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A review of Killer Whale interactions with other marine mammals: predation to co-existence

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ABSTRACT

Killer Whales are well-known as predators of other marine mammals, including the large Sperm and baleen whales. Members of all marine mammal families, except the river dolphins and manatees, have been recorded as prey of Killer Whales; attacks have been observed on 20 species of cetaceans, 14 species of pinnipeds, the Sea Otter, and the Dugong. Ecological interactions have not been systematically studied and further work may indicate that the Killer Whale is a more important predator for some populations than previously believed. Not all behavioural interactions between Killer Whales and other marine mammal species result in predation, however. Some involve 'harassment' by the Killer Whales, feeding by both species in the same area, porpoises playing around Killer Whales, both species apparently 'ignoring' each other, and even apparently unprovoked attacks on Killer Whales by sea lions. These non-predatory interactions are relatively common. We conclude that interactions between Killer Whales and marine mammals are complex, involving many different factors that we are just beginning to understand.

CONTENTS

INTRODUCTION

The diverse feeding habits of Killer Whales *Orcinus orca* have fascinated biologists and laymen for centuries. Like other odontocete cetaceans, Killer Whales are known to feed

on a wide variety of fish and cephalopods (see reviews in Perrin, 1982; Hoyt, 1984). But, unlike other cetaceans, they also regularly consume other prey, including seabirds (Taverner, 1943; Condy, Van Aarde & Bester, 1978; Straneck, Livezey & Humphrey, 1983; Stacey & Baird, 1989a) and marine turtles (Caldwell & Caldwell, 1969). They have even been seen feeding on a deer (*Odocoileus* sp.) carcass (Pike & MacAskie, 1969), and recently remains of a pig (*Sus* sp.) were recovered from the throat of a stranded animal (R. W. Baird and P. J. Stacey, unpubl.). Killer Whales are perhaps best known, however, for their habits of attacking, killing, and eating other marine mammals, including the large mysticetes and Sperm Whales.

This is not to say that other marine mammals do not also occasionally prey on their warm-blooded relatives. In fact, ten species have been implicated as marine-mammal feeders: Polar Bears *Ursus maritimus* (Freeman, 1973; Stirling & Archibald, 1977), Steller or Northern Sea Lions *Eumetopias jubatus* (Gentry & Johnson, 1981), New Zealand Sea Lions *Phocarctos hookeri* (Mattlin, 1987), Southern Sea Lions *Otaria flavescens* (Majluf, 1987; Harcourt, 1989), Walruses *Odobenus rosmarus* (Fay, 1960; Lowry & Fay, 1984), Leopard Seals *Hydrurga leptonyx* (Hamilton, 1939; Siniff & Bengston, 1977), Short-finned Pilot Whales *Globicephala macrorhynchus* (Perryman & Foster, 1980), Pygmy Killer Whales *Feresa attenuata* (Perryman & Foster, 1980), False Killer Whales *Pseudorca crassidens* (Perryman & Foster, 1980; Hoyt, 1983), and Sperm Whales *Physeter macrocephalus* (Lambertsen & Kohn, 1987). However, with the exception of the Leopard Seal and Polar Bear, these species appear to pursue marine mammal prey 'as a hobby'. Some Killer Whales, on the other hand, 'make a living' feeding on marine mammals.

Several studies in different parts of the world have identified the existence of two forms of Killer Whale, and have suggested that one feeds primarily on marine mammals, and the other mainly on fish (Berzin & Vladymirov, 1983; Bigg *et al.*, 1987). In the eastern North Pacific, these two forms have been termed 'transients' and 'residents', respectively (Bigg, 1982). As Guinet (1990a) notes, these terms are not as accurate in describing the movement patterns and site tenacity of the two forms as they were originally thought to be, but they are still in common use, due to their entrenchment and the lack of appropriate alternative designations. From Washington State through Alaska, resident fish eaters and transient marine-mammal eaters are sympatric, but can be distinguished by differences in behaviour, morphology, and mitochondrial DNA (Bigg, 1982; Bigg *et al.*, 1987; Baird & Stacey, 1988a,b; Stevens *et al.*, 1989). It is important to distinguish between these two types, and their analogues elsewhere in the world, when examining relationships between Killer Whales and their potential prey species.

This paper reviews what is known about how Killer Whales interact with other species of marine mammals and identifies behavioural trends apparent in the literature. The term 'interaction' is here used loosely to denote any occurrence of two or more species in close proximity, whether or not a change in behaviour of either species was observed. It deals primarily with behavioural interactions (as opposed to ecological interactions, e.g. Baird, Abrams & Dill, 1990). Little work has been undertaken on ecological interactions between Killer Whales and their prey, such as the influence of predation on prey populations, co-evolution of predator and prey, or competition for resources. Such work is needed to understand more fully the role Killer Whales play in their ecosystem.

Sources of information were the published and unpublished literature, unpublished records of many colleagues, and personal observations by the authors. Some of the

records come from reports of whalers and other untrained observers, and so must be viewed with caution. Appendices I and II summarize the records of interactions assembled. We do not imply that species not listed in the appendix tables do not interact with Killer Whales. On the contrary, although more common in colder nearshore waters, the Killer Whale is a cosmopolitan species (Leatherwood & Dahlheim, 1978; Heyning & Dahlheim, 1988) and we presume that interactions occur with virtually all species, at least occasionally. Such interactions have yet to be observed or reported for other species, however. We hope that this paper will guide the interpretation of future observations and promote their publication in the scientific literature.

PREDATION AND HARASSMENT OF MARINE MAMMALS

Cetaceans

Killer Whales have been observed attacking or harassing 20 species of cetaceans (Table 1, Appendix I). Five additional species are represented by stomach contents, but have not been directly observed being attacked: Pygmy Sperm Whale *Kogia breviceps*, Baird's Beaked Whale *Berardius bairdii*, Short-finned Pilot Whale, Striped Dolphin *Stenella coeruleoalba*, and Finless Porpoise *Neophocaena phocaenoides* (Nishiwaki & Handa, 1958; Perrin, 1982). Also, beaked whales of the genus *Mesoplodon* have been suggested as victims of Killer Whale attacks, based on scars that appear to correspond to *Orcinus* or *Pseudorca* tooth marks (Mead, 1989). Hoyt (1984) cited Nishiwaki & Handa (1958) as the source of a record of Pacific White-sided Dolphin *Lagenorhynchus obliquidens* remains in Killer Whale stomach contents, but this is apparently a mistake, as this species is not specifically mentioned by Nishiwaki & Handa.

Included among the victims are members of every cetacean family except Platanistidae (river dolphins), although Castello (1977) mentions the Franciscana *Pontoporia blainvillei*, which is commonly found in marine waters, as a possible prey item. Killer Whales are known to ascend rivers (e.g. Scammon, 1874; True, 1904; Shepherd, 1932; Tomilin, 1957), but do so uncommonly and almost never in the tropical and subtropical regions where river dolphins are concentrated. Conspicuously absent from Appendix I are the vast majority of the some 31 species in the family Delphinidae. Many delphinids are tropical, open-ocean species, and this may explain their absence. On the other hand, certain species, such as *Lagenorhynchus* spp. and *Lissodelphis* spp., have distributions that overlap areas of Killer Whale abundance, so their absence from the list is surprising and somewhat puzzling.

Fin Whales *Balaenoptera physalus*, Minke Whales *Balaenoptera acutorostrata*, Humpback Whales *Megaptera novaeangliae*, Bowhead Whales *Balaena mysticetus*, and Grey Whales *Eschrichtius robustus*, Narwhals *Monodon monoceros* and Dall's Porpoises *Phocoenoides dalli* are the most commonly recorded cetacean prey species, with over 10 records of predation or harassment each (Table 1).

Killer whale group sizes during predation or harassment episodes are shown graphically in Fig. 1 for various groupings of cetacean prey types. Somewhat surprisingly, most reported attacks on large whales have been by small groups of one to five killer whales. This is somewhat at odds with the findings of Felleman (1986). Attacks on large herds of dolphins or small whales show a tendency to have involved the largest groups of Killer Whales, most commonly six to ten animals, and often used some type of herding (see Brown & Norris, 1956; Rice, 1968; W. F. Samaras & S. Leatherwood, unpubl.). Attacks on single Minke Whales or small pods of medium-sized whales have mostly involved six to ten Killer Whales. Finally, predation on small groups of dolphins or

Table 1

Interactions between Killer Whales Orcinus orca *and other marine mammals. Number of reported incidents by marine mammal species (details given in Appendices I (predatory) and II (non-predatory), see pp. 173–180*

Family	Species	Interaction	
		Predatory	Non-predatory
Cetaceans			
Balaenopteridae	Blue Whale	4	2
	Fin Whale	15	22
	Sei Whale	2	14
	Bryde's Whale	1	1
	Minke Whale	17	56+
	Humpback Whale	21+	22+
Balaenidae	Bowhead Whale	12	—
	Northern Right Whale	1	—
	Southern Right Whale	8+	1
Eschrichtiidae	Grey Whale	24+	7+
Physeteridae	Sperm Whale	6+	33+
Ziphiidae	Arnoux's Beaked Whale	—	1
	Northern Bottlenose Whale	2	2
	Southern Bottlenose Whale	—	6
	Cuvier's Beaked Whale	1	—
Monodontidae	Narwhal	19	—
	White Whale	8	1
Delphinidae	Long-finned Pilot Whale	5	4
	False Killer Whale	—	1
	Risso's Dolphin	—	3+
	Common Dolphin	3	1
	Spinner Dolphin	—	1
	Dusky Dolphin	1	8
	White-beaked Dolphin	—	6
	Atlantic White-sided Dolphin	—	3
	Pacific White-sided Dolphin	—	1
	Bottlenose Dolphin	—	2
	Indo-Pacific Humpback Dolphin	—	1
Phocoenidae	Dall's Porpoise	16	46+
	Harbour Porpoise	12	7+
Pinnipeds			
Phocidae	Northern Elephant Seal	3	—
	Southern Elephant Seal	250+	—
	Grey Seal	3+	—
	Hooded Seal	1	—
	Harbour Seal	68+	8+
	Harp Seal	3	2
	Crabeater Seal	2	1
	Weddell Seal	2	2+
	Leopard Seal	1	—
Odobenidae	Walrus	12+	1
Otariidae	California Sea Lion	16+	1
	Steller Sea Lion	21+	10+
	Southern Sea Lion	200+	—
	Northern Fur Seal	3+	—
Sirenians			
Dugongidae	Dugong	3	—
Carnivores			
Mustelidae	Sea Otter	1	5

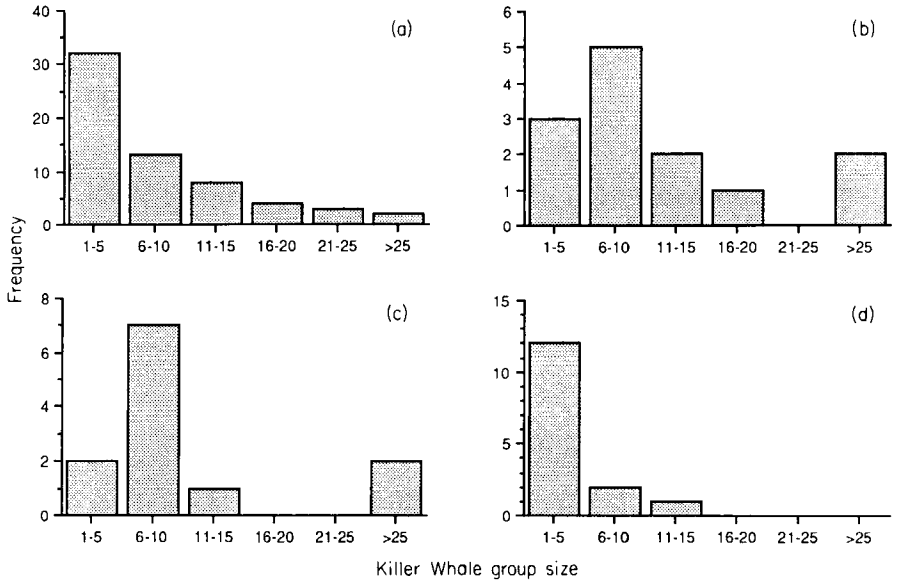

Fig. 1. Killer Whale group sizes involved in predation and harassment of (a) large whales (Sperm Whales and all mysticetes except Minke Whales), (b) large herds of dolphins or small whales (10 or more prey), (c) Minke Whales or small pods of medium-sized whales, and (d) small groups of dolphins or porpoises (nine or fewer prey).

porpoises generally has required only one to five Killer Whales, and large groups appear never to have been reported.

