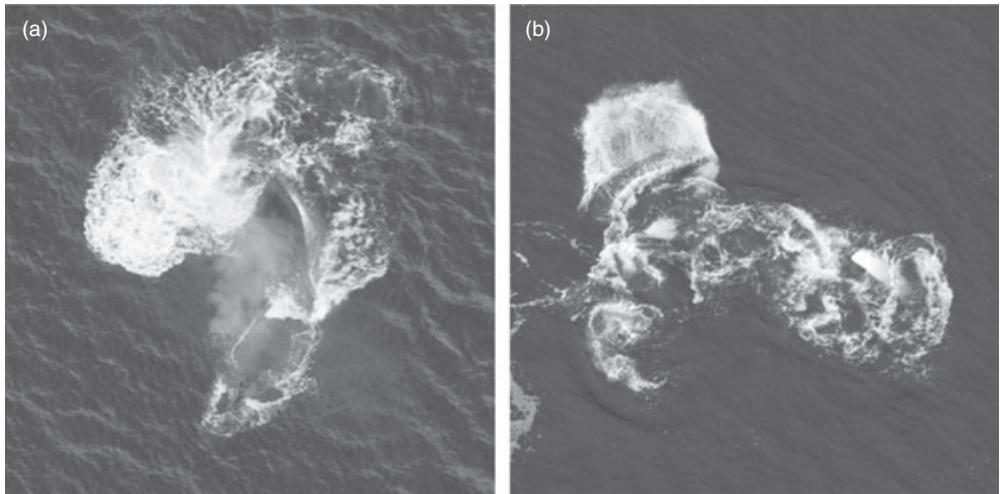


Fig. 2. Humpback whale, in upright (a) and inverted (b) positions, slashing tail flukes towards harassing killer whales (not visible in photos), Tenakee Inlet, south-eastern Alaska, 2 November 2007. Photos by J. Moran.

Humpback whale

Fifteen predatory interactions between killer whales and humpback whales are described in the Appendix. Ten of these involved groups of two or more humpbacks. Humpback whales responded to harassment or attack by killer whales by grouping tightly together (when more than a single humpback was involved) and mounting a vigorous physical defence, including slashing tail flukes at the predators, rolling and thrashing the water's surface with their long pectoral flippers, and head shaking (Fig. 2). These actions were often accompanied by loud 'wheezing' exhalations (also termed 'trumpet blows') that are typical of excited or highly agitated humpback whales (Dolphin, 1987). Single calves were present in six interactions, and in most cases they were reported as being positioned close alongside their presumed mother or within tight groups of adults. On two occasions, a young whale under attack was joined by adult humpbacks, which then displayed apparently defensive or protective behaviour.

Common minke whale

Predatory interactions between common minke whales and killer whales are documented in 17 cases described in the Appendix. All involved single minke whales. In each case where the initial response of the minke whale was observed, the animal fled at high speed from the killer whales, usually on a highly directional course towards open water. Such chases often reached speeds of 25–30 km/h, with both the minke whale and the killer whales adopting a 'porpoising' manner of swimming (Fig. 3), and covered distances of 15 km or more. In five predatory interactions, the killer whales abandoned the chase after pursuing the fleeing minke whale for 20 min to 1 hour. On one occasion, the minke was captured and killed in open water, and twice the minke was killed after stopping close to boats in an apparent attempt to hide from the predators. On three occasions, the chase ended when the minke whale entered a small, confined bay and was surrounded and killed by the killer whales. During five interactions, the minke whale entered shallow water and became partially or completely stranded on shore. On two of these occasions, the minke whale was attacked while in the shallows and subsequently killed. On the other three occasions, the minke stranded beyond reach of the pursuing killer



Fig. 3. Minke whale fleeing at high speed from pursuing group of four killer whales, Blackfish Sound, British Columbia, 28 August 2005. Photo by T. Aumeier.

whales, which eventually departed the scene. The stranded minke subsequently died on two of these occasions, but on one occasion it managed to swim off when the tide rose.

Although common minke whales showed a strong flight response to pursuing killer whales, when this tactic failed and an attack ensued, the minkes made no effort to defend themselves. During attacks, killer whales rammed the minkes repeatedly over periods of several minutes to several hours, yet in no case was any physical retaliation observed.

Antarctic minke whale

Antarctic minke whales appear to be important prey of killer whales in the Southern Ocean (Shevchenko, 1975; Horwood, 1990; Pitman & Ensor, 2003), but we could find only a single detailed description of a predatory interaction with this species. This involved a single Antarctic minke whale that was found stranded in shallow water and under attack by nine killer whales in Tierra del Fuego. Although wounded and bleeding, the minke whale made no apparent attempt to defend itself or retaliate.

Bryde's whale

Five predatory interactions involving killer whales and Bryde's whales, four of which are previously unpublished, are described in the Appendix. All interactions took place in the Gulf of California, and all involved single Bryde's whales. In each case, the whale's response to the approaching or pursuing killer whales was to flee at high speed on a straight course. On three occasions, no attack took place, but on two occasions the Bryde's whale was killed and eaten by the killer whales. During both attacks, the Bryde's whale made no physical defence while being rammed, bitten and forced underwater.

Sei whale

Two interactions between sei whales and killer whales are summarized in the Appendix. Both interactions were observed from shore in Tierra del Fuego after sei whales, being chased at

high speed by killer whales, became beached in shallow waters. In each case, the sei whale showed no defensive actions while the killer whales pushed at or bit it. In both instances, the killer whales were unable to gain sufficient access to the stranded sei whale to complete the kill and departed after several hours; both sei whales were later found dead.

Fin whale

Three interactions involving killer whales and fin whales are described, all from the Gulf of California (Appendix). Of these, two were high-speed chases that attained speeds of up to 30–40 km/h. In one case, a pair of fin whales pursued by three killer whales appeared to escape, but in the other the single fin whale was attacked and killed by 16 killer whales following a 60-min chase. No defensive actions by the fin whale were observed during this attack. The third interaction involved a single fin whale that was observed from the air while under attack for 1.5 hours. Again, no physical defence was seen.

Blue whale

Six interactions between killer whales and blue whales are documented in the Appendix. The response to approach or pursuit by killer whales in each interaction was high-speed flight. In one case, the killer whales inflicted substantial wounds on the blue whale while it fled, but abandoned the chase after 5 hours. No defensive actions were noted in this or any other incident.

DISCUSSION

The antipredator responses of the 11 species of baleen whales described here fall clearly into two distinct categories, which we term the *fight* and *flight* strategies. The *fight* strategy is characterized by active physical defence, including self-defence by single individuals, the defence of calves by their mothers and coordinated defence by groups of whales. Retreat to the protective cover of a nearby refuge (e.g. shallows, kelp beds or dense ice) is also a common response of *fight* strategists. The *flight* strategy is characterized by high-speed directional swimming away from killer whales, and the lack of defence by individuals should they be overtaken and attacked.

Fight species

Five species of baleen whales show *fight*-type reactions to killer whales: southern right whale, North Atlantic right whale, bowhead whale, humpback whale and grey whale. The North Pacific right whale likely belongs to this group, but interactions with killer whales have not been well documented enough to include it. Although these species share an overall response strategy, differences exist in some of the tactics they employ. When confronted with harassing or attacking killer whales, *fight* species tend to group tightly together and mount a physical defence (Figs 1 and 2). Calves, if present, are surrounded by adult whales, and groups of southern right whales may form a 'rosette', with heads towards the centre and tails facing the killer whales [a phenomenon first described by Nishiwaki (1962) based on observations of sperm whales under attack by whalers; also see Pitman *et al.* (2001)]. In southern right whales and humpback whales, individuals have been reported to join single whales or groups being harassed. Tail flukes and pectoral flippers are the primary weapons used to strike out at killer whales, though right whales and humpback whales occasionally also lunge or swing their heads at the attackers. Grey whales appear less inclined than other *fight* species to strike at attacking killer whales, though they will do so especially when defending calves. Instead, they often roll at the surface so that their dorsal surface rather than their ventral surface is exposed

to attack from below. Killer whales often debilitate and kill baleen whales by ramming forcefully and repeatedly into the ventral sides of their prey (Ford *et al.*, 2005; Appendix); thus, rolling upside down may protect the vulnerable underside from attack. Grey whale mothers often roll over and hold their young calf out of the water on their ventral surface, out of the reach of attacking killer whales (Walker, 1949; Ternullo & Black, 2002; Appendix).

All *fight* strategists, with the possible exception of humpback whales, appear to seek refuge from killer whales whenever possible. This is most notable in grey whales, which regularly attempt to head for the nearest shallow waters in response to killer whales. They may escape detection by hiding quietly in the cover of kelp or breaking surf, especially when they employ a low-profile breathing technique known as 'snorkelling', where the grey whale exposes only the blowholes in order to respire (Andrews, 1914; Dahlheim & Heyning, 1999; Reeves *et al.*, 2006). This method of respiration may be quieter underwater than normal respiration, thereby providing less of an aural cue as to the whale's presence. Andrews (1914, 1916a) noted that in addition to heading for shallow water, grey whales may respond to attacking killer whales by rolling upside down and remaining motionless at the surface, as if 'paralysed by fright'. This may be a defensive posture combined with crypsis or, as suggested by Reeves *et al.* (2006), capture myopathy or capture stress, as seen in ungulates.

