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Short Note

Gray Whale (*Eschrichtius robustus*) Predation and the Demise of Amphipod Prey Reserves in Clayoquot Sound, British Columbia

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Resource use by apex predators can redirect energy in dynamic systems, creating or relieving stress on prey populations. Even those ecosystems considered archetypal bottom-up systems, such as a marine system, experience strong localized top-down pressure. As whale populations recover from commercial whaling, their influence as apex predators on communities becomes more apparent. The concept of prey limitation has seldom been discussed for baleen whales, yet it may well play an important role in population size and distribution. The general case is discussed herein, as well as our observations, to examine one of the more accessible baleen whale/prey systems—the role of the eastern Pacific gray whale (*Eschrichtius robustus*) as an ecological architect of its foraging grounds. Data presented by those working in their primary Arctic feeding grounds are considered, not least Coyle and colleagues (2007). In addition, long-term datasets from more spatially restricted locales along their migration route are incorporated.

Responding to intensive whaling from 1850 to 1874 and then again in the early 20th century into the 1930s (Alter et al., 2012), the eastern Pacific gray whale population declined to lows of 1,000 to 2,000 individuals (Rice & Wolman, 1971). A bottleneck in the population is seen in the genetic data nearly 100 y or six generations ago, coinciding with the end of whaling and the classification of gray whales as "commercially extinct" (Alter et al., 2012). The current estimated number of gray whales is 19,126 individuals (Laake et al., 2012). This increase places pressure on foraging areas, leading to the suggestion that the carrying capacity of primary prey stocks in the Bering and Chukchi Seas and specifically the Chirikov Basin had been exceeded (Highsmith & Coyle, 1992; Le Boeuf et al., 2000; Moore et al., 2001). Coyle et al. (2007) suggest that the predation by gray whales has been the dominant factor in declines of dense patches of sediment-dwelling amphipods (Order Ampeliscidae). The gray whale response to these decreases, as an opportunistic predator, may be to utilize alternative foraging areas or other prey sources. Gray whales have been increasingly observed foraging in secondary foraging sites at the southern extent of the Bering Sea, as well as at tertiary areas that extend the length of their migration, particularly from Alaska to northern California (Kim & Oliver, 1989; Moore et al., 2001, 2007; Perryman & Lynn, 2002). Typically benthic feeders, gray whales have been documented to exploit more epibenthic or pelagic prey, in particular mysid shrimp (Family Mysidae) swarms (Dunham & Duffus, 2001, 2002).

Particular attention is given to foraging by gray whales in Clayoquot Sound on the west coast of Vancouver Island, Canada, between 49° 14' 36" N, 126° 6' 10" W and 49° 18' 51" N, 126° 14' 30" W (Figure 1). This area mirrors the community composition and ecological processes of northern latitudes but demonstrates the dynamic aspect of predator–prey relationships with multiple prey switching events. Clayoquot Sound has been noted as a feeding site for summering whales for more than 40 y, first recorded there by Hatler & Darling (1974). Gray whale feeding was noted in Clayoquot Sound in the sandy embayment of Ahous Bay on the west coast of Vargas Island. This site is protected from oceanic swell by surrounding reefs and islands. Detailed descriptions of the site were made by scuba diver observation and side scan sonar, in the summer months (July to September) of 1983 and 1984, mapping an area of 8 km^2 of dense amphipod tube mats, extending from the shallows to approximately 22-m water depths. Infaunal amphipods are the only known gray whale prey in Ahous Bay, with their coverage in the bay a result of its ubiquitous fine to medium sand-silt sediment (Oliver & Kvitek, 1984).

Infaunal prey likely had consistent annual use and removal by gray whales for 20 y, although

detailed records of foraging pressure are scant. Results from prey sampling programs in the early 1990s showed a decline in density of amphipod populations (Table 1), leading to the relocation of foraging and prey switching by gray whales (Duffus, 1996). Although foraging continued in Clayoquot Sound, the use of Ahous Bay became peripheral and was limited to a few whale

