

Use of Nearshore and Estuarine Areas of the Southeastern Bering Sea by Gray Whales (*Eschrichtius robustus*)

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ABSTRACT. During spring aerial surveys of the coast of the southeastern Bering Sea significant numbers of gray whales were seen in nearshore waters along the north side of the Alaska Peninsula. Many (50-80%) of these animals were observed surfacing with mud trails or lying on their sides, characteristics both associated with feeding. A migration route close to shore (within 1-2 km) was used until whales neared Egegik Bay, where they began to head west 5-8 km offshore, across northern Bristol Bay. Smaller numbers of gray whales were present throughout summer in nearshore waters and estuaries along the north side of the Alaska Peninsula. At Nelson Lagoon gray whales normally used the lagoon in spring, were absent during early summer, returned in mid-summer, and then were present until late November when they departed for the wintering grounds. Gray whales were present in the lagoon most often during periods of peak tidal flow; those that appeared to be feeding were oriented into the current. Three behaviors that appeared to be associated with feeding were observed: side-feeding from a stationary position within shallow waters of lagoon channels, diving within the lagoon and in nearshore waters, and elliptical side-feeding in the surf zone along the outer coast. Large crustaceans of the genus *Crangon* were available to and probably eaten by gray whales at Nelson Lagoon.

Key words: gray whale, *Eschrichtius robustus*, feeding, behavior, estuaries, Bering Sea, Alaska

RÉSUMÉ. Un nombre significatif de baleines grises de Californie ont été aperçues près du littoral nord de la péninsule de l'Alaska, lors d'inventaires aériens printaniers de la côte sud-est de la mer de Béring. Un bon nombre (50-80%) de ces animaux se déplaçaient vers la surface laissant une traînée de boue, ou reposaient sur leur côté, deux caractéristiques associées à l'alimentation. Les baleines suivaient une voie migratoire nageant à 1 ou 2 km du littoral jusqu'à la baie Egegik, où elles s'éloignaient vers l'ouest à entre 5 et 8 km du littoral, en traversant le nord de la baie Bristol. Quelques baleines fréquentaient les estuaires du littoral nord de la péninsule de l'Alaska et les eaux adjacentes tout le long de l'été. D'ordinaire, les baleines grises de Californie se déplaçaient dans la lagune Nelson au printemps, quittaient la région au début de l'été, y retournaient au milieu de l'été et y demeuraient jusqu'à la fin-novembre lorsqu'elles partaient pour les eaux d'hivernage. Ces baleines étaient présentes dans la lagune surtout pendant les périodes d'écoulement maximal de la marée; celles qui semblaient se nourrir faisaient face au courant. Trois comportements semblaient être associés à l'alimentation: l'alimentation stationnaire reposant sur le côté dans les eaux peu profondes des chenaux de lagunes, la plongée dans les lagunes et dans les eaux près du littoral, et l'alimentation elliptique reposant sur le côté dans la zone des brisants le long de la côté extérieure. Des gros crustacés du genre *Crangon* sont trouvés dans la lagune Nelson et servaient probablement de nourriture aux baleines grises de Californie qui s'y trouvaient.

Mots clés: baleine grise de Californie, *Eschrichtius robustus*, alimentation, comportement, estuaires, mer de Béring, Alaska

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РЕЗЮМЕ. В течение воздушного обзора юго-восточного, Берингского побережья наблюдалось значительное количество серых китов (*Eschrichtius robustus*), в море недалеко от берега вдоль северного берега Аляского Полуострова много (50-80%) из тех китов которых мы наблюдали всплыли с грязями следами или лежали в море на боку. Оба этих чертах характеризуются поведением в течение кормления. Миграционный путь использован китами находится близко от берега (в пределах 1-2 км) до эгегикского Залива, отсюда киты начали направиться на запад 5-8 км от берега, через северную часть Бристольского Залива. Небольшая группа китов присутствует все лето в прибрежном море и устьях вдоль северного берега Аляского Полуострова. В Нелсонской Лагуне обычно присутствуют серые киты весной и отсутствуют раннее лето, возвращающиеся в середине лета и тогда присутствует там до позднего ноября когда они отбыли в зимнее местожительство. Серые киты присутствовали в лагуне часто всего во время максимума ного прилива, и те которые кормили ориентировали прямо в ток. (1) Кормление сбоку в постоянное положение в неглубокой воде лагунского протока, (2) когда нырнули киты в лагуну и в прибрежную воду, (3) и эллиптическое кормление сбоку в прибойном поясе вдоль внешнего берега. Большие ракообразные рода *Crangon* существуют там в Нелсонской Лагуне и несомненно использованы китами.