Shallow water may prevent killer whales from attacking their prey from below, and could further restrict the attackers' manoeuvrability. Retreating towards shore appears to be an effective tactic for grey whales, as killer whales usually abandon their harassment or attack soon after they enter shallow water (Appendix). Similarly, southern right whales on their nearshore nursery grounds at Peninsula Valdés, Argentina, successfully escape from killer whales by swimming into shallow water (Cummings, Fish & Thompson, 1972; Payne, 1995; Sironi *et al.*, 2004; Appendix). Bowhead whales seek protection from killer whales by entering cracks in dense ice or, when no ice is available, shallow water (Mitchell & Reeves, 1982; Finley, 2001), a behaviour described by the Inuit people of eastern Canada as *ardlingayuq*, or 'fear of killer whales' (Finley, 1990). Unlike right, grey and bowhead whales, humpback whales have not been reported attempting to swim towards the shallows even though some of the interactions described in the Appendix took place in nearshore areas.

Flight species

The *flight* strategists all belong to the genus *Balaenoptera*: common minke whale, Antarctic minke whale, Bryde's whale, sei whale, fin whale and blue whale. The antipredator responses to killer whales of these *Balaenoptera* species are a consistent and striking contrast to the responses of *fight* species. *Flight* species react to pursuit by killer whales, and occasionally simply to the predators' approach, by fleeing at speeds of 20–40 km/h. Flight trajectories tend to be highly directional without shoreward orientation, and may end within several minutes if no chase ensues, but can continue for 1 hour or more when the whale is pursued.

Although most documented predatory interactions with *flight* species (see Appendix) involved single baleen whales, there appeared to be no tendency for individuals to join together when multiple whales were involved. Vidal & Pechter (1989) reported that an aggregation of fin whales dispersed slowly and quietly towards open sea while a high-speed chase involving killer whales and a pair of fin whales was underway nearby. Bryde's whales and blue whales fled at high speed when approached by killer whales, but did not group together (Appendix). Minke whales also flee towards open sea when chased, but occasionally run into shallow bays and become stranded. Beaching by minke whales and sei whales pursued by killer whales was noted by Goodall, Boy & Schiavini (2007), who suggested that the chased whales beached themselves intentionally to avoid predation. However, patterns of

flight responses observed in minke whales suggest that the whales more likely blunder into confined spaces or shallow water inadvertently while fleeing, or possibly get driven ashore by the pursuing killer whales (Ford *et al.*, 2005). Minke whales were twice observed to end a high-speed flight from killer whales by positioning themselves close to the hull of a nearby vessel, possibly to hide from the predators. This was unsuccessful in both cases (Ford *et al.*, 2005).

Another remarkable contrast to the *fight* strategy is the lack of physical defence seen in *flight* species. Seventeen attacks on *Balaenoptera* whales in which there were opportunities for the whale to defend itself are summarized in the Appendix. The sole observation that might be interpreted as an attempt at defence involved a Bryde's whale that was under attack for 1.5 hours and on one occasion 'forcefully wave[d] its tail laterally' (Silber, Newcomer & Perez-Cortez, 1990). Otherwise, the Bryde's whale responded in a manner typical of *flight* species – it submitted to the assault without any obvious defensive action until it was killed. *Flight* species do not even display passive resistance, such as rolling upside down as seen in grey whales. *Balaenoptera* species seem to rely on rapid escape and appear unable to defend themselves or retaliate should flight fail. Some terrestrial mammals that rely on speed and stamina for escape, such as wildebeest *Connochaetes taurinus* and Thomson's gazelle *Gazella thomsonii*, also lack retaliatory defence towards their predators (Edmunds, 1974). Intraspecific aggression associated with mating, as seen in some *fight* species, has not been observed in *Balaenoptera* whales, although the mating system and related behaviour of these whales are virtually unknown (Brownell & Ralls, 1986; Boness, Clapham & Mesnick, 2002).

Morphological and life history correlates with antipredator strategy

In addition to the disparate behavioural responses associated with the two broad classes of antipredator strategy, several important morphological attributes and life history features further differentiate and define the lifestyles of *fight* and *flight* species. Although these traits likely serve a variety of purposes, we suggest that a significant selective force driving the evolution of at least some of them has been predation pressure.

Adaptations for speed

Fight and *flight* strategists differ dramatically in their swimming performance abilities. Despite their diverse phylogenies, the *fight* species are all relatively slow swimmers (Chittleborough, 1953; Mackintosh, 1965; Reeves & Leatherwood, 1985; Clapham & Mead, 1999; Williams, 2002; Woodward, Winn & Fish, 2006). Members of the genus *Balaenoptera*, in contrast, are all fast swimmers (Andrews, 1916a; Mackintosh, 1965; Bannister, 2002; Fish, 2002) and share morphological adaptations for fast and efficient swimming. *Balaenoptera* whales have elongated, streamlined body forms, which give them the highest fineness ratios (the ratio of body length to maximum body width; Bose & Lien, 1989) among the mysticetes. They tend to have small flippers relative to their body size for reducing drag, and high-aspect-ratio flukes (a measure of surface area relative to fluke length) for propulsive efficiency and high speed (Bose & Lien, 1989; Bose, Lien & Ahia, 1990; Woodward *et al.*, 2006).

Although accurate measurements of the top speed of mysticetes are scarce, it is clear that the *Balaenoptera* whales can reach and sustain far greater swimming speeds than other species. Scammon (1874) considered the blue whale to be 'the swiftest whale afloat'. Andrews (1916a) called the fin whale 'the greyhound of the sea', but also remarked that there was 'little doubt that for short bursts of speed no other large whale can approach *Balaenoptera borealis*' and claimed that sei whales could reach speeds of 30 miles/h (48 km/h) (Andrews, 1916b, p. 326). Table 2 provides a summary of estimated and measured swimming speeds of baleen

Table 2. Reported speeds (km/h) of baleen whales during routine swimming (e.g. feeding, travelling, migration) and during bursts or sprints

Species	Speed (km/h)		Source
	Routine	Sprint	
<i>Fight species:</i>			
North Atlantic right whale	6.5	13	Tomilin (1957)
	1.1–3.5*		Mate, Nieukirk & Kraus (1997)
Southern right whale	2.7–4.2		Bannister (2002)
Bowhead	7.5	13–17	Tomilin (1957)
	1.5–6	22.7*	Reeves & Leatherwood (1985)
	5–6		Würsig & Clark (1993)
	4*		Rugh (1990)
	5*		Mate, Krutzikowsky & Winsor (2000)
Gray whale	0.9–4.5*		Heide-Jørgensen <i>et al.</i> (2003)
		16	Gilmore (1956)
		13	Tomilin (1957)
	7–9		Rice & Wolman (1971)
	7.2*		Sumich (1983)
	4–5*		Mate & Harvey (1984)
	5.9–6.3*		Swartz <i>et al.</i> (1987)
Humpback whale	5.6*		Mate & Urbán-Ramirez (2003)
	8.0		Chittleborough (1953)
	6.3		Hubbs (1965)
	2–12*		Watkins <i>et al.</i> (1981)
	4.5–6.2*		Mate, Gisiner & Mobley (1998)
		15	Williams (2002)
	23*	Noad & Cato (2007)	
<i>Flight species:</i>			
Common minke whale	8.3*		Stern (1992)
		30	Williams (2002)
		20–30*	Ford <i>et al.</i> (2005)
Bryde's whale	5.7*		Rankin & Barlow (2005)
	2–7	20–25	Kato (2002)
Sei whale		29	Williams (2002)
		48	Andrews (1916b)
Fin whale	6.4		Tomilin (1957)
		30–33	Gunther (1949)
	5–14	40–50	Tomilin (1957)
	9*		Ray <i>et al.</i> (1978)
	9*		Watkins (1981)
	7.4–12.6*		Watkins <i>et al.</i> (1984)
		>37	Gambell (1985)
		30–40	Vidal & Pechter (1989)
Blue whale	1.5–5.9*		Watkins <i>et al.</i> (1996)
	4		Notarbartolo di Sciara <i>et al.</i> (1997)
		40	Williams (2002)
	5.4–7.2	34	Notarbartolo di Sciara <i>et al.</i> (2003)
		40*	G. Heckel (see Appendix)
		37	Gawn (1948)
		Lockyer (1981)	
	2–6.5		Mate, Lagerquist & Calambokidis (1999)
	2.4–7.2*		
	2–8	32–36	Sears & Calambokidis (2002)
		32	Williams (2002)

Speeds measured by methods such as satellite tracking or GPS are marked with an asterisk. All others are either estimated or the means of determining speed was not indicated in the source.

