

Killer Whale (*Orcinus orca*) Predation of Marine Mammals

Bibliography

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Background & Scope

This bibliography is a comprehensive look at killer whale (*Orcinus orca*) predation of marine mammals. The goal is to better understand whether killer whales are successful marine mammal group hunters by evaluating their social structure and hunting strategies by analyzing examples from the literature describing mammal-hunting killer whale predation events. Understanding the costs of failure and success and the pivotal role social units' play in their hunting success could reveal how top-down predator dynamics influence marine ecosystems. The scope of this bibliography focused on academic and peer-reviewed literature, omitting news stories and second-hand accounts. It is broken up by year encompassing 1968-2020.

Sources Reviewed

Clarivate Analytics' Web of Science: Science Citation Index Expanded and Social Science Index; ProQuest's Science and Technology database, including Aquatic Science Fisheries Abstracts; Elsevier's Science Direct; JSTOR; EBSCO's Academic Search Complete and Environment Complete; NOAA's Institutional Repository; BioOneComplete; and Google Scholar,

Bibliography

Jonsgård, Å. (1968). A Note on the Attacking Behavior of the Killer Whale (*Orcinus orca*). *Norsk Hvalfangst-Tidende*, 57, 84-85

No abstract

Rice, D. W., Wolman, A. A., & American Society of, M. (1971). *The Life History and Ecology of the Gray Whale (Eschrichtius robustus)*. [Stillwater, Okla.]: American Society of Mammalogists. Retrieved from <https://www.biodiversitylibrary.org/item/87699>

No abstract

Baldrige, A. (1972). Killer Whales Attack and Eat a Gray Whale. *Journal of Mammalogy*, 53(4), 898-900
<https://doi.org/10.2307/1379230>

An attack on a gray whale and calf by 5 or 6 killer whales off the Californian coast was witnessed by several observers. The gray whales retreated towards the kelp but the calf was harassed and later floated to the surface apparently dead. The carcass was subsequently washed ashore and showed that most of the blubber on the ventral surface and the tongue had been eaten. The behaviour of the killer whales during their feeding is described. Meanwhile the adult gray whale, possibly the parent of the juvenile, was seen to take evasive action in the kelp-filled shallows and disappeared.

Condy, P., Aarde, R. V., & Bester, M. (1978). The Seasonal Occurrence and Behaviour of Killer Whales *Orcinus orca*, at Marion Island. *Journal of Zoology*, 184(4), 449-464
<https://doi.org/10.1111/j.1469-7998.1978.tb03301.x>

The paper describes the occurrence of Killer whales at Marion Island (Prince Edward group) in the south Indian Ocean from August 1973 to November 1976. They occur seasonally, being most numerous from October to December. Their occurrence is synchronized with the seasonal haul out of Southern elephant seals, but the seasonality of King, Rockhopper and Macaroni penguins is also likely to influence their occurrence. The largest herds occur in October, the month during which mean group size is also largest. Sex and age composition are given, adult males being significantly more numerous than adult females, while 36.3% of the latter had calves. Hunting activity appears to be greatest between 15.00 and 17.00 hrs, and most Killer whales were seen within 100 m of the shore. Aspects of hunting, attacking, feeding and resting behaviour are discussed. The body measurements of a young male found on a beach are given.

Smith, T. G., Siniff, D. B., Reichle, R., & Stone, S. (1981). Coordinated Behavior of Killer Whales, *Orcinus orca*, Hunting a Crabeater Seal, *Lobodon carcinophagus*. *Canadian Journal of Zoology*, 59(6), 1185-1189 <https://doi.org/10.1139/z81-167>

A pod of seven killer whales (*Orcinus orca*) was seen to attack a lone crabeater seal (*Lobodon carcinophagus*) which was lying on an ice floe. The whale located the seal, moved away from the floating

ice, then swam as a group close to the floe. This caused a wave which tipped up the ice floe and broke over it, causing the seal to be thrown into the water. The whales swam immediately to the vicinity where the seal disappeared but it was not possible to ascertain if a kill was made.

Ljungblad, D. K., & Moore, S. E. (1983). Killer Whales (*Orcinus orca*) Chasing Gray Whales (*Eschrichtius robustus*) in the Northern Bering Sea. *Arctic*, 36(4), 361-364 Retrieved from <https://www.jstor.org/stable/40509596>

Sixteen killer whales (*Orcinus orca*) were observed for 90 minutes as they approached and then chased gray whales (*Eschrichtius robustus*) in the Bering Sea north of St. Lawrence Island, Alaska. The killer swam in four discrete lines that blew synchronously as they approached an area in which gray whales were feeding. Once in the gray whales' feeding area, the killer whales broke into small groups and dispersed. The gray whales, which had been dispersed while feeding, formed groups of three to six and swam away from the killer whales, except for one individual. That whale was pursued by four killer whales swimming nearly abreast in a loose crescent formation with about 300 m between individuals. Although a sonobuoy was deployed throughout the observation period, no sounds were recorded from either species. The absence of whale sounds raises questions about how the whales detected one another and communicated between nearby conspecifics.

Steltner, H., Steltner, S., & Sergeant, D. (1984). Killer Whales, *Orcinus orca*, Prey on Narwhals, *Monodon monoceros*: An Eyewitness Account. *Canadian Field-Naturalist*, 98(4), 458-462 Retrieved from <https://www.biodiversitylibrary.org/page/28064297>

A first hand description is given of a herd or herds of several hundred Narwhals, *Monodon monoceros*, attacked by a herd of several tens of Killer Whales, *Orcinus orca*, in Eclipse Sound, Northwest Territories, in open water. The Killer Whales encircled the Narwhals by dividing into two groups which moved around the periphery of the prey animals in opposing directions. The attack by many killers at once then followed.

Anderson, P. K., & Robert, I. T. P. (1985). Predation on Dugongs: Attacks by Killer Whales. *Journal of Mammalogy*, 66(3), 554-556 <https://doi.org/10.2307/1380933>

No abstract

Lopez, J. C., & Lopez, D. (1985). Killer Whales (*Orcinus orca*) of Patagonia, and Their Behavior of Intentional Stranding While Hunting Nearshore. *Journal of Mammalogy*, 66(1), 181-183 <https://doi.org/10.2307/1380981>

No abstract

Whitehead, H., & Glass, C. (1985). Orcas (Killer Whales) Attack Humpback Whales. *Journal of Mammalogy*, 66(1), 183-185 <https://doi.org/10.2307/1380982>

No abstract

Mazzone, W. S. (1987). Walrus, *Odobenus rosmarus*, and Whale Interactions: An Eyewitness Account. *Canadian Field-Naturalist*, 101(4), 590-591 Retrieved from <https://www.biodiversitylibrary.org/page/28090023>

An attack by killer whales (*Orcinus orca*) on a group of walruses, (*Odobenus rosmarus*) at Cape Peirce, Alaska, is described. The killer whales surrounded, isolated, and attacked one walrus. A gray whale (*Eschrichtius robustus*) encountered and killed a large adult male walrus in the same area.

Arnbom, T., Papastavrou, V., Weilgart, L. S., & Whitehead, H. (1987). Sperm Whales React to an Attack by Killer Whales. *Journal of Mammalogy*, 68(2), 450-453 <https://doi.org/10.2307/1381497>

No abstract

Lowry, L. F., Nelson, R. R., & Frost, K. J. (1987). Observations of Killer Whales, *Orcinus orca*, in Western Alaska: Sightings, Strandings, and Predation on Other Marine Mammals. *Canadian Field-Naturalist*, 101(1), 6-12 Retrieved from <https://www.biodiversitylibrary.org/page/28089427>

Recent observations confirm that killer whales (*Orcinus orca*) occur off the coast of western Alaska from at least Bristol Bay to north of Point Barrow. They have been seen in drifting ice in spring and in open water during summer. Three strandings involving 10 animals that occurred in 1982-1984 in the area from Nunivak Island to Norton Sound are described. Observations of killer whales chasing a minke whale (*Balaenoptera acutorostrata*) aground in Unalaska Bay, and of killer whales eating a gray whale (*Eschrichtius robustus*) in the Chukchi Sea are reported. The marine mammal prey of killer whales in the area include gray whales, minke whales, walruses (*Odobenus rosmarus*), beluga whales (*Delphinapterus leucas*), and seals (Phocidae).

Baird, R. W., & Stacey, P. J. (1988). Foraging and Feeding Behavior of Transient Killer Whales. *Whalewatcher*, 22(1), 11-15 Retrieved from <https://www.cascadiaresearch.org/staff/robin-baird/robin-w-baird-publications>

No abstract

Campbell, R. R., Yurick, D. B., & Snow, N. B. (1988). Predation of Narwhals, *Monodon monoceros*, by Killer Whales, *Orcinus orca*, in the Eastern Canadian Arctic. *Canadian Field-Naturalist*, 102(4), 689-696 Retrieved from <https://www.biodiversitylibrary.org/page/28243966>

Killer whales (*Orcinus orca*) are considered uncommon in Canadian Arctic waters and have not been thought to be frequent predators of narwhals (*Monodon monoceros*). Observations of killer whale attacks in the Eclipse Sound area off the north coast of Baffin Island, Northwest Territories indicate this

may not be the case. There is evidence to confirm that killer whales are predators of narwhals and that the narwhals have evolved specific defensive strategies in response to killer whale predation.

Baird, R. W. S., P. J. . (1989). Observations on the Reactions of Sea Lions, *Zalophus californianus* and *Eumetopias jubatus*, to Killer Whales, *Orcinus orca*; Evidence of "Prey" Having a "Search Image" for Predators. *Canadian Field-Naturalist*, 103, 426 Retrieved from <https://www.biodiversitylibrary.org/page/34348258>

Observations on the reactions of California Sea Lions (*Zalophus californianus*) and Steller Sea Lions (*Eumetopias jubatus*) to the presence of foraging transient Killer Whales (*Orcinus orca*) were made on three occasions. Alert and avoidance responses by sea lions were made in the presence of Killer Whales of typical appearance. In the presence of a single, foraging Killer Whale of atypical appearance, no alert or avoidance response was observed. It is possible that the sea lions did not recognize the atypical whale as a Killer Whale, suggesting that sea lions may have a perceptual "search image" for the detection of predators, based on visual cues.

Vidal, O., & Pechter, G. (1989). Behavioral Observations of Fin Whale, *Balaenoptera physalus*, in the Presence of Killer Whale *Orcinus orca*. *Fishery Bulletin*, 87, 370-373

No abstract

Silber, G. K., & Newcomer, M. W. (1990). Killer Whales (*Orcinus orca*) Attack and Kill a Bryde's Whale (*Balaenoptera edeni*). *Canadian Journal of Zoology*, 68(7), 1603-1606
<https://doi.org/10.1139/z90-238>

On 3 May 1988, we observed a group of killer whales that pursued, killed, and partially consumed a Bryde's whale in the northern Gulf of California, Mexico (31°01'N, 114°15'W). The attack was observed from 06:54 to 08:53 while circling in a single-engine aircraft at an altitude of 160 m. The group comprised about 15 killer whales, including two adult males and at least two calves. Females and (or) subadult males pressed the attack most intently. The killer whales tore skin and blubber from the right flank of the Bryde's whale, and on 11 occasions the killer whales swam onto the head or back of the Bryde's whale, which hindered its breathing. The respiration intervals of the Bryde's whale were short and irregular, and blow rates differed significantly from those of undisturbed Bryde's whales. Fatiguing the whale may have facilitated an easier kill by asphyxiation. After the death of the Bryde's whale, the two adult male killer whales surfaced slowly about 200–300 m away from the remainder of the group, which presumably fed on the submerged Bryde's whale carcass. Two days later, the drifting Bryde's whale carcass was located. A large wound was visible on the abdomen, and sections of the lower jaw had been removed. Like those of canids and some felids that hunt cooperatively when preying on ungulates, attacks by *Orcinus orca* exhibit coordination of activities and efficiency in dispatching prey.

Hoelzel, A. R. (1991). Killer Whale Predation on Marine Mammals at Punta Norte, Argentina; Food Sharing, Provisioning and Foraging Strategy. *Behavioral Ecology and Sociobiology*, 29(3), 197-204
<https://doi.org/10.1007/BF00166401>

The social dynamics of killer whales (*Orcinus orca*) that hunt marine mammals are apparently highly flexible, though strong individual associations do exist. The killer whales at Punta Norte offer an unusually detailed view of association patterns and foraging behaviour, and suggest a pattern of behaviour that optimizes hunting efficiency with exception only to strong associations between some individuals and the provisioning and training of offspring. The main points from this paper are as follows: First, hunting effort was concentrated where the capture rate was greatest. All pods selectively attacked the prey type for which they had the highest capture rate. The amount of southern sea lion prey captured was approximately equal to the estimated minimum energetic requirement for killer whales based on weight. Secondly, one whale in each pod did the majority of the hunting, and then provisioned the others in the pod. It was clear on numerous occasions that food was shared. A review of reported incidences of killer whales taking marine mammal prey suggests that it is common for a subset of the individuals in a pod to hunt. These results are discussed in the context of the evolution of foraging behaviour.

Hoelzel, A. R. (1991). Killer Whale Predation on Marine Mammals at Punta-Norte, Argentina - Food Sharing, Provisioning and Foraging Strategy. *Behavioral Ecology and Sociobiology*, 29(3), 197-204
<https://doi.org/10.1007/bf00166401>

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Jefferson, T. A., Stacey, P. J., & Baird, R. W. (1991). A Review of Killer Whale Interactions with Other Marine Mammals: Predation to Co-Existence. *Mammal Review*, 21(4), 151-180
<https://doi.org/10.1111/j.1365-2907.1991.tb00291.x>

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.

Frost, K. J., Russell, R. B., & Lowry, L. F. (1992). Killer Whales, *Orcinus orca*, in the Southeastern Bering Sea - Recent Sightings and Predation on Other Marine Mammals. *Marine Mammal Science*, 8(2), 110-119 <https://doi.org/10.1111/j.1748-7692.1992.tb00370.x>

An unusual number of killer whales appeared in inshore waters of the southeastern Bering Sea in summer 1989 and 1990. Multiple sightings occurred in Bristol and Kuskokwim bays where killer whales had been seen only rarely in previous years. Three animals became stranded on mud flats in Kuskokwim Bay but were able to free themselves on a high tide. Killer whales were observed interacting with salmon, harbor seals, Steller sea lions, walruses, and beluga whales. Detailed observations were made of killer whales attacking belugas in the Naknek River. Local conditions and behavioral adaptations may reduce the susceptibility of belugas to killer whale predation. Continued killer whale activity in this area would be unlikely to affect fish resources, but might have some influence on beluga whales.