Основные слова: серый кит (*Eschrichtius robustus*), кормление, поведение, устья, Берингское Море, Аляска.

Russian abstract provided by K. Galvin.

INTRODUCTION

Throughout its annual cycle the gray whale (*Eschrichtius robustus*) is the most coastal of the baleen whales (Mysticeti). The California stock breeds within the lagoons on the Pacific side of Baja California and migrates along the Pacific Coast of North America to and from its summering grounds on the continental shelf of the northern Bering and southern Chukchi seas (Pike, 1962; Rice and Wolman, 1971; Rugh and Braham, 1979; Hall, 1981; Lowry *et al.*, 1982; Marquette and Braham, 1982). Hall (1981) and Norris *et al.* (1982) have recently discussed the recovery of the population from past exploitation, particularly in relation to the species' extensive use of coastal areas throughout its life cycle. They speculated that the

species evolved considerable behavioral flexibility, perhaps because of its association with coastal areas that have undergone frequent and rapid changes in sea level and morphology throughout recent geologic time. However, other than on the breeding grounds (Norris *et al.*, 1982), information on use of nearshore and sublittoral habitats by gray whales is scarce. Darling (1977) studied a small population summering along the west coast of Vancouver Island, Canada, and Votrogov and Bogoslovskaya (1980) and Zimushko and Ivashin (1980) mentioned the use of lagoons by gray whales summering along the Chukchi Peninsula in eastern Siberia.

Between 1976 and 1982 we collected information on gray whales using nearshore and estuarine areas on summering

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grounds along the Alaska Peninsula. The purpose of this paper is threefold: 1) to describe use of these nearshore and estuarine areas by gray whales; 2) to discuss this use in relation to tidal cycles at Nelson Lagoon, a major estuary along the north side of the Alaska Peninsula; and 3) to describe probable feeding behaviors and potential foods of gray whales using Nelson Lagoon and other estuaries.

METHODS

Most of the data presented on the occurrence, behavior, and potential foods of gray whales were obtained ancillary to studies of birds at Nelson Lagoon between 1976 and 1980 (Fig. 1). One of us (RG) and eight other observers were present a total of 473 days during this period. We worked from a camp fronting the main channel of the lagoon, about 1 km east of the village of Nelson Lagoon, from which whales entering the lagoon could be readily seen. Information on numbers of whales and individual behavior was recorded during extensive

land-based bird surveys near this and other areas of the lagoon. Numerous aerial and small-boat surveys were also conducted, during which information on gray whales was recorded. Gill and Jorgensen (1979), Gill *et al.* (1981), and Petersen (1980, 1981) give detailed descriptions of the survey frequency and techniques. Data on gray whales' use of nearshore and estuarine areas elsewhere along the Alaska Peninsula and Bristol Bay were gathered during aerial surveys of birds along the coast. Surveys from the mouth of the Kuskokwim River to Unimak Pass (Fig. 1) were flown five times: 23 April 1976, 1-3 October 1979, 6-8 October 1980, 23-27 April 1981, and 4-7 October 1981. Surveys along the south side of the Alaska Peninsula from Unimak Pass to Wide Bay (Fig. 1) were flown three times: 24-27 April 1981, 7 October 1981, and 3 May 1982.

On most aerial surveys we were censusing water birds from low altitudes (100-300 m), so only whales within 1 km of shore were recorded. However, we flew three segments of the