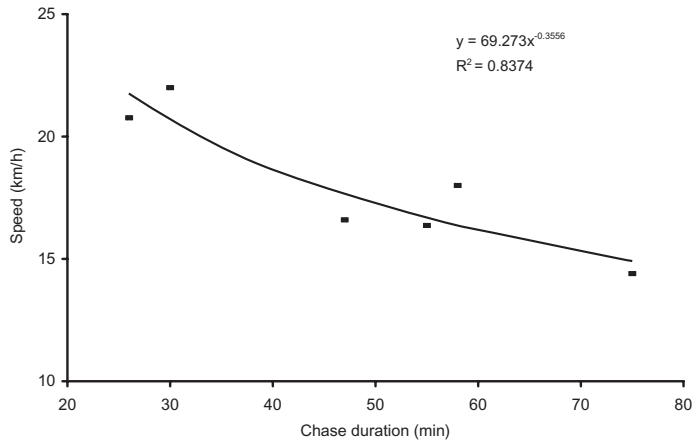


Fig. 4. Swimming speeds of killer whales chasing minke whales as a function of chase duration. Data from Ford *et al.* (2005) and Ford (unpublished data).

whales. Maximum sprint speeds of *Balaenoptera* whales are estimated to be 30–40 km/h. When moving at such high speeds, they adopt a ‘porpoising’ style of swimming, where they arch their bodies partly or mostly out of the water while surfacing to breathe (Gunther, 1949; Watkins, 1981; Ford *et al.*, 2005; Appendix; see also Fig. 3). Minke whales are somewhat slower than their larger congeners, with maximum speeds of about 30 km/h. The fastest measured burst of speed for a *Balaenoptera* is 40 km/h, which was determined by GPS for a fin whale fleeing from pursuing killer whales (G. Heckel, pers. comm.; see Appendix). In contrast, the maximum sprint speeds estimated for most *fight* species are 13–17 km/h, with exceptional top-measured speeds of about 23 km/h for a young bowhead whale and a group of humpback whales (Table 2).

For flight to be an effective antipredator strategy, baleen whales must achieve and sustain higher swimming velocities than the killer whales that pursue them. Killer whales are reportedly capable of swimming at speeds of up to 45 km/h (Williams, 2002), but are unable to maintain such speed for long. While chasing minke whales in coastal waters of the north-eastern Pacific, killer whales were observed swimming at speeds of at least 30 km/h at the outset, but this soon dropped as chases continued (Ford *et al.*, 2005). Average speeds of killer whales during relatively short (20–30 min) chases were 20–25 km/h, but were less than 20 km/h during 60-min chases, and only 15 km/h over a 75-min chase (Fig. 4). Although killer whales were able to match the speed of fleeing minke whales early in a chase, the minke whales appeared to have superior endurance and often outdistanced pursuing killer whales and escaped (Ford *et al.*, 2005; Appendix). Larger *Balaenoptera* whales have burst speeds (Table 2) and endurances that likely exceed that of minke whales. For example, Gawn (1948) reported that blue whales can swim at 20 knots (37 km/h) for 10 min and 14.5 knots (27 km/h) for 2 hours. Bose & Lien (1989) determined from morphological measurements and hydrodynamic calculations that fin whales can maintain efficient propulsion over a broad range of speeds, but their best propulsive efficiency is at speeds of 21–29 km/h. Lockyer (1981) noted that large *Balaenoptera* whales in the Southern Ocean easily outran pursuing vessels by swimming at speeds in excess of 12 knots (22 km/h) for 40 min or longer, without showing great fatigue. While attempting to deploy ‘Discovery’ tags on fin whales, Gunther (1949) observed that ‘a ship of 10–12 knots (19–22 km/h) has no hope of overtaking these whales and

they were usually abandoned by us after an hour's chase'. If the speed of killer whales during protracted minke whale chases reflects their maximum swimming ability (Fig. 4), it would appear that larger *Balaenoptera* whales are able to sustain speeds sufficient to outpace pursuing killer whales. The same cannot be said for *fight* species, whose top-burst speeds are well within the swimming performance abilities of killer whales. High-speed flight is clearly not an antipredator option for these slower species.

Adaptations for manoeuvrability

The morphological design of *fight* species may result in poor high-speed swimming performance, but it enhances their manoeuvrability compared with *flight* species. Humpback, grey, right and bowhead whales have flippers that are relatively longer and larger than those of *Balaenoptera* whales. This enables them to turn quickly and tightly and to undertake sculling and rowing manoeuvres when forward velocity is near zero. Humpback whales have exceptionally long flippers with protuberances on their leading edge that reduce drag and add lift, which further enhances turning ability (Miklosovic *et al.*, 2004). *Fight* species also tend to have larger fluke areas for their body size, which allows them to generate large acceleration forces to facilitate rapid turning at low speeds (Woodward *et al.*, 2006). Enhanced manoeuvrability would clearly be an advantage for animals physically defending themselves from attacking killer whales. Rapid and precise turning and positioning are no doubt critical when confronting multiple attackers and directing blows towards them with tail flukes, flippers or head. Sculling and rowing motions would allow grey whales to roll at the surface, which may be intended to prevent ventral ramming and to hold calves out of the water for protection. Also, *fight* species that retreat into shallow water would need good manoeuvrability to negotiate obstacles and prevent accidental stranding. Humpback whales seem not to seek refuge even though they frequently occur in or near shallow water. Perhaps, the proficiency with which adult humpbacks fend off attacking killer whales means that there is little incentive for them to seek refuge. *Balaenoptera* whales, with their relatively small flippers and flukes, cannot easily make quick starts and sharp turns (Gunther, 1949; Woodward *et al.*, 2006) and likely lack the manoeuvrability necessary to effectively defend themselves or retaliate against attacking killer whales.

Weapons and armour

Most *fight* species have encrustations over parts of their body that may play a role in defence during killer whale attacks. Right whales have raised hardened patches of skin on the dorsal, lateral and ventral surfaces of their head, known as callosities. Although callosities are found on both sexes, they tend to cover the head of males more extensively than females. Payne & Dorsey (1983) proposed that callosities serve as weapons during aggressive interactions among competitive male right whales, noting that their use leaves visible scrape marks on the whales' skin. Such a function does not explain why females also have callosities. It is conceivable that callosities provide both sexes with some protection from attacking killer whales. Male right whales show clear indications that being scraped by these rough and jagged callosities is painful (Payne & Dorsey, 1983), and it seems reasonable that killer whales would be wary of being struck by these encrustations while right whales roll and thrash during attacks.

Sessile barnacles can be found attached to many species of cetaceans, but none are encrusted to the extent seen on grey and humpback whales (Christensen, 1986; Fertl, 2002). At least three species of barnacles, the acorn barnacles *Coronula diadema* and *C. reginae* and a stalked barnacle *Conchoderma auritum*, occur on humpback whales (Cornwall, 1927;

Clarke, 1966). These are concentrated around the head, along the throat pleats, genital slit and leading edges of the flippers, and on the tips of the tail flukes (Clarke, 1966; Fertl, 2002). *C. diadema* in particular is quite large, reaching 5 cm in diameter and protruding 3 cm from the whale's skin surface, and individuals of this species can serve as an attachment substrate for up to 40 *Conchoderma* barnacles (Clarke, 1966). Individual humpbacks may carry as much as 450 kg of barnacles (Slijper, 1962). Barnacles on humpbacks may act as weapons during aggressive interactions among males. Male humpbacks engage in often-violent physical exchanges in competitive groups while on their breeding grounds. These exchanges include head butting and ramming, and striking blows with their long flippers and tail flukes (Tyack & Whitehead, 1983; Baker & Herman, 1984; Silber, 1986). These parts of the body are all areas where concentrations of barnacles are found, and a blow from a barnacle-encrusted surface would likely have enhanced effectiveness in aggressive physical interactions (Pierotti, Swatland & Ewald, 1985). We propose that barnacles may also play an important role as weapons when humpbacks are actively defending themselves from attack by killer whales. Humpbacks use the head, flippers and flukes to butt and strike out at killer whales, and barnacles may increase the chance of causing injury to killer whales and thereby provide more effective deterrence.

Grey whales carry extensive concentrations of the barnacle *Cryptolepas rhachianecti* (Kasuya & Rice, 1970; Rice & Wolman, 1971). These often form a continuous mass over the dorsal surface of the rostrum and anterior portion of the back, and can be found in dense clusters on the flippers, tail flukes and elsewhere on the body (Rice & Wolman, 1971). Unlike humpbacks and right whales, grey whales do not exhibit intraspecific aggression associated with male competition (Norris *et al.*, 1977, 1983; Jones & Swartz, 2002). Grey whales are also less inclined than humpback and right whales to retaliate by striking out at attacking killer whales. Barnacles on the skin of grey whales could help deter attacking killer whales as they try to ram or bite their potential prey.

Not all *fight* species are encrusted with barnacles. Right whales and bowhead whales are usually barnacle free, though concentrations of the barnacle *Tubicinella major* are embedded in the callosities of southern right whales (Tomilin, 1957; Scarff, 1986). Encrustations of barnacles and callosities are both absent on *flight* species.

Migratory patterns

Most mysticete species migrate between low-latitude winter calving areas and high-latitude summer feeding grounds. Some species, such as the grey whale and humpback whale, undertake extensive migrations and may travel 5000–9000 km (one-way) between feeding and calving areas (Rice & Wolman, 1971; Rasmussen *et al.*, 2007). Others, such as the sei whale and bowhead whale, have relatively diffuse or shorter-distance migrations that may vary with environmental conditions. Certain populations of blue, fin, Bryde's and humpback whales may be essentially non-migratory and remain in low-latitude waters throughout the year (Mikhalev, 1997; Bannister, 2002; Hucke-Gaete *et al.*, 2004).

