

Killer whales and whaling: the scavenging hypothesis

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Killer whales (*Orcinus orca*) frequently scavenged from the carcasses produced by whalers. This practice became especially prominent with large-scale mechanical whaling in the twentieth century, which provided temporally and spatially clustered floating carcasses associated with loud acoustic signals. The carcasses were often of species of large whale preferred by killer whales but that normally sink beyond their diving range. In the middle years of the twentieth century floating whaled carcasses were much more abundant than those resulting from natural mortality of whales, and we propose that scavenging killer whales multiplied through diet shifts and reproduction. During the 1970s the numbers of available carcasses fell dramatically with the cessation of most whaling (in contrast to a reasonably stable abundance of living whales), and the scavenging killer whales needed an alternative source of nutrition. Diet shifts may have triggered declines in other prey species, potentially affecting ecosystems, as well as increasing direct predation on living whales.

Keywords: scavenging; whaling; killer whale; ecosystem

1. INTRODUCTION

The killer whale (*Orcinus orca*) is the apex non-human, marine predator. The diverse diet of killer whales includes the large whales (Jefferson *et al.* 1991), and it has been suggested that killer whales, through their dietary shifts, have had major impacts on populations and ecosystems (Estes *et al.* 1998). In a particularly controversial paper, Springer *et al.* (2003) specifically proposed that the destruction of the populations of large whales in the North Pacific by the modern whaling industry forced killer whales to increase their consumption of smaller marine mammals, generating declines of harbour seals, *Phoca vitulina*, Steller sea lions, *Eumetopias jubatus*, and sea otters, *Enhydra lutris*. Similarly, it has been proposed that declines of southern sealions (*Otaria flavescens*), elephant seals (*Mirounga leonina*) and minke whales (*Balaenoptera bonaerensis*) in the Southern Ocean resulted from killer whales switching predation from decimated populations of large whales (Branch & Williams *in press*).

The evidence that killer whale predation was the proximate cause of the decline of sea otters in the central Aleutian Islands is good (Estes *et al.* 1998),

and it is at least reasonable to suppose that killer whales can play a major role in natural mortality for pinniped populations (Heise *et al.* 2003; Williams *et al.* 2004; Branch & Williams *in press*). However, reports of killer whales attacking other whales seem to have risen, rather than declined, since about 1970 (Reeves *et al.* *in press*), suggesting that any increase in attacks on marine mammals over the past 35 or so years has been the result of a scarcity of some food source other than living large whales.

Here we show that scavenging by killer whales from carcasses made available by the whaling industry was commonplace during the twentieth century (and probably also during the centuries before), and that this supply of carcasses almost disappeared quite suddenly during the 1970s.

2. RESULTS

In a broad-scale search of the whaling literature, including hundreds of voyage logbooks as well as published narratives and monographs, Reeves *et al.* (*in press*) found ample anecdotal evidence of scavenging on the carcasses of whales killed by whalers. In the supplementary Electronic Appendix (table 1) we summarize some references in the whaling literature to scavenging by killer whales. Included are references from the early 1700s to the 1960s, from most oceans, as well as photographs and film footage. It is clear from this compilation that such behaviour was commonplace, especially during modern whaling, that it was geographically widespread, and that whalers expected it and took measures to offset it. There are also instances of cooperation between scavenging killers and the whalers (Andrews 1916; Dakin 1934).

The observations make it clear that the tongues of baleen whales were the main focus of the scavenging killer whales, although they also consumed blubber and skin from carcasses. This pattern of partial consumption, with the tongue regarded as a 'delicacy', is consistent with reports of consumption of whales killed by the killer whales themselves (Jefferson *et al.* 1991).

We estimated the availability of large cetaceans and minke whales (*Balaenoptera acutorostrata* and *B. bonaerensis*), both live and as carcasses, during the twentieth century in all oceans. We divided the whales into four classes:

- (i) The larger whales of the genus *Balaenoptera*. These animals usually sink when dead. Although the carcasses may later rise to the surface, they are then in an advanced state of decomposition, and therefore may not be of interest to killer whales.
- (ii) The minke whales. Minke carcasses also sink to later rise. Minkes are the smallest and most numerous of the whales considered.
- (iii) Other baleen whales: the bowhead (*Balaena mysticetus*), gray (*Eschrichtius robustus*), humpback (*Megaptera novaeangliae*) and right (*Eubalaena* spp.). Carcasses of these species (except some humpbacks and maybe grays) generally float.