Guinet, C. (1992). (Hunting Behavior in Killer Whales (*Orcinus orca*) around the Crozet Islands.). [Comportement de chasse des orques (*Orcinus orca*) autour des îles Crozet]. *Canadian Journal of Zoology*, 70(9), 1656-1667 <https://doi.org/10.1139/z92-231>

Killer whales around Crozet Islands consume a great variety of preys, including fish, penguins (*Eudyptes* sp.), elephant seals (*Mirounga leonina*), and, occasionally, large cetacea. Predation techniques used on elephant seals and penguins, which are easily observed from the shore, are described. The successful predation of 29 elephant seals was observed, 24 of which were weaned pups. Seals were captured along the banks (n = 3), near river outlets (n = 14), by voluntary stranding of the whales on the beaches (n = 7), or by attach of seals swimming in bays (n = 5). Hunting techniques were routinely used in "strategic" points apparently chosen specifically according to the location and climatic factors. King penguins were hunted along the banks (n = 13), particularly where algae prevailed, or offshore (n = 32). While hunting, whales tended to be very quiet and used acoustic signals sparingly, emitting a few isolated chicks and short distance contact calls. Reactions of whales exposed to artificial sounds tended to show that they localize their prey by passive listening.

Flórez-González, L., Capella, J. J., & Rosenbaum, H. C. (1994). Attack of Killer Whales (*Orcinus orca*) on Humpback Whales (*Megaptera novaeangliae*) on a South American Pacific Breeding Ground. *Marine Mammal Science*, 10(2), 218-222 <https://doi.org/10.1111/j.1748-7692.1994.tb00264.x>

No abstract

Dahlheim, M. E., & Towell, R. G. (1994). Occurrence and Distribution of Pacific White-Sided Dolphins (*Lagenorhynchus obliquidens*) in Southeastern Alaska, with Notes on an Attack by Killer Whales (*Orcinus orca*). *Marine Mammal Science*, 10(4), 458-464 <https://doi.org/10.1111/j.1748-7692.1994.tb00501.x>

Although a number of cetacean species occur in the inland waterways of southeastern Alaska, only two small cetaceans are thought to commonly inhabit this region: the harbor porpoise (*Phocoena phocoena*) and Dall's porpoise (*Phocoenoides dalli*). During our 1991-1993 surveys, the seasonal occurrence of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) was also noted.

Goley, P. D., & Straley, J. M. (1994). Attack on Gray Whales (*Eschrichtius robustus*) in Monterey Bay, California, by Killer Whales (*Orcinus orca*) Previously Identified in Glacier Bay, Alaska. *Canadian Journal of Zoology*, 72(8), 1528-1530 <https://doi.org/10.1139/z94-202>

A group of at least 17 killer whales (*Orcinus orca*) were observed attacking a gray whale (*Eschrichtius robustus*) mother and calf on 2 May 1992 in Monterey Bay, California, U.S.A. (36 degree 47.90'N, 122 degree 00.17'W). Small groups of killer whales took turns harassing the gray whales and prevented them from leaving the area. Three of the killer whales participating in this attack previously had been photographed on 6 August 1989 in Glacier Bay, Alaska, U.S.A. (58 degree 41'N, 136 degree 04'W). This linear distance nearly doubles the maximum range of movement previously reported for killer whales.

Baird, R. W., & Dill, L. M. (1995). Occurrence and Behaviour of Transient Killer Whales: Seasonal and Pod-Specific Variability, Foraging Behaviour, and Prey Handling. *Canadian Journal of Zoology*, 73(7), 1300-1311 <https://doi.org/10.1139/z95-154#Xz7HYuhKg2w>

We studied the occurrence and behaviour of so-called transient killer whales (*Orcinus orca*) around southern Vancouver Island from 1986 to 1993. Occurrence and behaviour varied seasonally and among pods; some pods foraged almost entirely in open water and were recorded in the study area throughout the year, while others spent much of their time foraging around pinniped haulouts and other nearshore sites, and used the study area primarily during the harbour seal (*Phoca vitulina*) weaning–postweaning period. Overall use of the area was greatest during that period, and energy intake at that time was significantly greater than at other times of the year, probably because of the high encounter rates and ease of capture of harbour seal pups. Multipod groups of transients were frequently observed, as has been reported for "residents," but associations were biased towards those between pods that exhibited similar foraging tactics. Despite the occurrence of transients and residents within several kilometres of each other on nine occasions, mixed groups were never observed and transients appeared to avoid residents. Combined with previous studies on behavioural, ecological, and morphological differences, such avoidance behaviour supports the supposition that these populations are reproductively isolated.

Barrett-Lennard, L. G. (1995). *The Impact of Killer Whale Predation on Steller Sea Lion Populations in British Columbia and Alaska : Report for the North Pacific Universities Marine Mammal Research Consortium Fisheries Centre, University of British Columbia*. University of British Columbia Vancouver, BC.

Steller sea lion populations in Alaska have declined precipitously over the last 25 years. Much research has been conducted on the role of anthropogenic factors in this decline. The retrieval of 14 sea lion flipper tags from a dead killer whale in 1992 underscored the need for a similar appraisal of predation. We used simulation models to examine (1) the extent to which killer whales contributed to the sea lion decline, and (2) the present effect of killer whale predation on depleted sea lion populations. We estimated the model parameters using three sources: a survey of researchers and mariners, the stomach contents of stranded killer whales, and killer whale identification photographs from several collections. The 126 survey respondents described 52 attacks including 32 reported kills. Eight out of 15 killer whale stomachs with identifiable contents contained marine mammals, and two contained Steller sea lion remains. The survey and stomach content data were consistent with earlier findings that only members of the transient killer whale population commonly prey on marine mammals. Based on identification photographs, we estimated that at least 250 transient killer whales feed in Alaskan waters. We ran Leslie matrix simulations under various assumptions concerning the functional responses of killer whales to changes in sea lion density. Our models suggest that killer whale predation did not cause the sea lion decline, but may now be a contributing factor. At present, approximately 18% of sea lions that die annually in Western Alaska may be taken by killer whales.

Guinet, C., & Bouvier, J. (1995). Development of Intentional Stranding Hunting Techniques in Killer Whale (*Orcinus orca*) Calves at Crozet Archipelago. *Canadian Journal of Zoology*, 73(1), 27-33 <https://doi.org/10.1139/z95-004#.X0ZwRMhKg2w>

This paper describes the trend in the practice of what we interpret to be the "intentional stranding" hunting technique of two juvenile female killer whales (*Orcinus orca*), A4 and A5, belonging to pod A on the beaches of Possession Island, Crozet Archipelago. Pod A was composed of three adult females, A2, A3, A6, and one adult male, A1. A2 is A4's mother and A3 is A5's mother. The year of birth and thus the probable age of the two juveniles were estimated from their growth curve determined by means of a photogrammetric technique. These observations indicate that at Crozet Archipelago, juvenile killer whales first practiced intentional stranding on their own when they were 4–5 years old. Their first attempt to capture elephant seal pups by means of this technique was observed when they were 5–6 years old. However, 5- to 6-year-old juveniles still needed the assistance of an adult female to return to the water with their prey. This study indicates that learning hunting techniques needs a high degree of skill and requires high parental investment to reduce the associated risk. Furthermore, social transfer, through apprenticeship, is probably one of the mechanisms that enables the high degree of adaptability observed in killer whales.

Baird, R. W., & Dill, L. M. (1996). Ecological and Social Determinants of Group Size in Transient Killer Whales. *Behavioral Ecology*, 7(4), 408-416 <https://doi.org/10.1093/beheco/7.4.408>

Most analyses of the relationship between group size and food intake of social carnivores have shown a discrepancy between the group size that maximizes energy intake and that which is most frequently observed. Around southern Vancouver Island, British Columbia, killer whales of the so-called transient

form forage in small groups, and appear to prey exclusively on marine mammals. Between 1986 and 1993, in approximately 434 h of observations on transient killer whales, we observed 138 attacks on five species of marine mammals. Harbor seals were most frequently attacked (130 occasions), and the observed average energy intake rate was more than sufficient for the whale's energetic needs. Energy intake varied with group size, with groups of three having the highest energy intake rate per individual. While groups of three were most frequently encountered, the group size experienced by an average individual in the population (i.e., typical group size) is larger than three. However, comparisons between observed and expected group sizes should utilize only groups engaged in the behavior of interest. The typical size of groups consisting only of adult and subadult whales that were engaged primarily in foraging activities confirms that these individuals are found in groups that are consistent with the maximization of energy intake hypothesis. Larger groups may form for (1) the occasional hunting of prey other than harbor seals, for which the optimal foraging group size is probably larger than three; and (2) the protection of calves and other social functions.

Barrett-Lennard, L. G., Ford, J. K. B., & Heise, K. A. (1996). The Mixed Blessing of Echolocation: Differences in Sonar Use by Fish-Eating and Mammal-Eating Killer Whales. *Animal Behaviour*, 51(3), 553-565 <https://doi.org/10.1006/anbe.1996.0059>

Despite well-documented experimental evidence of echolocation in toothed whales, virtually nothing is known about the use and functional significance of cetacean sonar in the wild. Here, the patterns of echolocation sounds produced by killer whales, *Orcinus orca*, off British Columbia and Alaska are described. Two sympatric populations with divergent food habits differed markedly in sonar sound production. Individuals belonging to the fish-eating 'resident' population produced trains of characteristic sonar clicks, on average, 4% of the time, 27 times more often than marine mammal-eating 'transient' killer whales. The click trains of residents averaged 7s, more than twice as long as the trains of transients. Click repetition rates within resident's trains were constant or changed gradually; within transient's trains they often fluctuated abruptly. Transients produced isolated single or paired clicks at an average rate of 12/h, four times as often as residents. In general, the isolated clicks and infrequent, short and irregular trains of transients were less conspicuous against background noise than the sonar of residents. This difference in acoustic crypticity may reflect a flexible response to the probability of alerting prey, because marine mammals have more acute hearing than fish in the frequency range of sonar clicks. In both populations, echolocation use per individual decreased with increasing group size, suggesting the sharing of information between group members. No relationships were found between echolocation activity and water clarity for whales of either population. Transient whales often travelled or foraged without discernibly echolocating, suggesting that passive listening provides cues for prey detection and orientation.

Constantine, R., Visser, I., Buurman, D., Buurman, R., & McFadden, B. (1998). Killer Whale (*Orcinus orca*) Predation on Dusky Dolphins (*Lagenorhynchus obscurus*) in Kaikoura, New Zealand. *Marine Mammal Science*, 14(2), 324-330 <https://doi.org/10.1111/j.1748-7692.1998.tb00721.x>

Killer whales (*Orcinus orca*) are known to prey on a wide variety of marine mammal species, including large and small cetaceans, as well as pinnipeds. No well-documented records of killer whales feeding on dusky dolphins (*Lagenorhynchus obscurus*) have been reported in the literature. Wuersig and Wuersig (1980) reported one second-hand account of predation on dusky dolphins off Peninsula Valdes, Argentina. Accounts of killer whales preying on other species in the genus *Lagenorhynchus* are also

infrequent, especially given that these animals are both regularly observed in similar habitats. We present accounts of four killer whales preying on dusky dolphins over a period of 11 d off Kaikoura, New Zealand.

Hatfield, B. B., Marks, D., Tinker, M. T., Nolan, K., & Peirce, J. (1998). Attacks on Sea Otters by Killer Whales. *Marine Mammal Science*, 14(4), 888-894 <https://doi.org/10.1111/j.1748-7692.1998.tb00775.x>

Few references to attacks on sea otters, *Enhydra lutris*, by killer whales, *Orcinus orca*, exist in the literature. In an extensive review of predatory and non-predatory interactions between killer whales and other marine mammals, Jefferson et al. (1991) cited only one reference (Nikolaev 1965) in which killer whales aggressively pursued sea otters. In another review of attacks on marine mammals by killer whales in the North Pacific Ocean, Matkin and Saulitis (1994) listed three other interactions between killer whales and sea otters, but with the exception of one personal communication, the references (Barabash-Nikiforov 1938, Tomilin 1957) alluded only to presumed attacks. Kenyon (1969) described only non-aggressive interactions between the two species. No descriptions of killer whale attacks on sea otters have been published. In this note we describe nine observations made between 1992 and 1996 of killer whales attacking sea otters in Prince William Sound and in the Aleutian Islands, Alaska.

Visser, I. N. (1999). A Summary of Interactions between Orca (*Orcinus orca*) and Other Cetaceans in New Zealand Waters. *New Zealand natural sciences*, 24, 101-112 Retrieved from <https://ir.canterbury.ac.nz/bitstream/handle/10092/100537/visser.pdf?sequence=1>

Interactions between orca (*Orcinus orca*) and other species of cetaceans in New Zealand waters are presented, involving six species, over a 36 year period. Forty four published (n =15) and previously unpublished (n - 29) accounts are reviewed. The first Southern hemisphere accounts of orca attacking common dolphins (*Delphinus delphis*) are presented. Details are given of a dead sperm whale (*Physeter macrocephalus*) which had been attacked by orca.

Saulitis, E., Matkin, C., Barrett-Lennard, L., Heise, K., & Ellis, G. (2000). Foraging Strategies of Sympatric Killer Whale (*Orcinus orca*) Populations in Prince William Sound, Alaska. *Marine Mammal Science*, 16(1), 94-109 <https://doi.org/10.1111/j.1748-7692.2000.tb00906.x>

Killer whales (*Orcinus orca*) feed on a wide variety of fish, cephalopods, and marine mammals throughout their cosmopolitan range; however, the dietary breadth that characterizes the species is not reflected in all populations. Here, we present the findings of a 14-yr study of the diet and feeding habits of killer whales in Prince William Sound, Alaska. Two non-associating forms of killer whale, termed resident and transient (Bigg et al. 1987), were identified. All prey seen taken by transients were marine mammals, including harbor seals (*Phoca vitulina*), Dall's porpoises (*Phocoenoides dalli*), Steller sea lions (*Eumetopias jubatus*), and harbor porpoises (*Phocoena phocoena*). Resident killer whales appeared to prey principally on salmon (*Oncorhynchus* spp.), preferring coho salmon (*O. kisutch*) over other, more abundant salmon species. Pacific herring (*Clupea pallasii*) and Pacific halibut (*Hippocampus stenolepis*) were also taken. Resident killer whales frequently were seen to interact in non-predatory ways with Steller sea lions and Dall's porpoises, while transients were not. Differences in the social organization

and behavior of the resident and transient killer whales in Prince William Sound are discussed in the light of the dietary differences documented here.