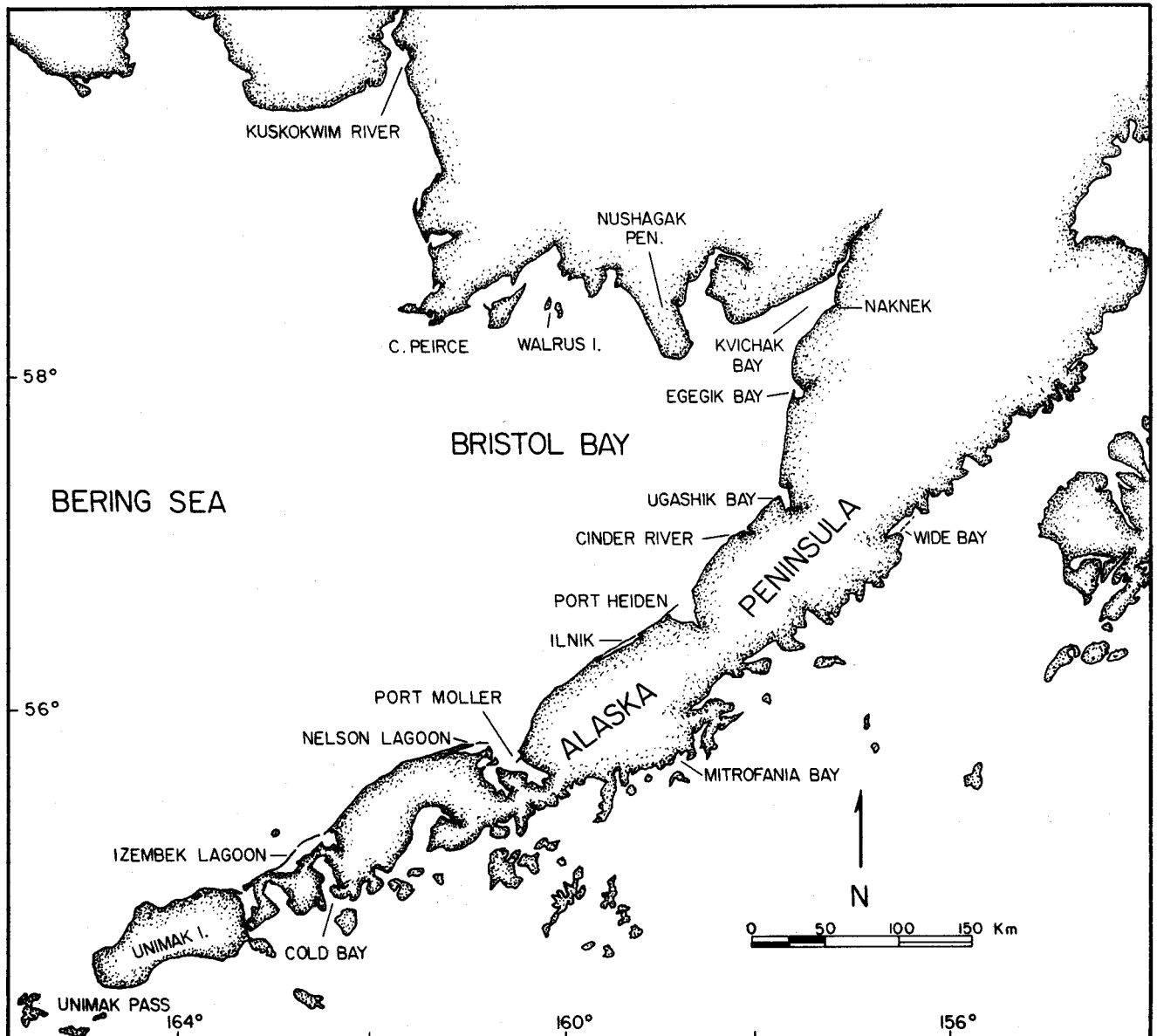


FIG. 1. Map of the southeastern Bering Sea showing locations mentioned in the text.

April 1981 survey (Izembek to Nelson Lagoon once; Ilnik to Naknek twice) at 800-1000 m altitude, specifically to census gray whales in nearshore waters. On these flights most whales within 5 km of shore were visible and we recorded some as far offshore as 8 km. During surveys of northern Bristol Bay in spring of both 1981 and 1982, densities of birds were low and we were able to devote considerable time to censusing whales. Surveys during these periods were flown at 500-800 m which allowed effective coverage of up to 6-8 km from shore. We realize that during our surveys some whales may have been migrating beyond the limits noted above; nevertheless, we feel our data accurately reflect use by gray whales of the immediate nearshore waters along the north side of the Alaska Peninsula and northern Bristol Bay. During all surveys we considered a whale to be feeding if it was observed with a mud trail in its wake or if it was seen maneuvering on its side in shallow water. Such observations have been suggested by others as evidence of feeding by gray whales (Fay *in Pike*, 1962; Ray and Schevill, 1974; Darling, 1977; Rice, 1978; Harrison, 1979; Norris *et al.*, 1982). We were able to record these characteristics reliably, however, only for whales within 1 km of shore.

