

Pacific walrus: Benthic bioturbator of Beringia

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Abstract

The dependency of walrus on sea ice as habitat, the extent of their feeding, their benthic bioturbation and consequent nutrient flux suggest that walrus play a major ecological role in Beringia. This suggestion is supported by several lines of evidence, accumulated during more than three decades of enquiry and leading to the hypothesis that positive feedbacks of walrus feeding strongly influence productivity and ecological function via benthic bioturbation and nutrient flux. Walrus annually consume an estimated 3 million metric tons of benthic biomass. Walrus prey species inhabit patches across the shelf according to sediment type and structure. Side-scan sonar and our calculations indicate that the area affected by walrus feeding is in the order of thousands of square kilometers per year. Annual to long-term walrus bioturbation results in significant, large-scale changes in sediment and biological-community structure, and magnifies nutrient flux from sediment pore water to the water column by about two orders of magnitude over wide areas. The combined effects of walrus feeding must be placed in the context of long-term, regional climate changes and responses. Should sea ice continue to move northward as a result of climate change, the walrus' ecological role could be diminished or lost, the benthic ecosystem could be fundamentally altered and native subsistence hunters would be deprived of important resources.

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1. Introduction

The Pacific walrus, *Odobenus rosmarus divergens*, is a year-long resident of Beringia. The total population of walrus annually consumes ~3 million tons of benthic biomass per year or about 3% of Beringian biomass, which rivals the total extraction of the entire Bering Sea fishery (noted by Fay, 1982 and still the case). Signs of walrus feeding in situ were first observed from a research submersible in March 1972 in the north-central Bering Sea (Ray, 1973), when Sam Stoker, the first observer aboard, exclaimed: “The bottom looks like

pigs had been at it!” Subsequent dives revealed furrows and pits about the width of a walrus muzzle and that these excavations were associated with remnants of walrus food items, such as broken or empty mollusk shells. As a result of these observations, Ray (1984) raised the questions: Does bioturbation associated with walrus feeding alter benthic structure and nutrient flux, and if so, to what extent? Are benthic communities altered to the extent that Beringian ecosystem function might be affected? At the time of our observations, there was little direct evidence for pursuit of these questions. We have since been able to develop an “historical narrative” (according to Mayr, 1997), based on walrus natural history and benthic ecology, in order to formulate testable hypotheses. Here, we present

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evidence on the effects of walrus bioturbation and hypothesize that positive feedbacks of walrus feeding strongly influence productivity and ecological function in Beringia via benthic bioturbation and nutrient flux.

Beringia (the combined continental shelves of the Bering, Chukchi, East Siberian and Beaufort Seas) is the world's largest continental-shelf system, extending to well over a million km², and among the most productive. The Beringian shelf is gently sloping and shallow, and is composed mostly of sandy to muddy substrata, with some gravel patches near islands. Essential features are overlying seasonal sea ice, strong benthic/water-column coupling, a rich benthic community and unique primary-production processes. This system remains relatively "natural" in comparison to most shelf seas (Smetacek and Nicol, 2005) and continues to support among the world's largest populations of sea birds and marine mammals. This abundance of seabirds and marine mammals and the rich benthic biota call attention to high nutrient availability that supports production processes. Three major nutrient sources are recognized. First, advection of nutrients from the shelf-edge has been proposed as the overriding factor in shelf biomass production (Springer and McRoy, 1993; Springer et al., 1996). Second, sea-ice biota (e.g., diatoms) are major contributors to production, particularly in spring (Arrigo, 2003; Lizotte, 2003; Clement et al., 2004). Third, sea-ice biota and suspended particulate organic matter support very high benthic biomass within the St. Lawrence Island polynya region southwest of St. Lawrence Island (Cooper et al., 2002; Grebmeier and Cooper, 1995; Grebmeier and Dunton, 2000; Lovvorn et al., 2005), and presumably other polynyas as well. However, many questions arise about the relationships among these three sources, the dynamics of production and the links to higher trophic levels. Furthermore, the role of bioturbation has been neglected.

2. The evidence

The following section reviews natural history and environmental observations from the 1970s to recently and provides the basis for our analyses of ecological effects.

2.1. Walrus ecology

Fay (1982) described the Pacific walrus' complex seasonal movements, illustrating that walruses have the potential to occupy virtually all of Beringia during their annual migratory cycle (Fig. 1). Walruses depend on

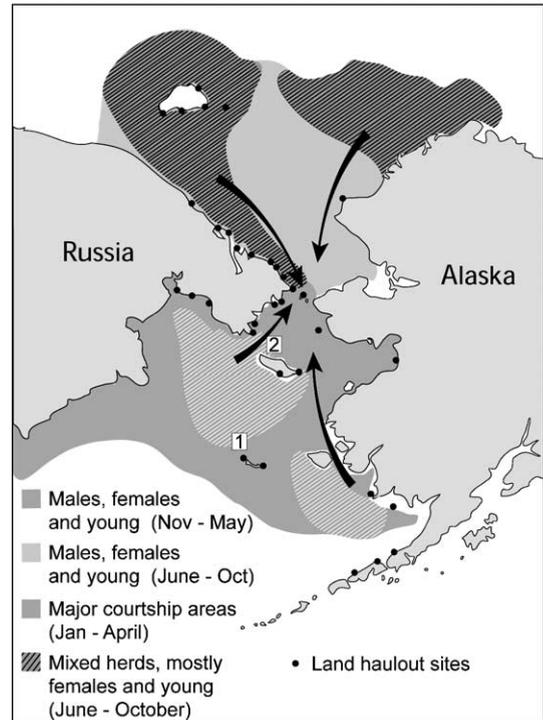


Fig. 1. Seasonal movements and concentrations of Pacific walruses in Beringia. Winter distribution is exclusively in the Bering Sea. Two reproducing subpopulations are, respectively, in the area of broken pack (see Fig. 2) and in the southeast Bering Sea. In summer, males and females segregate; most males occupy land haul-out areas (black dots) and females concentrate in the eastern and western parts of the Chukchi Sea. Segregation of sexes in summer is more marked in the Bering Sea, where adult males and females are almost totally segregated, than in the Chukchi Sea, where adult males and females may form mixed groups. Boxes 1 and 2 indicate locations of the two groups mentioned in the text (see Fig. 3). Recent changes in sea ice are affecting this distribution pattern in ways yet to be fully analyzed. Adopted from Fay (1982) and NOAA (1987).

sea ice not only for transport, but also as an essential habitat component. When walruses rest on sea ice, they passively move great distances, but males in summer also actively swim to and from land haul-outs and feeding areas. Historically, the population may have numbered at least 200,000 animals, which is assumed to be within the range of carrying capacity (Fay, 1957; Fay et al., 1989, 1997). One assessment in 1980 indicated a population of 300,000, but the most recent assessment of 1997 indicated a decline to about 188,000 (Gorbics et al., 1998; see Ray and McCormick-Ray, 2004 for an historical interpretation of walrus numbers). For purposes here, we assume a current population of ~200,000.

During late winter to early spring, the entire population occurs in large aggregations on sea ice

where they reproduce (Fay et al., 1984). At that time, most walrus occur in the “broken pack”, where ice floes are thick and large enough to support large groups of animals and within which individual flows are separated by leads and polynyas that afford access into and out of the water. Broken pack typically occurs in a large area from St. Lawrence Island and the Gulf of Anadyr south to St. Matthew Island in the mid-shelf region of the Bering Sea (Fig. 2) over depths of up to ~ 100 m, which appears to be the walrus’ maximum feeding depth (Fay and Burns, 1988). This depth also delimits the shallow region where the benthic food of walrus is most abundant and where primary productivity is partitioned largely to the benthos (Cooney and Coyle, 1982).

