Gray whale distribution relative to forage habitat in the northern Bering Sea: current conditions and retrospective summary

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Abstract: Hundreds of gray whales (Eschrichtius robustus) stranded dead along beaches from Mexico to Alaska in 1999 and 2000. The cause of the mortalities remains unknown, but starvation resulting from a reduction in prey, especially in the Chirikov Basin, was suggested as the cause. In the 1980s, the Chirikov Basin was considered a prime gray whale feeding area, but there has been no recent comprehensive assessment of whale or prey distribution and abundance. In 2002, a 5-day survey for gray whales revealed restricted distribution in the basin and a 3- to 17-fold decline in sighting rates. To put these data in context, a retrospective summary of gray whale and benthic fauna distribution and abundance was undertaken. During the 1980s, gray whale sighting rates in the Chirikov Basin were highly variable. Ampeliscid amphipods dominated the benthos where gray whale sighting rates were highest. Available measures of biomass suggest a downturn in amphipod productivity from 1983 to 2000, when estimates of gray whale population size were increasing, suggesting that the whales simply expanded their foraging range. We encourage long-term study of the Chirikov Basin as a location where predator–prey responses to changing ocean climate can be researched, because decadal time series data are available.

Résumé : En 1999 et 2000, des centaines de baleines grises (Eschrichtius robustus) se sont échouées mortes sur les plages, depuis le Mexique jusqu’en Alaska. La cause de cette mortalité est inconnue, mais on a suggéré qu’elle pouvait être due à la famine, à cause d’une réduction de la densité des proies, particulièrement dans le bassin de Chirikov. Durant les années 1980, le bassin de Chirikov était considéré comme un site d’alimentation de premier choix pour les baleines grises, mais il n’y a pas eu d’évaluation détaillée récente de la répartition ou de la densité des baleines et de leurs proies. En 2002, un inventaire de 5 jours a révélé que la répartition des baleines grises était restreinte dans le bassin et que le taux de repérage avait diminué de 3 à 17 fois. Pour mettre ces données dans leur contexte, nous avons entrepris une revue des répartitions et des densités des baleines grises et de la faune benthique au cours des années. Durant les années 1980, les taux de repérage des baleines grises dans le bassin de Chirikov étaient très variables et ils atteignaient leur maximum lorsque les amphipodes ampélisidés dominaient le benthos. Les données de biomasse disponibles montrent un déclin de la productivité des amphipodes de 1983 à 2000, au moment où la taille estimée de la population de baleines s’accroissait, ce qui laisse croire que les baleines ont simplement étendu leur aire de recherche de nourriture. Nous favorisons l’établissement d’études à long terme dans le bassin de Chirikov pour suivre les réactions des systèmes prédateurs–proies aux changements climatiques de l’océan, car il existe déjà des séries de données temporelles à l’échelle des décennies.

[Traduit par la Rédaction]

Introduction

Two populations of gray whales (Eschrichtius robustus) occur in the North Pacific, nominally called Eastern and Western stocks (LeDuc et al. 2002). The Eastern North Pacific (ENP) population was removed from the list of endangered and threatened species in 1994, after three decades of research supported the conclusion that it had recovered from removals during commercial whaling (Buckland and Breiwick 2002). In March 1999, a scientific panel convened to conduct a review of population status 5 years after the delisting also concluded that the population was healthy and not in need of legislative protection (Rugh et al. 1999). That same year, the counts of dead gray whales stranded on beaches along their migration route skyrocketed to 273, an order of magnitude higher than in any prior year. In 2000, 354 dead gray whales...
were reported. This dramatic increase in documented mortal-
ities and the emaciated condition of many of the whales, 
generated speculation that starvation linked to a downturn in 
benthic productivity in the Chirikov Basin was the primary 
cause of death (LeBoeuf et al. 2000). Unfortunately, there is 
no simple way to test this hypothesis, owing to the prey 
plasticity and extensive foraging range of gray whales (Moore 
et al. 2001).