Various hypotheses have been proposed to explain baleen whale migration. Most focus on the presumed thermoregulatory and energetic benefits that may result from leaving cold waters in winter when food availability is low (Brodie, 1975), and the increase in calf survival that may result from parturition in warm and relatively calm subtropical or tropical waters (Clapham, 1996, 2001). More recently, Corkeron & Connor (1999) discounted these earlier hypotheses and proposed that the primary selective factor driving baleen whale migration is predation by killer whales. They suggested that female baleen whales migrate to low-latitude waters to give birth because neonates are vulnerable to killer whale predation, and the density

of these predators is substantially greater in high latitudes. Males migrate as well to take advantage of mating opportunities on or near the calving grounds. This hypothesis was contested by Clapham (2001), who argued that killer whale predation is unlikely to have been the selective force driving mysticete migration, and that Corkeron & Connor's (1999) dismissal of the energetic explanation was not warranted.

If killer whale predation is not the primary selective force driving mysticete migration, it at least appears to have been important in shaping it. Patterns of migratory behaviour of baleen whales are consistent with the divergent antipredator strategies described here. *Fight* species generally use calving areas, and often migratory corridors, that provide favourable conditions for protecting neonates from killer whales. Eastern Pacific grey whales give birth and nurse their young in the inner parts of shallow lagoons in Baja California, where killer whales rarely occur (Reeves *et al.*, 2006). Calves migrating north with their mothers are targeted by killer whales at various localities, while older age classes are not (Goley & Straley, 1994; Ternullo & Black, 2002; Barrett-Lennard *et al.*, 2005; Appendix). Off central California, mother–calf pairs migrate within 200–400 m of shore. They follow the contour of the shoreline and often swim inside islets and through or along kelp beds (Poole, 1984). Other age/sex classes of grey whales, which migrate earlier than mother–calf pairs, use a migration corridor that is farther offshore (800–3200 m) and tend to travel from point to point rather than following the shore. Poole (1984) suggested that the nearshore route provides mother–calf pairs with protection from killer whales, as they can quickly find refuge in shallow water or kelp beds if needed. At the northern end of the migration, females with calves move into the coastal Chukchi Sea during the summer feeding season. Moore, Ljungblad & Schoik (1986) suggested that this could be due to predation pressure from killer whales, which are considered more abundant in the Bering Sea feeding grounds where other age/sex classes feed.

Like grey whales, North Atlantic and southern right whales tend to migrate to coastal, shallow-water calving areas where neonates can be defended from attack by killer whales. Female southern right whales in Argentina spend considerable time rearing their newborn calves in waters as shallow as 5 m, and retreat to these shallows if further offshore when killer whales approach or attack (Payne, 1995; Sironi *et al.*, 2004; Appendix). Other southern right whale calving areas include shallow, nearshore areas in southern Africa and Australia, while North Atlantic right whales calve in shallow coastal waters along the south-eastern United States (Kenney, 2002). Calving grounds for North Pacific right whales, which are extremely depleted due to whaling, are unknown.

Migration patterns and distribution of bowhead whales may also be influenced by killer whales. British whalers believed that adult male bowheads have 'the least to fear from natural enemies' (i.e. killer whales) and remain in the 'most exposed and open situations', while females with calves and juveniles 'keep to deeper situations amongst the ice, and disappear early in the season into its recesses' (Gray 1926, cited in Finley, 2001). Finley (1990) attributed the 'coast-hugging' tendencies of autumn-migrating bowheads to the proximity of shallow water for more effective defence from killer whales in the absence of protective ice cover.

Like those of most other *fight* species, the calving grounds of humpback whales are in shallow areas along continental coastlines or around offshore islands and reefs (Dawbin, 1966; Clapham & Mead, 1999). Killer whale predation is rarely observed on humpback calving grounds (Clapham, 2000), but the high incidence of killer whale teeth scars observed on humpback calves in some regions during their first high-latitude feeding season suggests that, like grey whale calves, they are targeted by killer whales during their first migration

(Katona *et al.*, 1990; Clapham, 2001; Mehta *et al.*, 2007; Steiger *et al.*, in press). In fact, a major drawback of a predictable, concentrated, nearshore migration is that it presents killer whales with a reliable stream of potential prey. Coastal migration must confer other advantages that outweigh or at least balance this risk of predation. If nothing else, it may be the shortest route between feeding and breeding grounds. Unlike those of grey whales, the migration routes used by humpback whales are sometimes not close along coastlines, and it is unclear what defensive tactics are employed by mothers during the period of calf vulnerability.

Compared with those of *fight* species, the migratory patterns and destinations of *flight* species are poorly understood. Most *Balaenoptera* species and populations move seasonally between high-latitude feeding areas and low-latitude waters for calving, but the locations of calving areas are unknown and may be spatially diffuse. These species are widely dispersed in offshore waters in tropical to warm temperate regions during the calving season (Mackintosh, 1965; Kasamatsu, Nishiwaki & Ishikawa, 1995; Clapham, Young & Brownell, 1999; Bannister, 2002; Stafford *et al.*, 2004). Discrete calving grounds where whales congregate in high densities, such as those seen in *fight* species, may not exist for *Balaenoptera* whales. Offshore calving and nursing is consistent with the antipredator strategy of this group. *Flight* species require open water in which to undertake a potentially lengthy escape sprint from pursuing killer whales. Risk of capture would increase with proximity to the coast, as killer whales could drive whales into confined embayments or fleeing whales could accidentally run into shallow water or ashore, as seen in minke whales (Ford *et al.*, 2005). Chases of *Balaenoptera* mother–calf pairs have rarely been observed, but it seems likely that in most circumstances they would be able to sustain sufficient speed to escape from killer whales. Blue, fin and sei whale neonates are close to the size of adult minke whales at birth or soon thereafter (Lockyer, 1981), and probably can attain comparable speeds. *Balaenoptera* neonates may well be precocial and ready to swim at high speed shortly after birth, as seen in terrestrial mammals that use flight to escape from predators (Kruuk, 1972). Gunther (1949) observed a fin whale mother and calf escape after being chased for 1.5 hours by a whale-marking vessel.

Predation as a selective force in mysticete evolution

As noted above, predation is one of the major selective forces influencing animal evolution. Adaptive traits to minimize predation can be seen in the morphology, physiology, chemistry, life history and behaviour of prey species (e.g. Edmunds, 1974; Sih, 1987). Together, these traits can shape and define a prey species' lifestyle, which may reduce predation risk but can also constrain a species ecologically (Sih, 1987; Lima, 1998). Prey can actively minimize the risk of predation in two main ways: (i) by avoiding encounters with predators (primary defence; Edmunds, 1974); and (ii) by escaping after an encounter (secondary defence). Baleen whales as a group appear to employ both forms of defence: the nearshore migratory corridor of grey whale mother–calf pairs may be an example of a primary defence trait, while the physical retaliation by *fight* species and high-speed escape by *flight* species may represent examples of secondary defence traits.

In order to assess the extent to which the morphological, behavioural and life history traits of mysticetes described above can be attributed to predation, the level of predation pressure under which these species live (or lived historically) must be evaluated. We emphasize, again, that our conception of predation pressure is broader than just killing and consuming; it encompasses the patterns of behavioural response exhibited by potential prey under risk of predation. The rarity of witnessed attacks by killer whales on baleen whales, especially the larger species, has often been taken as an indication that killer whales do not regularly attack

and kill these species (e.g. Jonsgård, 1968a,b; Heptner *et al.*, 1996; Mizroch & Rice, 2006), and thus do not represent a significant source of predation pressure (Clapham, 2001). However, the paucity of observed attacks is not necessarily a sign of minimal predation pressure, as low rates of attacks would be expected if antipredator adaptations of prey were effective (Sih, 1985, 1987; Connor & Corkeron, 2001). Also, current rates of predation may not be representative of levels in the evolutionary past, which would be the context in which successful antipredator responses evolved (Sih, 1985; Speakman & Rydall, 2000). Finally, the mere presence of predators, even if the risk of mortality is low, can have far-reaching effects on a prey species' behaviour and life history strategy (Sih, 1987; Lima & Dill, 1990; Lima, 1998).

Documented attacks by killer whales on baleen whales are rare, but the frequent presence of scars from killer whale teeth on the bodies of baleen whales suggests that predation pressure is significant in most species. Several studies have quantified the frequency of occurrence of such scars on mysticetes determined either from photographs of living animals or from examination of carcasses collected in whaling operations. For *fight* species, frequencies of 10–20% are common, though some populations have wider ranges, and such scars are virtually unknown in the current population of North Atlantic right whales (Mehta *et al.*, 2007). Scarring rates on bowhead whales were relatively low at 4–8% in the western Arctic (George *et al.*, 1994), but 31% in the eastern Arctic (Finley, 1990). Of 316 grey whales killed off California for research, 18% bore killer whale scars (Rice & Wolman, 1971). Frequencies of scarring are highly variable among humpback whale populations. In the North Pacific, they range from highs of 30–40% off Mexico to lows of 6–8% in waters of the Japanese islands of Ogasawara and Okinawa (Mehta *et al.*, 2007; Steiger *et al.*, in press). For *flight* species, frequencies also vary by species and population. Scarring rates reported for blue whales include 25% in the Gulf of California (Sears, 2002), 4% off south-eastern Australia and 42% off western Australia (Mehta *et al.*, 2007). High rates of scarring were described by Shevchenko (1975) for fin whales (53%) and sei whales (24%) in the Southern Ocean. Scars were observed most frequently on the pectoral flippers and tail flukes, but were also found on the caudal peduncle and dorsal fin of fin whales. The relatively low rate of scarring on southern minke whales (6.4%) was thought to reflect a high proportion of successful attacks on this small baleen whale species (Shevchenko, 1975). Variation in levels of scarring observed on baleen whales in different regions may reflect the local relative abundance of mammal-hunting killer whales.