Pinnipeds

Pinnipeds appear to comprise a regular and substantial portion of the diet of some populations of Killer Whales. There is evidence of predation from throughout the world, with more documented cases from sub-polar and polar latitudes where Killer Whales (and seasonally, pinnipeds) are most abundant. Included as prey species are all families and most major groups of pinnipeds: elephant seals, Antarctic seals, Northern Hemisphere seals, sea lions, fur seals, and the Walrus. Individuals of nine of the 18 or 19 species of phocids, four of the 14 species of otariids, and the single odobenid, have been observed being attacked (Table 1, Appendix I). Two other phocids, the Bearded Seal *Erignathus barbatus* and Ringed Seal *Phoca hispida* are known as Killer Whale prey only from stomach contents (Zenkovich, 1938; Tomilin, 1957; Nishiwaki & Handa, 1958; Reeves & Mitchell, 1988).

Monk Seals (*Monachus* spp.) are the only major group not known to be preyed on by Killer Whales, and these are tropical animals. Sharks appear to replace Killer Whales as significant predators in warmer waters, taking species such as Hawaiian Monk Seals *Monachus schauinslandi* and Mediterranean Monk Seals *M. monachus* (Kenyon, 1981). Killer Whales were noted by Bonner (1981) as probable predators of the eight species of southern fur seals (*Arctocephalus*), although no attacks are known to us. It is probable that seals of all of the remaining species, except the inland Baikal Seal *Phoca sibirica* and the Caspian Seal *P. caspica*, have been victims of Killer Whale predation at one time or another. Of the pinnipeds, Southern Elephant Seals *Mirounga leonina* and Harbour Seals *Phoca vitulina*, Walruses and Steller, Southern and California Sea Lions

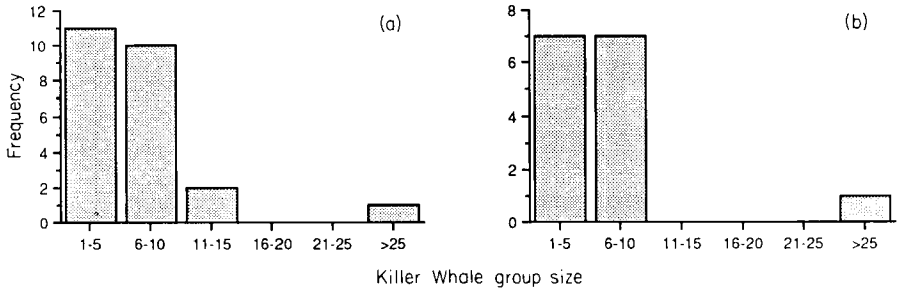

Fig. 2. Killer Whale group sizes involved in predation and harassment of (a) eared seals or Walruses, and (b) true seals.

Zalophus californianus have been most commonly recorded as Killer Whale prey species (Table 1).

Killer Whales attacked pinnipeds both offshore and near the haul-out sites where they concentrate. Prey handling time has varied from less than 1 minute (W. F. Samaras and S. Leatherwood, unpubl.) to several hours, although once the prey is killed, consumption can be very rapid (Anonymous, 1975). Pinnipeds are attacked by Killer Whales as singles and in groups of up to 30 whales, although the vast majority of reported attacks are by groups of 10 or fewer (Fig. 2).

Most events in Appendix I are incidental observations at a wide variety of locations, mainly cases of the observer being at the right place at the right time. Because of this lack of systematic study of Killer Whale predation, there is generally little information available on ecological importance, and this has led to the belief that Killer Whales are not significant predators of most species of pinnipeds. In two locations, Killer Whale predation on pinnipeds has been studied over a period of years. In both locations, southern Vancouver Island, British Columbia, Canada (Baird & Stacey, 1988b; Baird, Dill & Stacey, 1990) and Peninsula Valdes, Argentina (Lopez & Lopez, 1985; Hoelzel, 1989), Killer Whales were found to target certain marine mammal species. 'Preselection' of a particular species of available prey may be a general feature of social carnivores (see Kruuk, 1972a). In Argentina, Killer Whales have developed a strategy of beach stranding, sliding up on the beach and then wriggling back into the water (a behaviour also regularly seen in the Crozet Islands; Guinet, 1990b), which allows them to be more successful at capturing prey on gently sloping beaches (Lopez & Lopez, 1985). In nine years, 181 successful attacks on Southern Elephant Seals and Southern Sea Lions were observed (Lopez & Lopez, 1985). In the British Columbia study, Harbour Seals are preyed upon almost exclusively, with a total of over 50 kills observed in four years (Baird, Dill & Stacey, 1990; Fig. 3).

Other marine mammals

Of other marine mammals, only the Dugong *Dugong dugon* and the Sea Otter *Enhydra lutris* have been recorded as Killer Whale prey species (Table 1, Appendix I). Manatees (*Trichechus* spp.) are large, slow and fat, and would thus seem to be ideal prey for Killer Whales. They probably escape frequent predation, however, by being distributed primarily in inshore (and often freshwater) areas of the tropics, regions where Killer Whales are rare. Other 'marine' species are occasionally attacked, such as the River Otter *Lutra canadensis* (Campbell, 1985; Morton, 1987, 1990).

Fig. 3. Transient Killer Whale with live Harbour Seal pup in mouth, off southern Vancouver Island, British Columbia, Canada.

NON-PREDATORY INTERACTIONS

Cetaceans

Associations between Killer Whales and other marine mammals, with no evidence of predatory intent by the Killer Whales, have been recorded for 26 species of cetaceans, most of which have also been documented as prey species (Table 1, Appendix II). Here, as in the case of predation, all families except Platanistidae are represented. Interestingly, several species of dolphins not known as prey of Killer Whales have been seen interacting with Killer Whales in non-predatory contexts, including four species of *Lagenorhynchus*.

These interactions have included 'mixed groups' of the two species, both species being in close proximity with no observed response by either, concurrent feeding with both species in close proximity, apparent avoidance or flight from Killer Whales (despite no apparent attempts at predation by the whales), and apparent attraction to Killer Whale groups. Perhaps most interesting are incidents of the last type, including a report of several Humpback Whales closely approaching a group of Killer Whales that were attacking a Steller Sea Lion (Dolphin, 1987), and the many reports of Dall's Porpoises approaching Killer Whales apparently to play (Scheffer, 1949; Jacobsen, 1986; Jefferson, 1987). Estes & Goddard (1967) and Kruuk (1972a) discussed the phenomenon of 'curiosity' of ungulates toward their terrestrial predators.

Pinnipeds

Individuals of at least seven pinniped species have been recorded in association with Killer Whales in non-predatory contexts (Table 1, Appendix II). In most such cases, interactions consisted of Killer Whales passing by pinnipeds hauled-out or in the water, without any change in behaviour to indicate they noticed the potential prey. In one instance, the Killer Whales were busy feeding on cormorants (*Phalacrocorax* sp.) (Rice & Saayman, 1987). In many other cases, the pinnipeds appeared aware of the presence of the predators, but did not react noticeably.

Other marine mammals

Only the Sea Otter, among other marine mammals, has been recorded interacting with Killer Whales in non-predatory contexts (Table 1, Appendix II). In fact, such reports appear to be more common than reports of attacks. Otters may be less desirable prey items for Killer Whales, given that they are relatively small and furry, with no blubber layer.

DISCUSSION

Indirect evidence of interactions

Although we have discussed primarily observations of behavioural interactions between Killer Whales and other marine mammals, we recognize that there are other types of evidence for such interactions (especially predation). Stomach-content studies of Killer Whales have added several species of marine mammals to the list of known prey, but in such cases one can never be sure if the animal was killed by the predators or fed upon as carrion.

Several authors have described injuries to marine mammals that they attribute to Killer Whale attacks (e.g. Andrews, 1914; Bertram, 1940; Voison, 1972; Shevchenko, 1975; Morejohn, 1979; Best, 1982; Fay, 1982). These injuries are typically tooth rakes and punctures, various external wounds, mutilated extremities, blood in the body cavity, contusions, or broken bones (especially ribs and scapulae), sometimes with few or no external injuries visible. The lack of external wounds adjacent to internal injuries generally indicates that the victim was struck by a large blunt object, and this is consistent with the observed behaviour of Killer Whales leaping upon and striking marine mammals with their snouts (Scheffer & Slipp, 1948; Norris & Prescott, 1961; Rice, 1968; Fay, 1982). Such aggressive behaviour towards other species may also be used in non-feeding circumstances. It should be kept in mind that some marine mammals that escaped from attacks by Killer Whales may have sustained extensive internal injuries that later resulted in death, and as Samaras & Leatherwood (1974) noted, not all prey killed are eaten.

Ecological interactions

Piscivorous forms of Killer Whale may compete with other marine mammals for food, but the degree of this potential interaction is not known at present (Baird, Abrams & Dill, in press). For most species and populations, there is little evidence that Killer Whale predation is a major mortality factor affecting prey populations, but this may largely reflect inadequate information. Predation can have far-ranging effects on the behaviour of prey species, such as on grouping behaviour in Walruses (Taggart, 1987) and Harbour Seals (da Silva & Terhune, 1988). Killer Whale predation on Harbour Seals in North America has been regarded as incidental (Food and Agricultural Organization, 1976). However, Fisher (1952) considered Killer Whales the most important natural predators of the Harbour Seal. According to Fay (1982), mortality from attacks by Killer Whales may have a greater impact on the Walrus population than 'just the removal of a few calves'. Laws (1977) noted that young Crabeater Seals *Lobodon carcinophagus* are subject to heavy predation by Killer Whales, and in fact Killer Whale attacks are probably the chief cause of mortality for this species (Bertram, 1940). For most species of marine mammals, the Killer Whale may, in fact, play a more important role as a predator than is commonly suspected.

Zenkovich (1938, p. 4 of translation), based on observations in the western North Pacific, concluded that the Killer Whale is a 'rapacious beast of prey, causing great

damage to our fur seal industry at the Komandorski Islands and exterminating herds of pinnipeds in all of our seas, especially along the Chukchi coast.' Although many authors have claimed that Killer Whales take great numbers of Northern Fur Seals *Callorhinus ursinus* (Turner, 1886; Hanna, 1922; Ognev, 1935; Zenkovich, 1938), we were able to find very few actual descriptions of attacks (see Appendix I).

In the case of a rare or depleted species, such as the Bowhead Whale, Killer Whales could be an important source of mortality even with low absolute levels of predation (Mitchell & Reeves, 1982; Reeves & Mitchell, 1988; Finley, 1990). Populations of more abundant species that spend most of their life within the home range of a locally abundant population of predatory Killer Whales may be significantly affected by the predation. Such may be the case with the resident population of Harbour Seals off southern Vancouver Island. Members of the transient community of Killer Whales in the area appear to specialize in feeding on this species (Baird, Dill & Stacey, 1990b).

Questions about Killer Whale predation on marine mammals

Do Killer Whales successfully attack healthy adult baleen whales? Jonsgard (1968a,b) suggested that Killer Whales are incapable of attacking and feeding on healthy adult baleen whales under normal circumstances. Although many of the incidents listed in Appendix I involve uncertain kills (of course, Killer Whales can successfully feed on a large whale without killing it) or attacks on young or sick animals, there is ample evidence that, at least occasionally, healthy non-calf baleen whales are fed upon (Eschricht, 1866; Bullen, 1898; Cummings, Fish & Thompson, 1972; Cummings & Wolman, 1977; Tarpy, 1979; Whitehead & Glass, 1985; Silber, Newcomer & Perez-Cortes, 1990).

Do Killer Whales attack Sperm Whales? If the Killer Whale has a most formidable adversary among the marine mammals, it is surely the Sperm Whale. Sperm Whales are larger than Killer Whales, possess teeth and powerful tails, and usually live in groups. None of the incidents listed in Appendix I involved documented kills and all referred to attacks on Sperm Whale groups with calves (and in one case, on a group with a female apparently giving birth) or wounded animals. Schevchenko's (1975) report of Killer Whale bite marks on 65% of Southern Hemisphere Sperm Whales taken by whalers must be viewed with caution, because he did not mention how he discriminated marks made by Killer Whales from those by conspecifics (Rice, 1989). Thus, the evidence supports Berzin's (1972, p. 273) conclusion that attacks are 'too rare for us to brand killer whales as serious enemies of the sperm whale'.

Are large groups required to attack large whales successfully? That there should be a relationship between group size and prey body size seems intuitive, i.e. the larger the predator's group size, the larger the prey that can be captured, and more food can be divided among the group. But one may well wonder whether small groups of Killer Whales are capable of subduing large whales, for instance. Although not all attacks on large whales by large groups of Killer Whales (over five animals) were seen to be successful, most instances in which a kill or feeding took place involved relatively large groups of predators. There is some evidence, however (much of it from the whaling literature), to suggest that singles or groups of two or three Killer Whales can, at times, overcome and kill large baleen whales (Eschricht, 1866; Bullen, 1898; D. L. Kelly, unpubl.; Reeves & Mitchell, 1988). It is possible, however, that larger Killer Whale groups may have split up in some of these instances to feed on several whales. Killer

Whales specializing on certain types of marine mammal prey may be expected to optimize group size, thereby maximizing food intake. Recent work on transient Killer Whales around southern Vancouver Island indicates that such optimization of group sizes may help explain group size differences between transients and residents in that area (Baird, Watts & Stacey, 1989; Baird, Dill & Stacey, 1990).