Guinet, C., Barrett-Lennard, L. G., & Loyer, B. (2000). Co-Ordinated Attack Behavior and Prey Sharing by Killer Whales at Crozet Archipelago: Strategies for Feeding on Negatively-Buoyant Prey. *Marine Mammal Science*, 16(4), 829-834 <https://doi.org/10.1111/j.1748-7692.2000.tb00976.x>

Killer whales are known to prey on a wide array of species, including fish, seabirds, and marine mammals (Scammon 1874, Jefferson et al. 1991). At Crozet Archipelago (southern Indian Ocean, 46 degree E 25'S, 51 degree E 45'E) the same killer whales have been observed attacking fish, penguins, pinnipeds, and large cetaceans (Guinet 1991, 1992). Here, we describe the attack and kill of a minke whale (*Balaenoptera acutorostrata*) calf and the sharing of a young elephant seal carcass (*Mirounga leonina*) by killer whales at Crozet, based on both surface and underwater observations. To our knowledge, this is the first description by divers of the underwater behavior of killer whales feeding on marine mammals. The observations led us to consider the problems that killer whales face when feeding on large, negatively buoyant prey, and we discuss possible mitigating strategies.

Mann, J. (2000). *Cetacean Societies : Field Studies of Dolphins and Whales*. Chicago: University of Chicago Press. Retrieved from <https://press.uchicago.edu/ucp/books/book/chicago/C/bo3683255.html>

Long-Lived, slow to reproduce, and often hidden beneath the water's surface, whales and dolphins (cetaceans) have remained elusive subjects for scientific study even though they have fascinated humans for centuries. Until recently, much of what we knew about cetaceans came from commercial sources such as whalers and trainers for dolphin shows. Innovative research methods and persistent efforts, however, have begun to penetrate the depths to reveal tantalizing glimpses of the lives of these mammals in their natural habitats." "Cetacean Societies presents the first comprehensive synthesis and review of these new studies. Groups of chapters focus on the history of cetacean behavioral research and methodology; state-of-the-art reviews of information on four of the most-studied species: bottlenose dolphins, killer whales, sperm whales, and humpback whales; and summaries of major topics, including group living, male and female reproductive strategies, communication, and conservation, drawn from comparative research on a wide range of species. Appendixes cover cetacean phylogeny, evolution, and taxonomy." "Written by some of the world's leading cetacean scientists, this volume will benefit not just students of cetology but also researchers in other areas of behavioral and conservation ecology as well as anyone with a serious interest in the world of whales and dolphins.

Pitman, R. L., Ballance, L. T., Mesnick, S. I., & Chivers, S. J. (2001). Killer Whale Predation on Sperm Whales: Observations and Implications. *Marine Mammal Science*, 17(3), 494-507 <https://doi.org/10.1111/j.1748-7692.2001.tb01000.x>

In October 1997 we observed a herd of approximately 35 killer whales (*Orcinus orca*) attack a pod of nine sperm whales (*Physeter macrocephalus*) 130 km off the coast of central California. During the four hours we watched, adult female killer whales, including some with calves, attacked in waves of four to five animals in what was apparently a "wound and withdraw" strategy. Adult male killer whales stood by until the very end when one charged in and quickly killed a seriously wounded sperm whale that had

been separated from the group. The sperm whales appeared largely helpless: their main defensive behavior was the formation of a rosette ("marguerite"-heads together, tails out). When the killer whales were successful in pulling an individual out of the rosette, one or two sperm whales exposed themselves to increased attack by leaving the rosette, flanking the isolated individual, and leading it back into the formation. Despite these efforts, one sperm whale was killed and eaten and the rest were seriously, perhaps mortally, wounded. We also present details of two other encounters between sperm whales and killer whales that we observed. Although sperm whales, because of various behavioral and morphological adaptations, were previously thought to be immune to predation, our observations clearly establish their vulnerability to killer whales. We suggest that killer whale predation has potentially been an important, and underrated, selective factor in the evolution of sperm whale ecology, influencing perhaps the development of their complex social behavior and at-sea distribution patterns.

Rendell, L., & Whitehead, H. (2001). Culture in Whales and Dolphins. *BEHAVIORAL AND BRAIN SCIENCES*(24), 309–382 Retrieved from <http://primate.uchicago.edu/2001BBS.pdf>

Studies of animal culture have not normally included a consideration of cetaceans. However, with several long-term field studies now maturing, this situation should change. Animal culture is generally studied by either investigating transmission mechanisms experimentally, or observing patterns of behavioural variation in wild populations that cannot be explained by either genetic or environmental factors. Taking this second, ethnographic, approach, there is good evidence for cultural transmission in several cetacean species. However, only the bottlenose dolphin (*Tursiops*) has been shown experimentally to possess sophisticated social learning abilities, including vocal and motor imitation; other species have not been studied. There is observational evidence for imitation and teaching in killer whales. For cetaceans and other large, wide-ranging animals, excessive reliance on experimental data for evidence of culture is not productive; we favour the ethnographic approach. The complex and stable vocal and behavioural cultures of sympatric groups of killer whales (*Orcinus orca*) appear to have no parallel outside humans, and represent an independent evolution of cultural faculties. The wide movements of cetaceans, the greater variability of the marine environment over large temporal scales relative to that on land, and the stable matrilineal social groups of some species are potentially important factors in the evolution of cetacean culture. There have been suggestions of gene-culture coevolution in cetaceans, and culture may be implicated in some unusual behavioural and life-history traits of whales and dolphins. We hope to stimulate discussion and research on culture in these animals.

Janetzki, H. A., & Paterson, R. A. (2002). Aspects of Humpback Whale, *Megaptera novaeangliae*, Calf Mortality in Queensland. *Memoirs of the Queensland Museum.*, 47(2), 431-435 Retrieved from <https://www.biodiversitylibrary.org/part/249851>

The Queensland Museum has records of 19 humpback whale *Megaptera novaeangliae* calf mortalities. The cause of death in the majority was not determined. Three resulted from shark net drowning; two from shark attack and one from boat strike. Killer whale, *Orcinus orca*, attacks on calves are considered to be an uncommon cause of death in southern Queensland waters.

Nottestad, L., Fernoe, A., & Axelsen, B. I. (2002). Digging in the Deep: Killer Whales' Advanced Hunting Tactic. *Polar Biology*, 25(12), 939-941 <https://doi.org/10.1007/s00300-002-0437-0>

We document one of the most spectacular predator-prey interactions observed in a marine ecosystem, in which groups of killer whales force tens of tons of herring out of their safe deep-water habitat to the surface where the whales are superior. Killer whales performing this hunting tactic congregate in large groups, dive to the limit of their capacity, lift herring vertically more than 150 m by coordinated action, and split large aggregations of fish into small, dense schools before attacking them.

Heise, K., Barrett-Lennard, L. G., Saulitis, E., Matkin, C., & Bain, D. (2003). Examining the Evidence for Killer Whale Predation on Steller Sea Lions in British Columbia and Alaska. *Aquatic Mammals*, 29(3), 325-334 Retrieved from https://aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=237&catid=10&Itemid=157

The discovery of flipper tags from 14 Steller sea lions (*Eumetopias jubatus*) in the stomach of a dead killer whale (*Orcinus orca*) in 1992 focused attention on the possible role of killer whale predation in the decline of Steller sea lions in western Alaska. In this study, mariners in British Columbia and Alaska were surveyed to determine the frequency and outcome of observed attacks on sea lions, the age classes of sea lions taken, and the areas where predatory attacks occurred. The 126 survey respondents described 492 killer whale/sea lion interactions, of which at least 32 were fatal attacks on the sea lion. The greatest rate of observed predation occurred in the Aleutian Islands. The stomach contents of dead and stranded whales also were examined. Stomachs that were not empty contained only fish or marine mammal remains, but not both. This supports earlier evidence of dietary segregation between fish-eating resident and marine mammal-eating transient killer whales in Alaska. Steller sea lion remains were found in two of 12 killer whale stomachs examined from Alaska between 1990 and 2001. Stomach contents from two offshore killer whales provided the first direct evidence that this third form of killer whale feeds on fish.

Shelden, K. E. W., Rugh, D. J., Mahoney, B. A., & Dahlheim, M. E. (2003). Killer Whale Predation on Belugas in Cook Inlet, Alaska: Implications for a Depleted Population. *Marine Mammal Science*, 19(3), 529-544 <https://doi.org/10.1111/j.1748-7692.2003.tb01319.x>

Killer whale predation on belugas in Cook Inlet, Alaska, has become a concern since the decline of these belugas was documented during the 1990s. Accordingly, killer whale sightings were compiled from systematic surveys, observer databases, and anecdotal accounts. Killer whales have been relatively common in lower Cook Inlet (at least 100 sightings from 1975 to 2002), but in the upper Inlet, north of Kalgin Island, sightings were infrequent (18 in 27 yr), especially prior to the 1990s. Beach cast beluga carcasses with teeth marks and missing flesh also provided evidence of killer whale predation. Most observed killer whale/beluga interactions were in the upper Inlet. During 11 of 15 observed interactions, belugas were obviously injured or killed, either through direct attacks or indirectly as a result of stranding. Assuming at least one beluga mortality occurred during the other four encounters, we can account for 21 belugas killed between 1985 and 2002. This would suggest a minimum estimate of roughly 1/yr and does not include at least three instances where beluga calves accompanied an adult that was attacked.

Naessig, P., & Lanyon, J. (2004). Levels and Probable Origin of Predatory Scarring on Humpback Whales (*Megaptera novaeangliae*) in East Australian Waters. *CSIRO Wildlife Research*
<https://doi.org/10.1071/WR03086>

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

Williams, T. M., Estes, J. A., Doak, D. F., & Springer, A. M. (2004). Killer Appetites: Assessing the Role of Predators in Ecological Communities. *Ecology*, 85(12), 3373-3384 Retrieved from
www.jstor.org/stable/3450516

Large body size, carnivory, and endothermic costs lead to exceptionally high caloric demands in many mammalian predators. The potential impact on prey resources may be marked but is difficult to demonstrate because of the mobility, sparseness, and cryptic nature of these animals. In this study, we developed a method based on comparative bioenergetics and demographic modeling to evaluate predator effects and then used this approach to assess the potential impact of killer whales on sea otter and Steller sea lion populations in the Aleutian Islands. Daily caloric requirements of killer whales determined from allometric regressions for field metabolic rate show that an adult killer whale requires 51-59 kcal · kg⁻¹ · d⁻¹ (2.5-2.9 W/kg). Caloric values of prey items determined by bomb calorimetry ranged from 41 630 kcal for an adult female sea otter to sequentially higher values for male otters, sea lion pups, and adult Steller sea lions. Integrating these results with demographic changes in marine mammal populations show that fewer than 40 killer whales could have caused the recent Steller sea lion decline in the Aleutian archipelago; a pod of five individuals could account for the decline in sea otters and the continued suppression of sea lions. The collapse of the historical prey base of killer whales due to human whaling may have contributed to a sequential dietary switch from high to low caloric value prey, thereby initiating these declines. This study demonstrates that a combined physiological-demographic approach increases our ability to critically evaluate the potential impact of a predator on community structure and enables us to define underlying mechanisms that drive or constrain top-down forcing in dynamic ecosystems.

Harden, B. (2004). Have Gangs of Orcas Become the Serial Killers of the Ocean, Wiping out Sea Lions, Sea Otters, and Seals? If So, Some Scientists Blame Industrial Whaling for Eliminating the Orca's Favorite Dish. *DISCOVER* 25, 52-59. Retrieved from <https://www.discovermagazine.com/environment/killer-whales-cuisine>

No abstract

Santos, M. C. O., & F., N. D. (2005). Killer Whale (*Orcinus orca*) Predation on a Franciscana Dolphin (*Pontoporia blainvillei*) in Brazilian Waters. *Latin American Journal of Aquatic Mammals*, 4(1), 69 <https://doi.org/10.5597/lajam00072>

No abstract

Gaydos, J. K. B. R. W. (2005). Suspected Surplus Killing of Harbor Seal Pups (*Phoca vitulina*) by Killer Whales (*Orcinus orca*). *Northwestern Naturalist*, 86(3), 150-154 Retrieved from <https://www.jstor.org/stable/4095801>

No abstract

Ford, J. K. B., Ellis, G. A., Matkin, D. R., Balcomb, K. C., Briggs, D., & Morton, A. B. (2005). Killer Whale Attacks on Minke Whales: Prey Capture and Antipredator Tactics. *Marine Mammal Science*, 21(4), 603-618 <https://doi.org/10.1111/j.1748-7692.2005.tb01254.x>

We describe nine incidents of predation or attempted predation of minke whales (*Balaenoptera acutorostrata*) by mammal-hunting "transient" killer whales (*Orcinus orca*) in coastal waters of British Columbia, Washington, and southeastern Alaska. Pursuits of minke whales were characterized by prolonged chases on a straight heading at velocities of 15-30 km/h. In four of the nine cases the adult-sized minke whale gradually outdistanced the killer whales, which abandoned the high-speed pursuit after 0.5-1 h. In one case the minke beached itself and died. Four attacks were successful. In one instance a subadult minke was killed in open water following a chase. In two cases the fleeing minke entered a confined bay and was killed by the killer whales. One adult minke was taken after apparently attempting to seek cover beside a large sailboat. Minke whales made no attempt to physically defend themselves and were killed by repeated ramming or by asphyxiation. Although killer whales are capable of sprinting speeds greater than those of minke whales, it appears that adult minkes can maintain higher sustained speeds and evade capture if sufficient space for an extended escape trajectory is available. Successful predation of minke whales in coastal waters is rare compared to pinnipeds and small cetaceans, the main prey of transient killer whales.