We acquired information on foods available to (and probably eaten by) gray whales in Nelson Lagoon from two sources: identification of items eaten by birds shot while feeding at or just below the surface of water roiled by a whale that appeared to be actively feeding; and two epibenthic samples taken near whales that appeared to be feeding. These samples were obtained with a long-handled dip net (18 x 15 x 10 cm net dimensions, 1.0 mm mesh). For each sample the net was dragged first across the bottom and then 1 m above the bottom over a distance of 3-5 m. The samples were taken in water 2 m deep within 3-8 m of a whale swimming on its side.

Exact locations of places within the Nelson Lagoon-Port Moller complex that are frequently mentioned in the text (i.e., Mud Bay, Herendeen Bay, and Deer Island) can be found on U.S. Department of Commerce, National Oceanic and Atmospheric Administration nautical chart 16363 (Port Moller).

RESULTS AND DISCUSSION

Seasonal Use

Nearshore waters. Gray whales enter the Bering Sea in spring through Unimak Pass (Hessing, *in press*), and once there, a significant number of them appear to migrate along the north side of the Alaska Peninsula close to shore. In late spring 1976, when pack ice effectively blocked the coastline north of Izembek Lagoon, we saw 26 gray whales within 1 km of the shore of Unimak Island (Table 1). Hessing (*in press*), during extensive land-based and aerial surveys of gray whale migration through Unimak Pass and along the north side of Unimak Island in spring 1981, saw no animals farther offshore than 2.5 km. Our surveys in April 1981, which coincided with the peak of gray whale migration through Unimak Pass that spring (Hessing, *in press*), showed that after entering the Bering Sea many gray whales continued to migrate along the coast within 1 km of shore (Table 1). North of Ugashik Bay we began to see whales farther offshore. Indeed, of the 65 whales seen along the north side of the Alaska Peninsula more than 1 km offshore on 24 April 1981 (Table 1), 61 (94%) were seen north of Egegik Bay and were 5-8 km offshore. During the survey between Izembek Lagoon and Naknek on 27 April 1981, beginning at Ilnik we noted a few whales more than 1 km from the beach, but again the majority of animals remained close to shore until just beyond Egegik. Here gray whales were observed moving west across lower Kvichak Bay towards the Nushagak Peninsula (Fig. 1), roughly following the 14-18 m isobath. The paucity of observations of whales in nearshore waters west of the Nushagak Peninsula (Table 1) suggests that the animals migrate through northern Bristol Bay farther offshore (perhaps south of the Walrus Islands) than while along the Alaska Peninsula (Fig. 1). However, there is some indication that the migration route through this part of Bristol Bay may change as the season progresses. In spring 1976 Margaret Petersen (U.S. Fish and Wildlife Service, pers. comm. 1983) documented considerable movement of gray whales past Cape Peirce within 1 km of shore; however, the

TABLE 1. Numbers and behavior of gray whales seen during aerial surveys of nearshore waters along the Alaska Peninsula and northern Bristol Bay

Area surveyed	Dates surveyed	No. whales < 1 km from shore		No. whales 1-8 km from shore ^b
		No. seen	No. feeding (%) ^a	
South side of Alaska Peninsula				
Wide Bay to Unimak Pass	24-27 April 1981	14	2(14)	—
Mitrofanina Bay to Cold Bay	3 May 1982	21	2(9)	—
North side of Alaska Peninsula				
North Unimak Island ^c	23 April 1976	26	13(50)	—
Ilnik to Naknek	24 April 1981	69	52(75)	65
Izembek Lagoon to Naknek	27 April 1981	105	84(80)	17
Northern Bristol Bay				
Naknek to Kuskokwim R.	23 April 1981	3	0(0)	11
Naknek to Kuskokwim R.	3 May 1982	3	0(0)	0

^aSurfacing with mud trails or seen on their sides (see Pike, 1962; Darling, 1977; Rice, 1978; Harrison, 1979; Norris *et al.*, 1982).

^bDash indicates area not surveyed.

^cCoastal area from Nelson Lagoon north effectively blocked by ice.

majority of her 215 observations occurred in early June and involved primarily cow-calf pairs (cf. Hessing, in press). She recorded only six whales within 4 km of shore during late April and May, the usual period of peak spring migration of adult and subadult gray whales into the Bering Sea (Hessing, in press).