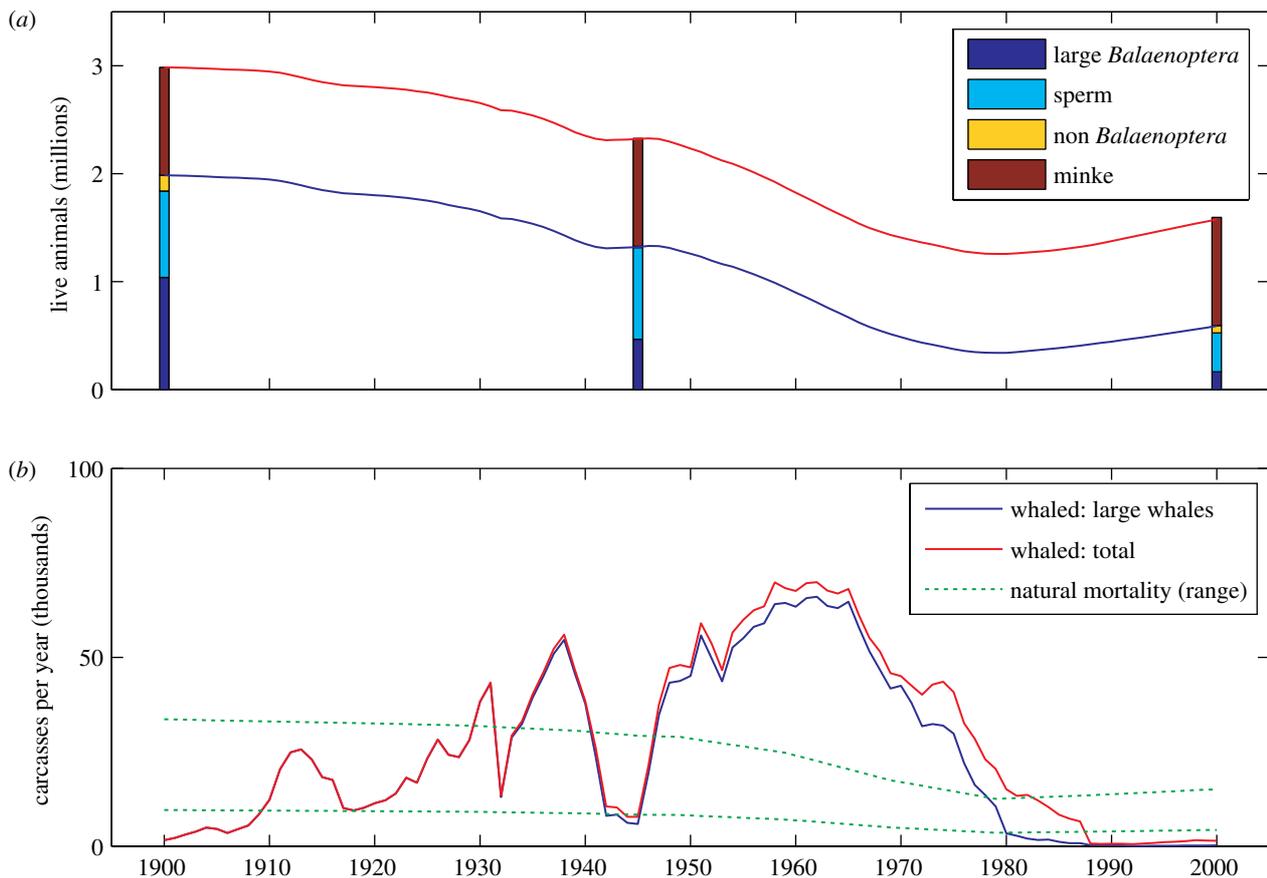


Figure 1. Estimated twentieth century trajectories for the number of whales alive (upper), and the number of carcasses available for scavenging killer whales from whaling and natural sources (lower), including and excluding minke whales.

(iv) Sperm whales (*Physeter macrocephalus*). Most sperm whale carcasses initially float.