There is strong evidence that scars on humpback whales result predominantly from unsuccessful killer whale attacks that take place when the animals are young calves, and this may be true for other mysticetes as well. Long-term photo-identification studies of humpback whales in the Gulf of Maine have revealed that virtually all killer whale scars are already present on individuals when they are first identified as calves (Clapham, 2000, 2001; Mehta *et al.*, 2007). Because killer whales are rare on both the calving and feeding grounds of this population, it is probable that the attacks occur primarily along the migratory corridor during the neonates' first migration (Clapham, 2001; Mehta *et al.*, 2007). Similar conclusions have been reached by researchers studying humpback whales in other regions (Chittleborough, 1953; Dolphin, 1987; Naessig & Lanyon, 2004; Steiger *et al.*, in press), though attacks on calves have been observed on some breeding grounds as well (Flórez-González, Capella & Rosenbaum, 1994; Appendix).

The frequency of killer whale scars indicates that a substantial proportion of humpback whale mother–calf pairs – almost one-third in some populations – are involved in predatory interactions with killer whales. Because neonates are likely incapable of defending themselves

from killer whales, their survival would depend on effective defensive actions by the mother and possibly other individuals involved in defensive groupings. Even if the proportion of successful (i.e. lethal) attacks on humpback calves was low, the frequency of unsuccessful attacks would appear to provide ample selective pressure to drive antipredator adaptations. As pointed out by Vermeij (1982, 1985), it is the unsuccessful attempts at predation (from the predator's perspective) that are most important in the evolution of antipredator traits, as it is the survivors that go on to reproduce. In the case of humpback whales, mothers can significantly enhance their reproductive success through active protection of their calves from predation.

Less is known of the life stages during which other mysticetes acquire killer whale scars, but it is reasonable to assume that calves are the most susceptible in all species. Calves on their first north-bound migration are clearly the primary targets in killer whale attacks on grey whales, and mothers are often able to successfully protect them by active defence and/or retreat to refuges. However, recently weaned grey whale calves and yearlings also are attacked in higher latitudes (Barrett-Lennard *et al.*, 2005; Melnikov & Zagrebin, 2005). Killer whales often target southern right whale calves on their calving grounds, though juveniles and adult-sized southern right whales are also attacked (Appendix). Most documented chases and attacks of *flight* species have involved adult-sized individuals on their feeding grounds, but this may be due at least partly to the fact that these species are rarely observed at all on the calving grounds, the locations of which are mostly unknown. Again, we stress that the strategy of *not having* a spatially concentrated calving ground may itself be a part of the *flight* species' antipredator strategy. Cotton (1944) reported a blue whale mother–calf pair fleeing at speed from killer whales off southern Australia and Pitman *et al.* (in press) observed killer whales feeding on a blue whale calf in offshore tropical waters, but the kill was not witnessed.

Although predation pressure is a potentially important selective force in baleen whale evolution, it is not clear whether what may well be antipredator traits as seen today arose primarily as a result of predation or instead evolved in response to other selective factors, with their antipredator role being a secondary benefit. Distinguishing between the adaptive results of different selective agents, including predation, is a common problem confronting evolutionary biologists (e.g. Vermeij, 1982; Abrams, 2000). Of particular interest with regard to mysticete evolution is the extent to which the morphological adaptations that facilitate the two divergent antipredator strategies – slow swimming speed and high manoeuvrability of *fight* species, vs. high-speed and limited manoeuvrability of *flight* species – were influenced by selection for reduced predation. Woodward *et al.* (2006) recently presented a comparative analysis of the morphology of representative baleen whale species with respect to their prey type, feeding behaviour and habitat. They concluded that the highly streamlined blue whale is 'designed for steady, high swimming speed efficient cruising in a pelagic environment', where the 'efficiency of travel from one prey patch to the next is more important in their foraging strategy than is a high degree of manoeuvrability' (Woodward *et al.*, 2006). This would presumably apply to other pelagic *Balaenoptera* species as well. The robust right whales, on the other hand, are designed for 'efficient slow speed cruising . . . optimal for their continuous filter feeding technique'. Woodward *et al.* (2006) propose that manoeuvrability is a priority over speed in the design of grey whales and humpback whales, due to their specialized feeding techniques. The relatively large flippers and flukes of humpbacks allow for the quick manoeuvrability needed to execute tight rolls and turns while bubble and lunge feeding. Grey whales are designed for 'enhanced low-speed manoeuvring in complex coastal habitats' where they feed on benthic or epibenthic prey.

It is reasonable to conclude that ecological factors related to foraging would be primary forces driving the divergence of baleen whales, but some traits of mysticetes can be more easily explained as antipredator adaptations. The *Balaenoptera* whales, for example, can reach swimming velocities far higher than other mysticetes, but there is little evidence that they make use of this exceptional swimming ability in their typical day-to-day lives. A review of swimming speeds measured or estimated for baleen whales (Table 2) shows that during routine activities, such as during foraging and migration, the *Balaenoptera* species generally swim at speeds of less than 10 km/h, and not appreciably faster than many of the slower *fight* species. We propose that the ability of *Balaenoptera* whales to swim at sustained speeds 3–5 times faster than these routine speeds, and the suite of morphological and physiological traits that enable them to do so, is primarily a result of their *flight* antipredator strategy. We also suggest that predation has been an important selective pressure leading to use of coastal calving grounds by *fight* species. The advantage afforded by shallow, nearshore waters in the defensive protection of neonates appears to be a selective force that has led to the convergent evolution of this behaviour in three different mysticete families.

It is interesting to consider whether the presence of callosities and barnacles on *fight* species represent adaptive traits that have arisen due to the benefits they confer to individuals when defending themselves or their calves from killer whales, or instead whether any offensive or defensive functions they serve are incidental. In some terrestrial mammals, such as many bovids and antelopes, both sexes have horns that serve as weapons in intraspecific interactions as well as in predator defence (Edmunds, 1974). As is often the case, determining which has been the primary selective force is difficult.

High densities of barnacles are found primarily on humpback whales and grey whales, which also happen to be *fight* strategists. Although there has been little critical discussion of why barnacles are less common on other cetaceans, it is generally stated or implied that such organisms are unable to settle and develop on faster-swimming whale species (e.g. Slijper, 1962; Fertl, 2002). This explanation seems overly simplistic and is less than satisfying. Right whales, which are as slow as or slower than grey and humpback whales (Table 2), are usually free of barnacles except for a single, non-protruding and rather cryptic species found in the callosities of southern right whales (Scarff, 1986). As discussed above, the routine swimming speeds of *Balaenoptera* whales are not substantially greater than those of barnacle-infested species such as grey and humpback whales, yet these *flight* species are free of embedded acorn barnacles (the stalked barnacles *Conchoderma* spp. and pseudo-stalked barnacles *Xenobalanus* spp. are occasionally found on these species; Clarke, 1966; Fertl, 2002). High densities of barnacles on the bodies of cetaceans would cause hydrodynamic drag and add to the energetic cost of locomotion regardless of swimming speed, and it seems possible that cetaceans have evolved anti-fouling mechanisms in their integument to prevent such infestation. The two notable exceptions, grey whales and humpback whales, may derive benefits from barnacles that outweigh their energetic cost and thus their integument may be specialized to tolerate or encourage barnacle attachment. Nogata & Matsumura (2006) provide evidence that larval settlement of the barnacle *C. diadema* results from a chemical cue from the host's tissue, in this case the humpback whale. We propose that selection may have favoured the evolution of a mutualistic relationship between host-specific barnacles and grey and humpback whales due to their beneficial role as armour or weapons in predatory interactions with killer whales. Pierotti *et al.* (1985) made a similar suggestion in the context of aggressive intraspecific interactions in humpback whales, likening barnacles to 'brass-knuckles' for use as weapons in competitive combat.

Effectiveness of antipredator strategies: are baleen whales profitable prey?

It is apparent from this review and others (e.g. Jefferson *et al.*, 1991; Mizroch & Rice, 2006; Reeves *et al.*, 2006) that successful predation by killer whales on baleen whales other than calves is fairly rare except possibly in the case of minke whales. Chases and harassment often end quickly without any physical attack. When attacks do take place, the killer whales most often abandon their potential prey without making a kill. Rates of acquisition of killer whale teeth rakes appear very low on adult humpback whales compared with calves, and this may well be true of other mysticetes as well. Field researchers who observe mammal-hunting killer whales in close proximity to baleen whales consistently report that the predators typically ignore these potential prey (Dolphin, 1987; Jefferson *et al.*, 1991; Ford & Ellis, 1999; Ternullo & Black, 2002). We believe that mammal-hunting killer whales seldom attack adult baleen whales because of the effectiveness of their antipredator strategies. *Flight* species offer low profitability (ratio of energy gain to pursuit and handling time per attack; Stephens & Krebs, 1986) due to the high cost associated with the prolonged chases needed to capture them, the high probability of failure, and, in the event of successful attack, the likelihood that only a small portion of the prey item can be consumed. This last point is particularly important because the negatively buoyant carcasses of *flight* species tend to sink quickly. At least in deep-water areas, such sinking puts a carcass effectively out of reach of killer whales (Guinet, Barrett-Lennard, & Loyer, 2000). This may not be an issue for small species such as minke whales or calves of larger *Balaenoptera* whales, which could be held near the surface long enough for consumption (e.g. Pitman *et al.*, in press). However, the carcass of a mature individual of a large species would be less easily managed, as appeared to be the case when 16 killer whales abandoned a sinking fin whale carcass after feeding on it for only 15 min following an hour-long high-speed chase and attack (G. Heckel, pers. comm., see Appendix).