Laidre, K. L., Heide-Jørgensen, M. P., & Orr, J. R. (2006). Reactions of Narwhals, *Monodon monoceros*, to Killer Whale, *Orcinus orca*, Attacks in the Eastern Canadian Arctic. *Canadian Field-Naturalist*, 120(4), 457-465 <https://doi.org/10.22621/cfn.v120i4.355>

A Killer Whale attack on Narwhals was observed at Kakiak Point in Admiralty Inlet, Nunavut, Canada, in August 2005. Behavioral responses of both Narwhals and Killer Whales were documented by direct

observation. Data collected from Narwhals instrumented with satellite-linked transmitters 5 days prior to the arrival of Killer Whales were used to examine changes in Narwhal movement patterns (e.g., dispersal and clumping) five days before the attack, during the attack, and five days after Killer Whales left the area. A minimum of four Narwhals were killed by 12-15 Killer Whales in a period of 6 hours. Narwhals showed a suite of behavioral changes in the immediate presence of Killer Whales including slow, quiet movements, travel close to the beach (<2 m from shore), use of very shallow water, and formation of tight groups at the surface. These behavioral changes are consistent with Inuit accounts of Killer Whale attacks on Narwhals. During the attack, Narwhals dispersed broadly, the groups were less clumped (standard deviation of inter-whale mean latitudes and longitudes), Narwhal space-use doubled from pre-attack home ranges of 347 km² to 767 km² (kernel 50% probability), and Narwhals shifted their distribution further south of the attack site. After the disappearance of Killer Whales, north-south dispersal of Narwhals contracted and was similar to pre-attack levels, total space use decreased slightly (599 km²), yet west-east dispersal remained high. Narwhals were distributed significantly ($P < 0.001$) more broadly offshore in areas not used before the occurrence of Killer Whales. In general, short-term reactions of Narwhals to Killer Whale presence were obvious; yet normal behavior (as observed from shore) resumed shortly after Killer Whales left the area. Long-term (five day) Narwhal behavioral responses included increased dispersal of Narwhal groups over large offshore areas. This is among the few reports of eyewitness Killer Whale attacks on Narwhals in the high Arctic and is the first time changes in Narwhal behavior have been documented in response to a predation event through the use of satellite telemetry.

Baird, R. W., McSweeney, D. J., Bane, C., Barlow, J., Salden, D. R., Antoine, L. K., . . . Webster, D. L. (2006). Killer Whales in Hawaiian Waters: Information on Population Identity and Feeding Habits. *Pacific Science*, 60(4), 523-530 <https://doi.org/10.1353/psc.2006.0024>

Killer whales (*Orcinus orca*) have only infrequently been reported from Hawaiian waters, and most of what is known about killer whales worldwide comes from studies in coastal temperate waters. Here we present 21 records of killer whales from within the Hawaiian Exclusive Economic Zone between 1994 and 2004. Killer whales were recorded nine months of the year, most around the main Hawaiian Islands. Although there were more records than expected during the period when humpback whales are abundant around the Islands, there is likely an increase in sighting effort during that period. Killer whales were documented feeding on both a humpback whale and cephalopods, and two species of small cetaceans were observed fleeing from killer whales. Although it is possible that there are both marine mammal-eating and cephalopod-eating populations within Hawaiian waters, it seems more likely that Hawaiian killer whales may not exhibit foraging specializations as documented for coastal temperate populations. Saddle patch pigmentation patterns were generally fainter and narrower than those seen in killer whales from the temperate coastal North Pacific. Analysis of skin samples from two animals indicated two mitochondrial haplotypes, one identical to the "Gulf of Alaska transient 2" haplotype (a mammal-eating form), and the other a new haplotype one base different from haplotypes found for mammal-eating killer whales in coastal Alaskan waters.

Barrett-Lennard, L. G., & Heise, K. A. (2006). The Natural History and Ecology of Killer Whales. In *Whales, Whaling, and Ocean Ecosystems*. J. A. Estes, D. P. Demaster, D. F. Doak, T. M. Williams, & R. L. Brownell (Eds.), (1 ed., pp. 163-173): University of California Press Retrieved from <http://www.jstor.org/stable/10.1525/j.ctt1ppsvh.18>

In his landmark book on marine mammals of the northeastern Pacific, whaling captain Charles Scammon remarked that killer whales "may be regarded as marine beasts, that roam over every ocean; entering bays and lagoons where they spread terror and death among mammoth balaenas and the smaller species of dolphins, as well as pursuing the seal and walrus, devouring, in their marauding expeditions up swift rivers, numberless salmon or other large fishes that may come in their way" (Scammon 1874:). Scammon's observations reflect the tendency, until very recent times, of most observers to describe killer whales—and other predators—from the

Branch, T., & Williams, T. (2006). *Legacy of Industrial Whaling: Could Killer Whales Be Responsible for Declines of Sea Lions, Elephant Seals, and Minke Whales in the Southern Hemisphere?*
<https://doi.org/10.1525/9780520933200-024>

Springer et al. (2003) hypothesized that the reduction of great whale biomass after industrial whaling resulted in killer whale dietary shifts, which in turn caused the sequential collapse of harbor seal, northern fur seal, Steller sea lion, and sea otter populations in southwest Alaska. We examined the applicability of this hypothesis to the Southern Hemisphere, where industrial whaling also decimated populations of great whales in the 20th century. Subsequent declines in southern sea lions and elephant seals, and possible declines in Antarctic minke whales, contrast starkly with rapid increases in populations of other marine mammals. These three species are often preyed on by killer whales, unlike the species that are increasing. Simple dietary models suggest that declines in southern sea lion and elephant seal populations are consistent with increased killer whale predation, but that the magnitude of the possible decline in Antarctic minke whales may be too great to be explained solely by predation. In view of these patterns, the predation hypothesis should not be casually dismissed for Southern Hemisphere marine mammal populations, even though supporting evidence remains largely circumstantial.

Mizroch, S. A., & Rice, D. W. (2006). Have North Pacific Killer Whales Switched Prey Species in Response to Depletion of the Great Whale Populations? *Marine Ecology Progress Series*, 310, 235-246
<https://doi.org/10.3354/meps310235>

Springer et al. (2003; Proc Natl Acad Sci USA 100:12223-12228) hypothesized that populations of seals, sea lions and sea otters in the northern North Pacific Ocean and Bering Sea declined because of increased predation by killer whales, in what they termed a 'sequential megafaunal collapse'. They hypothesized that the killer whales had been dependent on large whales for food, and that their increased predation on the smaller marine mammals was directly due to the depletion of great whale populations as a result of post-World War II industrial whaling. The maps presented by Springer et al. (2003) masked the development and precipitous decline of post-World War II industrial whaling. Our analysis shows that north of 50 degrees N, whaling developed slowly from 1948 to 1951, expanded steadily from 1952 to 1962, and increased very sharply from 1963 to 1967. By 1968, there was near total drop-off in catches north of 50 degrees N as the whaling fleets moved south. Because of the extraordinary whale biomass removals in the mid-1960s, any whaling-related prey shifting should have started by 1968, not the mid-1970s as they suggested. We also present data that refute their assumption that North Pacific killer whales depended on large whales as prey either prior to or concurrent with the whaling era. During the years of the development and pulse of whaling (i.e. prior to 1968), less than 3 % of the mammal-eating killer whales were observed to have large whale remains in their stomachs. Killer whales attack healthy, adult large whales only rarely, and such attacks are usually

unsuccessful. Neither minke nor gray whales were depleted by post-World War II industrial whaling, and they have always been available as prey for North Pacific killer whales.

Randall R. Reeves, Joel Berger, & Clapham, P. L. J. (2006). Killer Whales as Predators of Large Baleen Whales and Sperm Whales. In *Whales, Whaling, and Ocean Ecosystems*. J. A. Estes, D. P. DeMaster, D. F. Doak, T. M. Williams, & R. L. Brownell (Eds.), (pp. 174-187): University of California Press Retrieved from <https://www.ucpress.edu/ebook/9780520933200/whales-whaling-and-ocean-ecosystems#table-of-contents>

No abstract

Maniscalco, J. M., Matkin, C. O., Maldini, D., Calkins, D. G., & Atkinson, S. (2007). Assessing Killer Whale Predation on Steller Sea Lions from Field Observations in Kenai Fjords, Alaska. *Marine Mammal Science*, 23(2), 306-321 <https://doi.org/10.1111/j.1748-7692.2007.00103.x>

The behavioral and predatory patterns of Gulf of Alaska (GOA) transient killer whales (*Orcinus orca*) were studied between 2000 and 2005 using remote video and vessel-based observations near the Chiswell Island Steller sea lion (*Eumetopias jubatus*) rookery and in the broader Kenai Fjords (KF) region of the northern GOA. GOA transient killer whales were observed on 118 d over the 6-yr period; the median group size was two (range: 1-9). Nine predation events were observed from vessels and an additional sixteen were inferred from remote video studies; all involved Steller sea lions. Estimates from field observations suggest that fifty-nine sea lions were consumed over the summer seasons of 2002-2005; whereas estimates based on published caloric requirements of transient killer whales would suggest a loss of 103 sea lions over the same time period. GOA transients spent a large proportion (43%) of their time resting which may be a strategy for conserving energy. Predation on sea lion pups at the Chiswell Island rookery was greatest during years when a single killer whale was foraging alone and when a 1.5-yr-old calf was evidently being trained to handle prey. Predation on pups was low during years when killer whales were foraging in groups and were observed and presumed to be taking mostly juvenile sea lions. Our study suggests that GOA transients are having a minor effect on the recovery of Steller sea lions in the GOA.

Matkin, C. O., Barrett-Lennard, L. G., Yurk, H., Ellifrit, D., & Trites, A. W. (2007). Ecotypic Variation and Predatory Behavior among Killer Whales (*Orcinus orca*) Off the Eastern Aleutian Islands, Alaska. *Fishery Bulletin*, 105(1), 74-87 Retrieved from <https://spo.nmfs.noaa.gov/content/ecotypic-variation-and-predatory-behavior-among-killer-whales-orcinus-orca-eastern-aleutian>

From 2001 to 2004 in the eastern Aleutian Islands, Alaska, killer whales (*Orcinus orca*) were encountered 250 times during 421 days of surveys that covered a total of 22,491 miles. Three killer whale groups (resident, transient, and offshore) were identified acoustically and genetically. Resident killer whales were found 12 times more frequently than transient killer whales, and offshore killer whales were encountered only once. A minimum of 901 photographically identified resident whales used the region during our study. A total of 165 mammal-eating transient killer whales were identified, and the majority (70%) were encountered during spring (May and June). The diet of transient killer whales in spring was primarily gray whales (*Eschrichtius robustus*), and in summer primarily northern fur seals (*Callorhinus ursinus*). Steller sea lions (*Eumetopias jubatus*) did not appear to be a preferred prey or major prey item

during spring and summer. The majority of killer whales in the eastern Aleutian Islands are the resident ecotype, which does not consume marine mammals.

Matkin, D. R., Straley, J. M., & Gabriele, C. M. (2007, October 26–28, 2004). *Killer Whale Feeding Ecology and Non-Predatory Interactions with Other Marine Mammals in the Glacier Bay Region of Alaska*.

Populations of killer whales in southeastern Alaska overlap with populations inhabiting Prince William Sound, Alaska and British Columbia, Canada. We synthesize the results of a 20-year study in Glacier Bay and Icy Strait, Alaska. Individuals were photo-identified and predation events documented. Foraging strategies of killer whales were compared to those documented in similar studies in adjacent areas. One hundred twenty of the resident form of killer whales, 150 of the West Coast transients, 13 of the Gulf of Alaska transients and 14 of the offshore form were photo-identified in the study area. Residents preyed primarily on silver salmon and Pacific halibut. The prey of transients were harbor seals (40 percent), harbor porpoise (23 percent), Steller sea lions (16 percent), seabirds (14 percent), Dall's porpoise (5 percent) and minke whale (2 percent). Humpback whales were observed closely approaching transient groups that were attacking other marine mammals. Nonpredatory interactions also occurred between killer whales and Steller sea lions.

Pitman, R. L., Fearnbach, H., LeDuc, R., Gilpatrick, J. W., Jr., Ford, J. K. B., & Ballance, L. T. (2007). Killer Whales Preying on a Blue Whale Calf on the Costa Rica Dome: Genetics, Morphometrics, Vocalisations and Composition of the Group. *Journal of Cetacean Research and Management*, 9(2), 151-157 Retrieved from <https://archive.iwc.int/?r=264>

Killer whale (*Orcinus orca*) populations in high latitude, nearshore areas appear to regularly exhibit prey specialisation among two or more sympatric ecotypes, but nearly nothing is known about populations that inhabit open ocean areas or tropical latitudes. On 26 September 2003, during a cetacean survey in the eastern tropical Pacific Ocean, a group of an estimated 19 killer whales was encountered feeding on a calf of a blue whale (*Balaenoptera musculus*); the location was 10 degree 58'N, 88 degree 40'W, 230km west of Nicaragua. The whales were studied for 2.5 hours and during this time skin biopsy samples were collected, acoustic recordings made, aerial and lateral photographs taken and behavioural observations recorded. The 19 individuals identified included 4 males (3 adults, 1 subadult), 5 cow-calf pairs and 5 other females/subadult males. Using aerial photogrammetry, body lengths of 17 different animals were measured: the largest male (who carried the carcass most of the time) was 8.0m long; and the largest female (with a calf) was 6.1m. From 10 biopsy samples, two distinct haplotypes were identified that differed from resident (i.e. fish-eating ecotype) killer whales in the northeastern Pacific by one and two base pairs, respectively. The single discrete call recorded was a typical killer whale call but it had a two-part pitch contour that was structurally distinct from calls recorded to date in the North Pacific. These observations reaffirm that calves of even the largest whale species are vulnerable to predation, although by migrating to calving areas in the tropics, where killer whale densities are lower, baleen whales should be able to increase their overall reproductive fitness, as suggested by Corkeron and Connor (1999).