Do Killer Whales cooperate in hunting marine mammals? There is abundant evidence that groups of Killer Whales use coordinated techniques to hunt large whales (Baldridge, 1972; Tarpy, 1979; Whitehead & Glass, 1985; Silber *et al.*, 1990), small cetaceans (Brown & Norris, 1956; Jonsgard, 1968a; Steltner, Steltner & Sergeant, 1984; Hall & Cornell, 1986; King, 1989), and pinnipeds (Norris & Prescott, 1961; Samaris & Leatherwood, 1974; Smith *et al.*, 1981; Lopez & Lopez, 1985; Felleman, 1986; Baird & Stacey, 1988b). This cooperation often takes the form of some Killer Whales biting the flukes and flippers of large whales presumably to slow or stop their movement, striking pinnipeds with their bodies or extremities, lunging or leaping onto the backs of large whales to impede their progress (or possibly to drown them), or encircling or herding groups of smaller marine mammals to prevent their escape. In the Antarctic, Killer Whales have been seen to tip over ice floes and devour seals that are thus dumped into the water (Smith *et al.*, 1981). An analogue in the Northern Hemisphere may be the report of Killer Whales in Washington ramming a log boom to knock off hauled-out Harbour Seals (Scheffer & Slipp, 1948). Killer Whales have also been seen coralling small numbers of pinnipeds out of a larger group, then attacking the isolated animals (W. F. Samaras and S. Leatherwood, unpubl.). It is possible that cooperation was occurring, but was not noticed or reported, in many of the briefly observed instances, listed in Appendix I.

Of particular interest here is the case of human–Killer Whale 'cooperation' that apparently existed for at least 80 years at Twofold Bay, New South Wales, Australia (Dakin, 1938; Wellings, 1944; Mead, 1986). During the mid-1800s, an association developed between a group of about 30 Killer Whales and local shore whalers, both hunting Humpback and Right Whales *Eubalaena australis*. The reports tell of cooperation between the predators and the whalers, with the Killer Whales sometimes actively attracting the attention of shore lookouts when a baleen whale was detected. After the kill, which involved the coordinated actions of the humans and Killer Whales, the whalers allowed the predators to feed, unmolested, on the tongue and lips of the sinking large whale. The following day, the whalers returned to the refloated carcass, and claimed their prize, complete except for the less commercially valuable tongue and lips. This practice finally died out as, over the years, the Killer Whales apparently died or moved elsewhere, and the technique became less profitable for the whalers. Such apparent cooperation between humans and wild animals is not unprecedented; Isack & Reyer (1989) described the apparently symbiotic relationship between the Greater Honeyguide *Indicator indicator* and the Boran people of Kenya and there are several reports of dolphins cooperating with fisherman to herd fish (Busnel, 1973; Pryor *et al.*, 1990).

Several hypotheses might account for cooperative hunting in Killer Whales. Hunting cooperatively may increase net energy intake or decrease risk of injury. In one study of transient Killer Whale predation on Harbour Seals, it was shown that benefits occur from group hunting of marine mammals, because the predators were most efficient, in terms of individual food intake, in groups of three (Baird, Dill & Stacey, 1990b). Conversely, coordinated hunting may in some cases be an artifact of other benefits of

group living. It is important to distinguish between group hunting and cooperative hunting, as not all group behaviour need be cooperative (e.g. Packer & Ruttan, 1988). For instance, resident Killer Whales in the coastal waters of the eastern North Pacific live in groups, but during foraging often spread out and feed more or less individually on fish.

Lamprecht (1981) argued that in most social terrestrial carnivores, the primary function of social hunting is not to increase the ability to overcome larger and faster prey (the 'hunting hypothesis'), but rather more effectively to defend a kill from other predators, or alternatively that it is a side-effect of other benefits of sociality. The fact that most attacks on large whales involve small groups of Killer Whales suggests that the 'hunting hypothesis' may not be as important as commonly believed for this marine carnivore either. Another benefit of foraging in groups, termed the 'skill pool effect' by Graldeau (1984), allows individuals with different skills or abilities to forage together and thus increase the types of prey available to the group. Some 'division of labour' by age/sex class has been noted in Killer Whales (see below), but this potential function of group foraging warrants further study.

Are young or weak marine mammals preferred as prey? Many of the attacks listed in Appendix I involved as prey calves or pups, or animals injured or debilitated in some way (e.g. Jonsgard, 1968a; Gaskin, 1972; Bloch & Lockyer, 1988). Young animals or those weakened by illness or injury are certainly more vulnerable to attack, and Killer Whales (like other predators—see Schaller, 1972) would be expected to take advantage of this. There are several reports of apparent preference for pinniped young (Scammon, 1874; W. F. Samaras and S. Leatherwood, unpubl.), and many instances in which cetacean calves were apparently singled out for attack (Scammon, 1874; Baldridge, 1972; Berzin, 1972; D'Vincent, Haley & Sharpe, 1989). In some areas, Killer Whales may frequent pinniped rookeries during the time of year when breeding takes place, or when the young enter the water for the first time (Tomilin, 1957; Voison, 1972; Condy *et al.*, 1978; Lopez & Lopez, 1985; Guinet, 1990b; R. W. Baird and P. J. Stacey, unpubl.), preying selectively on pups. We suggest that many occurrences of 'harassment' by Killer Whales actually represent attempts by the predators to check for young or weakened animals, which would make easier prey. Such 'testing' of prey has been reported in Wolves *Canis lupus* (Mech, 1970) and Spotted Hyenas *Crocuta crocuta* (Kruuk, 1972a).

Is hunting of marine mammals done only by Killer Whale adults or adult males? Although there is some evidence that marine mammals form a more important part of the diet of large adult Killer Whales than of younger animals (Nishiwaki & Handa, 1958; Rice, 1968; Jonsgard & Lyshoel, 1970; W. F. Samaras and S. Leatherwood, unpubl.), all age and sex classes, including juveniles and calves, have been observed to participate in attacks on marine mammals and subsequent feeding (Budylenko, 1981; P. J. Stacey and R. W. Baird, unpubl.; J. D. Hall, *in litt.*). On the other hand, Silber *et al.* (1990) and Finley (1990) reported that the adult males did not participate in the attacks they observed on Bryde's Whales *Balaenoptera edeni* and Bowhead Whales, and in several attacks on Harbour Seals observed by R. W. Baird and P. J. Stacey (unpubl.) single adult males were not seen to participate in killing the prey, although on one occasion a

male did share in feeding. It has been suggested that adults in some areas may teach young how to capture pinnipeds (Lopez & Lopez, 1985; S. Leatherwood, pers. comm.).

Is there evidence of cannibalism? Stomach contents of two male Killer Whales from the Southern Hemisphere contained Killer Whale remains (Schevchenko, 1975). However, it is not known if these animals were dead or alive when they were fed upon. The only other known record of cannibalism is Gaskin's (1972, p. 120) report of a bleeding Killer Whale that had been shot being 'turned on by its companions and savagely attacked'.

Killer Whales form tight social bonds that apparently last for life, and both nurturant and succorant behaviour are known in this species (Caldwell & Caldwell, 1966). Thus, it seems likely that such incidents of cannibalism are examples of anomalous behaviour, rather than part of the normal feeding pattern of Killer Whales.

Do Killer Whales prefer the tongue and lips of baleen whales? The whaling literature indicates that Southern Hemisphere Killer Whales prefer to feed on the tongue and lips of baleen whales (Turner, 1886; Bullen, 1898; Dakin, 1938; Wellings, 1944; Gaskin, 1972). Killer Whales in the Northern Hemisphere have also been reported to favour the tongue, lips, and throat region of mysticetes (Bullen, 1898; Andrews, 1914; Hancock, 1965; Baldridge, 1972; Lowry, Nelson & Frost, 1987). Silber *et al.* (1990) suggested that Killer Whales may focus their attacks on the head region of baleen whales, at least partially, to avoid the danger of being struck by the flukes of the victim. Terrestrial predators similarly avoid the most dangerous parts of their victims' bodies during attacks (Estes & Goddard, 1967; Schaller, 1967; Mech, 1970).

Do Killer Whales always eat the prey they've killed? Surplus killing is seen in many terrestrial carnivores (Kruuk, 1972b; Breault & Cheng, 1988). Eschricht (1866) observed Killer Whales in Greenland kill many more White Whales *Delphinapterus leucas* than were eaten, and Samaras & Leatherwood (1974, unpubl.) watched Killer Whales kill an elephant seal but apparently not feed on it. Fay and colleagues (Fay & Kelly, 1980; Fay, 1982) observed several Walrus carcasses with extensive internal injuries, and attributed the injuries to Killer Whale attacks, but there was no evidence of Killer Whales having fed upon them. Many attacks on large whales resulted in only a minimal amount of feeding on the carcass (Tarpy, 1979; Silber *et al.*, 1990), which is in contrast to the situation in many terrestrial carnivores, where generally the entire carcass is eaten (e.g. Mech, 1970; Schaller, 1972).

Mueller & Hastings (1977) discussed the definition of surplus killing. They stated that a predator must kill an animal that is regularly taken by that species, and yet not eat part of the carcass, despite the fact that there is free access to it. Based on these criteria, we conclude that, for as yet unknown reasons, Killer Whales probably do engage in surplus killing of seabirds (Stacey & Baird, 1989a) and marine mammals (see above), although this warrants further investigation.

Aggressive killing, caching, playing, and teaching have all been offered to explain why animals may not always consume a prey immediately, or at all. Apparent teaching of young has been observed in Killer Whales (Lopez & Lopez, 1985) and Killer Whales have often been observed apparently 'toying' with prey items (e.g. Norris & Prescott, 1961; Felleman, 1986; Baird & Stacey, 1988b). Although confounded by many factors, another possible explanation for the observed practice of Killer Whales eating only portions of their prey may be within the framework of optimal-patch-use models. Sih

(1980) used such models to explain partial consumption of prey, noting that after consuming the most energy-rich parts of a large prey, it may be more beneficial for predators, in terms of maximizing net energy intake, to forage for other prey.

Marine-mammal responses to Killer Whales

Potential prey species have a number of options when threatened with the prospect of a Killer Whale attack. An obvious response is to fight back, and this may be a viable option, especially for the large whales, which use their flukes to strike at their attackers (Eschricht, 1866; Chittleborough, 1953; Cummings *et al.*, 1972; Best, Canham & MacLeod, 1984; Whitehead & Glass, 1985; D'Vincent *et al.*, 1989). Sperm Whales have been observed to form a 'spoke', with heads in and tails out and flailing, in response to being attacked by whalers (Nishiwaki, 1962). Because this same response has been observed to Killer Whale attacks on Right Whales (Payne, in press), it seems likely that this 'marguerite formation' may have evolved as a defense against Killer Whale (and shark) attacks. Although the effectiveness of fighting back is not always apparent, it can at times be successful. For example, Eschricht (1866) reported an instance in which a Bowhead Whale hit an attacking Killer Whale on the head with the edge of its flukes, apparently killing it. Large pinnipeds, such as Steller Sea Lions and Walruses, may be especially formidable prey, as they are very strong and manoeuvrable, and possess teeth capable of inflicting serious wounds (see Fay, 1982; Stirling, 1984; Bigg *et al.*, 1987; Hubbard-Morton, 1990). Matkin (*in litt.*) has even observed Steller Sea Lions attacking and nipping resting resident Killer Whales in south-east Alaska, a phenomenon similar to that observed between Lions *Panthera leo* and Buffalo *Syncerus caffer* by Prins & Iason (1989). Felleman (1986) has suggested that the large Killer Whale pod size involved in an attack on 200 Narwhals (Steltner *et al.*, 1984) was required by the danger involved in attacking these tusked small whales.

Large whales may not defend themselves, but instead turn belly-up in the event of an attack, presumably to protect their delicate undersides (Andrews, 1914; Zenkovich, 1938; Lockley, 1979; D'Vincent *et al.*, 1989) or may hold their flukes, rostrum, or flippers above the surface to restrict Killer Whale access to these appendages (Sharpe, D'Vincent & Nilson, 1990). Similar lack of active defense by ungulates has been observed in response to attacks by terrestrial predators (Kruuk, 1972a; Schaller, 1972).