Fight species also offer low profitability to killer whales due to the prolonged 'handling' time needed to attack these prey successfully. Perhaps even more importantly, these species pose a considerable risk of injury to attacking killer whales. A bowhead whale reportedly struck and killed a killer whale with its tail flukes (Eschricht, 1866), and right whales were observed to strike attacking killer whales during two encounters (Sironi *et al.*, 2004; Appendix). A grey whale was observed to strike and kill an adult walrus *Odobenus rosmarus* with its flukes (Mazzone, 1987), illustrating the effectiveness of the tail as a weapon. Mammal-hunting killer whales are cautious predators and exhibit considerable wariness while attacking dangerous prey such as Steller sea lions *Eumetopias jubatus*, which can inflict wounds if given the opportunity. Defensive actions of Steller sea lions appear often to be effective judging from the high rate of unsuccessful attacks (Ford *et al.*, 1998; Ford & Ellis, 1999). Thus, it would not be surprising if killer whales prefer less dangerous prey as an alternative to risking injury by attacking a baleen whale capable of retaliation.

CONCLUSIONS

Predation pressure from killer whales appears to have been a significant selective force influencing baleen whale evolution and behaviour. Mysticetes are certainly not unusual in this respect – predation is generally considered to be one of the most important factors driving animal evolution. Some authors have discounted the importance of killer whale predation as a selective force for baleen whales because of the rarity of observed attacks. However, we have attempted to show in this review that there are a number of good reasons to reconsider and temper that view. We propose that baleen whales exhibit two distinct and contrasting antipredator strategies: the *fight* and *flight* strategies. Many of the morphological, behavioural and life history traits of mysticetes are consistent with these strategies, though

the relative contributions of predation pressure vs. other selective forces in the evolution of these adaptations remain unclear and require further study. It is our hope that the hypotheses presented herein will stimulate discussion and encourage those who undertake field research on mysticetes to consider how their observations and findings do or do not fit into the hypothetical antipredator framework we have described.

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APPENDIX

Species	Date	Location	# KWs	# Prey	Killer whale behaviour	Baleen whale response	Kill?	Summary	Source
Balaenidae:									
Southern right whale	22 Sep 1965	Algoa Bay, South Africa	3	4	Harass	Group, defend	N	Two pairs of whales circled by killer whales reacted by grouping together; one whale lashed flukes at killer whale, making 'resounding slap'.	Donnelly (1967)
<i>Eubalaena australis</i>	27 Oct 1970	Mossel Bay, South Africa	3	8	Harass	Group, defend	Unk	Killer whales circled and rushed at group of right whales, which clustered tightly together, rolled and thrashed. Incident >3 hours in duration	P. Best, pers. comm., 2005
	4 July 1971	Golfo San José, Argentina	5	2	Harass	Group, defend	N	Right whales grouped tightly together, rolled and slashed with flukes and flippers while circled by killer whales, then retreated into shallow water after the 25-min long attack ended.	Cummings <i>et al.</i> (1972)
	24 Sep 1972	Golfo San José, Argentina	5	6+	Harass	Group, defend	N	Females assumed defensive posture with heads towards centre of ring and thrashed tail flukes. Mother swam into very shallow water with calf tight to side, and slashed tail at killer whales.	Sironi <i>et al.</i> (2004)
	28 Sep 1975	Punta Norte, Peninsula Valdés, Argentina	7	1	Attack	Defend	N	Lone male juvenile right whale reacted to attack by rolling repeatedly, apparently trying to hit killer whales with its head. Visual contact lost at dusk; attack duration >1 hour	Sironi <i>et al.</i> (2004)
	29 Sep 1975	Punta Norte, Peninsula Valdés, Argentina	7	8	Harass, attack	Group	N	Right whales formed 'rosette' with tails out and heads towards centre as killer whales approached. Killer whales disrupted formation and attacked same juvenile as 28 September 1975 incident. Whales ended attack after 40 min.	Sironi <i>et al.</i> (2004)
	28 Aug 1981	Golfo San José, Argentina	1	1	Attack	Defend, flee	Unk	Adult right whale slapped tail vigorously on water surface and swam rapidly along shore as killer whale swam 30–40 m offshore. Killer whale attacked right whale, biting it repeatedly, then whales lost from sight.	Sironi <i>et al.</i> (2004)
	30 Oct 1988	Caleta Valdés, Argentina	9–10	1	Attack	Defend, group	N	Lone adult right whale slashed tail at killer whales that surrounded and attacked it. After 1 hour, two adult right whales joined animal under attack and they formed a tight group and swam along shoreline. Killer whales followed for 90 min then departed.	Sironi <i>et al.</i> (2004)
	6 Sep 1996	Río Negro, Argentina	8	1	Attack	Defend	Not spec	Adult right whale seized by pectoral flippers rolled actively at surface and emitted loud vocalizations. One killer whale was struck with tail flukes. Attack lasted >150 min	Sironi <i>et al.</i> (2004)

14 Sep 2000	Punta Norte, Peninsula Valdés, Argentina	4	3	Harass	Group, defend	N	Two adult right whales swam closely on either side of calf, and slashed their tails towards approaching killer whales. Two more adult right whales joined harassed whales after 95 min and formed tight group, keeping calf in centre. Killer whales soon departed.	Sironi <i>et al.</i> (2004)
13 Oct 2000	Golfo San José, Argentina	2	4	Attack	Group, defend	N	Killer whales harassed three adult right whales and a very small calf. Intense splashing and flipper slapping observed. One adult right whale repeatedly pushed calf towards centre of group. One killer whale apparently struck by right whale tail, lifting animal above surface. Single adult right whale left group to chase after killer whales, then returned to group. Killer whales left after 30 min	Sironi <i>et al.</i> (2004)
21 Nov 2000	Peninsula Valdés, Argentina	5–8	4	Harass	Group, defend	N	Group of killer whales harassed right whale mother/calf pairs on two occasions. Adult right whales slapped water with flukes and pectoral flippers, positioned themselves between the killer whales and calf, and retreated into nearby shallow waters.	M. Iniguez, pers. comm. 2005
29 Sep 2004	Melkbosstrand, South Africa	2	2	Harass	Group, defend	Unk	Killer whales circled and rushed at mother with calf for almost 3 hours. Mother/calf rolled, thrashed water surface with flukes, emitted loud blows. Calf possibly killed.	P. Best, pers. comm., 2005
21 July 2005	East of Cape Cod, New England	10–11	4	Harass	Group, defend	Unk	Right whales grouped tightly together and thrashed their flukes at water and at killer whales, which circled, rushed at, and dove under right whales.	Fraser (2005)
Mid 1800s	Greenland	–	–	Harass	Defend	Not spec	Killer whales attacked by holding onto bowhead's tail and fins, and jumping on its blowholes apparently to obstruct breathing. Bowhead struck one killer whale with its tail flukes, possibly killing it in the process.	Eschricht (1866)
July 1922	Vicinity of Pond Inlet, Baffin Island	–	5	Chase	Hide	Not spec	Bowheads chased into narrow crack in ice by killer whales.	Munn, undated, cited in Mitchell & Reeves (1982)
Aug 1975	Frobisher Bay, Baffin Island	5	1	Harass	Defend	Unk	Five killer whales surrounded a large bowhead, which thrashed with its flukes in defence.	Mitchell & Reeves (1982)
11 Sep 1984	Isabella Bay, Baffin Island	4	1	Approach	Defend	Unk	Two of four killer whales approached single bowhead, after which there was much splashing and upwellings for 12 min.	Finley (1990)

APPENDIX (Continued)