Gray whales feed on a broad range of invertebrates. Nerini 
(1984) listed prey of 19 genera reported from gray whale 
stomachs, including a wide variety of amphipods (e.g., Anony-
ux, Atylus, Lembos, Pontoporeia), decapods (e.g., Chionoecetes,
Nectocrangdon, Nephrops), and other invertebrates, such as 
molluscs, polychaete worms, and even sponges. While all 
other mysticetes filter or scoop prey from the water column,
gray whales suction sediment and epi- and in-fauna from the 
sea floor (Nerini 1984) in addition to filtering zooplankton from 
the sea surface and water column where prey densities 
are high (Darling et al. 1998; Dunham and Duffus 2001,
2002). Suction feeding is highly disruptive to the benthos 
(Oliver and Slattery 1985) and may be considered a special-
ized type of niche construction (Odling-Smee et al. 1996). In 
the 1980s, gray whales fed extensively in the Bering Sea, es-
pecially in the Chirikov Basin between St. Lawrence Island 
and Bering Strait (Braham 1984; Moore et al. 1986, 2000).
In the basin, the whales’ primary prey were ampelicid am-
phipods (Yablokov and Bogoslovskaya 1984), which domi-
nated benthic samples obtained from the late 1970s through 
the mid-1980s (Stoker 1981; Grebmeier et al. 1989). In the 
mid-1980s, the Chirikov Basin was reported to have the 
highest secondary production rates of any extensive benthic 
community (Highsmith and Coyle 1990). However, the abun-
dance and biomass of the amphipod community appeared to 
be in decline by the end of that decade (Highsmith and 

Gray whales feed opportunistically from the lagoons of 
Baja California, Mexico, all along their migration route 
along the west coast of North America to Alaska (Nerini 
1984). Furthermore, it is clear that some whales spend the 
summer feeding offshore Vancouver Island (Kvitk and Oli-
ver 1986; Darling et al. 1998; Dunham and Duffus 2001,
2002), off the southeastern coast of Kodiak Island, Alaska 
(K. Wynne, personal communication), along the north and 
south coasts of the Chukotka Peninsula (Berzin 1984; Miller 
et al. 1985), at shoals in the northeastern Chukchi Sea 
(Moore et al. 2000), and in some years, as far east as the Ca-
nadian Beaufort Sea (Rugh and Fraker 1981). While this ex-
tensive foraging range begs the question of the relative 
importance of the Chirikov Basin as a prey source, when 
combined with prey plasticity it may suggest why this spe-
cies has recovered from whaling in the ENP.

Our interest in gray whales focuses on their potential role 
as conspicuous bio-indicators of environmental variability. 
Because gray whales forage where prey densities are high, 
they can reflect local areas of very high secondary productiv-
ity (hereinafter “hotspots”) and indicate when conditions that 
support that productivity change. The spike in gray whale 
mortalities, observation of emaciated whales, and reported 
decline in benthic biomass in the northern Bering Sea set the 
stage for inquiry into the current status of gray whale 
distribution and relative abundance in the Chirikov Basin. Thus,
in 2002, we conducted an abbreviated aerial survey to 
determine gray whale distribution and relative abundance to 
compare with data from the 1980s. The dramatic changes 
seen led us to prepare a fine-scale retrospective analysis to 
compare the distribution and relative abundance of gray 
whales with that of the benthic-community distribution in 
the early to mid-1980s. This is the first direct collation of 
relative-abundance measures for predator and prey in this 
formerly prime gray whale feeding area and provides a base-
line for future comparisons. This type of retrospective ap-
proach is fundamental to climate-change models that seek to 
include apex predators as indicators of environmental vari-
ability.

Methods

Gray whale distribution and relative abundance were de-

erived from sightings made during aerial surveys conducted 
in autumn 1980 and during the summers of 1981–1985 and 
2002. Survey protocols used during the 1980s were adopted 
for the 2002 surveys, to allow direct comparison of results. 
Line-transect surveys, with randomly derived start and end 
points, were flown in a fixed-wing aircraft at altitudes of 
150–450 m. Two observers maintained a continuous watch 
for whales, while a third observer–recorder entered data on a 
portable computer that was linked to the aircraft avionics. 
Search surveys were conducted to and from the start and end 
points of transect lines and the aircraft occasionally deviated 
from the trackline to circle a sighting, to allow observers to 
make certain species identification and obtain an accurate 
count. Additional details of this protocol are described in 
Moore et al. (1986).

The survey area was post stratified to three regions (Fig. 1), 
focused on the Chirikov Basin (regions 1 and 2) and waters 
south and east of St. Lawrence Island (region 3). Whale 
distribution was plotted and an index of relative abundance cal-
culated as the number of whales seen per survey kilometre. 
This index was uncorrected for whales missed owing to visi-
bility bias (i.e., observer fatigue) or availability bias (i.e., 
submergence; see Marsh and Sinclair 1989).