The extent of use of nearshore areas by gray whales in summer and fall in the southeastern Bering Sea is unclear. Our occasional incidental sightings ($n=17$) of gray whales 0-3 km offshore of Nelson Lagoon from June through September (1976-1979) indicates that nearshore areas were used in summer, but whether these animals represented summer residents, or late spring or early fall migrants, is unknown. We can shed little light on the use of these areas during fall migration as our aerial surveys at that time generally preceded by several weeks the southward movement of gray whales out of the Bering Sea (Rugh and Braham, 1979). During aerial surveys of nearshore waters from the Kuskokwim River to Unimak Pass during the first week of October 1979, 1980, and 1981, we saw one, two, and no whales, respectively, within 1 km of shore. Similarly, we saw no whales along the entire south side of the Alaska Peninsula during early October 1981.

Estuaries. Estuaries along the north side of the Alaska Peninsula also appeared to be important to gray whales, particularly in spring, and small, perhaps resident, populations used them throughout summer and fall. Within Nelson Lagoon between 1976 and 1979 we recorded 197 sightings of gray whales. The highest number of whales recorded in the lagoon at any one time was nine; these were seen during an aerial survey on 25 September 1977. Within the area of the Nelson Lagoon-Port Moller complex (Fig. 1) we also sighted whales as far inshore as the southern end of Deer Island and the mouth of Mud Bay. We never saw gray whales in the much deeper waters (30-100 m) of Herendeen Bay, nor have they been seen there by long-time residents of Nelson Lagoon (Paul Gundersen, pers. comm. 1978).

Other estuaries along the north side of the Alaska Peninsula at which we found gray whales included Ilnik, Port Heiden, Cinder River, and Ugashik and Egegik bays (Fig. 1). We saw no gray whales in Izembek Lagoon and only rarely have they been reported there previously (Robert Jones, Jr. and John Sarvis, U.S. Fish and Wildlife Service, pers. comm. 1982). Because we were primarily counting water birds on intertidal flats during our aerial surveys of these estuaries, we were not able to record all the whales present at these sites. However, M.E. Isleib (pers. comm. 1982) recorded considerable use of Ugashik Bay by gray whales in spring and summer. Between late May and early July 1982, Isleib estimated that he made over a thousand sightings of gray whales in the bay; 10-20% of these sightings were of whales as far as 15 km into the bay, and he estimated that on any given tidal cycle 50 whales were in the estuary.

It may be that gray whales use other estuaries along the Alaska Peninsula seasonally, as they use Nelson Lagoon. Generally, whales used Nelson Lagoon in spring, were absent for a brief period in early summer, and then were present

through late summer and fall (Fig. 2). Residents of Nelson Lagoon (P. Gundersen and Peter Kust, pers. comm. 1981-1983) reported a similar trend, but indicated that gray whales were usually absent during July, returned in August, and then used the lagoon steadily until their departure in middle to late November. The particular periods of use we recorded in spring 1976 and 1977 (Fig. 2) may have been related to the availability of food, which in turn might have been affected by ice scour. In 1976 the Bering Sea ice pack extended south of Nelson Lagoon and ice breakup in the lagoon did not occur until the first week of May. That spring whales were seen in the lagoon for only a brief period in late May. In 1977 no ice formed in the lagoon and whales were present throughout May and into mid-June.

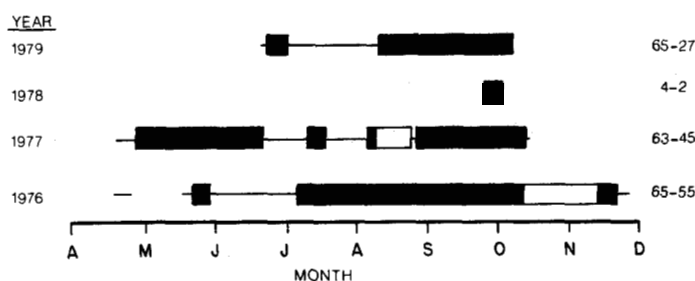


FIG. 2. Approximate temporal occurrence of gray whales in Nelson Lagoon, 1976-1979. The thin line represents the period when observers but no whales were present. The thick bar represents the period when whales were present. The open bar is the period when observers were absent, but residents of Nelson Lagoon reported whales present most days during those periods. Residents have reported that gray whales were never present in the lagoon between December and early March. Of the numbers on the right, the first represents the total number of whales recorded by us that year, and the second is the total number of days on which one or more whales was seen that year.