From estimates in the literature, and our own extrapolations, we estimated global populations of each of these species groups at three points in the twentieth century: 1900, 1945, 2000 (table 2 of supplementary Electronic Appendix). Then, for the aggregate total population, and the population without minke whales, we filled in population trajectories between 1900–1945 and 1945–2000 (figure 1; see supplementary Electronic Appendix for methods). Also shown in figure 1 are the reported catches of the worldwide whaling industry indicating the availability of whaled carcasses, as well as approximate confidence intervals for the availability of floating carcasses resulting from natural mortality. In figure 2, the curves of figure 1 are translated into whale biomass, using the mean adult masses of each species.

There are many sources of uncertainty and inaccuracy in the curves plotted in figures 1 and 2. These include inaccurate catch figures because of mistakes, falsification and the omission of catches by open-boat whalers of the early twentieth century and pirate whalers of the mid twentieth century; poor population estimates for almost all species (especially poor for some); the approximate nature of the interpolation models; uncertainty of the trajectory of minke whale populations; uncertainty as to which carcasses float and thus would be

available to scavenging killer whales; changes with time in methods of catching and processing whales, and thus in carcass availability to scavenging killer whales; and the lack of good data on natural mortality. Therefore, the details of these curves do not deserve any scrutiny. However, major, and real, features are:

- (i) there was no sudden global decline in either numbers or biomass of living whales during the 1970s;
- (ii) many more carcasses, and a much greater biomass of dead whales, were produced through whaling than by natural mortality of floating-carcass species during the middle part of the twentieth century;
- (iii) this carcass availability fell dramatically between 1970 and 1980.

For scavenging killer whales, whaled carcasses had several potential advantages over available naturally dying animals, which were mostly sperm whales. Whaled carcasses will have been generally of healthier, and thus more nutritious animals; they were more likely to be of baleen whales than sperm whales (baleen whales have large tongues and a much less tough skin than sperms); they were temporally and spatially clustered; and their availability was marked with loud acoustic signals audible at long range particularly from engines, winches, harpoon guns, and exploding harpoons.

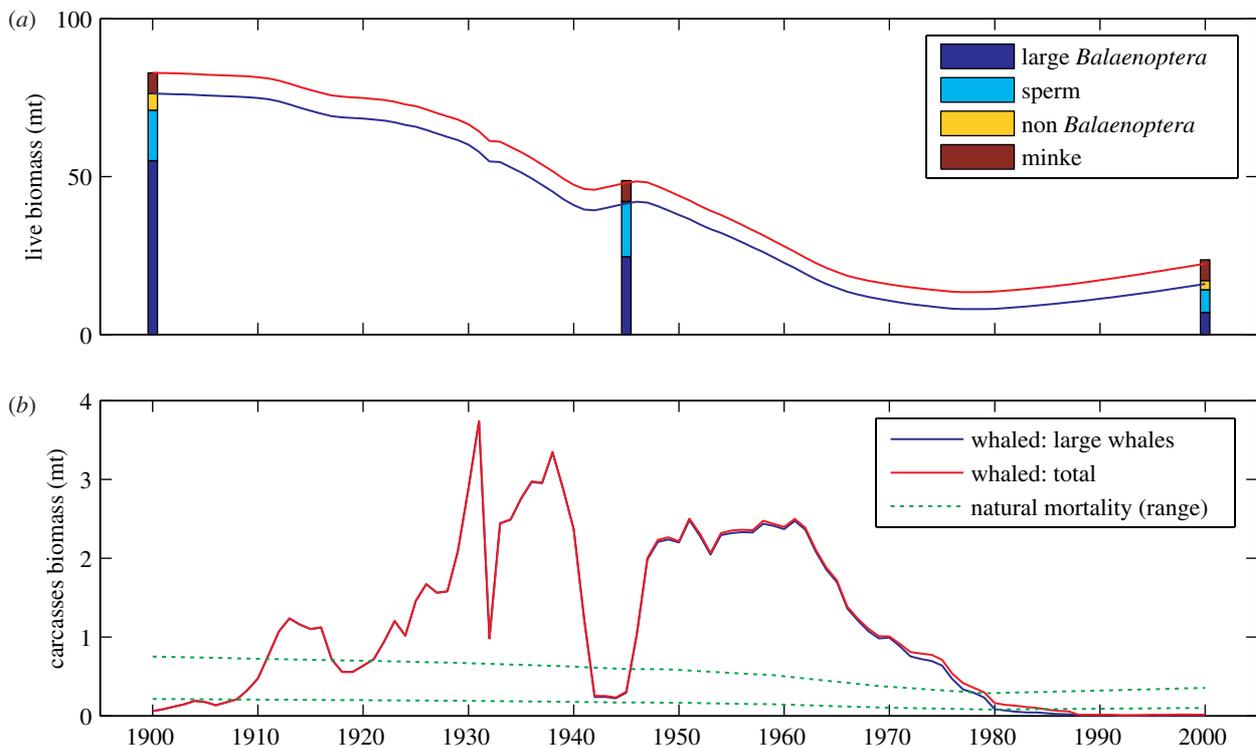


Figure 2. Estimated twentieth century trajectories for the biomass of whales alive (upper), and the biomass of carcasses available for scavenging killer whales from whaling and natural sources (lower), including and excluding minke whales.