Walrus are among the most gregarious of mammals and occur in extremely patchy aggregations. Large, contiguous herds seem to be randomly distributed in the broken pack and can number in the thousands of animals. Individual groups within herds may range from <10 to >1000 animals. In April 1975 and April 1976, we were able visually to observe walrus herds from a NASA CV-990 research aircraft, when Beringian sea-ice cover is at its annual maximum. The April 1975 herd was located at the southern extremity of the winter range (see Fig. 1 for location) and is illustrated in Fig. 3. Patchy distribution is indicated at three scales. The total number present on ice was at least 14,000 animals, no doubt an underestimate

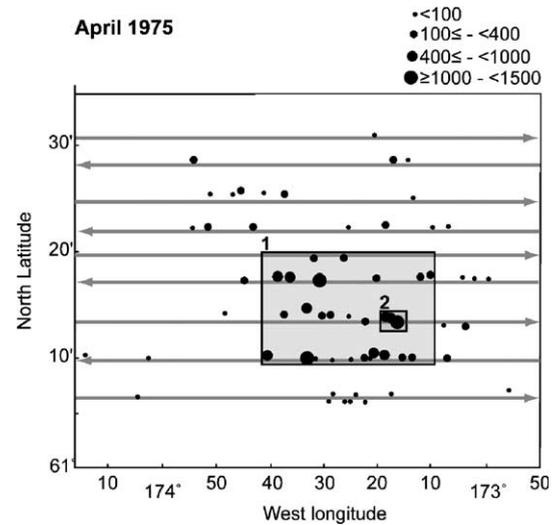


Fig. 3. On-ice walrus concentration recorded from NASA flights at 300–450 m altitude (see Fig. 1 for location). This very large group was observed in April 1975; box 1 encloses the bulk of the herd and box 2 encloses two particularly large groups. Sizes of filled circles represent order-of-magnitude numbers of animals visually observed. See text for further explanation. From Ray and Wartzok (1980) and Wartzok and Ray (1980).

as flight lines were ~ 6 km apart. This herd occupied an area of ~ 4000 km² or ~ 3.5 animals km⁻². The major portion of the herd (box 1) of $\sim 12,000$ animals was within ~ 600 km² or ~ 20 animals km⁻²; the largest

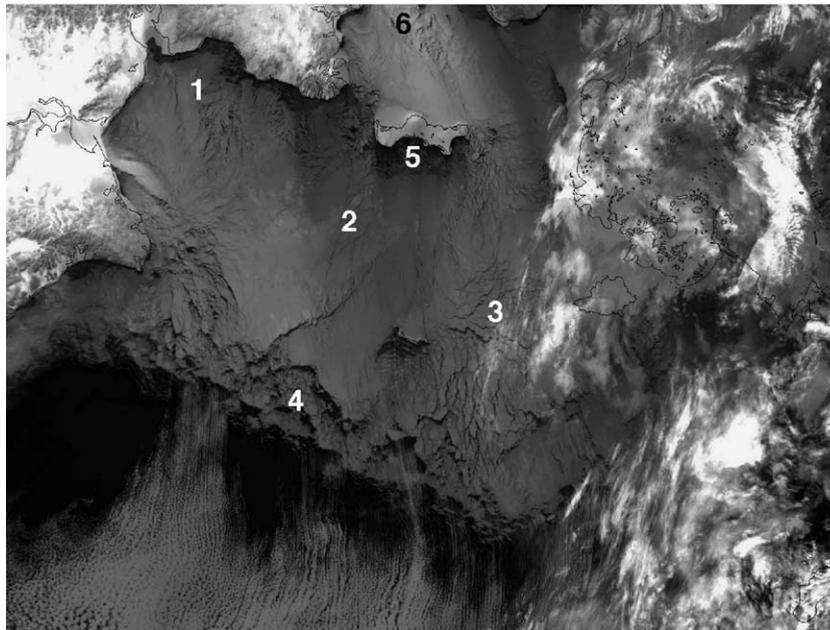


Fig. 2. NOAA AVHRR image of the Bering Sea ice pack in March 1988. Sea-ice types represent different habitats for marine mammals, seabirds and others: (1) pack ice with leads, (2) broken pack (where most walrus occur), (3) rounded pack, (4) loose pack (marginal ice zone (MIZ)), (5) open water and polynyas, (6) continuous ice. Adopted from Ray and Hufford (1989).

concentration within that area was ~ 2600 animals (box 2) within $\sim 24 \text{ km}^2$ or >100 animals km^2 . The April 1976 group (not illustrated, but see Fig. 1 for location) totaled ~ 840 animals in an area of $\sim 1800 \text{ km}^2$ or ~ 0.5 animals km^{-2} ; the major portion of the herd contained ~ 700 animals in 180 km^2 or $\sim 4 \text{ km}^{-2}$. Visual estimates have notoriously large variances, but our results seem reasonable given numerous observations from icebreakers and aircraft. This observed patchiness is an essential consideration for estimating the ecological impact of walrus feeding.

This on-ice distribution pattern approximates in-water feeding distribution as well, as walrus seem not to wander far from specific areas of moving sea ice to feed and to return to the same ice area after feeding. For example, we found that the April 1975 group of walrus remained in the same general sea-ice area for 3 days, even though GPS measurements revealed that the ice was moving $\sim 11 \text{ km day}^{-1}$ (Ray and Wartzok, 1980; Wartzok and Ray, 1980). This suggested that walrus “home” to specific or neighboring floes to haul out following feeding. Additionally, in July 1977, we unobtrusively followed a large group of >1000 animals by icebreaker for 13 days in the Chukchi Sea. During that time, we observed that these walrus alternated times spent on ice and in water (Fig. 4); times spent on ice were 39, 46 and 35 h, respectively, and intervals

spent in water were 24, 33 and 74 h. During this entire time, the ice moved $\sim 120 \text{ km}$ or $\sim 9 \text{ km day}^{-1}$, but the animals never moved far from this “home” sea ice. From these field observations, we concluded that times spent on ice are typically 1–2 days and in water 1–3 days, consecutively, and that movements of the whole herd in and out of water occur more or less concurrently.

Recent studies using telemetry support the above conclusions. Gjertz et al. (2001) found that walrus at Svalbard, Norway, spent on average, 56 h in the water followed by 20 h on land. Jay et al. (2001) found that walrus in Bristol Bay spent 76.6% of their time in the water, of which 60.3% was spent feeding; feeding trips lasted 0.3–9.4 days, but some short dives were not related to feeding. Born et al. (2003) found that, during one entire feeding cycle, 23 h were spent on land and 74 h were spent foraging in the water. In sum, ours and newer observations support the hypothesis that sea-ice movements determine the areal extent of feeding over time and that an intermittent feeding pattern is typical of walrus behavior. Fig. 5 is a representation of this diving behavior. From time 1 to times 2 and 3, sea ice is indicated to move several kilometers per day. During periods that walrus spend in water, benthic feeding is continuous; during periods when they are on ice, feeding is interrupted. This feeding pattern defines a semi-continuous track of bioturbation that varies in

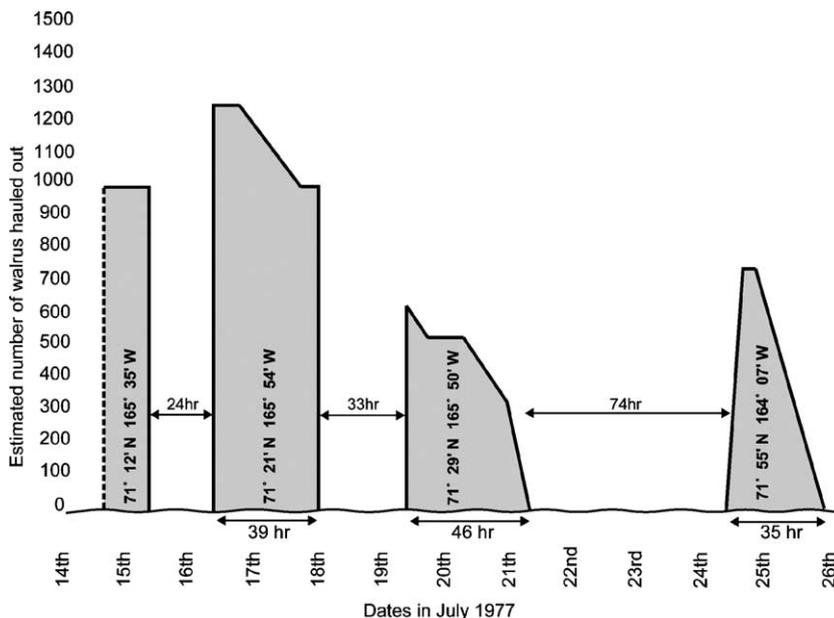


Fig. 4. Walrus movements in and out of water observed semi-continuously from icebreaker in July 1977 in the Chukchi Sea. Shaded areas indicate the approximate numbers of walrus hauled out on ice. Slopes on the shaded areas indicate that walrus moved in and out of the water during short periods of time. The dotted line on the first (left) shaded area indicates the beginning of our observations, when walrus were already on the ice. Geographic locations are included in the shaded areas. From Ray and Wartzok (1980) and Wartzok and Ray (1980).