Feeding

Nearshore waters. Although small numbers of gray whales have been reported feeding in nearshore waters during migration and while on the breeding grounds (Sund, 1975; Darling, 1977; Wellington and Anderson, 1978; Norris *et al.*, 1982), the majority are not known to begin feeding intensively until they reach the northern Bering Sea (Zimushko and Lenskaya, 1970; Rice and Wolman, 1971; Zimushko and Ivashin, 1980; Lowry *et al.*, 1982). During aerial surveys along the south side of the Alaska Peninsula in spring of both 1981 and 1982 we observed few gray whales that appeared to be feeding (Table 1); likewise, during spring of 1981 Hessing (in press) recorded probable feeding by gray whales in Unimak Pass on only 9 of 87 days of observations. However, our data suggest that once gray whales move into nearshore and estuarine waters along the north side of the Alaska Peninsula, many of them begin feeding. During our three spring aerial surveys (Table 1), 50-80% of the whales seen within 1 km of shore between Unimak Pass and Naknek were trailing mud plumes or were on their sides.

Some of the gray whales apparently feeding in nearshore waters were lying on their sides in shallow water, usually just beyond the surf zone. The animals appeared to be exhibiting a feeding behavior originally described by Ray and Schevill

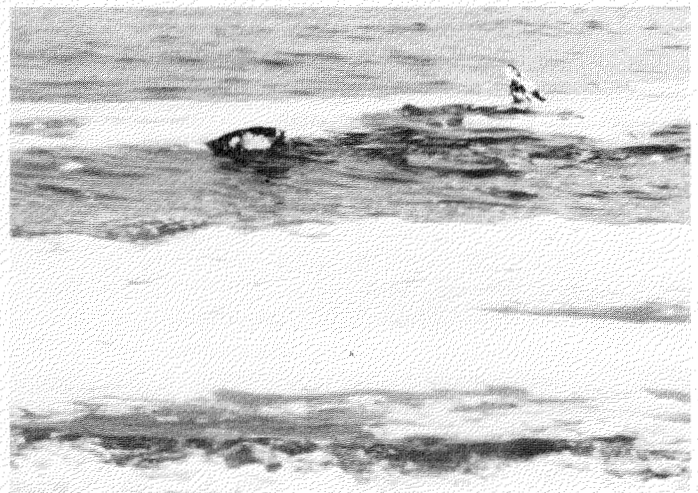
(1974) for a captive gray whale, whereby the whale sucked food from the bottom while swimming tipped over 120° from the vertical with its gape nearly parallel to the bottom. We also saw whales diving in deeper nearshore waters (6-20 m) of Bristol Bay and either surfacing with mud plumes behind them or swimming with bottom sediments washing from their bodies; these animals may have been feeding on their sides, but we could not determine this.

On one occasion we observed a different, and previously unreported, variation of "side-feeding". On 25 July 1982, while standing on shore about 8 km west of Nelson Lagoon, RG observed a whale, estimated at about 13 m total length, swimming on its side in and just beyond the surf in 2-3 m of

water, apparently feeding. At the time of the observation tidal currents were minimal. When first seen, the animal was on its side with its back facing and parallel to the beach (Fig. 3). Then, using its fluke and probably the submerged pectoral fin, the whale propelled itself along the bottom, moving in an ellipse with its body flexed in a moderate dorsal arch. As the whale moved, its exposed fin and fluke were in constant motion; sometimes they undulated actively and became almost completely exposed, the fluke to the notch of the tail and the fin to its base (Fig. 3a). After completing the ellipse, the animal rolled upright and breathed once as it slowly swam parallel to the shore for about two body-lengths. Then it again rolled onto its side and repeated the same motions. The whale



A



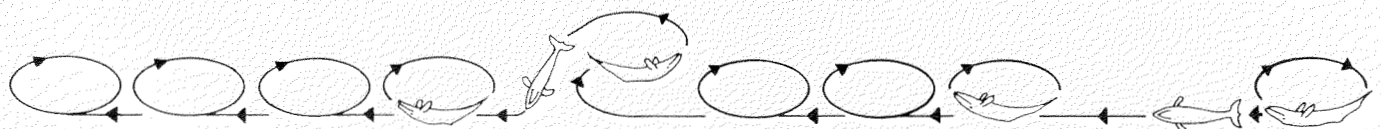
B



C



D



E

FIG. 3. Elliptical side-feeding by an adult gray whale. The whale is just beyond the surf and about 15 m from the beach. A. The animal is on its left side with its dorsal surface towards the beach, and its tail is flexed as it begins to move in a clockwise rotation. B. The body is moderately arched with the ventral surface of the right pectoral fin and the dorsal surface of the right fluke presented. C. The whale has passed the top of the ellipse and has begun to turn towards the beach. D. The whale is again parallel to the beach and on its left side. E. Schematic drawing of the elliptical side-feeding sequence observed 25 July 1982.