3. DISCUSSION

While the killer whale as a species has an extremely diverse diet, particular sets of animals are highly specialized (Baird 2000). In the northeastern Pacific two sympatric forms specialize on fish and marine mammals, respectively, rarely if ever eating the food of the other form (Ford *et al.* 1998). Similarly, three forms with distinct diets have been recognized from the Antarctic (Pitman & Ensor 2003). Social groups of killer whales can sometimes adopt new foraging behaviour, such as depredation on long-lines (Yano & Dahlheim 1995). These specializations are probably largely the result of social learning, i.e. they are cultural (Rendell & Whitehead 2001).

Thus the scavenging killers were likely specialists to some degree. Scavenging on carcasses resulting from natural mortality, including possibly predation by other killer whales, may have been a part of the repertoire of some killer whales before whaling, but given the spatial and temporal dispersion of the carcasses, it would probably have been difficult to subsist completely on the carcasses of large whales that they had not killed. Scavenging likely became more important during the era of open-boat whaling (Dudley 1725). We hypothesize that it was with modern whaling that scavenging became widespread and commonplace. Numbers of carcasses were being produced in reasonably small areas, with loud 'dinner-bells'. The large, fast animals of the genus *Balaenoptera* with their huge tongues and thin skin were suddenly available, already killed, inflated with air so that they did not sink, and often left floating unattended for several hours (Tønnessen & Johnsen 1982). Those killer whales for which scavenging was already a part of the feeding repertoire would have

had a bonanza, and possibly increased their reproductive rates, although mortality from armed, irate whalers (Robertson 1954) would have had the opposite effect. Other groups of killer whales, probably naturally mammal-eaters (fish-eaters seem loathe to eat mammals; Ford *et al.* 1998), were likely recruited to the scavenging way of life either through innovation, or by social learning from other killer whales already scavenging. During the carcass-rich decades of the mid twentieth century, as the scavenging culture spread, other ways of securing nutrients and energy could have receded from the behavioural repertoire, as well as perhaps the knowledge base, of these animals.

In this scenario, by about 1980 these scavenging killer whales faced a problem: the carcasses were almost gone. It seems reasonable that these animals would have turned to attacking pinnipeds, living large whales, small cetaceans and sea otters more frequently.

Killer whales have developed different feeding specializations in different parts of the world, and we should expect the significance of carcass scavenging, like natural predation, to have varied geographically. With variation in the cultures of the killer whales interacting with environmental differences, the switch from whale-carcass scavenging would have taken different paths in different areas, including, perhaps, significantly increased predation on sea otters and pinnipeds off Alaska (Springer *et al.* 2003), pinnipeds and minke whales in the Southern Ocean (Branch & Williams *in press*), and large whales off western North America (Reeves *et al.* *in press*). The extent to which killer whale predation has contributed to apparent declines of some populations of pinnipeds

and cetaceans is beyond the scope of this paper, and remains an open and controversial question.

Killer whales were not the only scavengers on whale carcasses. Flocks of seabirds scavenged from floating carcasses as well as the offal from whale processing (Dudley 1725; Robertson 1954). In the Arctic, polar bears (*Ursus maritimus*) still feast on bowhead whale carcasses (Todd O'Hara, personal communication); their opportunities for scavenging during the peak era of commercial whaling must have had a dramatic effect on bear numbers and distribution. Scavenging sharks were major nuisances to whalers in tropical areas (Reeves *et al.* 2001). Therefore, the ecological ramifications of whaling on predators cum scavengers, in addition to killer whales, likely had long-term consequences for at least some of their populations and prey.

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The supplementary Electronic Appendix is available at <http://dx.doi.org/10.1098/rsbl.2005.0348> or via <http://www.journals.royalsoc.ac.uk>.