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ARE GRAY WHALES HITTING "K" HARD?

Dead gray whales (*Eschrichtius robustus*) were reported along the North American coast, from Baja California, Mexico, to Alaska in record numbers in 1999 and 2000. A total of 273 whale carcasses were reported for the 1999 calendar year, with an unofficial tally of 361 in 2000. What is killing all these whales? Speculation usually focuses on starvation, disease, or anthropogenic impacts (*e.g.*, pollution, vessel strikes, *etc.*), or some synergistic combination of the three. In whatever combination, the response of gray whales to these or other factors may simply indicate that the Eastern North Pacific (ENP) population is reaching environmental carrying capacity (K). But even if gray whales are at or near K, why are they hitting this hypothetical boundary so hard?

Gray whales were commercially hunted during the 19th and early 20th centuries (Jones *et al.* 1984), which reduced the ENP population to perhaps as few as 1,000–2,000 whales (Rice and Wolman 1971). During the last half of the 20th century, this population grew at an estimated 3% per year and was estimated to number 26,635 (95% CI = 21,878–32,427) whales during the

1997–1998 southbound migration (Rugh *et al.* 1999). Through that year the population seemed robust. Counts of calves along the northward migration were high, and adult whales appeared to be healthy (*i.e.,* none appeared emaciated as in 2000; Perryman, unpublished data). Then, during the 1998–1999 migratory cycle, there was a sudden shift in population dynamics. Dead whales were reported in record numbers, starting in the Mexican breeding lagoons (LeBoeuf *et al.* 2000), and calf counts plummeted (Perryman, unpublished data). Some of the carcasses were rotund, others emaciated. More females were reported among the dead in 1999 (76 of 115 where sex was determined), but in 2000 this distinction was held by male whales (57 of 77 where sex was determined). In both years most carcasses could not be reached for examination, so sex and other vital statistics, as well as detailed evaluations on cause of death, are unavailable. When tissue samples could be obtained, preliminary evaluation of lipophilic contaminant levels were within the normal range reported for healthy whales (Krahn *et al.,* in press).

The suddenness of the demographic change and accompanying reports of emaciated whales are perplexing. While the number of carcasses does not exceed expected natural mortality (modeling exercises indicate that a population of 26,000 whales approaching K slowly should lose roughly 1,000 individuals annually [Wade, in press]), the number of adult whales among the stranded animals is surprising. Theoretically, as populations reach carrying capacity, heightened competition for food and other resources leads to increased mortality, especially among the oldest and youngest animals, and to decreased reproductive success (Eberhardt and Siniff 1977). However, in 1999 and 2000, over 60% of dead gray whales were adults, some seemingly in the prime of life. Simultaneously, reports of severely emaciated whales began to trickle in—only a few in 1999, but more in 2000. These whales were so thin that their scapulas protruded as bony humps aft of their blowholes as they swam (Fig. 1A, B), and their carcasses appeared serpentine (Fig. 1C). Causes for such emaciation are unknown. Epidemiological investigations are hampered by lack of fresh carcasses. Whales stranded in San Francisco Bay have been the best studied and, of the 29 carcasses examined to date, only one tested positive for domoic acid (a neurotoxin) and one other carried frustules of *Pseudonitzschia australis* in the feces. A third whale was emaciated and had heavy parasitic infection, with *Bulbosoma balanae* causing intestinal stenosis. The role of these conditions in the overall mortalities is unknown.