completed four such ellipses; midway into the fifth ellipse it rolled upright, took a breath, and then rolled onto its opposite (right) side and began to move in a counterclockwise ellipse. Just as the long axis of the body came perpendicular to the beach the animal rolled upright and moved so that it was again parallel to the shore just beyond the surf. The whale then moved about two body-lengths, turned onto its left side, and resumed a series of clockwise ellipses. The animal completed nine such ellipses, averaging 90-120 seconds per ellipse, during the 15 minutes it was observed (Fig. 3e). The long axis of a typical ellipse was about 20-25 m long. Although this behavior was seen only once, the repetitive pattern of the elliptical "side-feeding" suggested that it may be a regular component of the behavioral repertoire of this species.

Within Nelson Lagoon. Gray whales were most frequently seen in Nelson Lagoon during periods of highest tidal velocities, which occurred 1-2 hours before low or high tide (Fig. 4). Peak tidal ebb and flood velocities in Nelson Lagoon range between 70 and 120 $\text{cm}\cdot\text{sec}^{-1}$; velocities during mid-tide are about half of these values (Pearson *et al.*, 1981). We never observed whales in the lagoon during the hour before or after high tide; however, on occasion whales remained there during low tide, usually in the upper lagoon as far as 8 km from the entrance. During all of the 105 sightings within the lagoon for which we recorded whale behavior in relation to stage of the tide, the whale was oriented into the prevailing tidal current, a behavior presumably adapted for feeding (see below). Norris *et al.* (1982), studying gray whales in lagoons of Baja California, found that as tidal velocities increased the animals ceased courtship-mating patterns, congregated at the mouths of lagoons, and oriented themselves into prevailing currents, presumably to feed. As slack tide approached, the whales once again began to mill about and resumed courtship.

We suspected that any gray whale that maintained a stationary position on its side in shallow intertidal or subtidal water, or that was diving in the deeper channels of Nelson Lagoon, was feeding. Between 1976 and 1982 we observed

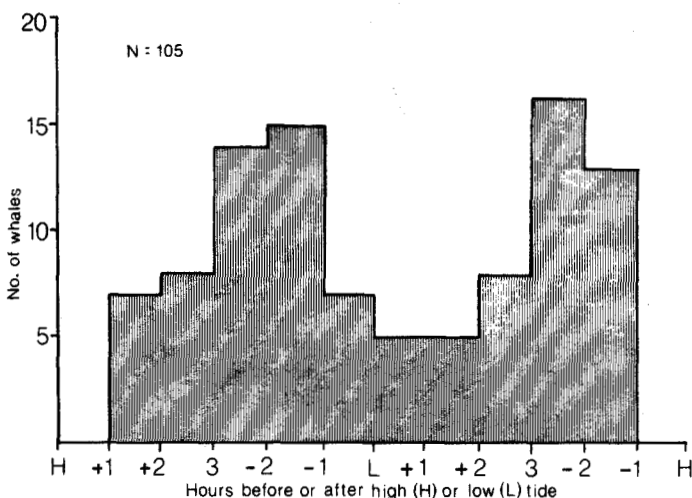


FIG. 4. Presence of gray whales suspected of feeding in Nelson Lagoon in relation to the stage of the tide. Observations cover the period 1976-1979. Peak tidal velocities occur 1-2 hours before low or high tide.

apparent side-feeding behavior in the lagoon on at least a dozen occasions, and in every instance the animal was oriented into the prevailing tidal current in shallow water (2-3 m deep) and kept its dorsal surface towards the deepest part of the tidal channel. A whale on its side in the lagoon usually exposed the upper third of both a fluke and pectoral fin (cf. Fig. 3), often undulating them slowly, but occasionally moving them vigorously. Where the tidal current was strong, this motion probably helped keep the animal stationary, but often the more vigorous motion occurred when the whale had worked its way into shallow water and was attempting to return to deeper water. We saw no evidence that whales favored one side of their bodies over the other when maneuvering on their sides (cf. Kasuya and Rice, 1970).