Most marine mammal species are gregarious to some extent, a pattern likely related partially to predator avoidance and protection, through increased vigilance and the 'encounter', 'dilution' and 'confusion' effects (see Landau & Terborgh, 1986; Inman & Krebs, 1987; Norris & Schilt, 1988). For small odontocetes, Wells, Irvine & Scott (1980) identified predation as an important pressure toward evolution of group-living, with those species that have the least predation pressure (i.e. riverine species) also tending to be the most solitary of the small toothed whales. Some beaked whales are also more or less solitary, but little else is known of their ecology.

Bunching-up, or tightening of inter-individual distances is a common response to stress or danger in many species of cetaceans (McBride & Hebb, 1948; Norris & Dohl, 1980), and grouping on haul-out sites appears to be related to predator avoidance in at least some pinnipeds (da Silva & Terhune, 1988). Grouping together during an attack has been observed in large whales (Ljungblad & Moore, 1983; Best *et al.*, 1984; Whitehead & Glass, 1985; Arnbom *et al.*, 1987), small cetaceans (Brown & Norris, 1956) and pinnipeds (W. F. Samaras and S. Leatherwood, unpubl.; T. A. Jefferson, unpubl.). This may sometimes, however, result more from herding by the Killer Whales than

from defensive manoeuvres by the prey, especially for smaller species (W. F. Samaras and S. Leatherwood, unpubl.). Young Walruses will reportedly ride on the mothers' backs during Killer Whale incidents (Scammon, 1872; Nikulin, 1941).

If possible, the intended prey may try to escape by fleeing from the predators (Saayman & Tayler, 1979; Würsig & Würsig, 1979; Jacobsen, 1986; Rice & Saayman, 1987; Baird & Stacey, 1989; Silber *et al.*, 1990) or by exhibiting conspicuous 'pursuit invitation' behaviour, thereby alerting the predator that it has been detected and that the element of surprise has been lost (Smythe, 1970; Jacobsen, 1986). It has been suggested that Killer Whales may sometimes vocalize to induce prey flight, and then use the noise of the fleeing animals to locate the prey (Mate, 1975). Killer Whales appear to be capable of chasing down and capturing even such fast-swimming species as Dall's Porpoise (Jacobsen, 1986; M. A. Bigg, *in litt.*). Even so, flight may be an effective strategy at times, because even though Killer Whales may be able to catch up, they may choose not to expend the energy required. This 'decision' would presumably depend on the predators' condition at the time, including when they had last eaten, the potential energetic value of the prey, and the availability of alternative prey.

Attempts to avoid or hide from Killer Whales in shallow water, kelp beds, river mouths, the surf zone (where the sound of the surf may help to 'acoustically hide' the animal), or among ice floes have been observed for many species. Large whales (Burrage, 1964; Morejohn, 1968; Baldridge, 1972; Poole, 1984; Finley, 1990), small cetaceans (Scheffer & Slipp, 1948; Saayman & Tayler, 1979; Würsig & Würsig, 1980; Rice & Saayman, 1987; Bloch & Lockyer, 1988; Campbell, Yurick & Snow, 1988), and pinnipeds (Zenkovich, 1938) all appear to use these tactics on occasion, and pinnipeds sometimes have the additional option of hauling out on shore to avoid Killer Whales (Moran, 1924; Tomilin, 1957). On the other hand, Killer Whales may intentionally herd cetaceans into coves to prevent their escape (Hancock, 1965; Hall & Cornell, 1986; Lowry *et al.*, 1987). The superior diving capabilities of Sperm and Beaked whales and some pinnipeds (such as elephant seals, *Mirounga* spp.—see Le Boeuf *et al.*, 1989) may provide these species with an additional escape option when they are not limited by the presence of young calves or shallow water. This would probably only be effective if they were far away from the predators or had not been detected yet, as Killer Whales may otherwise be able to corral the animals and thus prevent their escape, or chase and tire them, reducing their diving capabilities.

Marine mammals under attack have been observed hiding behind boats (Branson, 1971; Hoyt, 1984; Hall, 1986; T. A. Jefferson, unpubl.), and pinnipeds have even climbed or attempted to climb aboard vessels, buoys, or other floating objects for protection (Turner, 1886; Stacey & Baird, 1989b). The effects of such human influences on Killer Whale predation should be considered in these cases.

If the potential prey has not yet been detected, it may become silent and motionless to avoid detection (Tomilin, 1957; Schevill, 1964; Ljungblad & Moore, 1983; Arnbom *et al.*, 1987; Thomas *et al.*, 1981; Thomas, Ferm & Kuechle, 1987; Stacey & Baird, 1989b), a response also noted from Grey and White Whales to playback of Killer Whale sounds (Cummings & Thompson, 1971; Fish & Vania, 1971). Another method, apparently used by large whales to avoid detection, is to blow less often, exhale less forcefully, or exhale underwater (Hubbs, 1965; Poole, 1984; Vidal & Pechter, 1989; S. Leatherwood, pers. comm.). In these ways, the blow may be made less visible or harder to detect acoustically.

Sea Otters and pinnipeds may become more alert (Kenyon, 1975; Beckel, 1980; Jacobsen, 1986; Baird & Stacey, 1989), and large whales may spy-hop (Cummings &

Thomspon, 1971) to assess the danger visually. Because transient Killer Whales generally are silent during foraging (Ford & Fisher, 1982; Hubbard-Morton, 1990), it is likely that marine mammals use vision more than hearing to detect and avoid Killer Whales (Baird & Stacey, 1989). As first suggested by Andersen & Amundin (1976), Dall's and Harbour Porpoises produce mostly high-frequency sounds (> 100 kHz) and may thus be largely 'acoustically invisible' to Killer Whales, which have their greatest sensitivity at lower freqencies (Hall & Johnson, 1971; D. Bain, pers. comm.).

There are many incidents in the literature which involve non-predatory interactions between Killer Whales and other marine mammal species. Certainly, as noted by Ydenberg & Dill (1986), the reaction of an animal to a potential predator should depend on its perceived risk. In general, transient Killer Whales prey on marine mammals and residents do not. Thus, there would be a selective advantage to a prey's ability to distinguish the two types where they are sympatric. In the eastern North Pacific, where dialect differences allow the two types to be distinguished (see Ford & Fisher, 1982; Ford, 1984), sound may be very important in mediating interactions between Killer Whales and other marine mammals. Potential prey would be expected to pay little attention to the discrete calls of the common resident pods, which vocalize often, especially when foraging for fish. However, when marine mammals detect the presence of Killer Whales (through active echolocation, passive listening, or other cues) without hearing resident calls, they would be expected to exhibit increased alertness or avoidance behaviour (Stacey & Baird, 1989b). Transients are generally silent during foraging (Ford & Fisher, 1982; Ford, 1984), and potential prey could be 'fooled' by resting resident killer whales, which produce very few calls. This may explain some of the cases of apparent avoidance of residents by porpoises, which may mistake resting resident Killer Whales for transients.

Transient and resident Killer Whales can also be distinguished visually by experienced human observers (Bigg *et al.*, 1987; Baird & Stacey, 1988a), and it is likely that marine mammals resident to certain areas frequented by Killer Whales can do the same. The importance of vision in predator recognition is suggested by the observations of Baird & Stacey (1989).

The 'dangerous transient/friendly resident' rule breaks down at times. There are several reports of southern residents (those in southern British Columbia and Washington State) attacking Dall's and Harbour Porpoises and Harbour Seals, all apparently involving a portion of L-pod (Balcomb *et al.*, 1980; Felleman, 1986; Heimlich-Boran, 1988; Felleman, Heimlich-Boran & Osborne, 1991).

There are also several reports of Dall's and Harbour Porpoises near known transients with no response by the potential prey (R. W. Baird and P. J. Stacey, unpubl.). In certain cases, the predators may not have been detected, but there is certainly the possibility that, even within the transient form, marine mammals can distinguish between hunting and non-hunting Killer Whales. Many ungulate prey species can apparently pick up on subtle cues (most importantly postures) the intent of terrestrial predators, such as Wolves and Wild Dogs (Estes & Goddard, 1967; Walther, 1969; Mech, 1970; Kruuk, 1972a; Schaller, 1972). We agree with Dolphin (1987) that behavioural interactions between Killer Whales and marine mammals resemble those between terrestrial predators and their prey, with the normal existence of an 'uneasy truce' and wariness on the part of the potential prey. Fleeing at the appearance of every potential predator would be a waste of energy for both terrestrial and marine species. Instead, increased alertness toward the behaviour of the predator would generally allow for the normal pursuit of activities until there is evidence of real danger. As well, it is possible

that in areas with high abundance of more profitable prey (higher energy gain per handling cost), less preferable prey may be taken only infrequently, if at all. The use of 'prey' or 'diet models' (see Stephens & Krebs, 1986) may be a valuable tool in interpreting such observations.

CONCLUSION

Dolphin's (1987) classification of predator–prey interactions is helpful as a starting point in examining relationships between Killer Whales and other marine mammals, but does not cover all types of interactions reviewed in this paper. His comparative approach, using examples of better-known terrestrial mammal predator–prey interactions, cannot fail to provide insight into the complex interactions between Killer Whales and other marine mammals. This paper provides an attempt to assess the behavioural interactions between all marine mammals and their potential predator, the Killer Whale. It has previously been pointed out that not all interactions between Killer Whales and other species involve predation (Dolphin, 1987). As is the case with terrestrial predator–prey interactions, complicated and often subtle signs and signals appear to mediate the interactions. Prey species have much to lose by not detecting and responding to cues that a predator may give (whether deliberate or not) regarding its intentions. Marine mammals use their eyes and ears both above and below water to assess the danger in such situations. So far, human observers have looked almost exclusively from above the surface, with eyes from a distance. Now that we can recognize Killer Whales in many parts of the world as individuals, detailed observations including acoustic recordings and underwater observations, may begin to clarify the 'blurry' picture we have provided here.

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Appendix I

Interactions between Killer Whales (KWs) and other marine mammals involving harassment, chases, attacks, or presumed attacks by the Killer Whales