A grid of water column and benthic sampling stations 
were occupied, both north and south of Bering Strait, from 
July to September 1984–1986, with four stations occupied 
opportunistically through 2000. Details of sampling protocol 
are given in Grebmeier et al. (1989). In brief, benthic sam-
ples (0.1 m² van Veen grabs) were washed on 1 mm sieve 
screens; then, to determine abundance and wet-mass (wet-
weight as used in Grebmeier et al. (1989)) biomass, animals 
were identified to family level, counted, and weighed. 
Highly mobile epifauna, such as crabs and sea stars, were 
excluded from the analysis, while relatively sessile epifauna 
and infauna were included. Abundance data were then entered 
into a numerical clustering program, which grouped sampling 
stations according to faunal similarities, as developed by 
Stoker (1981) and Feder et al. (1985).

Results

Aerial surveys (a total of 39 462 km) were flown in 
spring, summer, and autumn from 1980 to 1985 (Table 1). 
Gray whales were never seen during April surveys, nor in 2
of the 4 years when surveys were conducted in May (Table 2). Comparatively high counts of gray whales were recorded in October and November 1980 (the only year of substantive survey effort in autumn), May and June 1981, and July 1983. Differences in sighting rates indicate substantial intra- and inter-annual variability in gray whale distribution. For example, in October 1980, sighting rates were similar in regions 1 and 2 but, by November, the sighting rate in region 1 was nearly twice that in region 2. This suggests that either whales aggregated in the more northern region late in the feeding season that year or that whales migrating south from the Chukchi Sea moved into region 1, while whales in region 2 had already migrated south. Intra-annual shifts among regions are also evident in 1981, in which highest sighting rates jumped from region 2 in May, northward to region 1 in June, back to region 2 in July, and south to region 3 in August. Among years, 1983 stood out as a year of peak gray whale abundance in the Chirikov Basin, coincident with a strong El Niño condition in the ENP. Conversely, 1982 and 1984 were low-abundance years, although this may in part reflect low survey effort, especially in 1984.

July was the only month in which surveys were flown over 5 consecutive years and corresponds best with the timing of benthic sampling. Combined July survey effort consisted of 14 224 km (Fig. 2A). Gray whale distribution was clustered along a central axis in regions 1 and 2, off the northwest coast of St. Lawrence Island in region 2, and off the southeast coast of the island in region 3 (Fig. 2B). Finescale sighting rates were highest in regions 1 and 2 and southeast of St. Lawrence Island in region 3 (Fig. 3A) and provide a pattern of whale distribution for scaled comparison with benthic-community sampling stations.

Six benthic communities were identified in the study area, clustered on the basis of similarities in relative percentage of faunal composition (Fig. 3B). Four faunal groups (FGs I, III, IV, and XI) were associated with the comparatively cold, saline, nutrient-rich Bering Shelf – Anadyr Water (BSAW), with two groups (FG VIII and FG X) associated with warm, less saline, and nutrient-poor Alaska Coastal Water (ACW). Biomass of amphipods in FG I was especially high in midregion 1, with one station measuring 30–40 g C/m² and numerous stations showing 20–30 g C/m² (>10 000 individuals/m²). Conversely, biomass at most stations in regions 2 and 3 ranged from 10 to 20 g C/m², with the highest measure at 20–30 g C/m².

Of the six benthic communities characterized, abundance and biomass were exceptionally high in FG I and FG III (Ta-
Ampeliscid amphipods dominated (70%) the FG I community, but comprised only 21% of the abundance within FG III. The correspondence of feeding whales with FG I, but not with FG III, suggests that the prey abundance threshold was somewhere between 21 and 70% Ampeliscidae. Conversely, some feeding whales occurred in the area of FG IV, where Ampeliscidae comprised only 11% of the community. Sediment composition is key to tube-building organisms, such as *Ampelisca macrocephala*, and it is not surprising that substrate associated with FG I was composed primarily of fine and very fine sand, the type of material required for tube construction. Conversely, sediments associated with FG III and FG IV contained substantial proportions of silt and clay.