Whales that were diving, and presumably feeding, in the lagoon always faced into the current and often appeared to remain stationary, as judged by their locations when they surfaced to breathe. Norris *et al.* (1982) also observed gray whales diving in this manner in lagoons on the wintering/calving grounds. They speculated that such behavior allowed the whales to take advantage of foods being carried to them by the currents, and that because of the absence of evidence that any of the animals had been "grubbing" in the bottom sediments (cf. Pike, 1962), they were probably feeding on organisms in the water column. Whales observed diving within Nelson Lagoon may have been feeding in this manner because none was seen surfacing with bottom sediments streaming from its mouth or body (cf. whales feeding in nearshore waters). We regularly observed organisms, particularly gammarid amphipods, concentrated in eddies and along fronts of tidal currents in the main channel of the lagoon, and suspected that other epibenthic forms may have been similarly concentrated and transported by currents in the deeper waters of the lagoon, and thus available to whales diving and feeding in these areas.

Probable Foods

On 22 and 23 September 1977 Bonaparte's Gulls (*Larus philadelphia*) and Mew Gulls (*L. canus*) in a mixed flock were observed in upper Nelson Lagoon plunge-diving and seizing items from the surface next to a gray whale that was on its side and appeared to be feeding. The whale was observed from a

TABLE 2. Items identified from bird stomachs and epibenthic samples collected near gray whales exhibiting side-feeding behavior in Nelson Lagoon

Sample source	No. prey	Species	Length ^a
Birds (n=4) (Bonaparte's and Mew gulls)	12	<i>Crangon septemspinosus</i>	51.8 ± 6.5 mm, 41-67 (\bar{X} ± SD, range)
Epibenthic 31 May 1977	6	<i>Crangon septemspinosus</i>	43.6 ± 14.9 mm, 34-72
	2	<i>Saduria entomon</i>	30.8, 39.5 mm
	1	<i>Anisogammarus pugettensis</i>	6.0 mm
	2	<i>Oncorhynchus keta</i>	39.0, 40.0 mm FL
2 October 1977	2	<i>Crangon septemspinosus</i>	48.0, 58.0 mm

^aLength measurements: FL = fork length; all other measurements are total length.

distance of 10-50 m for about two hours each day during the low-water cycle as it wallowed on its side in water 1.5-2.5 m deep. Two Bonaparte's Gulls and two Mew Gulls were shot while they fed around the whale. Whole, freshly ingested sand shrimp (*Crangon septemspinosa*) were the only items found in the bird stomachs (Table 2). These typically epibenthic shrimp are common in Nelson Lagoon; it seems probable that the whale was feeding on them and that those eaten by the birds were brought to the surface by upwelling caused by the constant movement of the whale's flukes and fins as it maintained a side-feeding posture. *Crangon* were the most commonly found organisms in the epibenthic samples, which also suggests that they may have been eaten by gray whales in Nelson Lagoon, although other foods were also available (Table 2).

CONCLUDING REMARKS

Our observations suggest that gray whales begin feeding extensively over nearshore and estuarine areas once they reach the north side of the Alaska Peninsula in spring, and that they probably use at least three different feeding methods to exploit food resources in these areas. The suggestion that the species has developed considerable behavioral flexibility, an adaptation that has probably helped allow gray whales to recover from severe overharvesting, is strengthened by these observations. However, the importance to the species of nearshore and estuarine areas, relative to the overall gray whale population on the summering grounds, is unclear. As a beginning, we propose two lines of inquiry. First it is necessary to determine, in spatial and temporal contexts, what segment of the population uses coastal areas of the southeastern Bering Sea and whether individual whales exhibit site fidelity to specific estuaries. Clearly not all whales migrating along the north side of the Alaska Peninsula use estuaries, yet at Nelson Lagoon a small number of animals is present for most of the summer. Second, we must determine the importance to gray whales of "peripheral" feeding areas, such as those along the north side of the Alaska Peninsula. Are the energy demands of gray whales migrating along the north side of the Alaska Peninsula (after several months of near-fasting) such that initiation of feeding after their lengthy spring migration is a requisite for survival? Or is it possibly a behavior still retained from earlier geologic times when feeding south of the present "traditional" areas was mandatory because of much lower sea levels during glacial periods?

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