Date	Location	Description	Cooperation?	Kill?	Source
Cetaceans					
Blue Whale *Balaenoptera musculus*					
Pre-1925	Antarctica	5 KWs attack adult Blue Whale	Y	Y	Villiers (1925)
December 1943	Port MacDonnell, S. Australia	11 KWs chasing Blue Whale cow–calf pair	?	?	Cotton (1944)
1977	Baja, California, Mexico	*c.* 30 KWs attack a young Blue Whale	Y	?	Tarpy (1979)
23 September 1986	Monterey Bay, CA, U.S.A.	Second-hand report of a single Blue Whale attacked by KWs	?	N	Baldridge (1986)
Fin Whale *Balaenoptera physalus*					
6 March 1884	Strait of Gibraltar, W. Mediterranean	About 12 KWs attacking single Fin Whale	?	?	Ferguson & Stair (1936)
Pre-1886	Tigalda Island, AK, U.S.A.	2 KWs attack a large Fin Whale	Y	?	Turner (1886)
6 July 1908	Sukkertoppen, W. Greenland	Whaler record of 2 KWs killing a Fin Whale*	?	Y	Reeves & Mitchell (1988)
14 June 1960	Marble Island, B.C., Canada	Attack on a Fin Whale	?	?	Pike & MacAskie (1969)
August 1979	New Hampshire, U.S.A.	12–30 KWs attack 3 Fin Whales	?	?	Gormley (1990)
2 March 1982	Gulf of California, Mexico	3 KWs attack pair of Fin Whales—no *kill* observed	?	?	Vidal & Pechter (1989)
1983–87	Greenland	8 observations of chases or attacks (involving 4–5, 8–10, 2, 2, 2, 2, 2–4 KWs)	?	?	Heide-Jorgensen (1988)
7 July 1984	Faroe Islands	2 KWs attack a Fin Whale (report from fishermen)*	?	?	Bloch & Lockyer (1988)
Sei Whale *Balaenoptera borealis*					
1962–74	Southern Hemisphere	2 KWs pursue single Sei Whale	?	?	Shevchenko (1975)
1967	Antarctica	2–3 KWs harass Sei Whales cow-calf pair	?	?	Gaskin (1972, 1982)
Bryde's Whale *Balaenoptera edeni*					
May 1988	Gulf of California, Mexico	Single Bryde's Whale chased, attacked and killed by 15 KWs	Y	Y	Perez-Cortes, Silber & Newcomer (1988), Silber *et al.* (1990)
Minke Whale *Balaenoptera acutorostrata*					
1940–87	Greenland	6 observations of attacks on Minkes (involving 30, 40–50, 6 KWs)	?	Y	Heide-Jorgensen (1988)
26 May 1964	Barkley Sound, B.C., Canada	7 KWs kill and eat a Minke	?	Y	Hancock (1965)
15 September 1971	Off Durban, S. Africa	About 10 KWs observed attacking a single Minke	?	Y	Best (1982)
5 August 1975	Amaknak Island, Bering Sea	7 KWs chase a Minke, which then stranded and died	?	Y	Lowry *et al.* (1987)
29 April 1976	Gulf of Alaska, U.S.A.	6 KWs attack and kill a Minke	?	Y	Fiscus *et al.* (1976), Anonymous (1976)
Winter 1977	Yakutat, AK, U.S.A.	6–7 KWs attacking a Minke, which was killed by ramming	?	Y	Hall (1986)
January 1980	Ross Island, Antarctica	Second-hand report of an attack on a Minke	?	?	Leatherwood, Thomas & Awbrey (1981)
February 1980	Antarctica	Possible attack on Minkes by 15–20 KWs	?	?	Horwood (1990)
14 August 1980	Port Hardy, B.C., Canada	Presumed attack—partial carcass of Minke discovered near I pod (residents)	?	?	Ford & Ford (1981)
Pre-1981	Southern Hemisphere	Attack observed	?	?	Mikhalev *et al.* (1981)
1982	Prince William Sound, AK, U.S.A.	10–15 KWs attack and kill Minke	?	Y	Mehlberg (1986)
16 September 1984	Gulf of St Lawrence, Canada	3 KWs attack and kill a single Minke	?	Y	Wenzel & Sears (1988), Gormley (1990)
Pre-1988	Gulf of St Lawrence, Canada	10 KWs kill and eat a Minke	?	Y	Gormley (1990)
Humpback Whale *Megaptera novaeangliae*					
1830	Narparsok, Greenland	1 Humpback killed by single KW (whaler record)*	N	Y	Eschricht (1866)
Mid 1800s–early 1900s	Twofold Bay, N.S.W., Australia	Many accounts of KWs aiding whalers in taking Humpbacks	Y	Y	Dakin (1938), Wellings (1944), Mead (1986)
1940–86	Greenland	4 observations of chases or attacks by KWs (one involving 90 KWs)	?	?	Heide-Jorgensen (1988)
October 1951	Exmouth Gulf, Western Australia	4–5 KWs attack 3 Humpbacks, one beat KWs with flukes (second-hand report)	?	N	Chittleborough (1953)
8 March	Santa Isabela Island, Baja, Mexico	Single KW (later joined by 5 others) encounters 2 Humpbacks—no attack observed, but KWs appear to give chase	Y	N	E. D. Asper (*in litt.*)
Pre-1979	Southern AK, U.S.A.	9 KWs attack 2 Humpbacks	Y	N	Lockley (1979)
16 September 1979	Halibut Point, MA, U.S.A.	KWs attacking small Humpback	?	?	Katona *et al.* (1988), Gormley (1990)
4 July 1982; 25, 26 June 1983	Newfoundland, Canada	3 attacks on Humpbacks by groups of 10–12, 17, and 17 KWs	Y	N	Whitehead & Glass (1985)
August 1983	South-east AK, U.S.A.	KWs attack a juvenile Humpback, defended by 2 adults	Y	?	D'Vincent *et al.* (1989)
June 1985	South-east AK, U.S.A.	5 KWs following 3 Humpbacks—apparent attack on one	?	?	P. Folkens (*in litt.*)
Summer 1987	South-east AK, U.S.A.	2 KWs attempt to attack a Humpback calf	?	N	D'Vincent *et al.* (1989)
Pre-1988	Western North Atlantic	Whaler record of about 5 KWs attacking a cow and calf Humpback*	?	?	Katona *et al.* (1988)
3 July 1988	South-east AK, U.S.A.	7 KWs harass at least 7 Humpbacks—no attack	N	N	T. A. Jefferson (unpubl.), D'Vincent *et al.* (1989)
Pre-1990	Brandt Pt, MA, U.S.A.	2 reported attacks on Humpback Whales	?	?	Gormley (1990)

Appendix I
(*Continued*)

Date	Location	Description	Cooperation?	Kill?	Source
Cetaceans (*Contd.*)					
Bowhead Whale *Balaena mysticetus*					
1800s	Sea of Okhotsk	3 KWs attack and mortally-wound a large Bowhead*	Y	Y	Bullen (1898)
1830s(?)	Holsteinsborg, Greenland	KWs attacking Bowhead—one KW hit on head and apparently killed (second-hand report)	?	N	Eschricht (1866)
Mid-1800s–1956	Eastern Canadian Arctic	4 second-hand or whaler reports of chases or attacks on Bowheads*	?	Y	Reeves & Mitchell (1988)
1922–75	Eastern Canadian Arctic	4 second-hand reports of attacks by KWs on Bowheads	?	Y	Mitchell & Reeves (1982)
11 September 1984	Baffin Island, eastern Canada	2 KWs presumably attack single Bowhead, while 12 other Bowheads socialize nearby	?	?	Finley (1990)
17 September 1985	Baffin Island, eastern Canada	Possible attack on Bowheads involving 22 KWs	?	?	Finley (1990)
Northern Right Whale *Eubalaena glacialis*					
Pre-1982	British Columbia, Canada	Second-hand report of an attack	?	?	Gaskin (1982)
Southern Right Whale *Eubalaena australis*					
Mid–1800s–early 1900s	Twofold Bay, N.S.W., Australia	Many accounts of KWs aiding whalers in taking RWs	Y	Y	Dakin (1938), Wellings (1944), Mead (1986)
22 September 1965	Algoa Bay, S. Africa	3 KWs closely circle and harass RWs	N	N	Donnelly (1967)
Early 1970s	Peninsula Valdes, Argentina	Second-hand report of KWs attacking 3 RW, which fled at high speed, almost ramming a small boat	?	N	B. Würsig (pers. comm.)
4 July 1971	Golfo San Jose, Argentina	5 KWs attack 2 RWs	?	N	Cummings *et al.* (1971), Cummings *et al.* (1972)
Pre-1972	Peninsula Valdes, Argentina	Second-hand report of an attack by 5 KWs	?	Y	Cummings *et al.* (1972)
24 September 1972	Peninsula Valdes, Argentina	5 KWs harass a group of RWs, which formed a protective group	?	N	Payne (in press)
December 1978	Southern Hemisphere	4–5 KWs attack a RW which stranded	?	?	C. Guinet (*in litt.*)
Grey Whale *Eschrichtius robustus*					
Spring 1858	Baja California, Mexico	3 KWs attack a cow–calf—calf killed	Y	Y	Scammon (1872, 1874)
Early 1900s	Korea	Several whaler records of KW attacks on GWs (one involved 7 Greys and 15 KWs)*	?	?	Andrews (1914)
1950	San Diego, CA, U.S.A.	Second-hand report of 6 KWs attacking 2 Greys	?	N	Gilmore (1961)
9 March 1952	Monterey Bay, CA, U.S.A.	Second-hand report of 6 KWs attacking 3 Greys	?	N	Rice & Wolman (1971)
10 September 1960	Langara Light, B.C., Canada	KW attack on a pair of Greys	?	?	Pike & MacAskie (1969)
November 1961	Southern CA, U.S.A.	Second-hand report of single KW attacking and killing single Grey	N	Y	W. F. Samaras and S. Leatherwood (unpubl.)
26 January 1964	San Diego, CA, U.S.A.	5 KWs 'chase' 6 Greys, which move close to shore	N	N	Burrage (1964)
February 1966	Southern CA, U.S.A.	Second-hand report of 2–3 KWs attacking 3 Greys, killing 1	?	Y	W. F. Samaras (*in litt.*)
2 May 1967	Monterey Bay, CA, U.S.A.	7 KWs attack 3 Greys including a calf	?	N	Morejohn (1968)
12, 18 May 1967	Monterey Bay, CA, U.S.A.	5–6 KWs attack cow–calf—calf killed; second-hand report of an attack on a Grey	Y	Y	Baldridge (1972)
4–6 January 1969	Central CA, U.S.A.	At least 6 KWs attack a large Grey, which disappeared	N	?	S. Leatherwood (pers. comm.)
August 1975	Point Hope, AK, U.S.A.	7 KWs attack a young Grey	Y	Y	Marquette (1978)
18 July 1980	St Lawrence Island, Bering Sea	10–12 KWs attack and kill a Grey	?	Y	Ljungblad & Moore (1983)
20 May 1981	St Lawrence Island, Bering Sea	16 KWs chase several Greys	?	N	Ljungblad & Moore (1983)
8 March 1982, 7 March 1983	Southern CA, U.S.A.	2 second-hand reports of KW attacks on Greys (involving 1 and 6 KWs)	?	Y	D. L. Kelly (unpubl.)
20 August 1983	Bering Strait	Presumed attack—carcass found near KW	?	?	Lowry *et al.* (1987)
25 July 1984	North-east Chukchi Sea	8 KWs observed feeding on Grey (presumed attack)	?	?	Lowry *et al.* (1987)
17 January 1987	California coast, U.S.A.	2 second-hand reports of attacks by 2 and 5 KWs (in one, a calf was killed)	?	Y	Baldridge (1987), Jones & Swartz (1989)
12 January, 23 April 1988	Monterey Bay area, CA, U.S.A.	2 second-hand reports of attacks by 6 and 3 KWs (in one, a calf was killed)	?	Y	Baldridge (1988)
Unidentified baleen whale Mysticeti					
23 February (year unknown)	Culebra Island, Caribbean	Second-hand report of 25 KWs attacking a large whale	?	?	Erdman (1970)
1912	Komandorskiye Islands, U.S.S.R.	Several KWs attack and kill whale	?	Y	Tomilin (1957)
Pre-1957	Near Bering Island	Second-hand report of 10–15 KWs attacking large whale	Y	?	Tomilin (1957)
20 October 1989	Southern Hemisphere	At least 10 KWs attack a possible Sei Whale	?	?	C. Guinet (*in litt.*)
Sperm Whale *Physeter macrocephalus*					
1961	Southern Hemisphere	KWs 'harrying a wounded sperm whale' (probably harpooned)	?	N	Gaskin (1972)
1962–74	Southern Hemisphere	Report of KW attack on Sperm Whale group, incl. calves	?	?	Schevchenko (1975)
6 April 1971	Off Durban, S. Africa	KWs circling pod of Sperm Whales, incl. one giving birth (many sharks also present)	?	N	Best *et al.* (1984)
Pre-1972	Kuril Islands, U.S.S.R.	Second-hand reports of KWs attacking Sperm Whale newborns	?	?	Berzin (1972)
Pre-1975	Southern Hemisphere	Second-hand observation of KW attack on Sperm Whale pod with calves	?	?	Yukhov, Vinogradova & Medvedev (1975)
18 April 1985	Galapagos Islands, Ecudaor	15–25 KWs attack at least 20 Sperm Whales	?	N	Arnbom *et al.* (1987)
Northern Bottlenose Whale *Hyperoodon ampullatus*					
1960s(?)	Jan Mayen, Norway	KWs attack 2 harpooned (alive) Bottlenoses, later killed by whalers	Y	N	Jonsgard (1968a)
June 1963	Spitsbergen, Norway	KWs kill and eat Bottlenose	?	Y	Jonsgard (1968a)
Cuvier's Beaked Whale *Ziphius cavirostris*					
1 October 1985	Mediterranean Sea	Single KW feeding on fresh carcass (probably killed by KW)	N	?	Notarbotolo-di-Sciara (1987)

Appendix I
(*Continued*)