Species	Date	Location	# KWs	# Prey	Killer whale behaviour	Baleen whale response	Kill?	Summary	Source
Grey whale <i>Eschrichtius robustus</i>	17 Sep 1985	Isabella Bay, Baffin Island	22	23	Approach, harass, attack?	Hide, group, defend	Unk	Bowheads grouped together and moved into shallow water at approach by killer whales. One bowhead offshore harassed and possibly attacked, with much associated splashing.	Finley (1990)
	1998	Chukotka Peninsula, Russia	4	11–12	Chase	Hide	Unk	Bowheads pursued by killer whales rapidly retreated into near-shore waters.	Melnikov & Zagrebin (2005)
Eschrichtiidae:									
Grey whale <i>Eschrichtius robustus</i>	14 Feb 1858	Magdalena Bay, Baja California	8–10	2	Attack	Defend	Unk	Killer whales attacked mother with calf close to shore. Mother defended calf by striking at killer whales with 'flukes and fins'. After 30 min, water was discoloured with blood and whales disappeared after a boat arrived on scene.	Saratoga 1857–58MS, in Reeves <i>et al.</i> (2006)
	Ca. 1910	Ulsan, Korea	15	7	Attack		Not spec	Grey whales rolled onto back and remained motionless when attacked.	Andrews (1914)
	26 Jan 1964	La Jolla, California	5	6	Approach	Avoid, hide	N	When approached by killer whales, grey whales reacted by swimming into shallow cove, near the line of breaking surf.	Burrage (1964)
	No date	Southern California	–	–	Approach	Hide	N	Observed grey whales react to presence of killer whales, at up to 2-km range, by exhaling underwater and only raising blowholes enough to inhale.	Hubbs (1965)
	No date	Central California	8	9	Approach	Avoid, hide, group	N	Grey whales grouped together and swam towards kelp beds when killer whales approached from 2-km distance. Gray whales remained near kelp beds after killer whales left, exposing blowholes only to inhale.	Dahlheim & Heyning (1999)
	2 May 1967	Monterey Bay, California	7	3	Harass, attack	Avoid, hide, defend	N	Grey whale rolled as killer whale tried to bite underside. Mother with calf moved into 2- to 3-m shallow water in surf, swam parallel to beach and attempted to swim under a pier.	Morejohn (1968)
	12 May 1967	Carmel, California	5–6	2	Attack	Avoid, hide	Y	Grey whale mother with calf retreated towards nearshore kelp bed when attacked. Calf killed and eaten. Presumed mother left area swimming slowly through kelp, exposing blowholes only to inhale.	Baldrige (1972)
	20 May 1981	Bering Sea, Alaska	16	27	Approach	Avoid, group	Unk	Scattered feeding grey whales formed tight groups of 3–6 individuals and slowly swam from area when pursued by 16 killer whales.	Ljungblad & Moore (1983)

2 May 1992	Monterey Bay, California	17+	2	Attack	Group, defend	Y	Mother with calf under attack rolled and splashed at surface, but made no attempt to flee. Calf and possibly mother killed.	Goley & Straley (1994)
22 April 1994	Tofino, British Columbia	6	2	Harass	Group, defend	N	Mother with calf harassed by killer whales rolled over on back, held calf on ventral surface. Killer whales departed soon after.	R. Palm, pers. comm. 1996; Ford <i>et al.</i> (1998)
June 1995	North of Vancouver Island, British Columbia	7	2	Attack	Group, defend	Unk	Killer whales surrounded and charged towards mother with calf. Mother reacted by slashing with tail flukes and rolling. On several occasions, mother rolled onto back with calf held above water on ventral surface.	M. Derry, pers. comm. 1996; Ford <i>et al.</i> (1998)
9 May 2004	Monterey Bay, California	12+	2	Harass	Avoid, hide	N	Mother with calf harassed by killer whales over 3.5 hours. Mother kept calf close alongside while she thrashed flukes and rolled at surface. Pair swam slowly towards shore, 5 km away; killer whales ended harassment when approximately 1 km from shore, in 16 m of water.	T. Kockhefer, pers. comm. 2005
23 May 2004	Catala Island, British Columbia	6-7	2	Harass	Defend	N	Killer whales rushed at mother with calf swimming slowly 5 m from steep rocky shore. Calf was positioned between mother and shore. Mother slashed vigorously and repeatedly with flukes towards approaching killer whales, which departed after grey whales entered shallow cove (4 m deep).	J. Ford, pers. obs.
1 Aug 2004	Pitun Bay, Sakhalin Is.	9	2	Harass	Avoid, hide	N	Killer whales observed circling mother with calf approximately 600-700 m from shore. After several unsuccessful attempts, mother-calf pair was able to break free of circling killer whales and swim underwater towards surf, at which point killer whales departed.	Vladimirov (2005)
9 Oct 2006	Clayoquot Sound, British Columbia	6	1	Harass	Defend, hide	N	Killer whales circled and rushed at adult-sized grey whale, which rolled and splashed at surface while retreating slowly towards kelp beds near shore. Killer whales left 10 min later, after grey whale entered shallows.	T. Perry, R. Orr, R. Palm, pers. comm. 2006
Balenopteridae: Oct 1951	Exmouth Gulf, Western Australia	4-5	3	Harass	Group, defend	N	While harassed by killer whales, humpback calf remained close to the presumed mother while the other adult charged the killer whales, beating them off with its flukes.	Chittleborough (1953)
4 July 1982	Grand Bank, Newfoundland	10-12	20-30	Attack	Group, defend	N	Feeding humpbacks reacted to killer whale attack by grouping together, turning and rolling, and thrashing at killer whales with tail flukes	Whitehead & Glass (1985)
25 June 1983	Grand Bank, Newfoundland	17	2+	Attack	Group, defend	N	Humpbacks vigorously defended themselves from killer whale attack, as in incident observed on 4 July 1982	Whitehead & Glass (1985)
26 June 1983	Grand Bank, Newfoundland	17	2+	Harass	Defend	N	Killer whales undertook 'weak' attack on humpbacks, which reacted with minimal defensive measures.	Whitehead & Glass (1985)

APPENDIX (Continued)

Species	Date	Location	# KWs	# Prey	Killer whale behaviour	Baleen whale response	Kill?	Summary	Source
	Aug 1983	Frederick Sound, Alaska		3	Approach, harass, attack	Group, defend	N	During attack on sea lion, killer whales began attacking juvenile humpback, which was then joined by two other adult-sized humpbacks. Humpbacks defended themselves by rolling over and slashing with flukes.	D'Vincent <i>et al.</i> (1989)
	Summer 1987	Chatham Strait, Alaska	2	3	Approach, harass	Group, defend	N	Humpback calf attacked by killer whales was joined by two adult humpbacks, which grouped closely one each side of calf. Position maintained until killer whales left after 20 min.	D'Vincent <i>et al.</i> (1989)
	15 Sep 1991	Gorgona Island, Colombia	10	3	Harass	Defend	N	Killer whales separated calf from two adult humpbacks, which swam erratically and produced 'wheeze' blows. Calf lashed at circling killer whales with its flukes. Skin and bits of blubber seen.	Floréz-González <i>et al.</i> (1994)
	20 Nov 1991	False Bay, South Africa	1	2	Harass	Defend	N	Single killer whale harassed humpback adult with calf. Presumed mother repeatedly struck sea surface with flukes, and killer whale left.	P. Best, pers. comm. 2005
	24 June 1994	Chatham Strait, Alaska	9	1	Harass	Defend	N	Adult humpback surrounded by killer whales reacted by splashing vigorously with flippers, shaking head, 'trumpet' blowing and exhaling underwater. Killer whales ended harassment after 45 min.	J. Straley, pers. comm., 2005
	18 Nov 1998	Eden, New South Wales, Australia	7	3	Attack	Group, defend	Y	Killer whales attacked group of two adults and one calf humpback. Calf was positioned between the two adults. Attack ended with death of calf.	Naessig & Lanyon (2004)
	28 Dec 2002	Bahia de Banderas, Mexico	3	1	Attack	Defend	N	Juvenile humpback attacked and wounded by killer whales struck at predators with tail flukes on several occasions.	M. Rodriguez, pers. comm. 2005
	15 Aug 2003	Langara Island, British Columbia	4-5	1	Attack	Defend	N	Single humpback rolled, thrashed tail flukes and flippers, and 'trumpeted' in response to attack.	B. Harrison, pers. comm. 2004
	30 Aug 2005	Off Eureka, California	3	5	Harass	Group	N	Four adult humpbacks grouped tightly around single calf as killer whales circled closely for <i>c.</i> 10 min before departing.	B. Pedro, pers. comm. 2004
	8 June 2006	Sitka Sound, Alaska	4	1	Attack	Defend	N	Four killer whales attacked subadult humpback by swimming onto its back in apparent attempt to submerge it. Humpback reacted by rolling vigorously at the surface to dislodge killer whales. Killer whales left after 20 min.	D. Lubin, via J. Straley, pers. comm. 2007