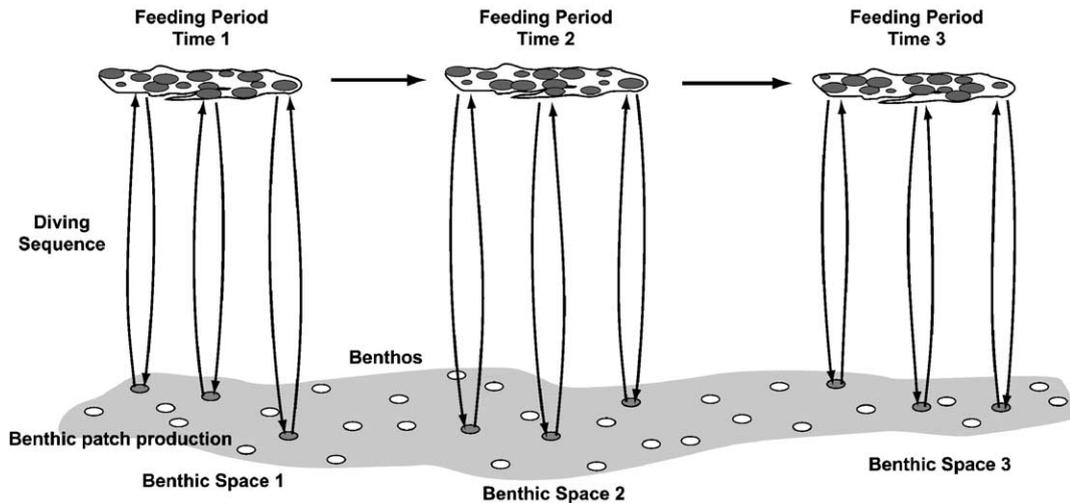


Fig. 5. Walrus movements and feeding behavior. The areas with filled circles above represent sea ice with hauled-out groups of walrus. The arrows show movements from “home” sea ice to the benthos to feed and return to the ice. The continuously shaded area below represents the benthos where walrus are feeding. Filled circles indicate areas where feeding occurred; open circles represent areas not fed upon. See text for further explanation.

intensity according to walrus group size and the rate of sea-ice movement. Presumably, not all benthic organisms are consumed, due to the fact that walrus are continuously conveyed by their sea-ice habitat. This sequence of alternate periods of gorging and resting is common among large predators and would seem to be energetically efficient for walrus as well.

2.2. Walrus feeding

Fay (1982) confirmed, from anatomical evidence and from direct observations of captives, that walrus feed by rooting in the bottom with their muzzles, in a manner similar to pigs, and extract clams from their shells by means of powerful sucking actions. Extraction of flesh from the shells is accomplished by means of a “vacuum pump”, powered by a “piston” (the tongue) within a “cylinder” (the oral cavity). Fay’s experiments indicated that oral suction could create a negative pressure of -0.914 bar.

Fay’s conclusions are verified by several studies. In 1972, our manned submersible dives (Ray, 1973) allowed observations of walrus feeding pits and furrows that strongly suggest rooting and vacuuming behavior (Fig. 6). Subsequently, Johnson and Nelson (1984) and Nelson and Johnson (1987) mapped 22,000 km² of the Chirikov Basin by side-scan sonar and recorded feeding patterns produced by walrus and gray whales (*Eschrichtius robustus*). Feeding furrows created by walrus averaged 47 m long by 0.4 m wide by 0.1 m deep, in contrast to larger, shallow pits created by the whales. At about the same time, Oliver et al. (1983)

observed by scuba-diving that walrus feeding furrows averaged 0.45 m wide by 0.17 m deep and that feeding pits were patchy in occurrence. They concluded that walrus excavate food items by rooting in benthic substrates and hypothesized that walrus also employ water-jetting (squirting water from the mouth) to uncover prey. They also concluded that walrus can consume six clams a minute and that the resulting bottom disturbance creates new habitats (e.g., resorted substrate and discarded shells) for other benthic biota.

2.3. Food consumption

Fay (1982) concluded, from stomach contents of wild walrus and from captives that had recently fed, that stomachs of adults may contain a maximum of 43.5 kg of ingesta. He calculated a consumption rate of 4.2–6.2% of total body weight day⁻¹ for captive adults, subadults and juveniles of both sexes weighing 250–700 kg. For fully grown adults of 1500 kg, this rate extrapolates conservatively to ~ 60 kg day⁻¹. Based on these data, Fay assumed that walrus feed twice a day to fulfill their metabolic requirements and that 8–12 h of feeding would be required to do so. Fay (op. cit.) also found that walrus consume about 60 species of benthic fauna, mostly infauna, presumably relying primarily on clams (e.g., *Mya*, *Serripes*, *Hiattella*, *Macoma*, *Nucula* and *Yoldia*). More recent evidence indicates that walrus consume an even wider assortment of prey within more than a dozen phyla, but that many soft-bodied food items can be digested in 1–6 h, hence may be missed by most stomach analyses



Fig. 6. Depiction of the natural history of walrus. The walrus in- and on-ice are from photographs taken by G.C. Ray in the central Bering Sea in April 1972. The benthos showing bioturbation is from observations and photographs taken by G.C. Ray during submersible operations at that same time and place. The underwater walrus are taken from living animals at the New York Aquarium during the 1960s. Painting by Robert Hynes from Ray and Curtsinger (1979), with permission of the National Geographic Society Image Collection.

(Sheffield, 1997; Sheffield et al., 2001). Nevertheless, feeding on large clams would appear to be most energetically efficient for the reasons that clams are relatively large food items, and are relatively abundant and easily detected and excavated.

A series of observations on the anatomy and behavior of captives support and extend Fay's conclusions (Kastelein and Mosterd, 1989; Kastelein and van Gaalen, 1988; Kastelein et al., 1990, 1991, 1994, 1997; Kastelein and Gerrits, 1990): (1) walrus root with their muzzles to detect clams; (2) blindfolded walrus can distinguish objects as small as 3 mm thick and 0.4 cm in surface area, and scan times for prey are in the order of seconds; (3) muzzle muscles are related to the vibrissae, which are important for food detection, identification, excavation, manipulation and processing; (4) the vibrissae can be erected en masse to form a rigid, sensitive "rake"; (5) walrus use water jets supported by oral musculature to uncover prey; (6) the upper lip is strong, sensitive and flexible; (7) the tongue can create very low oral pressures of -0.879 bar in air and -1.188 bar in water; and (8) by using these features, a

single walrus may typically discover, uncover and consume about 6000 clams in a single feeding of ~ 16 – 17 h duration.

Observations of walrus feeding at Young Sound, East Greenland, generally support these calculations. Born et al. (2003) recorded 412 dives by satellite telemetry, and found that walrus' aerobic limit while actively diving is ~ 10 min and that walrus spent $\sim 57\%$ of their time diving to 6–32 m. Underwater diving observations showed that walrus consumed an average of 53.2 clams (range 34–89: *Mya truncata*, *Hiattella arctica* and *Serripes groenlandica*) or 583 g wet weight (range 242–1000) per dive. Born et al. (op. cit.) also found that food consumption averaged 57 (range 41–72) kg day⁻¹ or 4.7% of total body weight of walrus that were immobilized and weighed, and that the average consumption rate was ~ 9 clams min⁻¹, which is higher than the ~ 6 clams min⁻¹ of Oliver et al. (1983) and Kastelein et al. (1997). This relatively high feeding rate is not unexpected, as the area in which Born et al. worked supports relatively few walrus, and clams may be relatively old and abundant.

2.4. Clam density

The dimensions of benthic patches containing clams and clam density within patches are critical for estimating the scale of walrus perturbation and its ecological effects. Patch size and clam density are expected to be highly variable, depending on clam recruitment and growth, and whether patches have been fed upon by walruses. Unfortunately, density information for high-latitude mollusks is sparse and highly variable (Richard Warwick, personal communication). Roseberry et al. (1991) found an average density of *Mya arenaria* in the St. Lawrence estuary, where walruses do not occur, of 177 individuals m^{-2} . Sejr et al. (2002) found an average density of 57 *Serripes* m^{-2} with a biomass of 6.2 g shell-free dry weight in eastern Greenland, where walruses do occur but are not abundant. Oliver et al. (1983) did not measure clam density per se, but presented an illustration showing a 21-m portion of a walrus feeding furrow containing 34 excavated clam pits (*Mya* and *Serripes*). Furrow width was ~ 0.5 m; thus, the total area depicted was ~ 10 m^2 . Each pit appeared to contain a single clam, indicating that this area contained ~ 3 clams m^{-2} . Born et al. (2003) found a much higher density of 89 clams in a 2–3-m diameter patch that walruses had excavated or about 10–20 clams m^{-2} , which is probably high for reasons given above.

Stoker (1973) examined infauna from the area southwest of St. Lawrence in which walruses are most concentrated (Fig. 1). Densities ranged from 10 to 732 m^{-2} , indicating extreme patchiness. He found an average clam density of 121 m^{-2} with a total wet weight of 84 g. He was not able adequately to sample large *Mya* that live deep in the sediment, but assuming *Mya* body weights at ~ 6 g each (see below), his results suggest a density of ~ 15 *Mya* m^{-2} (84 divided by 6). Therefore, because Stoker extensively quantified infauna from the area of concern in this paper, we conservatively assume a density of 15 clams m^{-2} for our calculations below.

3. Ecological effects

Walrus feeding activity has at least four ecological dimensions: food consumption, benthic community changes, sediment restructuring and nutrient mobilization. Our calculations are based on two sources: first, the natural history of walruses given above and, second, observations on the Beringian benthos, given below.

The importance of sediment for macro-invertebrate benthic community structure has often been demon-

strated (Weston, 1988), including for Beringia (Grebmeier et al., 1989). The Bering Sea shelf is dominated by sands, muds and gravels (Fig. 7A), and these sediments are poorly sorted (Fig. 7B), strongly suggesting effects of bioturbation. Clams and other infauna are major bioturbators in the Bering Sea, and mobilized sediments are resorted by the infauna in ways unpredicted by physical laws of sedimentation (Burrell et al., 1988). When sediment particles are mixed by infaunal activities, benthic structure changes and the distribution and abundance of other benthic fauna also changes.