Date	Location	Description	Cooperation?	Kill?	Source
Cetaceans (*Contd.*)					
Narwhal *Monodon monoceros*					
1885–1963	Eastern Canadian Arctic	9 second-hand or whaler records of KW chases, attacks, or kills of Narwhals*	?	Y	Reeves & Mitchell (1988)
1976–85 (exact dates unknown)	Greenland	7 observations of chases or kills by KWs (incl. 15 KWs chasing 20–40 Narwhals)	?	?	Heide-Jorgensen (1988)
30 August 1980	Eclipse Sound, N.W.T., Canada	Several hundred Narwhals attacked by 30–40 KWs	Y	Y	Steltner *et al.* (1984)
15–20 August 1985	Canadian Arctic	12 KWs attack Narwhals, which swam into shallows	?	Y	Newman & Cavanaugh (1986)
20 August 1985	Pond Inlet, eastern Canadian Arctic	3 groups of Narwhals in shallow water—one group likely attacked by 9 KWs	?	?	Campbell *et al.* (1988)
White Whale *Delphinapterus leucas*					
1827	Godhaven, Greenland	KW attack on a pod of White Whales (second-hand report)	?	Y	Scammon (1872, 1874), Eschricht (1866)
1911–56	Eastern Canadian Arctic	3 second-hand or whaler records of chases or attacks on White Whales*	?	Y	Reeves & Mitchell (1988)
Pre-1930	Greenland	Attack observed	?	?	Degerbøl & Nielsen (1930)
Pre-1952	Western Pacific	8 KWs attack White Whales	Y	?	Sleptsov (1952)
1985	Greenland	KWs 'hunting belugas'	?	?	Heide-Jorgensen (1988)
April 1989	Bristol Bay, AK, U.S.A.	8 KWs attack about 50 White Whales, killing 3–4*	Y	Y	King (1989)
Long-finned Pilot Whale *Globicephala melas*					
1950	New England, U.S.A.	KW 'feeding on a pod of pilot whales'	N	?	Clark (1950)
1980, 1986	Greenland	2 observations of chases by KWs (in one instance by a single KW)	?	?	Heide-Jorgensen (1988)
1984, date unknown	Faroe Islands	2 attempts by 10 and 50 KWs to attack Pilots (one successful)	?	Y	Bloch & Lockyer (1988)
Common Dolphin *Delphinus delphis*					
Fall 1947	Baja California, Mexico	15–20 KWs attack 100 Common Dolphins	Y	Y	Brown & Norris (1956)
2 May 1973	Robbe Berg Pt, S. Africa	About 1000 Common Dolphins flee from 3 pursuing KWs	?	?	Saayman & Tayler (1979)
8 March 1982	Southern CA, U.S.A.	Second-hand report of 6 KWs chasing large school (species ID of dolphins not positive)	?	?	D. L. Kelly (unpubl.)
Dusky Dolphin *Lagenorhynchus obscurus*					
Pre-1980	Peninsula Valdes, Argentina	Second-hand report of an apparent attack	?	?	Würsig & Würsig (1980)
Unidentified dolphin (Delphinidae)					
1968–80	Eastern tropical Pacific	3 reports of KWs attacking or chasing unidentified dolphins (probably *Stenella* or *Delphinus*)	?	?	Perryman & Foster (1980)
1979	Near Cape Town, S. Africa	Second-hand report of 5 KWs killing dolphin in small school*	?	Y	Rice & Saayman (1987)
17 October 1982	Cape Town, S. Africa	2 KWs hunting a school of fleeing dolphins	?	?	Rice & Saayman (1987)
11 April 1986	False Bay, S. Africa	Second-hand report of apparent attack on 12 dolphins by 1 KW*	?	?	Rice & Saayman (1987)
Dall's Porpoise *Phocoenoides dalli*					
May 1962, 1963	British Columbia, Canada	2 observations of attacks on Dall's (one by 12 KWs)	Y	?	Pike & MacAskie (1969)
30 October 1971	South-east AK, U.S.A.	2 KWs attack single Dall's	?	?	Barr & Barr (1972)
Summer 1982	Johnstone Strait, B.C., Canada	Single transient KW lunges on top of fleeing Dall's	N	?	Jacobsen (1986)
Dall's Porpoise *Phocoenoides dalli* (*Contd.*)					
July 1982	Greater Puget Sound, WA, U.S.A.	L pod subgroup (residents) attack Dall's	Y	?	Felleman (1986), Heimlich-Boran (1988), Felleman *et al.* (1991)
July 1983	Johnstone Strait, B.C., Canada	O pod KW (transient) attacks a Dall's calf	N	?	J. Jacobsen (pers. comm.)
27 May 1984	South-east AK, U.S.A.	Dall's disappeared near KWs—presumed attack	N	?	S. Leatherwood (pers. comm.)
1984–88	British Columbia, Canada	Transient KWs pursue Dall's	?	N	Morton (1990)
6 August, 7 September 1985	Prince William Sound, AK, U.S.A.	2 attacks (first involved 2 transients and 1 resident, second 4 transients)	Y	Y	Hall & Cornell (1986)
9 February 1987	Vancouver Island, B.C., Canada	8 transients attack several Dall's	?	?	M. A. Bigg (*in litt.*)
Summer 1987	South-east AK, U.S.A.	2 transient KWs attack a Dall's	?	N	D'Vincent *et al.* (1989)
7 September 1987	South-east AK, U.S.A.	2 transient KWs chasing 1–2 Dall's	?	?	F. Sharpe (pers. comm.)
July 1988, date unknown	South-east AK, U.S.A.	2 observations of KWs attacking several Dall's	?	Y	P. Folkens (*in litt.*)
Harbour Porpoise *Phocoena phocoena*					
September 1962	Haro Strait, WA, U.S.A.	2 KWs chase a Harbour Porpoise (second-hand report)	?	?	Hoyt (1984)
August 1976	Haro Strait, WA, U.S.A.	L pod subgroup (residents) attack single Harbour Porpoise	Y	?	Balcomb *et al.* (1980), Felleman (1986), Heimlich-Boran (1988), Felleman *et al.* (1991)
Pre-1980	SW Ireland	KWs pursue porpoises	?	?	Evans (1980)
1984–88	British Columbia, Canada	5 attacks by transient KWs on Harbour Porpoises	?	Y	Morton (1990)
11 June, 5 August 1985	Prince William Sound, AK, U.S.A.	2 observations of 6 and 2 transient KWs killing single Harbour Porpoises	Y	Y	Hall & Cornell (1986)
7 August 1987	Faroe Islands	Single bull KW eats single Harbour Porpoise (second-hand report)	N	?	Bloch & Lockyer (1988)
Unidentified small cetacean (Delphinidae or Phocoenidae)†					
May 1949	Southern CA, U.S.A.	3 KWs attack 8 porpoises	?	?	Norris & Prescott (1961)
November 1964	Near Napier, New Zealand	At least 4 KWs attack a school of dolphins	Y	Y	Robson (1976)
Unidentified cetacean (Cetacea)					
Summer 1976	Barrow, AK, U.S.A.	3–4 KWs attack an unidentified cetacean	?	?	Marquette (1978)
Pre-1982	Wainwright, AK, U.S.A.	2 second-hand reports of attacks on whales*	Y	?	Nelson (1982)

Appendix I
(Continued)

Date	Location	Description	Cooperation?	Kill?	Source
Pinnipeds					
Northern Elephant Seal *Mirounga angustirostris*					
28 December 1973	Islas San Benitos, Baja, Mexico	2 KWs attack and kill Elephant Seal, not eaten	Y	Y	Samaras & Leatherwood (1974)
26 October 1987	Cypress Pt, CA, U.S.A.	Presumed attack—KWs breaching, tail-slapping around area where an Elephant Seal submerged (bloody cloud seen and pink tissue seen in KW mouth)	?	?	N. A. Black (pers. comm.)
20 September 1988	Victoria, B.C., Canada	Attack by M1 pod (3 transients) on an Elephant Seal	Y	Y	Stacey & Baird (1989a)
Southern Elephant Seal *Mirounga leonina*					
1966	Possession Island, southern Indian Ocean	Reports of KWs 'patrolling' the surf, hunting for seals	N	N	Voison (1972)
Early 1970s	Marion Island, southern Indian Ocean	Several attacks by 4 and 3 KWs	?	Y	Condy *et al.* (1978)
1975–85	Punta Norte, Argentina	33 attacks by a solitary male (17 successful) and 535 attacks by groups (164 successful) on either Southern Elephant Seals or Southern Sea Lions	Y	Y	Lopez & Lopez (1985)
Summer 1982	Crozet Islands, southern Indian Ocean	KWs noted several times feeding on Elephant Seals	?	Y	Ridoux (1987)
1987–88	Punta Norte, Argentina	Many attacks on Southern Elephant Seals	Y	Y	Hoelzel (1989)
November 1987–December 1988	Crozet Islands, southern Indian Ocean	10 kills of weaned Elephant Seal pups	?	Y	Guinet (1990b)
Grey Seal *Halichoerus grypus*					
Pre-1980	North Rona and mainland coast of Scotland	Attacks observed	?	?	Evans (1990)
Pre-1988	Faroe Islands	Second-hand report of KW attack on a Grey Seal	N	?	Bloch & Lockyer (1988)
Hooded Seal *Cystophora cristatus*					
July 1940	Greenland	30 KWs eat a Hooded Seal	?	Y	Heide-Jorgensen (1988)
Harbour Seal *Phoca vitulina*					
May 1919	Green Island, B.C., Canada	About 6 KWs attack 1 Harbour Seal, which hauled-out to escape	?	N	Moran (1924)
July 1939	Dean Channel, B.C., Canada	Second-hand report of KWs chasing seals to shore	?	N	Fisher (1952)
Pre-1940s	Estero de Punta, Baja, Mexico	Small groups of KWs seen feeding on seals (second-hand report)	?	Y	Norris & Prescott (1961)
Pre-1948	Washington, U.S.A.	4 attacks observed	Y	Y	Scheffer & Slipp (1948)
1970s	British Columbia, Canada	Transient M1 observed to eat a Harbour Seal	N	Y	Balcomb *et al.* (1980)
1980s	Near San Juan Island, WA, U.S.A.	4 attacks by transient KWs	Y	Y	Felleman (1986), Felleman *et al.* (1991)
1982–84	Glacier Bay, AK, U.S.A.	2 observations of predation or attempted predation near land haulout sites, also second-hand reports	?	?	Calambokidis *et al.* (1987)
1984–88	British Columbia, Canada	Attack on a Harbour Seal by transient KWs	?	Y	Morton (1990)
11 June 1985	Prince William Sound, AK, U.S.A.	2 attacks by 6 transients	?	Y	Hall & Cornell (1986)
1986–89	Victoria, B.C., Canada	Over 50 kills of Harbour Seals by transient KWs	Y	Y	Baird & Stacey (1987, 1988b), Baird, Dill & Stacey (1990)
Summer 1987	Near San Juan Island, WA, U.S.A.	2 resident killer whales (from L pod) attack a Harbour Seal	?	Y	Felleman *et al.* (1991)
Harp Seal *Phoca groenlandica*					
May 1950	Greenland	4–5 KWs following Harp Seals	?	N	Heide-Jorgensen (1988)
April 1977	Newfoundland, Canada	KWs seen 'feeding on harp seal pups and other seals'	?	?	N. Oien (*in litt.*)
23 September 1979	Lancaster Sound, Canada	KWs seen chasing many Harp Seals	?	?	Koski & Davis (1980)
Crabeater Seal *Lobodon carcinophagus*					
January 1973	Antarctic	8 KWs attack seal on ice floe	Y	?	Yukhov *et al.* (1975)
12 November 1979	Gerlache Strait, Antarctica	7 KWs attack seal on ice floe, wash seal off ice	Y	?	Smith *et al.* (1981)
Weddell Seal *Leptonychotes weddelli*					
20 January–5 February 1981	Ross Sea, Antarctica	Single case of a chase by KWs of a Weddell	?	?	S. Leatherwood (pers. comm.)
January 1957	Antarctica	6–7 KWs pull a seal off the ice	?	Y	Cromie (1963)
Leopard Seal *Hydrurga leptonyx*					
30 October 1975	Antarctica	Attack by at least 2 KWs	?	Y	Siniff & Bengtson (1977)
Walrus *Odobenus rosmarus*					
Pre-1866	Norsuak, Greenland	Second-hand report of an attack on a Walrus	Y	?	Eschricht (1866)
Pre-1872	Bering Sea	Many attacks, especially on young	?	Y	Scammon (1872, 1874)
1933, 1936	Anadyr Zaliv and Bering Strait	Several attacks on Walruses observed	Y	?	Zenkovich (1938)
1935	Kolyuchinski Bay, U.S.S.R.	2 reports of KWs pursuing Walrus (one instance involved 2 KWs)	?	?	Nikulin (1941)
September 1936	Cape Providence, U.S.S.R.	15 KWs attack small group split off from larger group of 60–70 Walrus	?	?	Zenkovich (1938)
20 August 1983	Bering Strait	Presumed attack—Walrus remains found near KWs	?	Y	Lowry *et al.* (1987)
18 July 1985	Cape Pierce, AK, U.S.A.	4 KWs attack 3 Walrus, from group moving towards shore	Y	?	Mazzone (1987)
California Sea Lion *Zalophus californianus*					
Date unknown	Santa Catalina Island, CA, U.S.A.	Second-hand reports KWs jumping onto rocks to get at Sea Lions*	?	Y	W. F. Samaras (*in litt.*)
April 1952 (?)	Magdalena Bay, Baja, Mexico	5–7 KWs attack 10–15 Sea Lions	Y	Y	Norris & Prescott (1961)
August 1955	Near Santa Barbara Island, CA, U.S.A.	Attack by 6 KWs, played with prey	?	?	Norris & Prescott (1961)
1959	California, U.S.A.	4 KWs attack a Sea Lion	Y	Y	W. F. Samaras and S. Leatherwood (unpubl.)