Causes of the recent spate of gray whale deaths may never be discovered. A decline of productivity in the North Pacific following the regime shift of the late 1970s (Francis *et al.* 1998) has been postulated as resulting in prey limitation for gray whales (LeBoeuf *et al.* 2000). However, gray whales' unique capacity to forage by suctioning dense mats of tube-building amphipods from the sea floor (Oliver and Slattery 1985), coupled with the temporal and spatial breadth of prey species and feeding opportunities (Nerini 1984), confounds a comprehensive assessment of prey availability. Indeed, the capability of gray whales to exploit a relatively untrammeled prey base may have aided their recovery. Removed from the Endangered Species List in 1994, ENP gray

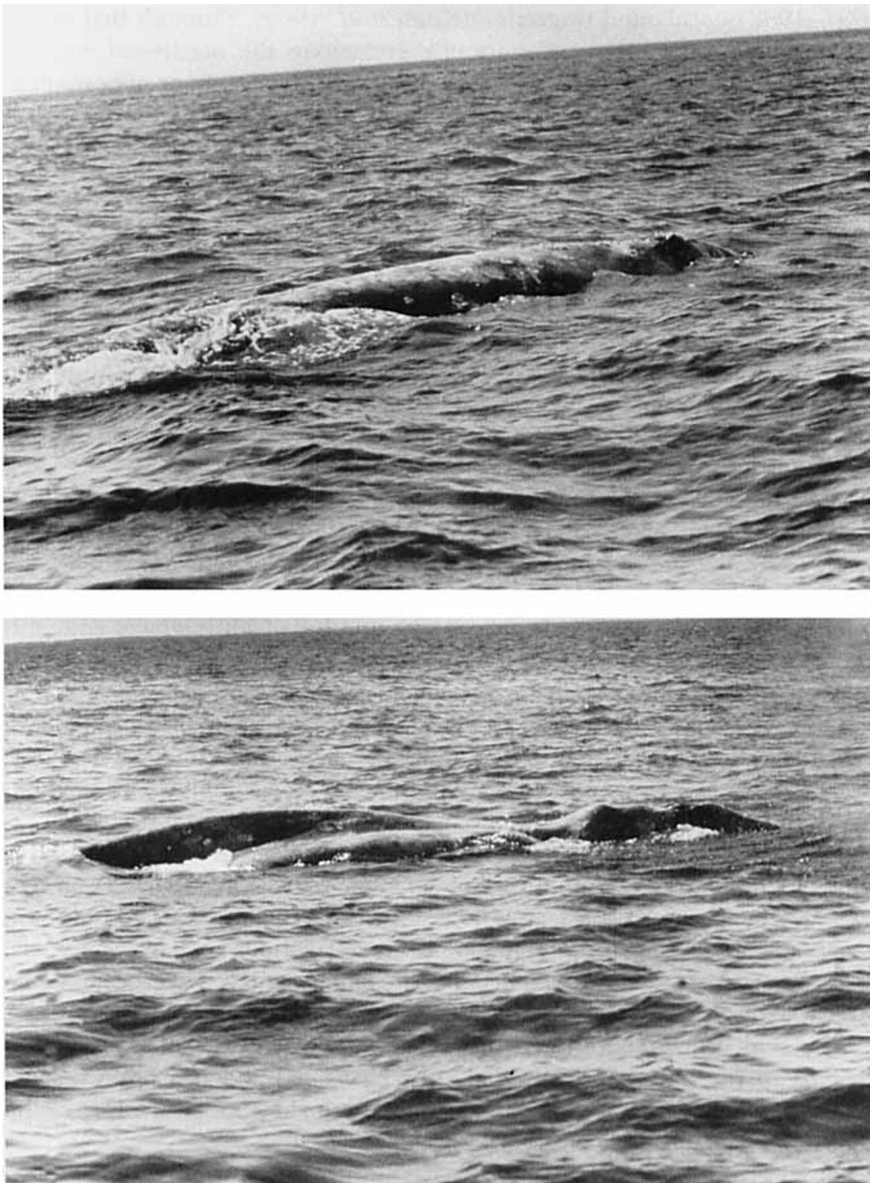

Figure 1. Comparison of: healthy (top), emaciated living (bottom), and emaciated dead (opposite) gray whales. Photo credits: Jorge Urban R. (top and bottom); Frances Gulland (opposite).

whales remain a standout success story in the annals of mysticete whale recovery after commercial exploitation. The life history characteristics that brought the population back from that challenge will, in all likelihood, support their response to the current trial.

Figure 1. Continued.

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