The Bering/Chukchi soft-sediment system exhibits at least eight major faunal assemblages of considerable complexity. These assemblages are strongly correlated with sediment type, particle size, bottom temperature, depth, sedimentation rates, circulation intensity and suspended particulate content of near-bottom water. Densities vary according to the structural heterogeneity described by grain size and sorting coefficients (Grebmeier et al., 1989). Stoker (1973, 1981) identified 472 benthic macrofaunal species at varied densities across Beringia. Of these, 95% came from four dominant phyla: Mollusca (bivalves, gastropods), Annelida (polychaetes), Arthropoda (amphipods) and Echinodermata (asteroids, ophiuroids). One to five species dominated each of these groups and the majority of other groups contained only one to two species. Of the 292 genera and total of 16 phyla, polychaetes were most ubiquitous and speciose, with a mean density of 190 individuals m^{-2} . Mollusks were close behind polychaetes in frequency, with a mean density of 166.6 individuals m^{-2} . Faunal abundance is important for describing benthic communities. However, for a predator, biomass is more relevant. Thus, while polychaetes are dominant in abundance, bivalve biomass seems to be greater in areas where walruses feed, particularly south of St. Lawrence (Simpkins et al., 2003).

Wheatcroft and Drake (2003) observed that macrofauna that live deep in sediments are often larger than the smaller, more surficial tube-dwelling fauna, and their contribution to sediment reworking is likely to be substantial. By increasing the porosity and erodibility of the sediment, by ingesting small sediment particles and by egesting larger fecal pellets at the sediment surface, these deep, subsurface macrofauna may alter the vertical distribution of sediment grain sizes, as well as change the spectrum of grain sizes. These activities result in both sequestration and releases of trapped gases and nutrients, and also influences on the distribution and abundance of benthic inhabitants. This alteration of sediment structure by benthic infauna clearly has the

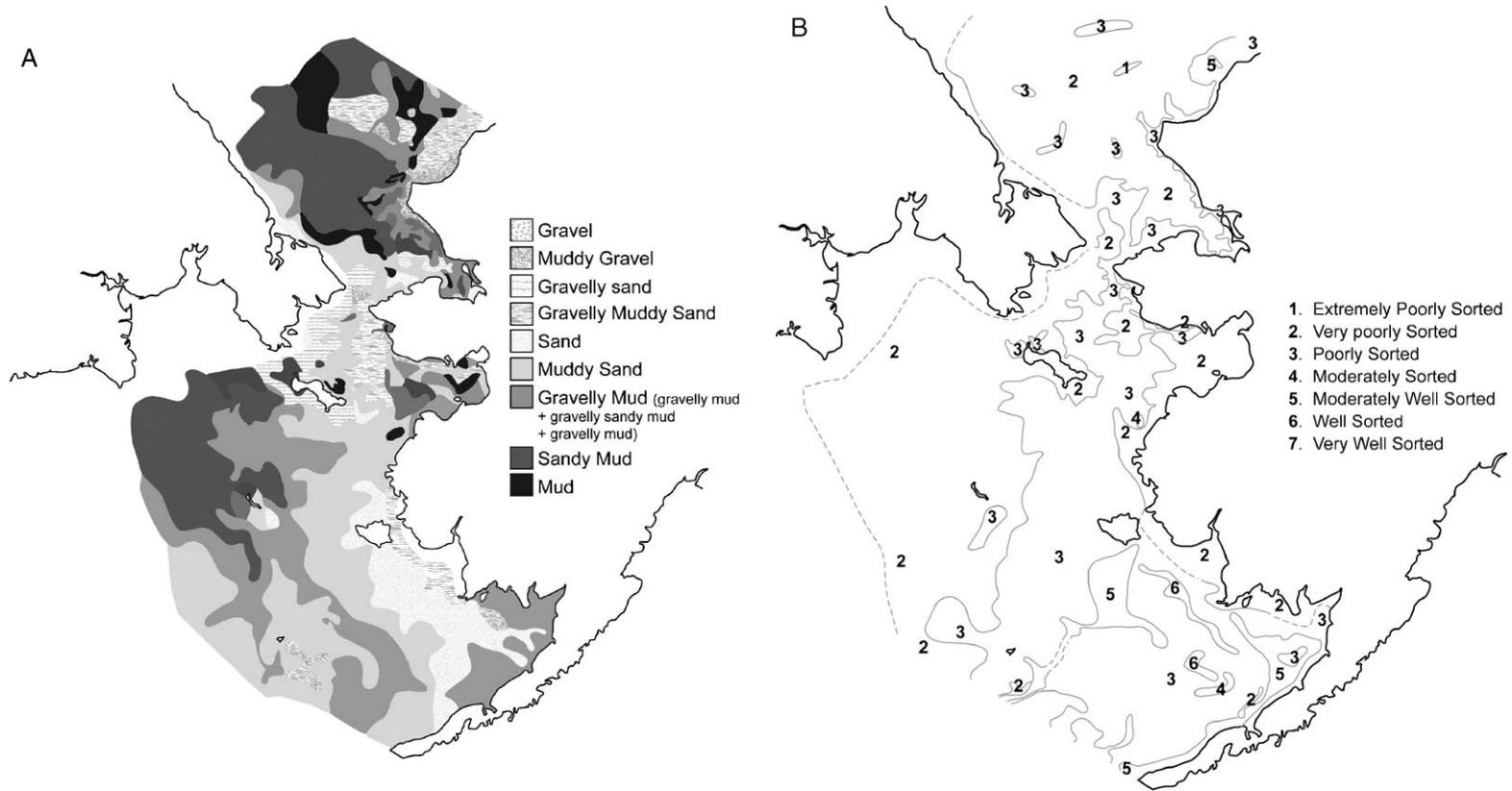


Fig. 7. Beringian sediments. (A) Sediment structure and (B) sediment sorting. Sediments throughout the Bering and Chukchi Seas range from gravel to mud, with the greatest majority being sands and muds. Sorting is generally very poor, indicating a high degree of biological activity, including bioturbation. Adopted from [Naidu \(1987\)](#).

potential to alter species recruitment and community structure.

3.1. Walrus biomass removal

Fay (1982) estimated that food consumption for wild walrus may be 5–7% of total body weight, somewhat higher than for captives (see above). However, the number and biomass of organisms consumed by wild walrus are difficult to estimate because different food organisms have different caloric values, consumption rates vary and wild walrus probably require more food than captives. Compounding factors are that Pacific walrus numbers are imprecisely known, that feeding is inconsistent throughout the year and that the sex/age structure of the population (therefore, relative weights of sex/age classes) is uncertain. Adult males feed little if at all during the winter reproduction period and adult females with newborns do not feed at all for weeks to a month or so after giving birth; contrarily, pregnant females increase consumption during late pregnancy. These uncertainties mean that total consumption by a herd of walrus is difficult to measure.

An average wet weight for clams consumed is difficult to assess considering: (1) different sizes among food species; (2) the different proportions and sizes among food species; and (3) the possible ingestion of clam soft parts other than siphons and feet. Therefore, in order to calculate walrus consumption, two assumptions are initially required. First, we recognize that walrus

eat a wide variety of foods. Research to date strongly suggests that clams, particularly *Mya truncata*, are preferred. We base our calculations on this species, assuming that it reasonably reflects a walrus' overall metabolic requirements. Second, Welch and Martin-Bergmann (1990) have shown that *Mya* siphons from the Canadian Arctic average ~6 g wet weight, and “when pulled [they] almost always break at the mantle unless the sediment is very soft, when occasionally the entire clam can be removed”. We have observed that *Mya* siphons from walrus stomachs in the Bering Sea may considerably exceed 6 g (Fig. 8), but considering that walrus eat a variety of smaller prey, we assume 6 g as a reasonable overall dietary surrogate. Next, we define each daily feeding event as a “bout”, that is the approximate “mealtime” needed for a walrus to consume 4000–6000 clams (see above); we define a “period” as a 3-day time spent in the water during which feeding concurrently occurs. Consumption of 4000–6000 clams day⁻¹ with an average weight of 6 g per *Mya* results in a daily food intake of 24–36 kg day⁻¹, which is a conservative average result for groups containing juvenile to adult walrus (Table 1). A consumption rate of 6–9 clams min⁻¹ for each bout would require 450–1000 min (~7–17 h), a greater time range than given by Fay (1982), but less than Kastelein et al. (1997). However, feeding is not continuous and feeding times must account for intervals at the surface. Furthermore, rates of consumption would vary according to varying prey species and density. Walrus must



Fig. 8. Clam siphons and feet from the stomach of an adult walrus, taken by St. Lawrence hunters. The siphons are from *Mya*; the feet are unidentified as to species. The weights are more than the 6 g clams average mentioned in the text. Photograph by G. Carleton Ray.