Appendix I
(*Continued*)

Date	Location	Description	Cooperation?	Kill?	Source
Pinnipeds (*Contd.*)					
California Sea Lion (*Cont'd*)					
1959 or 1960	Santa Catalina Island, CA, U.S.A.	Second-hand report of 50–60 Sea Lions attacked by 12–15 KWs	Y	?	W. F. Samaras and S. Leatherwood (unpubl.)
1960	Santa Barbara Island, CA, U.S.A.	KWs seen to 'jump up onto the rocks' to grab Sea Lions (second-hand report)*	?	Y	W. F. Samaras (*in litt.*)
25 May 1965	Farallon Islands, CA, U.S.A.	8 KWs attack a male Sea Lion (second-hand report)	Y	?	Rice (1968)
9 February 1967	*Islas San Benitos, Baja,* Mexico	*At least 6 KWs attack a Sea Lion*	?	?	Rice (1968)
Autumn 1973	Los Angeles, CA, U.S.A.	7–8 KWs kill 4 of a group of 10–12 Sea Lions	Y	Y	W. F. Samaras and S. Leatherwood (unpubl.)
14 February 1982	Coronado Island, Baja, Mexico	6 KWs seen eating Sea Lions	Y	Y	D. L. Kelly (unpubl.)
8 March 1982	Southern CA, U.S.A.	6 KWs eat 2 Sea Lions	?	Y	D. L. Kelly (unpubl.)
2 November 1986	Near Pt Reyes, CA, U.S.A.	10 KWs attack a California Sea Lion (second-hand report)	?	?	Baldridge (1986)
3 December 1986	Vancouver Island, B.C., Canada	4 transient KWs attack a California Sea Lion	Y	N	Bigg *et al.* (1987)
20 May 1988	Monterey, Bay, CA, U.S.A.	Second-hand report of 2 KWs 'breaching, feeding on, or playing with sea lion', probably a California Sea Lion*	?	?	Baldridge (1988)
14 January 1989	Point Piños, CA, U.S.A.	4 KWs attack 5–6 Sea Lions, killing 1	Y	Y	Jefferson (unpubl.)
Steller Sea Lion *Eumetopias jubatus*					
Pre-1886	Bering Sea	Group of KWs chases 5 Sea Lions, tearing throat from 1	?	?	Turner (1886)
Pre-1872	British Columbia, Canada or Alaska, U.S.A.	4 KWs seen eating Sea Lions	?	Y	Scammon (1872)
June 1933	*Cape Shipunskiy,* Bering Sea	Approach by several dozen KWs to rookery, attacking those in water	?	?	Zenkovich (1938)
9 May 1959	Triangle Island, B.C., Canada	Group of KWs toying with wounded Sea Lion	?	?	Pike & MacAskie (1969)
20 August, 4 September 1960	Langara Light, B.C., Canada	2 KW attacks on Sea Lions	?	?	Pike & MacAskie (1969)
23 January 1971	Bering Sea	7 KWs pursue 20–25 Sea Lions	?	?	Branson (1971)
13 March 1975	Vancouver Island, B.C., Canada	Attack by 3 KWs	?	Y	Harbo (1975)
Pre-1981	North Pacific Ocean	KWs seen feeding on Steller Sea Lions	?	Y	Mikhalev *et al.* (1981)
1982	Shelikof Strait, AK, U.S.A.	About 150 Sea Lions hauled-out onto small islet as KWs circled	Y	?	Leatherwood, Bowles & Reeves (1983)
August 1983	Frederick Sound, AK, U.S.A.	KWs attacking bull Sea Lion	?	?	D'Vincent *et al.* (1989)
13 August 1983	Frederick Sound, AK, U.S.A.	Attack by 6 KWs	Y	?	Dolphin (1987)
Pre-1984	Vancouver Island, B.C., Canada	KWs attacking Sea Lions forced into water by tide	?	Y	Hoyt (1984)
1984–88	Vancouver Island, B.C., Canada	3 attacks by transient KWs on Steller Sea Lions	?	Y	Morton (1990)
Pre-1986	Prince William Sound, AK, U.S.A.	Second-hand reports of numerous attacks	?	Y	Hall (1986)
Pre-1987	Vancouver Island, B.C., Canada	6 transient KWs attack a Steller Sea Lion	?	Y	Bigg *et al.* (1987)
Southern Sea Lion *Otaria flavescens*					
1970–85	Punta Norte, Argentina	33 attacks by a solitary male (17 successful) and 535 attacks by groups (164 successful) on either Southern Elephant Seals or Southern Sea Lions	Y	Y	Lopez & Lopez (1985)
Pre-1975	Peninsula Valdes, Argentina	More than 20 attacks on pups in 1 hour, also second-hand report of thousands taken*	?	Y	Anonymous (1975)
Pre-1976	Peninsula Valdes, Argentina	Several attacks on Sea Lions observed	?	Y	Bartlett & Bartlett (1976)
21 January 1981	Isla Marta	Single KW chases young Sea Lion onto shore	N	N	S. Leatherwood (pers. comm.)
1987–88	Punta Norte, Argentina	Many attacks on Southern Sea Lions	Y	Y	Hoelzel (1989)
Northern Fur Seal *Callorhinus ursinus*					
Pre-1922	Pribilof Islands, Bering Sea	Second-hand reports of attacks each spring and autumn, first-hand observation of attack on pups	?	Y	Hanna (1922)
16 June 1964	Tyuleniy Island, U.S.S.R.	5 KWs attack a Fur Seal colony	?	?	Bychkov (1967)
Unidentified sea lion (Otariidae)					
Summer 1974	Long Beach, B.C., Canada	Second-hand report of an attack by 5 KWs on sea lions	Y	?	Ford & Ford (1981)
Unidentified pinniped (Pinnipedia)					
Pre-1872	Santa Barbara Island, CA, U.S.A.	KWs seen pursuing seals	Y	?	Scammon (1872)
19–29 August 1943	Lancaster Sound, Canada	Second-hand report of about 20 KWs terrorizing seals	?	?	Reeves & Mitchell (1988)
7 August 1954	*Greenland*	6 KWs chased but did not catch a seal	?	N	Heide-Jorgensen (1988)
Pre-1979	Alaska, U.S.A.	4 KWs attack a seal	?	?	Lockley (1979)
13 February 1986	Namibia, Africa	Second-hand report of a KW eating 4 seals	N	Y	Rice & Saayman (1987)
Sirenians					
Dugong *Dugong dugon*					
20–26 May 1983	Western Australia	3 incomplete observations or second-hand reports of KWs attacking Dugongs	?	?	Anderson & Prince (1985)
Carnivores					
Sea Otter *Enhydra lutris*					
Spring 1962	Kuril Islands, U.S.S.R.	Report of a KW catching a Sea Otter	?	?	Nikolaev (1965)

*Possibly unreliable record.
†Baird & Stacey (1988) reported a porpoise kill, but subsequent observations convinced the authors that it was a Harbour Seal, not a porpoise.

Appendix II

Interactions between Killer Whales (KWs) and other marine mammals involving no apparent aggressive actions by the Killer Whales

Date	Location	Description	Source
Cetaceans			
Blue Whale *Balaenoptera musculus*			
1961–79	Southern Hemisphere	2 observations of 'mixed groups' of KWs and Blue Whales	Mikhalev *et al.* (1981)
Fin Whale *Balaenoptera physalus*			
August 1933	Cape Olyutorsky, Bering Sea	Fin Whales feeding peacefully with Humpbacks and KWs on large school of herring	Zenkovich (1938)
7 October 1948	Western North Pacific	20 Fin Whales near KWs hunting herring	Sleptsov (1961)
1961–79	Southern Hemisphere	11 observations of 'mixed groups' of KWs and Fin Whales	Mikhalev *et al.* (1981)
14–28 June 1970	Newfoundland, Canada	4 reports of KWs 'associated with' Fin Whales being hunted, presence of KWs 'made whales very wild'	Mitchell & Reeves (1988)
5 September 1979	Ipswich Bay, MA, U.S.A.	40–50 KWs seen within 20 m of 2 Fin Whales	Gormley (1990)
16 September 1984	Gulf of St Lawrence, Canada	Single Fin Whale passes by 3 KWs attacking a Minke Whale—no apparent response by Fin	Gormley (1990)
23 October 1985	New Scantum Ledge, NH, U.S.A.	Single KW approaches 2 Fin Whales—Fin Whales not noticeably disturbed	Gormley (1990)
1980s	Cape Cod, MA, U.S.A.	KWs and Fin Whales pass through each other's ranks—no aggression observed	Gormley (1990)
Pre-1990	Ipswich Bay, MA, U.S.A.	Fin Whale travelling with over 100 KWs	Gormley (1990)
Sei Whale *Balaenoptera borealis*			
1961–79	Southern Hemisphere	14 observations of 'mixed groups' of KWs and Sei Whales	Mikhalev *et al.* (1981)
Bryde's Whale *Balaenoptera edeni*			
8 January 1987	Namibia, S. Africa	Second-hand report of KWs 'feeding with 2 Bryde's Whales'	Rice & Saayman (1987)
Minke Whale *Balaenoptera acutorostrata*			
April 1955	Graham Land, Antarctica	For several months, about 60 KWs, 120 Minke Whales, and 1 Arnoux's Beaked Whale were trapped in a pool in the sea ice—no aggression observed	Taylor (1957)
1961–79	Southern Hemisphere	34 observations of 'mixed groups' of KWs and Minke Whales	Mikhalev *et al.* (1981)
1979–82	Johnstone Strait, B.C., Canada	12 observations of non-predatory interactions between the two species	Jacobsen (1986)
Pre-1981	Vancouver Island, B.C., Canada	Several observations of Minke Whales near and among KWs	Ford & Ford (1981)
20 January–5 February 1981	Ross Island, Antarctica	Several observations of KWs and Minke Whales in close proximity, sometimes sharing the same breathing holes and in near physical contact	Leatherwood *et al.* (1981), S. Leatherwood (pers. comm.)
Pre-1984	Vancouver Island, B.C., Canada	Several observations of KWs near Minkes	Hoyt (1984)
Pre-1986	Greater Puget Sound, WA, U.S.A.	Resident KWs in vicinity of Minkes on several occasions—no attacks	Felleman (1986), Heimlich-Boran (1988), Felleman *et al.* (1991)
14 August 1988	Caamano Sound, B.C., Canada	2 Minkes pass by 5 KWs—no noticeable reaction	P. Axhorn (pers. comm.)
Humpback Whale *Megaptera novaeangliae*			
August 1933	Cape Olyutorsky, Bering Sea	Humpbacks feeding peacefully with Fin Whales and KWs on large school of herring	Zenkovich (1938)
1952	Western Australia	4 reports of KWs and Humpbacks in the same area, with no attack	Chittleborough (1953)
1961–79	Southern Hemisphere	5 observations of 'mixed groups' of KWs and Humpback Whales	Mikhalev *et al.* (1981)
Summer 1970	Johnstone Strait, B.C., Canada	Several observations of a Humpback Whale near KWs	Spong, Bradford & White (1970)
14–28 June 1970	Newfoundland, Canada	4 reports of KWs 'associated with' Humpbacks being hunted by whalers, presence of KWs 'made whales very wild'	Mitchell & Reeves (1988)
1982–83	South-east AK, U.S.A.	3 observations of Humpbacks and KWs in same area (once KWs were attacking a sea lion)	Dolphin (1987)
August 1983	Off Santa Cruz, CA, U.S.A.	3 Humpbacks 'cavorting with' single juvenile KW	Dohl *et al.* (1983)
7 March 1987	Cape Hatteras, SC, U.S.A.	3 KWs seen near single Humpback	Gormley (1990)
January 1989	Isla Socorro, Mexico	Approx. 4 KWs pass singing Humpback, Humpback stops singing, surfaces among passing KWs	J. Jacobsen (*in litt.*)
Southern Right Whale *Eubalaena australis*			
1961–79	Southern Hemisphere	One observation of a 'mixed group' of KWs and Right Whales	Mikhalev *et al.* (1981)
Grey Whale *Eschrichtius robustus*			
Pre-1961	San Diego, CA, U.S.A.	Several reports of Grey Whales and KWs in same area with no aggression	Gilmore (1961)
6-17 January 1963	Santa Barbara, CA, U.S.A.	2 Grey Whales using 'sneaking behaviour' with no visible blows and slower respirations as they passed KWs	S. Leatherwood (pers. comm.)
Pre-1965	North Pacific	Grey Whales using underwater exhalations to avoid KWs	Hubbs (1965)
19 August 1979	Chukotka, Bering Sea	14 KWs (in separate subgroups) near Grey Whales	Ivashin & Votrogov (1981)
21 April 1980	Central CA, U.S.A.	2 Grey Whales apparently avoid 5 KWs, and exhale underwater	Poole (1984)
27 February 1983	Southern CA, U.S.A.	Second-hand report of KW following 2 Greys—no aggression reported	D. L. Kelly (unpubl.)
Sperm Whale *Physeter macrocephalus*			
1961–79	Southern Hemisphere	31 observations of a 'mixed groups' of KWs and Sperm Whales	Mikhalev *et al.* (1981)
Pre-1988	South Africa	'Multi-species assemblages' of KWs, Sperm Whales, and Risso's Dolphins	Bloch & Lockyer (1988)
Arnoux's Beaked Whale *Berardius arnuxii*			
April 1955	Graham Land, Antarctica	For several months, about 60 KWs, 120 Minke Whales, and 1 Arnoux's Beaked Whale were trapped in a pool in the sea ice—no aggression observed	Taylor (1957)
Northern Bottlenose Whale *Hyperoodon ampullatus*			
April 1893, 1977	Eastern Canadian Arctic	2 second-hand or whaler records of Bottlenose Whales in the same vicinity as KWs*	Reeves & Mitchell (1988)
Southern Bottlenose Whale *Hyperoodon planifrons*			
1961–79	Southern Hemisphere	6 observations of 'mixed groups' of KWs and Bottlenose Whales	Mikhalev *et al.* (1981)
White Whale *Delphinapterus leucas*			
5 August 1881	Eastern Canadian Arctic	Report of KWs with a herd of White Whales*	Greely (1886)
Long-finned Pilot Whale *Globicephala melas*			
1961–79	Southern Hemisphere	One observation of a 'mixed group' of KWs and Pilot Whales	Mikhalev *et al.* (1981)
10 September 1962	Smith Sound, eastern Canadian Arctic	Second-hand report of possible Pilot Whale with KWs (species ID uncertain)*	Reeves & Mitchell (1988)
15 September 1975	Mt Desert Rock, ME, U.S.A.	5 'blackfish' being followed by KW	Gormley (1990)
7 July 1987	Faroe Islands	Pilot Whales and KWs in mixed groups	Bloch & Lockyer (1988)
False Killer Whale *Pseudorca crassidens*			
1970s	Eshamy Lagoon, AK, U.S.A.	Report of a single False Killer Whale staying with 7 KWs for several days	C. O. Matkin (*in litt.* to S. Leatherwood)