Newman, K., & Springer, A. M. (2008). Nocturnal Activity by Mammal-Eating Killer Whales at a Predation Hot Spot in the Bering Sea. *Marine Mammal Science*, 24(4), 990-999
<https://doi.org/10.1111/j.1748-7692.2008.00236.x>

No abstract

Ford, J. K. B., & Reeves, R. R. (2008). Fight or Flight: Antipredator Strategies of Baleen Whales. *Mammal Review*, 38(1), 50-86 <https://doi.org/10.1111/j.1365-2907.2008.00118.x>

1. The significance of killer whale *Orcinus orca* predation on baleen whales (Mysticeti) has been a topic of considerable discussion and debate in recent years. Discourse has been constrained by poor understanding of predator-prey dynamics, including the relative vulnerability of different mysticete species and age classes to killer whales and how these prey animals avoid predation. Here we provide an overview and analysis of predatory interactions between killer whales and mysticetes, with an emphasis on patterns of antipredator responses. 2. Responses of baleen whales to predatory advances and attacks by killer whales appear to fall into two distinct categories, which we term the fight and flight strategies. The fight strategy consists of active physical defence, including self-defence by single individuals, defence of calves by their mothers and coordinated defence by groups of whales. It is documented for five mysticetes: southern right whale *Eubalaena australis*, North Atlantic right whale *Eubalaena glacialis*, bowhead whale *Balaena mysticetus*, humpback whale *Megaptera novaeangliae* and grey whale *Eschrichtius robustus*. The flight strategy consists of rapid (20-40 km/h) directional swimming away from killer whales and, if overtaken and attacked, individuals do little to defend themselves. This strategy is documented for six species in the genus *Balaenoptera*. 3. Many aspects of the life history, behaviour and morphology of mysticetes are consistent with their antipredator strategy, and we propose that evolution of these traits has been shaped by selection for reduced predation. Fight species tend to have robust body shapes and are slow but relatively manoeuvrable swimmers. They often calve or migrate in coastal areas where proximity to shallow water provides refuge and an advantage in defence. Most fight species have either callosities (rough and hardened patches of skin) or encrustations of barnacles on their bodies, which may serve (either primarily or secondarily) as weapons or armour for defence. Flight species have streamlined body shapes for high-speed swimming and they can sustain speeds necessary to outrun pursuing killer whales (> 15-20 km/h). These species tend to favour pelagic habitats and calving grounds where prolonged escape sprints from killer whales are possible. 4. The rarity of observed successful attacks by killer whales on baleen whales, especially adults, may be an indication of the effectiveness of these antipredator strategies. Baleen whales likely offer low profitability to killer whales, relative to some other marine mammal prey. High-speed pursuit of flight species has a high energetic cost and a low probability of success while attacks on fight species can involve prolonged handling times and a risk of serious injury.

Visser, I. N., Smith, T. G., Bullock, I. D., Green, G. D., Carlsson, O. G. L., & Imberti, S. (2008). Antarctic Peninsula Killer Whales (*Orcinus orca*) Hunt Seals and a Penguin on Floating Ice. *Marine Mammal Science*, 24(1), 225-234 <https://doi.org/10.1111/j.1748-7692.2007.00163.x>

No abstract

Weller, D. W. (2009). Predation on Marine Mammals. In *Encyclopedia of Marine Mammals (Second Edition)*. W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), (pp. 923-932). London: Academic Press <https://doi.org/10.1016/B978-0-12-373553-9.00210-8>

Publisher Summary This chapter discusses the hunting and consumption of marine mammals by their predators. Specifically this chapter focuses predation on sirenians, mustelids, pinnipeds, and cetaceans. The relatively slow moving and rather lethargic behavior of sirenians makes them seem particularly vulnerable to predation. However, manatees and dugongs actually have few known natural predators and appear to experience only occasional mortality due to predation. Although large sharks, crocodiles (*Crocodylus* spp.), and killer whales (*Orcinus orca*) are all considered to be potential predators, few records exist to confirm these suspicions. Of all the marine mammal groups, pinnipeds are probably subjected to the highest level of predation. While some pinniped species experience little or no predation pressure, others are so intensively hunted that important aspects of their natural history, including reproductive strategies, have evolved in response. Several pinniped species are recognized as predators of other pinnipeds, and in some locations are responsible for a significant portion of the annual mortality incurred by regional populations. The most ferocious pinniped predators include the leopard seal in the Southern Hemisphere and the walrus in the Northern Hemisphere.

Miller, P. J. O. M., Shapiro, A. D., & Deecke, V. B. (2010). The Diving Behaviour of Mammal-Eating Killer Whales (*Orcinus orca*): Variations with Ecological Not Physiological Factors. *Canadian Journal of Zoology*, 88(11), 1103-1112 <https://doi.org/10.1139/z10-080>

Mammal-eating killer whales (*Orcinus orca* (L., 1758)) are a rare example of social predators that hunt together in groups of sexually dimorphic adults and juveniles with diverse physiological diving capacities. Day–night ecological differences should also affect diving as their prey show diel variation in activity and mammal-eating killer whales do not rely on echolocation for prey detection. Our objective was to explore the extent to which physiological aerobic capacities versus ecological factors shape the diving behaviour of this breath-hold diver. We used suction-cup-attached depth recorders (Dtags) to record 7608 dives of 11 animals in southeast Alaska. Analysis of dive sequences revealed a strong bout structure in both dive depth and duration. Day–night comparisons revealed reduced rates of deep dives, longer shallow dives, and shallower long-duration dives at night. In contrast, dive variables did not differ by age–sex class. Estimates of the aerobic dive limit (cADL) suggest that juveniles exceeded their cADL during as much as 15% of long dives, whereas adult males and females never exceeded their cADL. Mammal-eating killer whales in this area appear to employ a strategy of physiological compromise, with smaller group members diving nearer their physiological limits and large-bodied males scaling down their physiological performance.

Srinivasan, M., Grant, W. E., Swannack, T. M., & Rajan, J. (2010). Behavioral Games Involving a Clever Prey Avoiding a Clever Predator: An Individual-Based Model of Dusky Dolphins and Killer Whales. *Ecological Modelling*, 221(22), 2687-2698 <https://doi.org/10.1016/j.ecolmodel.2010.07.010>

Faced with an intermittent but potent threat, animals exhibit behavior that allows them to balance foraging needs and avoid predators and over time, these behaviors can become hard-wired adaptations with both species trying to maximize their own fitness. In systems where both predator and prey share similar sensory modalities and cognitive abilities, such as with marine mammals, the dynamic nature of

predator-prey interactions is poorly understood. The costs and benefits of these anti-predator adaptations need to be evaluated and quantified based on the dynamic engagement of predator and prey. Many theoretic models have addressed the complexity of predator-prey relationships, but few have translated into testable mechanistic models. In this study, we developed a spatially-explicit, geo-referenced, individual-based model of a prototypical adult dusky dolphin off Kaikoura, New Zealand facing a more powerful, yet infrequent predator, the killer whale. We were interested in two primary objectives, (1) to capture the varying behavioral game between a clever prey and clever predator based on our current understanding of the Kaikoura system, (2) to compare evolutionary costs vs. benefits (foraging time and number of predator encounters) for an adult non-maternal dusky dolphin at various levels of killer whale-avoidance behaviors and no avoidance rules. We conducted Monte Carlo simulations to address model performance and parametric uncertainty. Mantel tests revealed an 88% correlation (426 x 426 distance matrix, km²) between observed field sightings of dusky dolphins with model generated sightings for non-maternal adult dusky dolphin groups. Simulation results indicated that dusky dolphins incur a 2.7% loss in feeding time by evolving the anti-predator behavior of moving to and from the feeding grounds. Further, each evolutionary strategy we explored resulted in dolphins incurring an additional loss of foraging time. At low killer whale densities (appearing less than once every 3 days), each evolutionary strategy simulated converged towards the evolutionary cost of foraging, that is, the loss in foraging time approached the 2.7% loss experienced by evolving near shore-offshore movement behavior. However, the highest level of killer whale presence resulted in 38% decreases in foraging time. The biological significance of these losses potentially incurred by a dusky dolphin is dependent on various factors from dolphin group foraging behavior and individual energy needs to dolphin prey availability and behavior. (C) 2010 Elsevier B.V. All rights reserved.

Visser, I. N., Zaeschmar, J., Halliday, J., Abraham, A., Ball, P., Bradley, R., . . . Pace, D. S. (2010). First Record of Predation on False Killer Whales (*Pseudorca Crassidens*) by Killer Whales (*Orcinus orca*). *Aquatic Mammals*, 36(2), 195-204 <https://doi.org/10.1578/am.36.2.2010.195>

The first record of killer whale (*Orcinus orca*) predation on false killer whales (*Pseudorca crassidens*) is reported here. On 25 March 2010, a group of 50 to 60 false killer whales, including approximately 15 calves and accompanied by three to five bottlenose dolphins (*Tursiops* sp.), were sighted in the Bay of Islands, New Zealand. Within 30 min, they were approached by a group of approximately eight killer whales. Five false killer whales were attacked, with at least three rammed from below, forcing them out of the water. After 29 min, the killer whales were milling at the surface and feeding on the carcass of a false killer whale calf, possibly the only individual killed. The killer whales had prolific fresh and healed oval wounds, which were attributed to cookie cutter shark (*Isistius* sp.) bites.

Best, P. B., Meyer, M. A., & Lockyer, C. (2010). Killer Whales in South African Waters - a Review of Their Biology. *African Journal of Marine Science*, 32(2), 171-186 <https://doi.org/10.2989/1814232x.2010.501544>

The distribution, seasonality and schooling behaviour of killer whales *Orcinus orca* in South African waters have been investigated from 785 records compiled between 1963 and 2009, and their size, morphometrics, growth, reproduction, food and feeding behaviour described from the examination of 54 individuals, 36 of which were landed at the Durban whaling station between 1971 and 1975. Qualitatively, the species appears to be more frequently encountered offshore, where it forms small schools of generally less than six animals. Seasonality of occurrence is not marked, although

circumstantial evidence indicates that some individuals migrate from higher latitudes. Males reach 8.81 m and females 7.9 m, with 16.2% of males exceeding the size of the largest female. Stomach content and observational data suggest that the species can be characterised locally as an opportunistic predator of megavertebrates, rather than as the fish-feeding ecotype previously described. A stranded adult male with extreme tooth wear that was 1.5-2 m shorter than other males of equivalent age may be representative of a separate 'offshore' ecotype. Apparent differences between features of the population's life history and those of resident killer whales in the north-eastern Pacific might be attributed to either uncertainties in age determination using dentinal growth layer groups or sampling bias. The basis for the suggestion that killer whales in South African waters should be reclassified as Vulnerable (rather than Data Deficient) is challenged.

Dahlheim, M. E., & White, P. A. (2010). Ecological Aspects of Transient Killer Whales *Orcinus orca* as Predators in Southeastern Alaska. *Wildlife Biology*, 16(3), 308-322 <https://doi.org/10.2981/09-075>

In this study we present empirical data on predator numbers, movements and area usage, and predation obtained from tracking transient killer whales *Orcinus orca* throughout the inland waters of southeastern Alaska, USA. During 1991-2007, we documented 155 transient killer whales via photo-identification methodology within the large study area (27,808 km²). Transient killer whales were distributed throughout southeastern Alaska and were present during all seasons, although not all individuals were seen every year. Resighting data suggested that within southeastern Alaska, maternal groups may partition area usage of their environment. By following whales for 1,467 km, we calculated a mean travel speed of 7.2 km/hour with mean daily movements of 134 km plus or minus 88 km/24 hours and ranging within 59-240 km/24 hours. Photographic matches demonstrated that most of the transient killer whales (86%) identified in southeastern Alaska also utilized British Columbia and Washington State waters. In contrast, photographic matches between whales in southeastern Alaska and whales seen off of California, USA, were rare, suggesting that different transient killer whale stocks occupy these two regions. Transient killer whales preyed upon Dall's porpoise *Phocoenoides dalli*, Pacific white-sided dolphins *Lagenorhynchus obliquidens*, harbor porpoise *Phocoena phocoena*, minke whales *Balaenoptera acutorostrata*, Steller sea lions *Eumetopias jubatus*, harbor seals *Phoca vitulina* and seabirds. Potential prey species that were available, but not targeted, included humpback whales *Megaptera novaeangliae*, elephant seals *Mirounga angustirostris* and sea otters *Enhydra lutris*. Prey-handling techniques varied depending on the prey being targeted with no evidence of prey specialization. During 114 encounters totaling 332.5 hours of direct observations of transient killer whales, we documented 36 predation events for a calculated kill rate of 0.62 prey items/24-hour period/whale. The data we present in this article provide a foundation of transient killer whale ecology aimed at improving our ability to understand the impact of transient killer whale predation on southeastern Alaska prey populations.

Beck, S., Kuningas, S., Esteban, R., & Foote, A. D. (2011). The Influence of Ecology on Sociality in the Killer Whale (*Orcinus orca*). *Behavioral Ecology*, 23(2), 246-253 <https://doi.org/10.1093/beheco/arr151>

The persistence and size of social groups can be plastic and governed by ecological selection or be under greater genetic control and constrained by phylogenetic inertia. Comparing sociality of phylogenetically divergent populations under the same ecological conditions or between groups within a population under different ecological conditions can identify the relative influence of ecological selection on group

formation. Here, we compare the size and persistence of social groups within a community of Atlantic killer whales, comparing between data collected from an area around Scotland where the whales have mainly been seen to hunt seals and data collected from an area around Iceland where the whales have mainly been seen to hunt herring. Additionally, we compare the observed social structure with that of previously studied Pacific ecotypes. Atlantic killer whale groups in both locations had a stable long-term primary social tier (association index level > 0.8) similar to that of Pacific killer whales. However, associations between these groups were much lower when hunting for seals than for fish in both the Atlantic and the Pacific. The occurrence of these differences in sociality between Atlantic groups, which are linked in a single social network, suggests that ecological selection partially determines sociality in this species. Furthermore, if sociality was constrained by phylogenetic inertia, then the Atlantic killer whales would all be expected to be more similar to the Pacific fish-eating ecotype than the more phylogenetically distant Pacific mammal-eating ecotype. Our study suggests that sociality in killer whales is to some extent plastic and can be adapted to the local ecological conditions.

Guinet, C. (2011). Intentional Stranding Apprenticeship and Social Play in Killer Whales (*Orcinus orca*). *Canadian Journal of Zoology*, 69, 2712-2716 <https://doi.org/10.1139/z91-383>

Over three hunting seasons, killer whales (*Orcinus orca*) from two pods were observed stranding intentionally on the beaches of Possession Island, Crozet Archipelago. Intentional stranding was performed principally by adult females to catch elephant seals on shore and during social play. Within a pod significant differences existed in the number of intentional strandings performed by individual females during hunting and also during "social beaching play." During intentional stranding, calves were associated with an adult female. Two calves were systematically associated with their mother, but one calf was associated significantly more with the two other pod females. This calf's mother stranded intentionally significantly less than the two other females. This suggests that alloparental "teaching" may occur within a pod according to the specific skills of the pod members.