Table 1
Walrus consumption and sediment bioturbation

| <i>Walrus consumption: each walrus: 4000–6000 clams day⁻¹</i> | |
|--|---|
| Feeding bout, one walrus | |
| Feeding rate | 6–9 clams min ⁻¹ |
| Food consumption | 24–36 kg day ⁻¹ |
| Feeding period, 1000 walruses | |
| Total clams | 12–18 × 10 ⁶ |
| Total weight | 72–108 × 10 ³ kg |
| Five-month season in Bering Sea | |
| 140,000 walruses, total clams | 50–75 × 10 ⁹ |
| 140,000 walruses, total weight | 300–450 × 10 ³ mt |
| <i>Walrus benthic bioturbation: based on 15 clams m⁻²</i> | |
| Sediment affected | |
| One walrus, one bout, area | 260–400 m ² |
| One walrus, one bout, volume | 53–80 m ³ |
| 1000 walruses, one period, area | 780–1200 × 10 ³ m ² |
| 1000 walruses, one period, volume | 159–240 × 10 ³ m ³ |
| Five-month season in Bering Sea | |
| 140,000 walruses, total area | 3–5 × 10 ³ km ² |
| 140,000 walruses, total volume | 655–1000 × 10 ⁶ m ³ |

Calculations are based on *Mya* as a surrogate for overall consumption. A “bout” is 1-day feeding; a “period” is 3-day continuous feeding. See text for explanations.

first explore the benthos to discover clam patches, which they then exploit heavily. For all these reasons, it seems reasonable to assume an average of 1 bout 24 h⁻¹ and that a minimum of 3 bouts would occur in a 3-day feeding period.

Our calculations result in a consumption rate of 4–6 × 10³ clams (24–36 kg) for each walrus during one feeding bout or 12–18 × 10³ clams (72–108 kg) during one feeding period. We know from captives that adults may require up to 60 kg day⁻¹ or more; however, as an average for all age groups, our calculation seems reasonable. An extrapolation to a group of 1000 animals, as commonly occurs on sea ice, is 12–18 × 10⁶ clams (72–108 × 10³ kg). Extrapolation to larger scales or for longer periods is somewhat risky due to the caveats given by Fay (above). Nevertheless, we would expect about 30 feeding periods to occur from January through May, when walruses are in the central Bering Sea (150 total days divided by 5 days required for one feeding-and-resting period). Also, we may conservatively assume that a minimum of 10 herds the size of the one depicted in Fig. 3 (i.e., at least ~14,000 animals) or about 140,000 animals occur there. This assumption is based on the occurrence of two winter concentrations (Fig. 1), the larger one of which, perhaps containing three-fourths of the total population (as indicated by previous aerial surveys), occurs southwest of St. Lawrence. Therefore, we estimate the total

consumption of clams by the central Bering Sea subpopulation to be about 4200 times greater than that calculated for one period by 1000 animals (30 periods × 14 × 10 herds). The result approximates 5–8 × 10¹⁰ clams (3–5 × 10⁸ kg) consumed, equivalent to 3–5 × 10⁵ metric tons for the 5-month time that the central Bering Sea walrus subpopulation spends in the area south of St. Lawrence Island.

3.2. Walruses cause major shifts in benthic communities

Walrus feeding may quickly deplete areas of prey and alter community composition. Each of the assemblages mentioned above is likely to have different responses to walrus feeding. The effects of feeding may also be different among species that live at varying depths. *Mya* has a long, tough siphon and burrows to depths of ~30 cm (Oliver et al., 1983). *Macoma* has a shorter siphon and generally burrows to <20 cm. And *Serripes* has an even shorter siphon and lives in shallow burrows at the sediment surface. Oliver et al. (1983) and Born et al. (2003) found that benthic infauna were notably less abundant in pits and furrows dug by walruses, whereas other species (e.g., polychaetes, tunicates, epifaunal anemones and amphipods) were in great abundance. These authors also observed that mobile amphipods invaded walrus feeding patches within minutes and within 1–2 h devoured most of the soft remains. Oliver et al. (1983) observed that walrus feeding opens space for new species' invasions and leaves some unconsumed remains that can be an important source of food for benthic scavengers, such as asteroids, ophiuroids and crustaceans. Oliver et al. (1985) noted that walrus prey populations may recover slowly in cold, seasonally ice-covered, boreal seas.

Benthic communities and walrus prey may be slow to recover, possibly only during multi-year periods. Prey persistence and resiliency depend on life-history patterns, factors that must be considered for assessment of walrus feeding ecology. The large mollusks observed in walrus stomachs by Fay (1982) are mostly slow-growing species and these species are almost certainly vulnerable to over-exploitation. Size is related to age, and preliminary data of Will Ambrose (personal communication) suggest that Alaska *Serripes* with a shell height of ~50 mm are ~8 to 12.5 years old and *Mya* with a shell length of 22 mm are ~9 years old. Furthermore, benthic recruitment of clam populations might be intermittent. Stoker (1973) observed that individual clam populations in the Bering Sea were represented by single-sized (aged) individuals of 1-year class in one location and another single-aged class at

another location. A similar spatial, age-class distribution was observed by Maximovich and Guerassimova (2003) in the White Sea, where the beds of *M. arenaria* consisted of only 1-year class, other generations were scarce, and recruitment was not observed.

Growth and population recruitment of prey species also depend on their food supply. The quality and quantity of organic carbon reaching the benthos from the overlying water column sustains a rich benthic biomass, which Stoker (1981) suggested was detritus-based. However, due to seasonal ice cover, primary production is largely confined to the spring–summer growing season. In late winter under a polynya, water-column production does not support a direct, continuous linkage to the sediments, as it is then significantly lower than during and just after ice retreat (Cooper et al., 2002; Clement et al., 2004). Mollusks and other infauna are selective detritus and/or suspension feeders, adapted to seasonal water-column production (Grebmeier et al., 1989). Beringian mollusks may also be seasonal feeders. Thus, benthic fauna may not feed in winter, or may gain some benefit by switching from suspension to deposit feeding (Ólafsson, 1986; Lopez and Levinton, 1987).

3.3. Walrus restructure sediments

Walrus feeding may account for major restructuring and resorting of sediment (Fig. 7B). As walrus remove deep-dwelling clams and mobilize benthic particles, benthic sediment is mixed and oxygenated, and sediment structure is altered. The new surface becomes available for colonization by invertebrate larvae, for opportunists to enter, for trapped gases to be released and for sediment structure to be fundamentally different from undisturbed areas. Nelson and Johnson (1987) estimated that, if 200,000 walrus spent 100 days in the northeast Bering Sea and if each animal created only two average, 47-m long furrows a day, 75 million m³ (100 × 10⁶ mt) of sediment might be redistributed, which the authors acknowledged is an underestimation. For example, a 100-m furrow may contain 750 clams (100 m long × 0.5 m wide × 15 clams m⁻²), possibly only a fraction of a single walrus' daily requirement. While consuming 4000–6000 *Mya* (or their equivalent in weight), at a minimum density of 15 clams m⁻² (see above) and at a feeding depth of 20 cm in the sediment (an average between depths for shallow-living species and deeper-living *Mya*), one walrus could perturb 260–400 m² (53–80 m³) of sediment during each feeding bout, or 780–1200 m² (156–240 m³) for each feeding period (Table 1). Obviously, bioturbation beneath each individual group of walrus on ice may be greater or

lesser depending on ice movements and on prey species' patch size and density. But it seems safe to say that the ~140,000 walrus in the central Bering Sea could perturb ~3–5 × 10³ km² of area and resuspend ~650–1000 × 10⁶ m³ of sediment during the 5 months they spend there. This amounts to 2–3% of the Bering Sea shelf, which an ecologically significant amount, considering that the bioturbation takes the form of highly patchy pulses. Furthermore, it must be noted that the extent of bioturbation does not occur over the entire Beringian shelf every year, but rather is distributed largely according to areas where sea ice provides favorable habitat.

3.4. Walrus magnify nutrient flux to the water column

Benthic macrofauna in the Bering Sea are responsible for a substantial portion of total sediment respiration (Rowe and Phoel, 1992). Given the rate of sediment accumulation and of infaunal reworking of the sediment, the surface of a muddy sea floor could pass through the benthos at least once and in some cases several times each year (Rhoads, 1974). Sediment reworking results in important exchange processes, such as transport of higher organic content of surface sediments downwards into deeper sediment (Henriksen et al., 1993; Lomstein et al., 1989). Active irrigation by macrofauna through their burrows and tubes increases sediment oxygen uptake and nutrient flux between the sediment and overlying water column.

Dissolved organic compounds are often abundant in surficial pore waters of the benthos and biogenic mixing affects the depth of the benthic mixed oxidized zone, below which live the aerobic and anaerobic microfauna of the sulphide biome (Rhoads, 1974). Rowe and Phoel (1992) show that a seasonal buildup of ammonium over the mid-shelf of the Bering Sea is generated at least in part by benthic biota. Henriksen et al. (1993) and Lomstein et al. (1989) have measured the flux and pore-water concentrations of nitrogen in several locations in the northern Bering and southern Chukchi Seas during summer. They found that ammonium pore-water concentrations in upper sediments (0–12 cm) varied from 60 to 200 nmol cm⁻³ and ammonium fluxes varied from 0.22 to 1.00 mmol m⁻² day⁻¹ over the sediment–water interface. Lomstein et al. (1989) have also shown enhancement of sediment mineralization processes for an area of high macrofaunal concentrations on the western Bering Sea shelf.