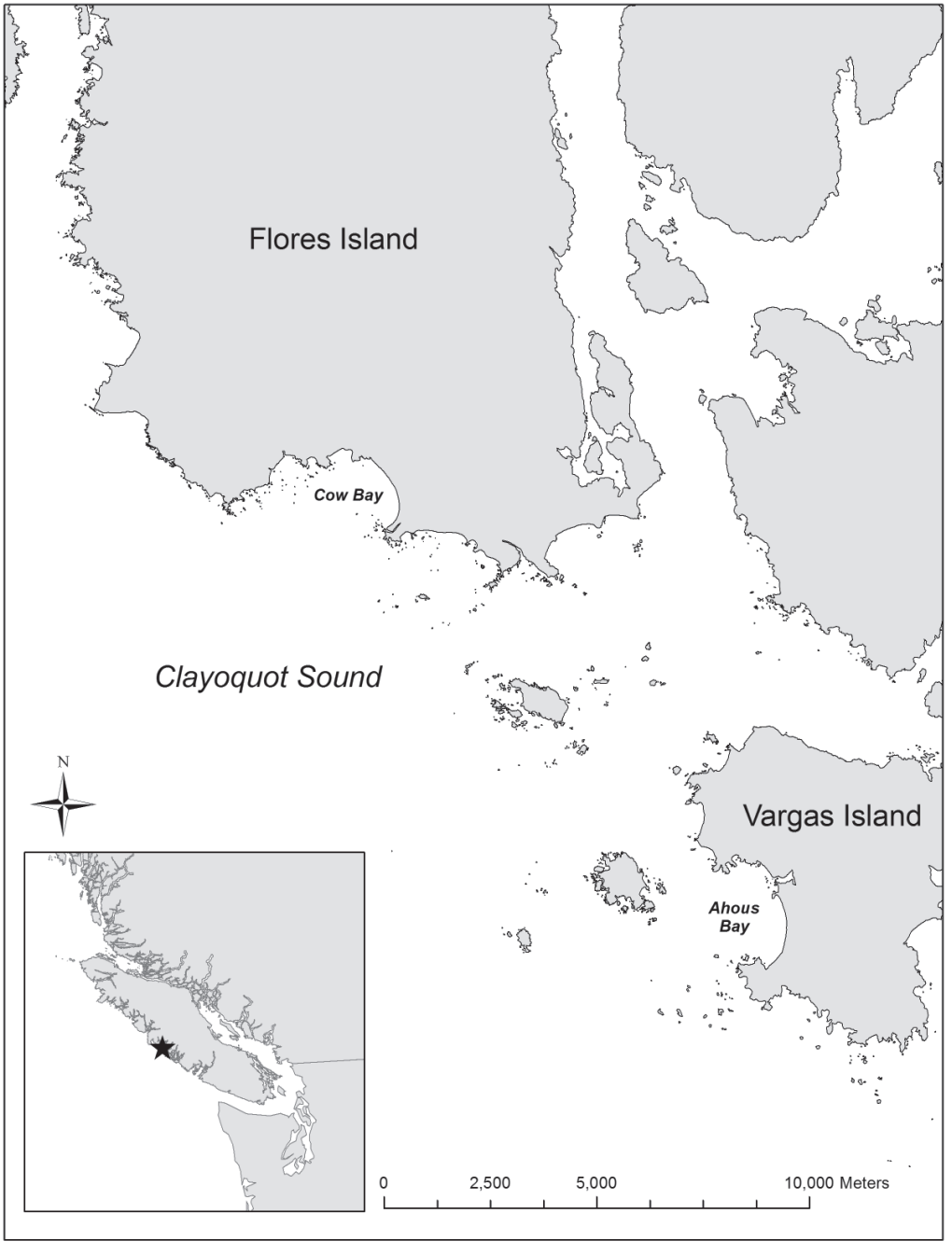

Figure 1. Map of study area of Clayoquot Sound (49° 14' 36" N, 126° 6' 10" W and 49° 18' 51" N, 126° 14' 30" W) indicating the two sample sites, Ahous Bay and Cow Bay

Table 1. Mean density estimations of amphipod prey in Ahous Bay over time

Ahous Bay			
Year	Number of samples	Density (ind/km^2)	Body length % ≥ 6 mm
1992	8	16,978	--
1995	17	15,832	--
1996	54	10,654	11.7
1997	29	12,186	19.0
2008	22	7,787	17.7

sightings in the early spring and late fall (Duffus, 1996; pers. obs., 1988-2014). This should have resulted in a predator release response for benthic amphipods in Ahous Bay. However, a sampling program of the bay a decade after the gray whales' abandonment found amphipod populations still unreplenished (Table 1). Continued but less frequent sampling from 2008 to 2013 found amphipods still very sparse and patchy. This suggests that the intensity of predation up until the mid-1990s may have pushed amphipod stocks into small population dynamics and/or energy decoupling from which they have yet to recover.