Reisinger, R. R. (2011). *Abundance and Predatory Impact of Killer Whales at Marion Island*. University of Pretoria, Retrieved from <https://www.repository.up.ac.za/bitstream/handle/2263/27643/dissertation.pdf?isAllowed=y&sequence=1>

Killer whales are the oceans' apex predator and are known to have important effects on ecosystems. At Subantarctic Marion Island, southern Indian Ocean, they have only been studied opportunistically, resulting in limited knowledge of their ecosystem impact here. This dissertation describes the prey and seasonal abundance, estimates the population size and assesses the predatory impact of killer whales on seals and penguins at Marion Island, using dedicated and opportunistic shore-based observations and photographic identification, from 2006 to 2009. During 823 sightings of killer whales at Marion Island (2006 to 2009) 48 predation events were recorded; in only 10 cases could prey be identified. Killer whales fed on fur seals, elephant seals and penguins. Constant effort (dedicated) observations (259 hours, 2008 to 2009) showed that killer whale abundance, which peaked in September to December with a secondary peak in April to May, is linked to the abundance of seals and penguins. Mark-recapture analyses were performed using nearly 10 000 photographs taken from 2006 to 2009. Following careful quality control criteria 37 individuals were identified and a population size of 42 (95% CI = 35-50) individuals estimated using the open population POPAN parameterization in the software program MARK. The analytical approach is more rigorous than that used in any previous population size

assessment at Marion Island. Finally, the above data were integrated to assess whether top-down control of seal and penguin populations at Marion Island is generally plausible using a simple process of elimination. Based on published data I predicted the energetic ingestion requirements of adult male and female killer whales as 1 394 MJ.day⁻¹ and 1 028 MJ.day⁻¹, respectively. Expanding these requirements to the 37 killer whales photographically identified at Marion Island, the population requires 40 600MJ.day⁻¹. Based on available energy density and mass data, I predicted the energy content of available seal and penguin prey and calculated the rates at which killer whales would consume these prey in various scenarios. Penguins and Subantarctic fur seals are relatively insensitive to killer whale predation owing to their large population sizes (10 000s to 100 000s), conversely, the smaller populations (100s to 1 000s) of Antarctic fur seals and southern elephant seals are sensitive to predation, particularly the latter as they have a high energy content (approximately 2 000 to 9 000 MJ). Populations of these seals are currently increasing or stable and I conclude that presently killer whale predation is not driving population declines, although they clearly have the potential for regulation of these smaller populations. Thus, if population sizes were reduced by bottom-up processes, if killer whale diet shifted, or if prey availability changed, top-down control by killer whales could become significant. This study provides baseline information for the informed management and conservation of killer whales at Marion Island, identifies avenues for further research, and provides a foundation for the continuation of structured and dedicated killer whale research at Marion Island.

Barrett-Lennard, L. G., Matkin, C. O., Durban, J. W., Saulitis, E. L., & Ellifrit, D. (2011). Predation on Gray Whales and Prolonged Feeding on Submerged Carcasses by Transient Killer Whales at Unimak Island, Alaska. *Marine Ecology Progress Series*, 421, 229-241 <https://doi.org/10.3354/meps08906>

As apex predators, killer whales *Orcinus orca* are expected to strongly influence the structure of marine communities by impacting the abundance, distribution, behavior, and evolution of their prey. Empirical assessments of these impacts are difficult, however, because killer whales are sparsely distributed, highly mobile, and difficult to observe. We present a 4 yr time series of observations of foraging and feeding behavior of >150 transient killer whales that aggregate annually during the northbound migration of gray whales past Unimak Island, Alaska. Most predatory attacks were on gray whale *Eschrichtius robustus* calves or yearlings and were quickly abandoned if calves were aggressively defended by their mothers. Attacks were conducted by groups of 3 to 4 killer whales, which attempted to drown their prey. Gray whales generally tried to move into shallow water along the shoreline when attacked; if they succeeded in reaching depths of 3 m or less, attacks were abandoned. Kills occurred in waters from 15 to 75 m deep or were moved into such areas after death. After some hours of feeding, the carcasses were usually left, but were re-visited and fed on by killer whales over several days. Carcasses or pieces of prey that floated onshore were actively consumed by brown bears *Ursus arctos*, and carcasses on the bottom were fed on by sleeper sharks *Somniosus pacificus*, apparently increasing the local density of both species.

Ferguson, S. H., Kingsley, M. C., & Higdon, J. W. (2012). Killer Whale (*Orcinus orca*) Predation in a Multi-Prey System. *Population Ecology*, 54(1), 31-41 <https://doi.org/10.1007/s10144-011-0284-3>

Predation can regulate prey numbers but predator behaviour in multiple-prey systems can complicate understanding of control mechanisms. We investigate killer whale (*Orcinus orca*) predation in an ocean system where multiple marine mammal prey coexist. Using stochastic models with Monte-Carlo

simulations, we test the most likely outcome of predator selection and compare scenarios where killer whales: (1) focus predation on larger prey which presumably offer more energy per effort, (2) generalize by feeding on prey as encountered during searches, or (3) follow a mixed foraging strategy based on a combination of encounter rate and prey size selection. We test alternative relationships within the Hudson Bay geographic region, where evidence suggests killer whales seasonally concentrate feeding activities on the large-bodied bowhead whale (*Balaena mysticetus*). However, model results indicate that killer whales do not show strong prey specialization and instead alternatively feed on narwhal (*Monodon monoceros*) and beluga (*Delphinapterus leucas*) whales early and late in the ice-free season. Evidence does support the conjecture that during the peak of the open water season, killer whale predation can differ regionally and feeding techniques can focus on bowhead whale prey. The mixed foraging strategy used by killer whales includes seasonal predator specialization and has management and conservation significance since killer whale predation may not be constrained by a regulatory functional response.

Ferguson, S. H., Higdon, J. W., & Westdal, K. H. (2012). Prey Items and Predation Behavior of Killer Whales (*Orcinus orca*) in Nunavut, Canada Based on Inuit Hunter Interviews. *Aquatic Biosystems*, 8(1), 3 <https://doi.org/10.1186/2046-9063-8-3>

Killer whales (*Orcinus orca*) are the most widely distributed cetacean, occurring in all oceans worldwide, and within ocean regions different ecotypes are defined based on prey preferences. Prey items are largely unknown in the eastern Canadian Arctic and therefore we conducted a survey of Inuit Traditional Ecological Knowledge (TEK) to provide information on the feeding ecology of killer whales. We compiled Inuit observations on killer whales and their prey items via 105 semi-directed interviews conducted in 11 eastern Nunavut communities (Kivalliq and Qikiqtaaluk regions) from 2007-2010.

Grandi, M. F., Loizaga de Castro, R., & Crespo, E. A. (2012). Killer Whales Attack on South American Sea Lion Associated with a Fishing Vessel: Predator and Prey Tactics. *Latin American Journal of Aquatic Research*, 40, 1072-1076 <https://doi.org/103856/vol40-issue4-fulltext-22>

Interactions between killer whales and sea lions are widely known. This work describes the predator-prey behaviour of killer whales and South American sea lion associated with a trawling fishery. In Argentina the predatory behaviours of killer whales and anti-predatory behaviours of South American sea lions have been described from coastal based observations, but predator-prey behaviour of these species is poorly known at open waters. Here we describe a killer whale group attack on an individual sea lion, using a video recorded from a trawling vessel and an interview of the ship captain. This predator-prey behaviour represents an example of the complexity of interactions between marine mammals and fisheries along the Patagonian coast.

Kryukova, N. V., Kruchenkova, E. P., & Ivanov, D. I. (2012). Killer Whales (*Orcinus orca*) Hunting for Walruses (*Odobenus rosmarus Divergens*) near Retkyn Spit, Chukotka. *Biology Bulletin*, 39(9), 768-778 <https://doi.org/10.1134/s106235901209004x>

Group hunting by killer whales for walruses was observed in August 18, 2008, in the littoral area (3 km from the haulout of walruses, Retkyn Spit, Chukotka). The group of killer whales consisted of seven adults (one adult male did not participate in attacks) and two calves. Based on prey type, these killer

whales were mammal-eating. The total duration of their hunt activity was not less than 95 min. The hunt consisted of three phases. The first phase was an attack on the group of walruses and choice of individual prey; the second phase was attacks on the chosen walrus; and the third (final) phase was a decrease in activity of killer whales and leaving group with walrus from sea shore. The main behavioral patterns of killer whales during the hunt were discerned. Two killer whales tried to kill walruses by chasing them and jumping out of the water on the shore. The video analysis of the "attack phase" showed that killer whales made 55 attacks on the walrus during 17.3 min. On average, each killer whale attacked the walrus seven times. The attack tactics of killer whales, the number of movements, and the location of killer whales (adults and calves) relative to each other and to the walrus were described. Well coordination of their movements and group actions was observed.

Pistorius, P. A., Meÿer, M. A., Reisinger, R. R., & Kirkman, S. P. (2012). Killer Whale Predation on Subantarctic Fur Seals at Prince Edward Island, Southern Indian Ocean. *Polar Biology*, 35(11), 1767-1772 <https://doi.org/10.1007/s00300-012-1216-1>

Killer whales at subantarctic Marion Island have been subjected to several scientific studies. In contrast, up until recently, there has been only one record of these animals documented for neighbouring Prince Edward Island. We here report on killer whale observations at Prince Edward Island during March 2012. During 3 days of opportunistic observations at a fur seal colony on the island, killer whales were sighted on six occasions. These probably represented three different pods numbering 11 individuals in total. During all sightings, individuals were seen hunting subantarctic fur seal pups, with four successful predatory events observed.

Pitman, R. L., & Durban, J. W. (2012). Cooperative Hunting Behavior, Prey Selectivity and Prey Handling by Pack Ice Killer Whales (*Orcinus orca*), Type B, in Antarctic Peninsula Waters. *Marine Mammal Science*, 28(1), 16-36 <https://doi.org/10.1111/j.1748-7692.2010.00453.x>

Currently, there are three recognized ecotypes (or species) of killer whales (*Orcinus orca*) in Antarctic waters, including type B, a putative prey specialist on seals, which we refer to as pack ice killer whale (PI killer whale). During January 2009, we spent a total of 75.4 h observing three different groups of PI killer whales hunting off the western Antarctic Peninsula. Observed prey taken included 16 seals and 1 Antarctic minke whale (*Balaenoptera bonaerensis*). Weddell seals (*Leptonychotes weddellii*) were taken almost exclusively (14/15 identified seal kills), despite the fact that they represented only 15% of 365 seals identified on ice floes; the whales entirely avoided taking crabeater seals (*Lobodon carcinophaga*; 82% relative abundance) and leopard seals (*Hydrurga leptonyx*; 3%). Of the seals killed, the whales took 12/14 (86%) off ice floes using a cooperative wave-washing behavior; they produced 120 waves during 22 separate attacks and successfully took 12/16 (75%) of the Weddell seals attacked. The mean number of waves produced per successful attack was 4.1 (range 1-10) and the mean attack duration was 30.4 min (range 15-62). Seal remains that we examined from one of the kills provided evidence of meticulous postmortem prey processing perhaps best termed butchering.

Testa, J. W., Mock, K. J., Taylor, C., Koyuk, H., Coyle, J. R., & Waggoner, R. (2012). Agent-Based Modeling of the Dynamics of Mammal-Eating Killer Whales and Their Prey. *Marine Ecology Progress Series*, 466, 275-291 Retrieved from www.jstor.org/stable/24876124

The role of mammal-eating, or transient, killer whales *Orcinus orca* in the decline of various marine mammal populations in Alaska is controversial and potentially important in their recovery. Classical predator–prey models are insufficient to describe the dynamics of a single predator on the number of prey types known for these predators, and there are few population-level data that could be used to parameterize such models. As an heuristic framework for this more complicated system, we developed an agent-based model of killer whales with plausible energetics and behavior. We calibrated and validated the model using single-prey scenarios (a community of generic ‘Seals’) against published expectations for prey consumption rates, killer whale group dynamics, and demography. We then explored the emergent properties of single-prey models and of 3-prey models using the ‘Seals’ as primary prey, a generic small population of ‘Sea Lions’, and seasonally available large ‘Whales’. The single-prey model gave results that were intuitively reasonable and responsive to underlying parameters but were also sensitive to encounter/killing rates, as expected in classic predator–prey models with similar parameters. However, the dynamics included long time lags (~30 yr) with strong shifts in predator age structure and vital rates. In multi-prey scenarios in which the importance of seasonally available large whale prey was manipulated, large whale prey had the potential to augment killer whale numbers somewhat but had a minimal effect on the overall dynamics, whereas perturbing the carrying capacity of the primary prey created strong numeric shifts in killer whale population size and consequent indirect effects on both alternate prey. No predictive utility is suggested due to the absence of such elements as spatial realism, explicit prey-switching and more realistic prey structure, but the models suggest that we consider more complicated numerical dynamics of killer whales in discussions of their impact on prey.

Alava, J. J., Smith, K. J., O'Hern, J., Alarcon, D., Merlen, G., & Denking, J. (2013). Observations of Killer Whale (*Orcinus orca*) Attacks on Bryde's Whales (*Balaenoptera edeni*) in the Galapagos Islands. *Aquatic Mammals*, 39(2), 196 <https://doi.org/10.1578/AM.39.2.2013.196>

The aim of this article is to describe a successful attack by a group of killer whales on a Bryde's whale in the Galapagos Islands, Ecuador, with a description of their attack behavior. This article presents information related to a resighting of one of the killer whales involved in the attack off the coast of Ecuador. Previous observations of killer whale interactions with marine mammals and attacks on baleen whales have frequently occurred in the past, but these observations were not documented in detail. In Galapagos waters, killer whales feed on and interact with a broad group of marine vertebrates, dolphins and large whales. The predatory attacks involving tropical baleen whales are of particular interest given that similar behaviors have been reported for transient killer whales. These insights might be used as evidence to further support future studies investigating population and feeding ecology, photo-identification, and the ecotypes occurring in the Galapagos region.

de Bruyn, P. J. N., Tosh, C. A., & Terauds, A. (2013). Killer Whale Ecotypes: Is There a Global Model? *Biological Reviews*, 88(1), 62-80 <https://doi.org/10.1111/j.1469-185X.2012.00239.x>

Killer whales, *Orcinus orca*, are top predators occupying key ecological roles in a variety of ecosystems and are one of the most widely distributed mammals on the planet. In consequence, there has been significant interest in understanding their basic biology and ecology. Long-term studies of Northern Hemisphere killer whales, particularly in the eastern North Pacific (ENP), have identified three ecologically distinct communities or ecotypes in that region. The success of these prominent ENP studies

has led to similar efforts at clarifying the role of killer whale ecology in other regions, including Antarctica. In the Southern Hemisphere, killer whales present a range of behavioural, social and morphological characteristics to biologists, who often interpret this as evidence to categorize individuals or groups, and draw general ecological conclusions about these super-predators. Morphologically distinct forms (Type A, B, C, and D) occur in the Southern Ocean and studies of these different forms are often presented in conjunction with evidence for specialised ecology and behaviours. Here we review current knowledge of killer whale ecology and ecotyping globally and present a synthesis of existing knowledge. In particular, we highlight the complexity of killer whale ecology in the Southern Hemisphere and examine this in the context of comparatively well-studied Northern Hemisphere populations. We suggest that assigning erroneous or prefatory ecotypic status in the Southern Hemisphere could be detrimental to subsequent killer whale studies, because unsubstantiated characteristics may be assumed as a result of such classification. On this basis, we also recommend that ecotypic status classification for Southern Ocean killer whale morphotypes be reserved until more evidence-based ecological and taxonomic data are obtained.