Walrus feeding activities occur on much larger spatial scales and much more abruptly than infaunal activities. Their bioturbation can, during short time

periods, potentially release significantly larger amounts of trapped organic materials and nutrients into the ice-covered, winter-mixed water column than can benthic fauna. Assuming an average sediment porosity of 0.5 (Lomstein et al., 1989), an average feeding depth to 20 cm by walrus digging (see above) and that each walrus feeding event (a day's bout) is one "disturbance", the potential ammonium release by a walrus may be calculated as:

$$[\text{concentration in sediment}] \times [\text{porosity}] \\ \times [\text{bioturbation depth}]$$

Therefore:

$$[60 - 200 \text{ nmol cm}^{-3}] \times [0.5] \times [20 \text{ cm}] \\ = 600 - 2000 \text{ nmol cm}^{-2} \text{ "disturbance"}^{-1} \\ \text{equivalent to } 6 - 20 \text{ mmol m}^{-2} \text{ "disturbance"}^{-1}.$$

Thus, each feeding bout results in a disturbance flux that may be as much as 2 orders of magnitude day^{-1} greater than normal flux rates at the sediment–water interface. This amount becomes even more significant when considering the extensive areas that walrus perturb. The result is a series of large nutrient pulses from the sediment to the bottom water that would not otherwise be released in so short a time. This release may be utilized by phytoplankton and we speculate that this has the potential to trigger a significant localized bloom that would not otherwise occur. High variance among nutrient releases is to be expected among seasons and geographically, depending on the movements of sea ice and walrus, and also depending on walrus group size. Caution must be exercised in prediction of the fate of these nutrients, as they may become distributed throughout the water column under conditions of non-stratification in winter, or they could remain in the bottom water due to summertime stratification and capping-off of the Bering Sea cold pool during this period. Furthermore, nutrients could be consumed by a variety of organisms, from microbiota to phytoplankton, or possibly assimilated directly by benthic organisms themselves.

4. The walrus as Beringian integrator

Our historical narrative spans more than three decades of natural-history field work and has been extended by a variety of multi-scaled observations that have more recently emerged. The narrative also contains a number of assumptions based on on-going research, for example, on sea-ice movements, benthic communities,

nutrient cycling, productivity and, perhaps most significantly, climate change. This history and recent developments have now allowed the statement of hypotheses that require a daunting research agenda, among which are:

- H1. Walrus preferentially occupy "broken pack" in winter months, the dynamics of which influence the areas where walrus feed;
- H2. Benthic areas where walrus feed exhibit altered structure and biota, and enhanced productivity; and
- H3. Climate change is significantly altering sea ice structure and walrus distributions, thereby altering ecosystem structure and production, as well as subsistence hunting at local to regional scales.

H1 expresses the need for better information on the sea-ice habitat of walrus. H2 requires that studies of walrus be undertaken in collaboration with benthic ecologists. And, H3 expresses concerns that climate change, as is already being observed, will significantly alter the functional role of walrus in Beringia. These three hypotheses, in combination, state the proposition that walrus constitute an agent of change, driven top-down by climate and sea ice, but also affected bottom-up by benthic dynamics, and with implications for Beringian ecology itself.

The high productivity of Beringia is widely acknowledged, as are the roles of the green belt, polynyas, marginal sea ice and nutrient fluxes from the sediments. This paper suggests that bioturbation is an equally important, but neglected, production process due to its effect on benthic structure and regeneration of nutrients. This suggestion is supported by recent research. Seitzinger and Giblin (1996) emphasize that the importance of benthic macrofauna to denitrification is to bring oxygen into sediments, thereby increasing coupled nitrification and denitrification processes. Lohrer et al. (2004) show that bioturbation can enhance production through changes in nutrient fluxes and biochemical interactions. And, Howe et al. (2004) show that denitrification and nitrification rates are significantly enhanced through the activities of two bioturbating shrimp.

However, the role of mesoscale benthic bioturbation by large, wide-ranging, gregarious consumers has yet to be fully acknowledged. Nelson and Johnson (1987) were impressed by the extent of both gray whale and walrus bioturbation and aptly observed: "In spite of the battlefield appearance of the sea floor, the feeding activities of the whales and walrus seem to be

beneficial to the area, enhancing its productivity”. Recognition of complex relationships among benthic bioturbation, altered benthic communities and increased nutrient cycling brought about by walrus raises the question of whether nutrients mobilized by walrus might increase production and benthic biomass via increased nutrient turnover within large, even sub-regional, scales. This possibility seems to be supported by benthic “hot spots” that co-occur with areas favored by walrus (Grebmeier and Dunton, 2000; Fig. 9). The findings of Naidu et al. (2004) on fluxes of nutrients and organic carbon also bear witness to this coincidental correlation; “...the highest values [in benthic oxygen uptake rates] are southwest of St. Lawrence Island and south of Bering Strait in Chirikov Basin”, which they attribute to “the relative abundance of the benthic biomass, which in turn is determined by the lateral variations in marine vs. terrigenous OC [organic carbon] and the total flux of OC depositing at the sea floor”. This conclusion begs the question: what role does bioturbation play? The effect of walrus bioturbation is to increase oxygenation of sediments, thereby increasing nitrification and subsequent denitrification, most especially nitrogen release from the sediment, which substantially increases the nitrogen available in the water column for phytoplankton production that is made available for benthic organisms.

In sum, the Pacific walrus’ consumption, uniqueness, size and gregarious behavior indicate a highly efficient benthic, food processing, coastal-shelf ecosystem engineer that has evolved with a rich, high-latitude shelf system. Assessing the effects of walrus bioturbation may take several avenues. The effect could be trivial if only one or a few walrus were involved, or ecologically highly significant if a large herd occupying a relatively limited area were involved. Our observations make clear that walrus integrate climate-controlled sea-ice dynamics with benthic production at hierarchical scales of interaction. Walrus are year-round residents of Beringia and the compounded effects of their feeding activities result in significant structural alterations of the benthos and large nutrient releases to the water column. Although released nutrients are translocated in ways not yet understood, local effects are almost certain to be highly significant. Further, it is critical to incorporate sea ice into interpretation of these effects, as ice dynamics are largely responsible for the temporal and spatial dynamics of walrus feeding, with feedbacks to the walrus population itself. That is, if sea ice failed to transport walrus herds, as might occur under varying ice conditions or climate-warming scenarios, access to mid-shelf food resources would be diminished,

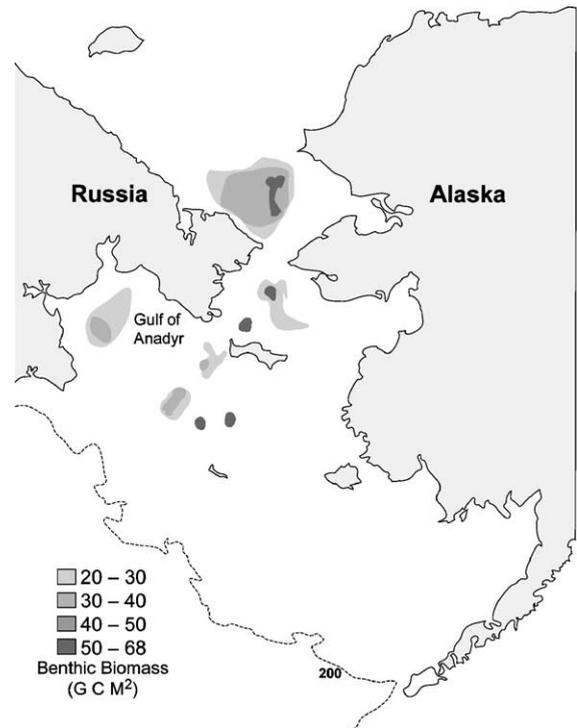


Fig. 9. High concentrations of benthic biomass obtained in the Bering and Chukchi Seas, 1984–1995. Many more samples were taken (not indicated here), all with a concentration of $<20 \text{ g cm}^{-2}$. From Grebmeier and Dunton (2000), with permission.

with implications for shelf ecology and productivity, and for indigenous people that depend on walrus for resources. Therefore, walrus, sea ice and climate-change interactions transcend beyond benthic ecology to potentially affect the entire Beringian system and its indigenous peoples.