At fine scale, the highest gray whale relative abundance (2–5 whales/km; Fig. 3A) was associated almost exclusively with FG I (Fig. 3B). Whale abundance was especially high in the central portions of mid-regions 1 and 2, where benthic biomass was measured at 30–40 g C/m² or higher. Conversely, gray whale distribution did not overlap FGs III, VIII, and X, where ampeliscids comprised 21% of the abundance; nor did it overlap FG IV, which was dominated by bivalves. Combined, these results suggest that, at least in the mid-1980s, gray whales were selectively foraging on high-density patches of ampeliscid amphipods, nearly to the exclusion of other possible prey.

After 1986, benthic station 1 (BS1; Fig. 3B) in region 1 was occupied four times, BS2 and BS4 were sampled on three occasions, and BS5 was occupied in 1999 and 2000 (Fig. 4). Dramatic declines in Ampeliscidae biomass (9–15 g C/m²) were measured at three stations, with some suggestion of recovery at BS1 since 1993 and at BS2 since 1999. Results of the 2002 aerial surveys depict a corresponding decline in gray whale distribution and relative abundance. Although the study area was nearly completely surveyed during the 5-day effort (Fig. 5A), gray whale distribution was restricted to the northern portion of the Chirikov Basin and waters offshore northeast and southwest St. Lawrence Island (Fig. 5B). Sighting rates in the three regions dropped 3- to 17-fold, with the greatest difference between survey periods evident in region 2 (Table 4). While this 1-week survey can be considered only a “snapshot” of gray whale occurrence, it does suggest a marked downturn in whale foraging since the 1980s.

### Discussion

This retrospective analysis of gray whale and benthic fauna distribution and relative abundance in the northern Bering Sea provides a baseline for comparing a period when gray whales fed in what was considered a prime foraging
habitat (i.e., the 1980s) with a time when this habitat may be less than optimal. Regional indices of relative abundance show that gray whales were dynamic in their movements through the Chirikov Basin from May through November. In some years, the highest regional indices occurred in autumn, suggesting that whales may have aggregated to feed in the basin prior to initiation of the southbound migration. In July, fine-scale indices of whale abundance were associated with the highest biomass of one particular amphipod-dominated faunal group, suggesting strong prey selection, as shown for
gray whales feeding offshore Vancouver Island (Dunham and Duffus 2001, 2002).

Coyle and Highsmith (1994) predicted that the gray whale foraging rate on the ampeliscid amphipod communities in the Chirikov Basin, as seen in the 1980s, could not be sustained. Yet collective data suggest that the 30% decline in the gray whale prey base reported for 1986–1988 (Highsmith and Coyle 1992) had no immediate measurable effect on whale recruitment. The ENP gray whale population was estimated to number 16,555 (SE = 690) whales in 1979–1980, increasing to 20,348 (SE = 726) whales by 1985–1986 (Buckland and Breiwick 2002). In 1987–1988, when amphipod biomass was dropping, the population was estimated to number 21,113 (SE = 688) whales (Buckland et al. 1993), with the estimate increasing slightly to 23,109 (SE = 144) individuals by 1993–1994 (Buckland and Breiwick 2002). In 1997–1998, the highest estimate, 26,635 (SE = 2681) gray whales in 1997–1998 (Rugh et al. 1999), overlapped further declines in the benthic biomass measured at sampling stations in the north-central Chirikov Basin (Fig. 4) and south of St. Lawrence Island (Grebmeier and Dunton 2000). This apparent delay in the response of gray whales to their diminished food resources seems to conflict with the Perryman et al. (2002) model that shows a fairly sensitive positive correlation between gray whale foraging time in the Chirikov Basin (as inferred by ice cover) and calf recruitment.

Because gray whales feed on such a wide variety of prey and at so many locations along their range, it seems an oversimplification to equate the high mortalities in 1999 and 2000 solely to (or to focus recruitment models on) whale foraging opportunities in the Chirikov Basin. However, this formerly prime feeding area may be a bellwether for the state of gray whale foraging habitat, if either prey abundance or quality has changed significantly. Grebmeier and Dunton (2000) note that, while benthic biomass north of Bering Strait has remained high, there has been a change in dominant fauna that is likely the result of changing hydrographic conditions. This is important, because gray whale forage quality varies with species composition. For example, large A. macrocephala are especially lipid rich compared with other common amphipod prey (e.g., Byblis spp.), so conditions that favor Byblis spp. over A. macrocephala will result in a poorer diet for gray whales even when biomass remains high. Of note, Byblis spp. are the dominant amphipod found in samples from the central southern Chukchi Sea (J.M. Grebmeier, unpublished data). Further, prey species size is