2 Nov 2007	Tenakee Inlet, Alaska	8	1	Harass	Defend	Unk	Adult-sized humpback harassed by killer whales responded by repeatedly slashing with tail flukes and pectoral flippers, often while lying with ventrum to the surface.	J. Moran, pers. comm. 2007
26 May 1964	Barkley Sound, British Columbia	7	1	Chase, attack	Flee	Y	Killer whales chased minke into confined bay, then attacked and killed it.	Hancock (1965)
5 Aug 1975	Amaknak Island, Alaska	7	1	Chase	Flee, strand	Y	Minke whale fled from killer whales and became stranded in shallows, at which point killer whales departed. Minke later died.	Lowry, Nelson & Frost (1987)
Winter 1977	Off Yakutat, Alaska	4-5	1	Chase, attack	Flee, hide	Y	Minke whale fled at high speed from killer whales, then appeared to stop and hide under observer's vessel. Killer whales then attacked and killed minke.	Hall (1986)
1980 or 1981	Korf, NE coast	2+	1	Attack	Flee, strand	N	Minke whale swam into shallow waters while being chased by killer whales. Killer whales milled offshore as tide dropped and minke became stranded, at which point they departed. Minke whale swam free several hours later on rising tide.	V. Burkanov, pers. comm. 2006
28 April 1993	Kamchatka Peninsula, Russia	6	1	Chase, attack	Flee, strand	Y	Minke whale 'rushed' into bay while being pursued by killer whales and became stranded in shallows. After several hours, the killer whales departed the vicinity and the minke whale refloated and began swimming offshore. Killer whales quickly returned, attacked, killed and consumed the minke whale.	Goodall <i>et al.</i> (2007)
12 July 1994	Johnstone St., British Columbia	2	1	Chase	Flee	N	Killer whales chased minke whale at speeds of up to 30 km/h for 28 min, but abandoned the chase as the minke whale continued to pull away.	Ford <i>et al.</i> (2005)
27 July 1996	Glacier Bay, Alaska	13	1	Attack	Flee, hide	Y	Minke whale swimming at high speed in front of pursuing killer whales suddenly stopped beside sailboat and was attacked and killed.	Ford <i>et al.</i> (2005)
7 Sep 1998	Cormorant Channel, British Columbia	9	1	Chase	Flee	N	Killer whales chased minke whale on straight course for 30 min at speed of 20-25 km/h, then gave up chase.	Ford <i>et al.</i> (2005)
23 Nov 1998	Possession Island, Crozet Archipelago	6	1	Chase, attack	Flee, strand	Y	Killer whales chased at high speed a minke whale calf into shore, where it temporarily stranded. The killer whales then pulled the calf into deeper water, and killed it after it attempted to flee again.	Guinet <i>et al.</i> (2000)
15 Oct 2002	Ganges Harbour, British Columbia	4	1	Chase, attack	Flee, strand	Y	Minke whale chased by killer whales into bay, where it stranded in shallows for 4.5 hours. Killer whales began attack in shallows, then continued as minke swam free at high tide. Minke whale killed and eaten.	Ford <i>et al.</i> (2005)

APPENDIX (Continued)

Species	Date	Location	# KWs	# Prey	Killer whale behaviour	Baleen whale response	Kill?	Summary	Source
	19 Aug 2003	Juan de Fuca Strait, Washington	4	1	Chase	Flee	N	Minke whale chased for 15 km at speeds of 15–30 km/h gradually outpaced killer whales, which gave up chase.	Ford <i>et al.</i> (2005)
	2 Sep 2003	Blackfish Sound, British Columbia	4	1	Chase, attack	Flee	Y	Killer whales chased minke whale at high speed for 13 km until it entered narrow bay, at which point it was attacked and killed.	Ford <i>et al.</i> (2005)
	5 Sep 2003	Glacier Bay, Alaska	2	1	Chase	Flee	N	Minke chased for 30+ min before killer whales gave up.	Ford <i>et al.</i> (2005)
	1 Dec 2003	Juan de Fuca Strait, Washington	6	1	Chase, attack	Flee	Y	Small minke whale chased for 18 km before being attacked and killed.	Ford <i>et al.</i> (2005)
	28 Oct 2004	Echo Bay, British Columbia	2	1	Chase, attack	Flee, strand	Y	Minke whale beached itself after being chased into small bay at high speed by killer whales. Killer whales waited for 8.5 hours as tide rose, but eventually left bay. Minke whale subsequently died on beach.	Ford <i>et al.</i> (2005)
	16 Aug 2005	Goletas Channel, British Columbia	4	1	Chase, attack	Flee	Y	Minke whale chased by killer whale into small bay with narrow entrance. Whales circled the bay at high speed, then killer whales attacked and killed minke in narrow entrance.	C. Tulloch, pers. comm. 2005
	28 Aug 2005	Blackfish Sound, British Columbia	4	1	Chase	Flee	N	Minke whale fled from killer whales on highly directional course towards open sea at average speed of 18 km/h for 58 min, at which point killer whales ended chase.	J. Borrowman & B. Mackay, pers. comm. 2005
Antarctic minke whale <i>Balaenoptera bonaerensis</i>	9 July 1986	Bahia Brown, Tierra del Fuego, Argentina	9	1	Attack	Strand	Y	Antarctic minke whale found beached at dusk, with head on shore and tail in deeper water. Killer whales took repeated 'swipes' at the bleeding minke whale, but no effort to defend or retaliate was reported. Minke found dead the next morning	Goodall <i>et al.</i> (2007)

Bryde's whale <i>Balaenoptera edeni</i>	3 May 1988	Northern Gulf of California	c. 15	1	Chase, attack	Flee	Y	Bryde's whale fled rapidly from killer whales, and continued to swim as the killer whales overtook and attacked it. No physical defence seen. Bryde's whale eventually killed and eaten.	Silber <i>et al.</i> (1990)
	11 Mar 1998	Isla Carmen, Gulf of California	c. 20	1	Chase	Flee	N	Bryde's whale initiated rapid flight as killer whales approached. Killer whales then gave chase for c. 5 min, before returning to original course and speed.	R. Sears, pers. comm. 2005
	4 Feb 2000	Isla Carmen, Gulf of California	c. 20	1	Chase, attack	Flee	Y	Killer whales first observed chasing adult-sized Bryde's whale at high speed. The Bryde's whale slowed during the 45 min long attack, and finally was killed.	M. Fishbach, pers. comm. 2005
	20 Mar 2003	Isla Carmen, Gulf of California	12	1	Approach	Flee	N	Bryde's whale (and two blue whales, see below) seen swimming rapidly towards north. Ten minutes later, killer whales found travelling on same course c. 2 km away.	C. Ramp, pers. comm., 2004
	6 Mar 2004	Isla San Jose, Gulf of California	10–12	1	Approach	Flee	N	Bryde's whale seen porpoising at high speed on straight course. Eight minutes later, killer whales observed swimming on same course at regular speed.	J. Urban R., pers. comm. 2004
Sei whale <i>Balaenoptera borealis</i>	15 May 1990	Bahia Brown, Tierra del Fuego, Argentina	9	2	Chase, attack	Flee, strand	Y	Two whales, one large and the other smaller, observed swimming at high speed. Large whale disappeared behind island, smaller whale stranded temporarily in shallows, then continued at high speed with a big 'bow' wave. Observers then noticed pursuing killer whales. Whale stranded once again, and killer whales approached and pushed at the whale repeatedly over several hours. By morning, killer whales had departed and whale was dead. Examined and found to be 12.5-m male sei whale.	Goodall <i>et al.</i> (2007)
	28 June 2004	Bahia Golondrina, Tierra del Fuego, Argentina	6	1	Chase, attack	Flee, strand	Y	Sei whale swimming at high speed and flanked by killer whales stranded in shallow water near coast. Killer whales pushed and bit at whale for 2.5 hours, then disappeared after being unable to gain access to whale. Subadult (11.3 m) female sei whale found dead next morning.	Goodall <i>et al.</i> (2007)

APPENDIX (Continued)

Species	Date	Location	# KWs	# Prey	Killer whale behaviour	Baleen whale response	Kill?	Summary	Source
Fin whale <i>Balaenoptera physalus</i>	2 Mar 1982	Gulf of California	3	2	Chase	Flee	Unk	Fin whales approached by killer whales abruptly changed direction and fled at speeds of 30–40 km/h, with killer whales in close pursuit. Chase continued until whales were out of sight. Other fin whales in vicinity slowly moved away from location of chase.	Vidal & Pechter (1989)
	Jan 1984	Gulf of California	7	1	Attack	–	Unk	Attack in progress on fin whale observed from air. Killer whales circled, held flippers, and repeatedly rammed fin whale. No defensive actions seen. Observation ended after 1.5 hours due to darkness.	R. Patterson, pers. comm. 2005
	17 Oct 2005	Canal de Balleas, Gulf of California	16	1	Attack	Flee	Y	Fin whale chased for 1 hour at speeds of up to 40 km/h. Fin whale slowed after fleeing for 10 km, and was attacked and killed. Killer whales fed on sinking carcass for c. 15 min, then left area.	G. Heckel & Y. Schramm, pers. comm. 2005
Blue whale <i>Balaenoptera musculus</i>	10 Dec 1942	Port MacDonnell, Australia	11	2	Chase	Flee	N	Blue whale mother with calf observed being chased at high speed by killer whales.	Cotton (1944)
	1977	South of Baja California	c. 30	1	Attack	Flee	N	C. 20-m blue whale attacked while attempting to flee at high speed. Killer whales bit whale repeatedly, removing blubber and flesh. No defensive actions noted. Killer whales ended attack after swimming 30 km over 5 hours. Injured blue whale continued to flee.	Tarpy (1979)
	Jan 1982	Isla Santa Catalina, Gulf of California	4–5	1	Chase	Flee	N	Killer whales gave chase to blue whale, which fled at high speed. Killer whales ended chase after 10 min.	R. Patterson, pers. comm. 2005
	21 Aug 2001	Off Carmel Bay, California	5	4	Approach	Flee	N	Four blue whales 'panicked' at the approach of killer whales, fleeing at speeds of >20 km/h for over 30 min.	R. Teruelo, pers. comm. 2006
	21 Oct 2001	Monterey Bay, California	5	1	Chase	Flee	N	Blue whale approached closely by killer whales fled at speeds of >20 km/h. Killer whales broke off chase after 4 min.	J. Calambokidis, pers. comm., 2005
	20 Mar 2003	Isla Carmen, Gulf of California	12	2	Approach	Flee	N	Pair of blue whales (and one Bryde's whale, see above) seen porpoising at high speed towards north for several min. Killer whales observed travelling on same course 10 min later, c. 2 km distant.	C. Ramp, pers. comm., 2004