We recognize that walrus are not the only large-sized agents of bioturbation in Beringia. Gray whales in the northern Bering and southern Chukchi seas in summer (Moore et al., 2003), and birds (spectacled eiders, *Somateria fischeri*, Grebmeier and Dunton, 2000; Lovvorn et al., 2003) in the St. Lawrence Island polynya in winter also significantly contribute. Walrus may be most prominent, as they are year-round residents and pervasive consumers throughout almost all of Beringia at one time or another. The effect of bioturbation by any or all of these is best understood as a series of pulsed events that collectively enrich the Beringian system. Odum et al. (1995) described “nature’s pulsing paradigm” with regard to ecosystem restructuring, e.g., small-scale events that have the capacity to alter ecosystems at much larger scales, in both time and space, than individual events alone. An

analogy may be made to forests that are fundamentally restructured by tree-fall events, which open gaps in the forest canopy and bring about structural change (Shugart, 1984).

Our conclusion is that the ecology of Beringia cannot be interpreted absent consideration of bioturbation. We suggest that Beringian bioturbators play key roles on a regional scale, even to the extent that they may “cultivate their own garden” through their feeding activities. For example, Nelson and Johnson (op. cit.) state that gray whales maintain a sandy substrate by winnowing fine sediments away from their feeding area, thereby maintaining habitat for the amphipods that are their major food supply. Ironically, Russian whalers have named the gray whale’s feeding area in the Chirikov Basin of the northern Bering Sea the “large kitchen garden” (Votrogov and Bogoslovskaya, 1980). We suggest that walrus bioturbation may have the same or similar effect. This is to say that walruses and other bioturbators have evolved with their food supply for millennia, strongly implying that benthic communities and high regional productivity are, at least in part, the result of the activities of these species.

This conclusion brings environmental change into question. Beringia is experiencing fundamental ecological alterations, especially through the agency of climate change. Sarmiento et al. (2004) conclude that the greatest regional, marine change currently being caused by climate change may be within Beringia, especially with respect to sea ice. Smetacek and Nicol (2005) add that air-breathing predators play significant roles in polar ecosystem functioning and that a decrease in their populations or feeding can “have cascading effects down the food chain and lead to marked shifts in ecosystem function”. The monitoring of such changes, including benthic restructuring and nutrient release by bioturbation and their ecological feedbacks, are therefore essential for future monitoring and management of Beringia and its resources as a whole. The “footprint” of benthic-pelagic coupling in the sediments can provide a sentinel indicator of global-change effects (Grebmeier et al., 1988, 1989; Grebmeier and McRoy, 1989; Grebmeier and Cooper, 2004). Moore et al. (2003) have observed changes in gray whale distributions and a decline in productivity in whale feeding areas, and point out that: “physical forcing, which directly affects benthic coupling of

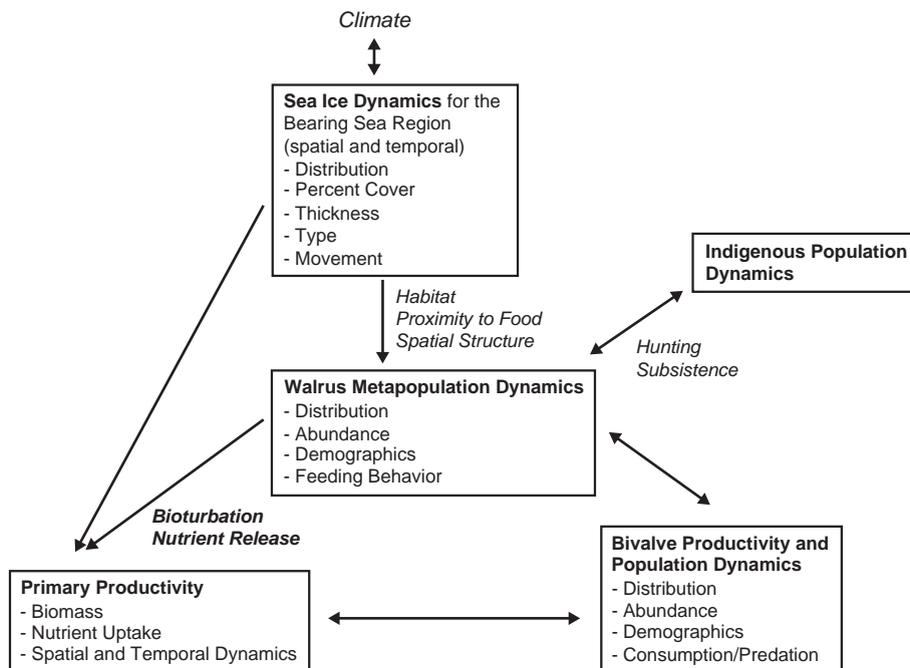


Fig. 10. A model of walrus relationships, illustrating the necessity for a multi-scaled, integrative approach towards interpreting the effects of walrus activities on Beringian ecology and native peoples. Top-down controls include climate and sea-ice dynamics. Walruses exert bottom-up controls on bivalves and other benthic communities through sediment alteration, consumption and the effects of nutrient cycling. These nutrient dynamics also have the potential to affect the walrus population itself. Native indigenous peoples depend on walruses and can influence these dynamics through their hunting activities.

biological processes...is key to any assessment of gray whale prey availability”.

In conclusion, we ask: What if walruses and other similar bioturbators were to move northward in response to changes in climate and sea ice, and their activities were to cease in the Bering Sea? Or, as Grebmeier and Dunton (2000) also ask: “How will a reduced ice cover impact higher trophic level populations and their associated predation on the benthos?” In this regard, we must consider that Beringia is a habitat for among the world’s greatest concentrations of ecologically “expensive” endothermic consumers, i.e., marine birds and mammals. The ecological importance of their activities will vary according to their numbers, aggregation size, time of year and location. However, whether or to what extent their activities cascade to whole ecosystems will only be resolved, if at all, by means of integration across multiple scales including climate, sea-ice habitat, feeding behavior, production regimes, patchiness of their food supply and the possible effects of subsistence hunting (Fig. 10).

The pioneering oceanographer Max Dunbar (1968) has hypothesized that many characteristics of polar and subpolar systems and their biota are a product of the short time that they have existed in their present condition: “...we have been looking at evolution in the polar regions as an ecological problem, which indeed it is, and have emphasized the development of the ecosystem as a whole rather than the evolution of individual species within the system”. Whether one adopts Dunbar’s evolutionary metaphor or not, it becomes apparent that the famed productivity of Beringia cannot be explained by any single factor, but is rather due to the combined interaction of climate, sea ice, oceanographic circulation and the biota, all of which operate at different scales.

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References

- Arrigo, K.R., 2003. Primary production in sea ice. In: Thomas, D.N., Dieckmann, G.S. (Eds.), *Sea Ice: An Introduction to its Physics, Chemistry, Biology and Geology*. Blackwell Science, Oxford, UK, pp. 143–183.
- Born, E.W., Rysgaard, S., Ehlme, G., Sejr, M., Acquarone, M., Levermann, N., 2003. Underwater observations of foraging free-living Atlantic walruses (*Odobenus rosmarus rosmarus*) and estimates of their food consumption. *Polar Biology* 26, 348–357.
- Burrell, D.C., Tomos, K., Naidu, A.S., Hoskin, C.M., 1988. Some geochemical characteristics of Bering Sea sediments. In: Hood, D. W., Kelly, E.J. (Eds.), *Oceanography of the Bering Sea*. Occasional Publication, vol. 1. Institute of Marine Science, University of Alaska, Fairbanks, pp. 305–319.
- Clement, J.L., Cooper, L.W., Grebmeier, J.M., 2004. Late-winter water column and sea ice conditions in the northern Bering Sea. *Journal of Geophysical Research* 109 (CO3022), 1–16.
- Cooney, R.T., Coyle, K.O., 1982. Trophic implications of cross-shelf copepod distribution in the southeastern Bering Sea. *Marine Biology* 70, 187–196.
- Cooper, L.W., Grebmeier, J.M., Larsen, I.L., Egorov, V.G., Theodorakis, C., Kelly, H.P., Lovvorn, J.R., 2002. Seasonal variation in sedimentation of organic materials in the St. Lawrence Island polynya region, Bering Sea. *Marine Ecology. Progress Services* 226, 13–26.
- Dunbar, M.J., 1968. *Ecological Development in Polar Regions: A Study in Evolution*. Prentice-Hall, Inc, Englewood Cliffs, NJ.
- Fay, F.H., 1957. History and present status of the Pacific walrus population. *Transactions of the North American Wildlife Conference* 22, 431–443.
- Fay, F.H., 1982. *Ecology and Biology of the Pacific Walrus Odobenus rosmarus divergens* Illiger. North American Fauna, vol. 74. U.S. Department of the Interior, Fish and Wildlife Service.
- Fay, F.H., Burns, J.J., 1988. Maximal feeding depth of walruses. *Arctic* 41 (3), 239–240.
- Fay, F.H., Ray, G.C., Kibal’chich, A.A., 1984. Time and location of mating and associated behavior of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. Soviet–American Cooperative Research on Marine Mammals. In: Fay, F.H., Fedoseev, G.A. (Eds.), vol. 1—Pinnipeds. NOAA Tech. Rept. NMFS 12, pp. 89–99.
- Fay, F.H., Kelly, B.P., Sease, J.L., 1989. Managing the exploitation of Pacific walruses: a tragedy of delayed response and poor communication. *Marine Mammal Science* 5 (1), 1–16.
- Fay, F.H., Eberhardt, L.L., Kelly, B.P., Burns, J.J., Quakenbush, L.T., 1997. Status of the Pacific walrus population, 1950–1989. *Marine Mammal Science* 13 (4), 537–565.
- Gjertz, I., Griffiths, D., Kraaft, B.A., Lydersen, C., Wiig, Ø., 2001. Diving and haul-out patterns of walruses *Odobenus rosmarus* in Svalbard. *Polar Biology* 24, 214–219.
- Gorbics, C.S., Garlich-Miller, J.L., Schliebe, S.L., 1998. Alaska Marine Mammal Stock Assessments 1998: Sea Otters, Polar Bear and Walrus. Marine Mammal Management, U.S. Fish and Wildlife Service, Anchorage, Alaska.