<table>
<thead>
<tr>
<th>Benthic faunal group</th>
<th>Water type</th>
<th>Mean abundance (no./m²)</th>
<th>Mean Ampeliscidae (%)</th>
<th>Mean biomass (g C/m²)</th>
<th>Sediment composition (%)</th>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>I</td>
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<td>6940</td>
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<tr>
<td>III</td>
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<tr>
<td>XI</td>
<td>BSAW</td>
<td>1684</td>
<td>0</td>
<td>12.5</td>
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</tbody>
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*SC, silt and clay; VFS, very fine sand; FS, fine sand; MS, medium sand; CS, coarse sand; GR, gravel; —, no data.

Fig. 4. Biomass time series for dominant benthic amphipod at four stations in the northern Chirikov Basin, 1983–2000 (data from Stoker 1981; Grebmeier et al. 1989; Grebmeier 1993; Grebmeier and Dunton 2000; J.M. Grebmeier, unpublished data).
influenced by organic-matter flux, with the density of small amphipods (e.g., *Ampelisca birulai*) favored when organic flux is low (Coyle and Highsmith 1994). Finally, warming seas will elevate amphipod food requirements, which may lead to elevated predation rates, both selecting for smaller prey species (Coyle and Highsmith 1994). Thus physical forcing, which directly affects pelagic–benthic coupling of biological processes in the northern Bering and Chukchi Seas (Grebmeier 1993; Grebmeier and Cooper 1995), is key to any assessment of gray whale prey availability.

The Chirikov Basin and areas southwest of St. Lawrence Island and north of Bering Strait are at the downstream end of the productive current that follows the edge of the continental shelf in the Bering Sea called the “Green Belt” (Springer et al. 1996). These productive benthic zones are the result of carbon and nutrient transfer to the shallow shelves of the northern Bering and Chukchi seas (Grebmeier 1993; Grebmeier and Cooper 1995), is key to any assessment of gray whale prey availability.

The Chirikov Basin and areas southwest of St. Lawrence Island and north of Bering Strait are at the downstream end of the productive current that follows the edge of the continental shelf in the Bering Sea called the “Green Belt” (Springer et al. 1996). These productive benthic zones are the result of carbon and nutrient transfer to the shallow shelves of the northern Bering and Chukchi seas (Grebmeier and Barry 1991). Productivity along the “Green Belt” is strongly influenced by the Pacific Decadal Oscillation (PDO), which reflects the relative position and strength of the Aleutian Low (Francis et al. 1998). Overall, a decline in seabird and marine mammal populations in the North Pacific correlates with the PDO, although linking mechanisms remain poorly understood (Springer 1999). Recent reports of an overall decline in carrying capacity in the Bering Sea during the past two decades (e.g., Schell 2000) are countered by observations of increases in concentrations of various species of zooplankton there (e.g., Napp et al. 2002). So, as yet there is no clear picture of marine ecosystem response to atmospheric oscillations, and its affect on benthic environments such as the Chirikov Basin.

Perhaps most important to benthic infauna, sediment grain size is directly related to current strength. Recent evidence points to a weakening in current flow in the Gulf of Anadyr and through Bering Strait (Roach et al. 1995). Changes in current strength and flow directly impact carbon deposition, sediment composition, and benthic-community structure (Grebmeier 1993). Individual species of benthic infauna require specific sediment regimes within which to feed and grow. Over the last decade, the sediment structure in the northern Bering Sea has changed and sediments in the Chirikov Basin have become coarser, suggesting a changing hydrographic regime. Since the dominant ampeliscid amphipod in the FG I group (Fig. 3B) is a tube builder that agglutinates fine sediment into its tubes, coarser sediments could lead to a reduction in amphipod numbers. In addition, a 30% decline in sediment oxygen uptake in the productive areas to the southwest of St. Lawrence Island was observed during the 1990s (Grebmeier and Cooper 1995). This decline in sediment oxygen uptake is another indication of a reduction of carbon supply to the benthos.

As the ENP gray whale population has increased, top-down (predation) and bottom-up (production) effects have acted negatively and synergistically to reduce available prey in the Chirikov Basin. Seemingly, gray whales have responded to this by expanding their foraging range. Still, we encourage long-term study of the Chirikov Basin as the best location to investigate predator–prey responses to changing

<table>
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<th>Region</th>
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<td>0.209</td>
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