Appendix II
(*Continued*)

Date	Location	Description	Source
Cetaceans (*Contd.*)			
Risso's Dolphin *Grampus griseus*			
Pre-1988	South Africa	'Multi-species assemblages' of KWs, Sperm Whales, and Risso's Dolphins	Bloch & Lockyer (1988)
27 November 1988	Monterey Bay, CA, U.S.A.	Single KW moving with group of 8 Risso's Dolphins and 10 Pacific White-sided Dolphins	N. A. Black (pers. comm.)
Common Dolphin *Delphinus delphis*			
19 March 1989	Monterey Bay, CA, U.S.A.	About 1200 Common Dolphins turn 180 and flee suddenly from 3 KWs	Jefferson (unpubl.)
Spinner Dolphin *Stenella longirostris*			
Pre-1973	Hawaii, U.S.A.	Report of a single KW that escaped from captivity associating with Spinners	Pryor (1973)
Dusky Dolphin *Lagenorhynchus obscurus*			
1973–76	Peninsula Valdes, Argentina	6 instances of Dolphins moving in tight groups away from KWs in area, in 3 instances especially close to shore	Würsig & Würsig (1980)
Pre-1987	Kaikoura, New Zealand	Dusky Dolphins suddenly move north, very close to shore, as group of KWs moved into area	B. Würsig (pers. comm.)
Pre-1989	Otago Peninsula, New Zealand	5 Dusky Dolphins following 5 KWs—no aggression	Hawke (1989)
White-beaked Dolphin *Lagenorhynchus albirostris*			
August 1977	Pentland Firth, Scotland	At least 15 KWs associated with Dolphins	Evans (1980)
1986	Iceland	5 observations of both species in the same area (once they fed together)	Sigurjonsson *et al.* (1988)
Atlantic White-sided Dolphin *Lagenorhynchus acutus*			
8 April 1978	Off Labrador, eastern Canada	Second-hand report of 2 KWs 'accompanied by' a dolphin (dolphin species ID uncertain)*	Mitchell & Reeves (1988)
June 1982	Isle of Shoals, ME, U.S.A.	Single KW 'swimming with White-sided Dolphins'	Gormley (1985), Katona *et al.* (1988)
15 October 1985	Iceland	KWs 2–5 miles from White-sided Dolphins, which were taking flight (possible coincidence)	S. Leatherwood (pers. comm.)
Pacific White-sided Dolphin *Lagenorhynchus obliquidens*			
27 November 1988	Monterey Bay, CA, U.S.A.	Single KW moving with group of 8 Risso's Dolphins and 10 Pacific White-sided Dolphins	N. A. Black (pers. comm.)
Bottlenose Dolphin *Tursiops truncatus*			
1974–76	Peninsula Valdes, Argentina	2 instances of Dolphins moving away from KW groups in area, towards open sea	Würsig & Würsig (1979)
Indo-Pacific Humpback Dolphin *Sousa chinensis*			
Pre-1979	Algoa Bay, S. Africa	About 20 Dolphins apparently avoid 3 KWs, by swimming very close to shore	Saayman & Tayler (1979)
Unidentified dolphin (Delphinidae)			
1961–79	Southern Hemisphere	One observation of a 'mixed group' of KWs and unidentified dolphins	Mikhalev *et al.* (1981)
March 1974	Southern CA, U.S.A.	6–7 KWs follow a school of dolphins at about 1 mile—no aggression observed (second-hand report)	W. F. Samaras (*in litt.*)
9 March 1976	Brazil	4–5 KWs in same vicinity as a school of unid. dolphins	Notobartolo-di-Sciara (1977)
Pre-1987	South Africa	Several observations of KWs in same vicinity as dolphins, with no aggression	Rice & Saayman (1987)
Dall's Porpoise *Phocoenoides dalli*			
4 August 1947	Cape Uyak, AK, U.S.A.	5–6 Dall's play near 5 KWs	Scheffer (1949)
4 November 1954	Southern CA, U.S.A.	2 Dall's feeding together on anchovies with 2 KWs	Brown & Norris (1956)
June–September 1970, 1971	Johnstone Strait, B.C., Canada	Several observations of Dall's and KWs feeding in the same area, and 2 reports of Dall's swimming with pods of KWs	Spong *et al.* (1970), Spong, Michaels & Spong (1972)
1979–82	Johnstone Strait, B.C., Canada	4 observations of Dall's Porpoises playing around KWs	Jacobsen (1986)
Pre-1981	Prince William Sound, AK, U.S.A.	Numerous instances of Dall's approaching and swimming with KWs	Matkin (1981)
Pre-1981	Vancouver Island, B.C., Canada	Several observations of Dall's near KWs, with no aggression	Ford & Ford (1981)
Pre-1982	Alaska, U.S.A.	Several reports of Dall's 'seen near and occasionally directly interacting' with KWs	Braham & Dahlheim (1982)
Pre-1984	Vancouver Island, B.C., Canada	Several observations of Dall's and KWs in close proximity	Hoyt (1984)
20 April–10 September 1984	South-east AK, U.S.A.	Several observations of Dall's swimming across the path of KWs and travelling in front of KWs	S. Leatherwood (pers. comm.)
20–July–23 September 1984	Prince William Sound, AK, U.S.A.	Single Dall's swam with resident pod of KWs, acted like a KW	C. O. Matkin (*in litt.*)
Summer 1984	Johnstone Strait, B.C., Canada	10 observations of Dall's and resident KWs the same area; observation of 5 Dall's playing around resident KWs	Jefferson (1987)
29 July 1984	Johnstone Strait, B.C., Canada	Lone Dall's avoids 4 resting resident KWs	Jefferson (1987)
28 August 1984	Kodiak Island, AK, U.S.A.	Several Dall's in close proximity to at least 103 KWs	S. Leatherwood (pers. comm.)
Pre-1986	Greater Puget Sound, WA, U.S.A.	Resident KWs and Dall's seen in close proximity several times	Felleman (1986)
22 August 1987	Boundary Pass, B.C., Canada	Several Dall's appear to avoid K pod (residents)	L. Fontaine (pers. comm.)
24 June 1988	Boundary Pass, B.C., Canada	Two groups of Dall's amidst J pod (residents)—no apparent reaction	L. Fontaine (pers. comm.)
13–May–19 August 1989	Victoria, B.C., Canada	2 observations of Dall's avoiding transient KWs, one of residents	R. W. Baird (unpubl.)
3 September 1988–26 August 1989	Victoria, B.C., Canada	6 occurrences of Dall's near transient KWs, and once with residents—no behavioural interactions	R. W. Baird and P. J. Stacey (unpubl.)
Harbour Porpoise *Phocoena phocoena*			
Pre-1948	Nisqually River, WA, U.S.A.	Harbour Porpoises apparently taking refuge from hunting KWs in a river (second-hand report)	Scheffer & Slipp (1948)
Pre-1986	Greater Puget Sound, WA, U.S.A.	Resident KWs and Harbour Porpoises seen in close proximity several times	Felleman (1986)
7 April–26 August 1989	Victoria, B.C., Canada	4 instances of porpoises within a few hundred metres of transient KWs—no reaction	R. W. Baird and P. J. Stacey (unpubl.)
Pinnipeds			
Harbour Seal *Phoca vitulina*			
1970s	British Columbia, Canada	Numerous accounts of pods passing close to hauled-out seals, with no reaction	Ford & Ford (1981)
1979–82	Johnstone Strait, B.C., Canada	3 reports of KWs and Harbour Seals in same area, with little reaction by seals	Jacobsen (1986)
1980s	Southern Vancouver Island, B.C., Canada	Resident KWs passing by hauled out Harbour Seals	R. W. Baird and P. J. Stacey (unpubl.)
Pre-1986	Greater Puget Sound, WA, U.S.A.	Harbour Seals and resident KWs in same area (often < 50 m away)	Felleman (1986), Felleman *et al.* (1991)

Appendix II
(*Continued*)

Date	Location	Description	Source
Pinnipeds (*Contd.*)			
Harp Seal *Phoca groenlandica*			
May 1950	Greenland	4–5 KWs 'following harp seals'	Heide-Jorgensen (1988)
February 1987	Finnmark, Norway	KWs circled around Harp Seals—no attack observed	N. Oien (*in litt.*)
Crabeater Seal *Lobodon carcinophagus*			
April–November	Graham Land, Antarctica	KWs trapped in sea-ice pool made no apparent attempts to attack seals present	Taylor (1957)
Weddell Seal *Leptonychotes weddelli*			
January 1981	Ross Sea, Antarctica	Several reports of KWs and Weddell Seals in same area	Thomas *et al.* (1981)
Walrus *Odobenus rosmarus*			
26 June 1922	Bering Strait	KWs following Walruses—no aggression reported	Bailey & Hendee (1926)
California Sea Lion *Zalophus californianus*			
12 October 1987	Victoria, B.C., Canada	Lone adult male KW swims within group of Steller and California Sea Lions, with no reaction by sea lions	Baird & Stacey (1989)
Steller Sea Lion *Eumetopias jubatus*			
June 1922	Green Island, B.C., Canada	2 sea lions (presumably Stellers) observed group of 15 KWs at close range, as whales were lobtailing	Moran (1924)
1979–82	Johnstone Strait, B.C., Canada	5 reports of KWs and Stellers in same area, with no evidence of avoidance (in one case, sea lions entered water as KWs passed)	Jacobsen (1986)
Pre-1982	Alaska, U.S.A.	Several observations of Stellers 'seen near and on occasion directly interacting with killer whales' with no aggression	Braham & Dahlheim (1982)
17 September 1984	Prince William Sound, AK, U.S.A.	3 Stellers feeding on herring with about 35 resident KWs, 2 sea lions attacked and bit KWs (unprovoked)	C. O. Matkin (*in litt.*)
12 October 1987	Victoria, B.C., Canada	Lone adult male KW swims within group of Steller and California Sea Lions, with no reaction by sea lions	Baird & Stacey (1989)
Unidentified pinniped (Pinnipedia)			
2 August 1983	Cape Point, S. Africa	Hundreds of seals in area feeding, upon appearance of KWs they disappeared	Rice & Saayman (1987)
14 February 1986	Namibia, S. Africa	KWs swimming around rocks near seals	Rice & Saayman (1987)
8 April 1986	Namibia, S. Africa	2 KWs feeding on seabirds and ignoring seals in the water	Rice & Saayman (1987)
Carnivores			
Sea Otter *Enhydra lutris*			
1 March, 9 April 1959	Amchitka Island, AK, U.S.A.	2 observations of KWs near otters, otters 'sensed' KWs, but not alarmed	Kenyon (1975)
1960 (?)	Rat Island, AK, U.S.A.	6 KWs near at least 200 otters	Kenyon (1975)
19, 26 July 1978	Prince William Sound, AK, U.S.A.	2 observations of KWs and otters in same area, otters become alert and alarmed (respectively)	Beckel (1980)