Dunn, C., & Claridge, D. (2014). Killer Whale (*Orcinus orca*) Occurrence and Predation in the Bahamas. *Journal of the Marine Biological Association of the United Kingdom*, 94(6), 1305-1309
<https://doi.org/10.1017/s0025315413000908>

Killer whales (*Orcinus orca*) have a cosmopolitan distribution, yet little is known about populations that inhabit tropical waters. We compiled 34 sightings of killer whales in the Bahamas, recorded from 1913 to 2011. Group sizes were generally small (mean = 4.2, range = 1-12, SD = 2.6). Thirteen sightings were documented with photographs and/or video of sufficient quality to allow individual photo-identification analysis. Of the 45 whales photographed, 14 unique individual killer whales were identified, eight of which were re-sighted between two and nine times. An adult female (Oo6) and a now-adult male (Oo4), were first seen together in 1995, and have been re-sighted together eight times over a 16-yr period. To date, killer whales in the Bahamas have only been observed preying on marine mammals, including Atlantic spotted dolphin (*Stenella frontalis*), Fraser's dolphin (*Lagenodelphis hosei*), pygmy sperm whale (*Kogia breviceps*) and dwarf sperm whale (*Kogia sima*), all of which are previously unrecorded prey species for *Orcinus orca*.

Ford, J. K. B., & Ellis, G. M. (2014). You Are What You Eat: Foraging Specializations and Their Influence on the Social Organization and Behavior of Killer Whales. In *Primates and Cetaceans: Field Research and Conservation of Complex Mammalian Societies*. J. Yamagiwa & L. Karczmarski (Eds.), (pp. 75-98). Tokyo: Springer Japan https://doi.org/10.1007/978-4-431-54523-1_4

The feeding ecology of predators can have a profound effect on their life history and behaviour. The killer whale—the apex marine predator—has a cosmopolitan distribution throughout the world's oceans. Globally, it is a generalist predator with a diverse diet, but regionally, different socially and genetically isolated killer whale populations can have highly specialized foraging strategies involving only a few types of prey. In the eastern North Pacific, the three sympatric killer whale lineages have distinct dietary specializations: one feeds primarily on marine mammals, another on salmon, and the third appears to specialize on sharks. These ecological specializations are associated with distinct patterns of seasonal distribution, group size, social organization, foraging behavior, and acoustic activity. Divergent foraging strategies may have played a major role in the social isolation and genetic divergence of killer whale populations.

Pitman, R. L., Totterdell, J. A., Fearnbach, H., Ballance, L. T., Durban, J. W., & Kemps, H. (2015). Whale Killers: Prevalence and Ecological Implications of Killer Whale Predation on Humpback Whale Calves Off Western Australia. *Marine Mammal Science*, 31(2), 629-657
<https://doi.org/10.1111/mms.12182>

Reports of killer whales (*Orcinus orca*) preying on large whales have been relatively rare, and the ecological significance of these attacks is controversial. Here we report on numerous observations of killer whales preying on neonate humpback whales (*Megaptera novaeangliae*) off Western Australia (WA) based on reports we compiled and our own observations. Attacking killer whales included at least 19 individuals from three stable social groupings in a highly connected local population; 22 separate attacks with known outcomes resulted in at least 14 (64%) kills of humpback calves. We satellite-tagged an adult female killer whale and followed her group on the water for 20.3 h over six separate days. During that time, they attacked eight humpback calves, and from the seven known outcomes, at least three calves (43%) were killed. Overall, our observations suggest that humpback calves are a predictable, plentiful, and readily taken prey source for killer whales and scavenging sharks off WA for at least 5 mo/yr. Humpback "escorts" vigorously assisted mothers in protecting their calves from attacking killer whales (and a white shark, *Carcharodon carcharias*). This expands the purported role of escorts in humpback whale social interactions, although it is not clear how this behavior is adaptive for the escorts.

Strange, E. L. (2016). *Assessing Southern Resident Killer Whale (Orcinus orca) Prey Abundance: The Effects of Chinook Salmon (Oncorhynchus Tshawytscha) Ocean Fishery Reductions and Related Hatchery Production*. California State University, Sacramento, CA. Retrieved from
<http://hdl.handle.net/10211.3/171230>

Predator-prey dynamics and their ecological drivers have absorbed the interest of population ecologists since models were first developed describing the cyclical nature of predator-prey populations in a static framework. Empirical data has demonstrated that species life histories evolve over ecological timescales in response to changes in broad ecological processes or specific changes in population densities and/or spatial distributions. Anthropomorphic environmental impacts have influenced ecological processes on a broad scale and in many cases impacted predator-prey relationships. Southern Resident killer whale, *Orcinus orca*, and its preferred prey, Chinook salmon, *Oncorhynchus tshawytscha*, provide an opportunity to evaluate human impacts from Chinook salmon ocean harvest and hatchery production to the predator-prey dynamic between these co-evolved species. This is particularly important when considering the management of ocean fisheries and hatcheries that support those fisheries relative to the recovery of the Southern Resident killer whale population, a federally-endangered marine mammal species. The purpose of this study was to: 1) investigate the impacts of modifications in Chinook salmon ocean harvest and hatchery production inputs on their abundance as a prey species for Southern Resident killer whale; and 2) evaluate how the Southern Resident killer whale population responds to the subsequent prey availability. Time-series (1984-2011) Chinook salmon terminal run (freshwater harvest plus spawning population) and ocean fishery harvest data from British Columbia, Washington, Oregon and California, were analyzed under twelve scenarios involving different combinations of ocean fishery harvest and hatchery production. Chinook salmon terminal run results were used as input to the Southern Resident killer whale population dynamics model to evaluate the whale population response to varying levels of prey availability. Two covariates were chosen for the Chinook salmon time-series analysis: reduction in ocean fishery harvest and reduction in hatchery production. The primary response

variable chosen for this analysis was Chinook salmon terminal run, although ocean fishery harvest and Chinook salmon total abundance were also evaluated. Linear regression was used to evaluate the influence that reductions in ocean harvest and hatchery production have on the relative absolute change in Chinook salmon terminal run, fishery harvest, and total abundance between the status quo and each scenario. A Mann-Whitney Test was used to determine trends between early and late periods in the Chinook salmon time-series. Results of this study indicate significant interactions between covariate and response variables, revealing that reduction in ocean fishery harvest explains the amount of Chinook salmon in the terminal run to a weak degree, while the reduction in hatchery production explains the amount of Chinook salmon in the terminal run to a moderate degree. Although percent reduction calculations showed decreasing ocean harvest as hatchery production decreased, the linear regression showed that percent reduction in hatchery production does not explain the amount of Chinook salmon ocean fishery harvest. The ocean fishery harvest reduction percentage weakly explains the Chinook salmon fishery harvest. In addition, reduction in hatchery production explains the total abundance of Chinook salmon in the ocean to a weak degree, while ocean harvest reduction explains the total abundance of Chinook salmon in the ocean to a moderate degree. Results also indicate a significant decrease in fishery impacts from an early time period (1984-1997) to a late time period (1998-2011), while no significant difference was demonstrated between the two timeframes for terminal run and total abundance. Southern Resident killer whale modeling results revealed that all of the Chinook salmon scenarios (terminal run data) resulted in a positive Southern Resident killer whale population growth response. However, statistical analysis between scenarios indicated no significant difference in the Southern Resident killer whale population growth over a 10-year projection. These results have value to fishery managers with regard to potential modifications to Chinook salmon ocean fishing harvest and hatchery production that may result in a greater prey base for the Southern resident killer whale population. Identification of the Chinook salmon populations most important as prey to Southern resident killer whale could focus natural/wild Chinook salmon population restoration and hatchery reform efforts with the target of increasing the numbers of Chinook salmon produced in those important watersheds. Chinook salmon management decisions directed at changing the focus of hatchery operations to support naturally spawning populations and improving freshwater habitats to support natural/wild spawning Chinook salmon populations may provide more prey over the long-term for Southern resident killer whale than management actions directed at further restrictions on the commercial ocean Chinook salmon fishery. However, based on prior research (Ward et al. 2013) and the results of this study, Chinook salmon management practice involving a complete closure of the ocean fishery while maintaining current levels of hatchery production may produce a higher likelihood that the Southern Resident killer whale population would reach their recovery target.

Beerman, A., Ashe, E., Preedy, K., & Williams, R. (2016). Sexual Segregation When Foraging in an Extremely Social Killer Whale Population. *Behavioral Ecology and Sociobiology*, 70(1), 189-198
Retrieved from www.jstor.org/stable/44848823

Resident, fish-eating killer whales in the northeastern Pacific Ocean live in multi-generational matrilineal societies containing both sexes. The degree of maternal fidelity and natal philopatry in this killer whale society is extreme even by the standards of lions, elephants or any highly social mammal. Benefits of group living include cooperative foraging and alloparental care, but few studies have explored how killer whales avoid within-group competition for prey. This study measured focal animal behaviour from one population in its legally designated critical habitat. Adult males and females overlapped spatially whilst resting, travelling and socialising, but during feeding bouts, females foraged nearshore in shallower waters, whilst adult males distributed foraging effort throughout the study area, with no statistically

significant depth preference. We postulate that sex-biased dispersal in foraging ecology reflects physiological capacity for deeper diving in males than females, which may be either a driver or consequence of extreme sexual dimorphism in the species; alternative interpretations exist. Killer whales appear to be a cosmopolitan species complex including populations that range widely in body size and diet. Our physiological limitation theory could be tested with other ecotypes. For the northern resident killer whale population we studied, we postulate that our finding may indicate a mechanism to avoid or reduce competition for food within the family unit whilst ensuring group cohesion. Investigating sex differences in foraging habitat informs area-based management and conservation of this threatened population, but studies on other ecotypes are needed to improve our understanding of the evolution of sociality in this species.

Wellard, R., Lightbody, K., Fouda, L., Blewitt, M., Riggs, D., & Erbe, C. (2016). Killer Whale (*Orcinus orca*) Predation on Beaked Whales (*Mesoplodon* Spp.) in the Bremer Sub-Basin, Western Australia. *Plos One*, 11(12) <https://doi.org/10.1371/journal.pone.0166670>

Observations of killer whales (*Orcinus orca*) feeding on the remains of beaked whales have been previously documented; however, to date, there has been no published account of killer whales actively preying upon beaked whales. This article describes the first field observations of killer whales interacting with, hunting and preying upon beaked whales (*Mesoplodon* spp.) on four separate occasions during 2014, 2015 and 2016 in the Bremer Sub-Basin, off the south coast of Western Australia.

Breed, G. A., Matthews, C. J. D., Marcoux, M., Higdon, J. W., LeBlanc, B., Petersen, S. D., . . . Ferguson, S. H. (2017). Sustained Disruption of Narwhal Habitat Use and Behavior in the Presence of Arctic Killer Whales. *Proceedings of the National Academy of Sciences of the United States of America*, 114(10), 2628-2633 <https://doi.org/10.2307/26480080>

Although predators influence behavior of prey, analyses of electronic tracking data in marine environments rarely consider how predators affect the behavior of tracked animals. We collected an unprecedented dataset by synchronously tracking predator (killer whales, N = 1; representing a family group) and prey (narwhal, N = 7) via satellite telemetry in Admiralty Inlet, a large fjord in the Eastern Canadian Arctic. Analyzing the movement data with a switching-state space model and a series of mixed effects models, we show that the presence of killer whales strongly alters the behavior and distribution of narwhal. When killer whales were present (within about 100 km), narwhal moved closer to shore, where they were presumably less vulnerable. Under predation threat, narwhal movement patterns were more likely to be transiting, whereas in the absence of threat, more likely resident. Effects extended beyond discrete predatory events and persisted steadily for 10 d, the duration that killer whales remained in Admiralty Inlet. Our findings have two key consequences. First, given current reductions in sea ice and increases in Arctic killer whale sightings, killer whales have the potential to reshape Arctic marine mammal distributions and behavior. Second and of more general importance, predators have the potential to strongly affect movement behavior of tracked marine animals. Understanding predator effects may be as or more important than relating movement behavior to resource distribution or bottom-up drivers traditionally included in analyses of marine animal tracking data.