In addition to density calculations, measurement of prey resources for gray whales considers the percentage of individuals exceeding 6 mm in length (Table 1), the minimum size believed to be retained in gray whale baleen (Dunham & Duffus, 2001). Between 1997 and 2005, the proportion of sufficiently large individuals fell from 19 to only 10% of the population.

The use of Ahous Bay effectively ended in 1992 (Duffus, 1996; Dunham & Duffus, 2001, 2002). Foraging gray whales moved progressively into inshore waters over rocky reefs and kelp bed areas, primarily in Cow Bay, 5 km to the northeast. In Clayoquot Sound, this is habitat for swarms of mysids, and adjacent open water provided examples of opportunistic feeding on pelagic crab larvae. In the intervening years since the amphipod failure, gray whales occasionally searched Ahous Bay, although efforts were typically short lived and occurred later in the summer (pers. obs., 1988-2014). Our research vessel(s) in the local whale-watching fleet transit the bay daily during the whale foraging season, so reports of whale presence are always noted.

Several complementary ecological processes may be preventing amphipod recovery. First, following predation, the recolonization of patches is impeded by low dispersal of young amphipods due to the destruction of tube mats that they reinhabit. Second, those individuals that are not retained in baleen are widely redistributed and are susceptible to predation once they are removed from their tubes (Kim & Oliver, 1989). Third, from continued, occasional sediment sampling, it appears that the niche occupied by amphipods may have been colonized by other infaunal filter feeding invertebrates. The energy and resources once used by amphipods may now be the province of small clams (*Macoma* spp.) that have shown very large increases in the samples. Finally, the occasional appearance of gray whales in Ahous Bay, apparently testing the benthos for prey, may locate and decimate remnant amphipod stands, further retarding population recovery.

Furthermore, the amphipod species present in Clayoquot Sound have intrinsic barriers to rapid recolonization. Slow growth in colder winter waters does not allow amphipods to exploit the seasonal release from whale predation to recover from the summer losses. Also, the maturation time of Amplescid species (*Ampelisca aggassizi* and *A. careyi*) exceeds 2 y (Dunham & Duffus, 2002), which also hampers population recovery. Amphipod body size from between 1996 to 1997 clearly shows the evidence for elongated maturation time (Dunham & Duffus, 2001).

Despite these barriers to recovery, we believe the major factor in amphipod decline is the powerful nature of removal—that is, the intense annual predation by gray whales over a long time period. Although a pulse perturbation predation may stimulate higher rates of production and greater species diversity, a disturbance regime of such strength and consistency as seen in Ahous Bay by gray whales acts more like a press perturbation. This continued stressor may have pushed amphipod communities past the point of recovery, indicated by the lack of amphipods found in sediment samples and the continued disinterest of foraging whales in the area.

Typically, the release of predator pressure allows population recovery. In this example, paradoxically, the discontinued use by gray whales of certain locales can contribute to reduced productivity overall. The lack of sediment and nutrient mixing, which would result from the sifting of the substrate due to the filter-feeding methods of gray whales, may reduce resources for benthic filter feeders and alter sediment composition. Indeed, in addition to predation disturbance, there are other means by which gray whales can shape their environment—for example, when foraging, the whales are both removing energy and adding nutrients through defecation, a process Lavery et al. (2010) have termed a "manuring mechanism" (first used in Smetacek, 2008, p. 47) in the ocean system. This implies that gray whale predation has a greater influence on the ecological architecture of its foraging area and may impact prey populations through direct and indirect pathways.

These findings and conclusions are consistent with the work by Coyle et al. (2007) in similar but much more extensive benthic communities. In Clayoquot Sound, it is possible that amphipods may not show significant recovery and may not return as the prominent food source for gray whales. The new principal prey, epibenthic mysids, are apparently better able to combat the annual removal with shorter growth and maturation times, with reproduction cycles on a monthly rather than a yearly basis. Although there are several contributory factors to the demise of the amphipod populations discussed, predation by gray whales initiates and maintains the disturbance regime. The same may be true for feeding locales at higher latitudes. The resurgent population of gray whales could become resource limited over a wider geographical area, and prey-switching options may become progressively more important or populations may see more frequent fluctuations as experienced in 1998.

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