George, J. C., Sheffield, G., Reed, D. J., Tudor, B., Stimmelmayer, R., Person, B. T., . . . Suydam, R. (2017). Frequency of Injuries from Line Entanglements, Killer Whales, and Ship Strikes on Bering-

Chukchi-Beaufort Seas Bowhead Whales. *Arctic*, 70(1), 37-46 Retrieved from www.jstor.org/stable/26379722

We analyzed scarring data for Bering-Chukchi-Beaufort (BCB) Seas bowhead whales (*Balaena mysticetus*) harvested by Alaska Native hunters to quantify the frequency of line entanglement, ship strikes, and killer whale-inflicted injuries. We had 904 records in our database for whales landed between 1990 and 2012, and after data quality screening, we found 521 records containing information on scarring. Logistic regression was used to evaluate different combinations of explanatory variables (i.e., body length, sex, year, year-group) to develop a prediction model for each scar type. We also list bowhead whales that were harvested, found dead, or observed alive entangled in commercial line/fishing gear. Our findings suggest that about 12% of harvested bowheads show entanglement scars. Their frequency is highly correlated with body length and sex: about 50% of very large bowheads (> 17 m) show such scars, while whales under 9 m rarely do, and males show a significantly higher rate than females. Scars associated with ship strikes are infrequent and occur on ~ 2% of all harvested whales; body length, sex, and year were not significant factors. Scarring from attempted killer whale predation was evident on ~ 8% of landed whales. As with entanglement injuries, the frequency of killer whale scars was much higher (> 40%) on whales more than 16 m in length and statistically more frequent in the second half of the study (2002-12). Increased killer whale injuries in the recent decade are consistent with studies conducted on bowheads of the Eastern Canada-West Greenland population. The findings presented here reflect the most thorough analysis of injury rates from entanglement, ships, and killer whales for the BCB bowheads conducted to date. They indicate that (1) entanglement rates primarily from pot fishing gear (crab or cod or both) are relatively high for very large and presumably older bowheads, (2) collisions with ships are infrequent at present, and (3) scarring from killer whales is frequent on very large adult whales (> 17 m). Considering that bowhead habitat is changing rapidly (e.g., sea ice reduction), industrial ship traffic in the Arctic is increasing, and commercial fishing operations are expanding to the north, we strongly recommend that monitoring of scarring and injuries on harvested bowheads continue into the future as a means of documenting change.

Jourdain, E., Vongraven, D., Bisther, A., & Karoliussen, R. (2017). First Longitudinal Study of Seal-Feeding Killer Whales (*Orcinus orca*) in Norwegian Coastal Waters. *Plos One*, 12(6) <https://doi.org/10.1371/journal.pone.0180099>

Killer whales (*Orcinus orca*) have been documented preying on either fish or marine mammals in several regions, suggesting that this odontocete species has the ability to specialize on different types of prey. Off Norway, killer whales have been shown to rely on the Atlantic herring (*Clupea harengus*) as a main prey resource. Infrequent observations have revealed seals as an additional component of their diet, yet the extent of predation on marine mammals has remained largely unknown. Here, we present the findings of 29 years of photographic and observational data on seal-feeding killer whale groups identified in Norwegian coastal waters. Four groups have been observed preying and feeding on seals over several years, taking both harbor (*Phoca vitulina*) and grey (*Halichoerus grypus*) seals. These stable groups are shown to adopt small group sizes, were typically observed in near-shore areas and were not encountered on herring wintering grounds. Behavioral and social traits adopted by these groups are similar to those of pinniped-feeding killer whales from other regions. The potential ecological reasons and the extent of such prey specializations are discussed.

Pitman, R. L., Deecke, V. B., Gabriele, C. M., Srinivasan, M., Black, N., Denkinger, J., . . . Ternullo, R. (2017). Humpback Whales Interfering When Mammal-Eating Killer Whales Attack Other Species: Mobbing Behavior and Interspecific Altruism? *Marine Mammal Science*, 33(1), 7-58
<https://doi.org/10.1111/mms.12343>

Humpback whales (*Megaptera novaeangliae*) are known to interfere with attacking killer whales (*Orcinus orca*). To investigate why, we reviewed accounts of 115 interactions between them. Humpbacks initiated the majority of interactions (57% vs. 43%; $n = 72$), although the killer whales were almost exclusively mammal-eating forms (MEKWs, 95%) vs. fish-eaters (5%; $n = 108$). When MEKWs approached humpbacks ($n = 27$), they attacked 85% of the time and targeted only calves. When humpbacks approached killer whales ($n = 41$), 93% were MEKWs, and $\geq 87\%$ of them were attacking or feeding on prey at the time. When humpbacks interacted with attacking MEKWs, 11% of the prey were humpbacks and 89% comprised 10 other species, including three cetaceans, six pinnipeds, and one teleost fish. Approaching humpbacks often harassed attacking MEKWs ($\geq 55\%$ of 56 interactions), regardless of the prey species, which we argue was mobbing behavior. Humpback mobbing sometimes allowed MEKW prey, including nonhumpbacks, to escape. We suggest that humpbacks initially responded to vocalizations of attacking MEKWs without knowing the prey species targeted. Although reciprocity or kin selection might explain communal defense of conspecific calves, there was no apparent benefit to humpbacks continuing to interfere when other species were being attacked. Interspecific altruism, even if unintentional, could not be ruled out.

Capella, J. J., Felix, F., Florez-Gonzalez, L., Gibbons, J., Haase, B., & Guzman, H. M. (2018). Geographic and Temporal Patterns of Non-Lethal Attacks on Humpback Whales by Killer Whales in the Eastern South Pacific and the Antarctic Peninsula. *Endangered Species Research*, 37, 207-218
<https://doi.org/10.3354/esr00924>

The role and impact of killer whales *Orcinus orca* as predators of baleen whales has been emphasized by studies of humpback whales *Megaptera novaeangliae*. In this study, rake marks on the fluke were used as a proxy for predatory attacks in a sample of 2909 adult humpback whales and 133 calves from 5 breeding and 2 feeding locations in the eastern South Pacific and the Antarctic Peninsula. The goal of this study was to evaluate how often, at what age, where, and when humpback whales were more susceptible to attacks. Overall, 11.5 % of adults and 19.5 % of calves had rake marks on their flukes. Significant differences were found in the prevalence of scars in calves when comparing breeding (9 %) vs. feeding areas (34 %) ($\chi^2(2) = 10.23$, $p < 0.01$). Multi-year sighting analysis of scar acquisition in 120 adults (82 % site fidelity) and 37 calves in the Magellan Strait showed no new marks after the initial sighting for the subsequent 15 yr. This finding indicates that rake marks were most probably acquired when whales were calves, which supports the belief that scar acquisition is a once in a lifetime event. The odds of having rake marks increased with time but with a significantly higher rate in calves ($\chi^2(2) = 5.04$, $p < 0.05$), which suggests an increase in predation pressure over time. Our results support the earlier hypothesis that killer whale attacks occur mostly on calves, near breeding sites, and during the first migration to feeding areas.

Weller, D. W. (2018). Predation on Marine Mammals. In *Encyclopedia of Marine Mammals (Third Edition)*. B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), (pp. 772-780): Academic Press <https://doi.org/https://doi.org/10.1016/B978-0-12-804327-1.00206-5>

Summary Although marine mammals are regarded as accomplished and sophisticated hunters, they too are preyed upon by a variety of terrestrial, avian, and aquatic predators. While the risk of predation is of little or no concern for some species, others exist under high levels of predatory pressure. This review is focused on the hunting and consumption of marine mammals by their predators.

You, H., Hwang, J. H., & Park, Y. S. (2019). Mechanical Understanding of Hunting Waves Generated by Killer Whales. *Marine Mammal Science*, 35(4), 1396-1417 <https://doi.org/10.1111/mms.12600>

The wave wash hunting employed by *Orcinus orca*, also known as killer whales, is unique in that the prey is hunted outside of the water by generating waves. To quantitatively analyze the specific mechanism of the wave wash, data were obtained using computational fluid dynamics (CFD), and wave theory was introduced as the theoretical background to clarify the mechanism. The relationships between the swimming characteristics and wave parameters are defined in this paper. The results obtained by numerical investigation revealed that the wavelength increased with the swimming speed. Additionally, the wave height increased as the swimming speed increased and the swimming depth became shallower, and subsequently converged to a maximum of 2.42 m. The success of hunting is determined by two wave parameters, which indicate the intensity of the wave wash: the wave height and force exerted on the prey. The metabolic rate and the drag force are considered to evaluate the efficiency of the locomotion, which varied according to the swimming speed (V) and swimming depth (d) of the whales. To generate hunting waves efficiently, the optimal ranges of V and d were estimated to be 3 similar to 5 m/s and 0.5 m similar to 1.1 m respectively.

Gualtieri, D., & Pitman, R. L. (2019). Killer Whale (*Orcinus orca*) Predation on a Gervais' Beaked Whale (*Mesoplodon Europaeus*) in the Eastern Atlantic Ocean. *Aquatic Mammals*, 45(2), 244-245 <https://doi.org/10.1578/AM.45.2.2019.244>

Although killer whales (*Orcinus orca*) have been documented preying on numerous species of marine mammals, there are few records of attacks on beaked whales. At 0700 h on Oct 7, 2014, while sailing across the Atlantic Ocean from Cape Verde to Salvador, Brazil, aboard the MS National Geographic Explorer, DG sighted a group of seven killer whales approximately 1.5 km off the starboard bow; their position was 08° 16' N, 026° 20' W in water 4,000 to 5,000 m deep, approximately 930 km southwest of Cape Verde Islands. The sea conditions were flat calm. For the first 10 min of observation, the killer whales were spread out, coursing back and forth through an area of about 100 × 200 m. During that time, they saw no conspicuous surface behavior (e.g., splashing, lob-tailing, or spy-hopping). To their knowledge, this is only the third report of killer whale predation on free-ranging mesoplodonts and the first involving a Gervais' beaked whale.

Testino, J. P., Petit, A., Alcorta, B., Pacheco, A. S., Silva, S., Alfaro-Shigueto, J., . . . Gonzalez-Pestana, A. (2019). Killer Whale (*Orcinus orca*) Occurrence and Interactions with Marine Mammals Off Peru. *Pacific Science*, 73(2), 261-273 <https://doi.org/10.2984/73.2.7>

Killer whales (*Orcinus orca*) are widely distributed in all ocean basins, however, their occurrence, distribution, and ecology in the southeast Pacific, including Peru, is poorly defined. This study aims to describe the occurrence of killer whales in Peruvian waters, with additional description of predatory behaviors. Between 2003 and 2018 there were 29 reports of killer whales in Peruvian waters in which at least 110 individuals were observed, with pod sizes ranging between 1 and 15 individuals. Most sightings occurred in waters within the continental shelf or in close proximity to the shelf break. During eight of the sightings, killer whales displayed predatory behavior towards other marine mammals, including cetaceans (*Megaptera novaeangliae* and *Balaenoptera musculus*) and pinnipeds (*Otaria flavescens* and *Arctocephalus australis*). In addition, we present the first photo-analysis of the incidence of killer whale tooth rake marks on humpback whale flukes off northern Peru. Between 2009 and 2017, 897 unique individual humpback whales were photo-identified off northern Peru, of which 19.6% (n = 172) displayed rake marks in their flukes, suggesting that humpback whales in the southeast Pacific are exposed to the attack of killer whales. Our findings suggest that the occurrence of killer whales in Peruvian waters are more common than previously documented and that killer whales are preying marine mammals in this region. Further understanding killer whale distribution, foraging habitats, and movement patterns within Peruvian waters will be essential in promoting their conservation.

Matthews, C. J. D., Breed, G. A., LeBlanc, B., & Ferguson, S. H. (2020). Killer Whale Presence Drives Bowhead Whale Selection for Sea Ice in Arctic Seascapes of Fear. *Proceedings of the National Academy of Sciences*, 117(12), 6590-6598 <https://doi.org/10.1073/pnas.1911761117>

Behavioral responses of prey to perceived predation risk are now recognized as important components of predator-prey interactions, but have rarely been quantified in marine vertebrates. Using telemetry data from the eastern Canadian Arctic, we document pronounced and prolonged changes in bowhead whale behavior and selection for sea ice when under perceived predation threat by killer whales. Although the energetic or fitness costs of such nonconsumptive effects (NCEs) are difficult to quantify, our results strongly suggest the ecological impacts of killer whales as apex predators extend beyond consumptive/density-mediated effects (direct mortality). Killer whale-induced NCEs may compound the negative consequences of sea ice loss on Arctic endemic marine mammals as they cope with more-frequent, longer exposures to predator threat. The effects of predator intimidation on habitat use and behavior of prey species are rarely quantified for large marine vertebrates over ecologically relevant scales. Using state space movement models followed by a series of step selection functions, we analyzed movement data of concurrently tracked prey, bowhead whales (*Balaena mysticetus*; n = 7), and predator, killer whales (*Orcinus orca*; n = 3), in a large (63,000 km²), partially ice-covered gulf in the Canadian Arctic. Our analysis revealed pronounced predator-mediated shifts in prey habitat use and behavior over much larger spatiotemporal scales than previously documented in any marine or terrestrial ecosystem. The striking shift from use of open water (predator-free) to dense sea ice and shorelines (predators present) was exhibited gulf-wide by all tracked bowheads during the entire 3-wk period killer whales were present, constituting a nonconsumptive effect (NCE) with unknown energetic or fitness costs. Sea ice is considered quintessential habitat for bowhead whales, and ice-covered areas have frequently been interpreted as preferred bowhead foraging habitat in analyses that have not assessed predator effects. Given the NCEs of apex predators demonstrated here, however, unbiased assessment of habitat use and distribution of bowhead whales and many marine species may not be

possible without explicitly incorporating spatiotemporal distribution of predation risk. The apparent use of sea ice as a predator refuge also has implications for how bowhead whales, and likely other ice-associated Arctic marine mammals, will cope with changes in Arctic sea ice dynamics as historically ice-covered areas become increasingly ice-free during summer.

Young, B. G., Fortune, S. M. E., Koski, W. R., Raverty, S. A., Kilabuk, R., & Ferguson, S. H. (2020). Evidence of Killer Whale Predation on a Yearling Bowhead Whale in Cumberland Sound, Nunavut. *Arctic Science*, 6(1), 53-61 <https://doi.org/10.1139/as-2019-0014>

Accounts of killer whale (*Orcinus orca*) predation on marine mammals in the Canadian Arctic are relatively uncommon. Although second-hand reports of killer whale predation events in the Arctic are more common in recent years, these observations are a.) generally poorly documented and the outcome of attacks are often unknown. On 12 August 2016, a floating bowhead whale (*Balaena mysticetus*) carcass was found off-shore in Cumberland Sound, Nunavut presumably preyed by killer whales that were sighted in the area. Inspection of the carcass revealed injuries consistent with published accounts of killer whale predation on large whales and observations of killer whale predation on bow-heads described in Inuit traditional knowledge. The bowhead was male, 6.1 m long in good nutritional condition and estimated between 14 and 16 months old. As a recently weaned yearling, this whale would have been highly vulnerable to killer whale predation. With decreasing summer sea ice making some areas of the Arctic more accessible, the incursion and presence of killer whales in the Arctic is expected to increase. A better understanding of Arctic killer whale predation pressure is needed to predict the potential impact they will have on the eastern Canada-west Greenland bowhead population as well as on other marine mammal prey.