- Grebmeier, J.K., Cooper, L.W., 1995. Influence of the St. Lawrence Island polynya upon the Bering Sea benthos. *Journal of Geophysical Research* 100 (C3), 4439 (89-12-4460).
- Grebmeier, J.M., Cooper, L.W., 2004. Biological implications of arctic change. ACIA International Symposium on Climate Change in the Arctic, Reykjavik, Iceland, 9–12 November 2004.
- Grebmeier, J.M., Dunton, K.H., 2000. Benthic processes in the northern Bering/Chukchi Seas: status and global change. Impacts of Changes in Sea Ice and Other Environmental Parameters in the Arctic. Report of the Marine Mammal Commission Workshop, Girdwood, Alaska. U.S. Marine Mammal Commission, Bethesda, MD, USA, pp. 61–71.
- Grebmeier, J.M., McRoy, C.P., 1989. Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas: III. Benthic food supply and carbon cycling. *Marine Ecology. Progress Series* 53, 79–91.
- Grebmeier, J.M., McRoy, C.P., Feder, H.M., 1988. Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas: I. Food supply source and benthic biomass. *Marine Ecology. Progress Series* 48, 57–67.
- Grebmeier, J.M., Feder, H.M., McRoy, C.P., 1989. Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas: II. Benthic community structure. *Marine Ecology. Progress Series* 51, 253–268.
- Henriksen, K., Blackburn, T.H., Lomstein, B.A., McRoy, C.P., 1993. Rates of nitrification, distribution of nitrifying bacteria and inorganic fluxes in northern Bering–Chukchi shelf sediments. *Continental Shelf Research* 13 (5/6), 629–651.
- Howe, R.L., Rees, A.P., Widdicombe, S., 2004. The impact of two species of bioturbating shrimp (*Callianassa subterranea* and *Upogebia deltaura*) on sediment denitrification. *Journal of the Marine Biological Association of the United Kingdom* 84, 629–632.
- Jay, C.V., Farley, S.D., Garner, G.W., 2001. Summer diving behavior of male walrus in Bristol Bay, Alaska. *Marine Mammal Science* 17 (3), 617–631.
- Johnson, K.R., Nelson, C.H., 1984. Side-scan sonar assessment of gray whale feeding in the Bering Sea. *Science* 225, 1150–1152.
- Kastelein, R.A., Gerrits, N.M., 1990. The anatomy of the walrus head (*Odobenus rosmarus*): Part 1. The skull. *Aquatic Mammals* 16 (3), 101–119.
- Kastelein, R.A., Mosterd, P., 1989. The excavation technique for mollusks of Pacific walrus (*Odobenus rosmarus divergens*) under controlled conditions. *Aquatic Mammals* 15 (1), 3–5.
- Kastelein, R.A., van Gaalen, M.A., 1988. The sensitivity of the vibrissae of a Pacific walrus (*Odobenus rosmarus divergens*): Part 1. *Aquatic Mammals* 14 (3), 123–133.
- Kastelein, R.A., Stevens, S., Mosterd, P., 1990. The tactile sensitivity of the mystacial vibrissae of a Pacific walrus (*Odobenus rosmarus divergens*): Part 2. Masking. *Aquatic Mammals* 16 (2), 78–87.
- Kastelein, R.A., Gerrits, N.M., Dubbeldam, J.L., 1991. The anatomy of the walrus head (*Odobenus rosmarus*): Part 2. Description of the muscles and of their role in feeding and haul-out behavior. *Aquatic Mammals* 17 (3), 156–180.
- Kastelein, R.A., Muller, M., Terlouw, A., 1994. Oral suction of a Pacific walrus (*Odobenus rosmarus divergens*) in air and under water. *Zeitschrift für Säugetierkunde* 59, 105–115.
- Kastelein, R.A., Dubbeldam, de Bakker, M.A.G., 1997. The anatomy of the walrus head (*Odobenus rosmarus*): Part 5. The tongue and its function in walrus ecology. *Aquatic Mammals* 23 (1), 29–47.
- Lizotte, M.P., 2003. The microbiology of sea ice. In: Thomas, D.N., Dieckmann, G.S. (Eds.), *Sea Ice: An Introduction to its Physics, Chemistry, Biology and Geology*. Blackwell Science, Oxford, UK, pp. 184–210.
- Lohrer, A.M., Thrush, S.F., Gibbs, M.M., 2004. Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature* 431, 1092–1095.
- Lomstein, B.A., Blackburn, T.H., Henriksen, K., 1989. Aspects of nitrogen and carbon cycling in the northern Bering shelf sediment: I. The significance of urea turnover in the mineralization of NH_4^+ . *Marine Ecology. Progress Series* 57, 237–247.
- Lopez, G.R., Levinton, J.S., 1987. Ecology of deposit-feeding animals in marine sediments. *The Quarterly Review of Biology* 62 (3), 235–260.
- Lovvorn, J.R., Richman, S.E., Grebmeier, J.M., Cooper, L.W., 2003. Diet and body condition of spectacled eiders wintering in pack ice of the Bering Sea. *Polar Biology* 26, 259–267.
- Lovvorn, J.R., Cooper, L.W., Brooks, M.L., De Ruyck, C.C., Bump, J. K., Grebmeier, J.M., 2005. Organic matter pathways to zooplankton and benthos under pack ice in late winter and open water in late summer in the north-central Bering Sea. *Marine Ecology. Progress Series* 291, 135–150.
- Maximovich, N.V., Guerassimova, A.V., 2003. Life history characteristics of the clam *Mya arenaria* in the White Sea. *Helgolander Marine Research* 57, 91–99.
- Mayr, E., 1997. *This is Biology: The Science of the Living World*. Belknap Press, Harvard University Press, Cambridge, Massachusetts.
- Moore, S.E., Grebmeier, J.M., Davies, J.R., 2003. Gray whale distribution relative to forage habitat in the northern Bering Sea. *Canadian Journal of Zoology* 81, 734–742.
- Naidu, A.S., 1987. Marine surficial sediments. Map 1.4 in Bering, Chukchi, and Beaufort Seas Coastal and Ocean Zones Strategic Assessment: Data Atlas. National Oceanic and Atmospheric Administration, National Ocean Service, Strategic Assessment Branch. U.S. Government Printing Office, Washington, D.C.
- Naidu, A.S., Cooper, L.W., Grebmeier, J.M., Whitley, T.E., Hameedi, M.J., 2004. The continental margin of the north Bering–Chukchi Sea: distribution, sources, fluxes, and burial rates of organic carbon. In: Stein, R., MacDonald, R.W. (Eds.), *The Organic Carbon Cycle in the Arctic Ocean*. Springer-Verlag, Berlin.
- Nelson, C.H., Johnson, K.R., 1987. Whales and walrus as tillers of the sea floor. *Scientific American* 256 (2), 112–117.
- NOAA 1987. Bering, Chukchi, and Beaufort Seas Coastal and Ocean Zones Strategic Assessment: Data Atlas. National Oceanic and Atmospheric Administration, National Ocean Service, Strategic Assessment Branch. U.S. Government Printing Office, Washington, D.C.
- Odum, W.E., Odum, E.P., Odum, H.T., 1995. Nature's pulsing paradigm. *Estuaries* 18 (4), 547–555.
- Ólafsson, E.G., 1986. Density dependence in suspension-feeding and deposit-feeding populations of the bivalve *Macoma balthica*: a field experiment. *Journal of Animal Ecology* 55, 517–526.
- Oliver, J.S., Slattery, P.N., O'Connor, E.F., Lowry, L.F., 1983. Walrus, *Odobenus rosmarus*, feeding in the Bering Sea: a benthic perspective. *Fishery Bulletin* 81 (3), 501–512.
- Oliver, J.S., Kvitek, R.G., Slattery, P.N., 1985. Walrus feeding disturbance: scavenging habits and recolonization of the Bering Sea benthos. *Journal of Experimental Marine Biology and Ecology* 91, 233–246.
- Ray, G.C., 1973. Underwater observation increases understanding of marine mammals. *Marine Technology Science Journal* 7 (1), 16–20.

- Ray, G.C., 1984. Submersible systems for ecological research in polar regions. *Marine Technology Science Journal* 18 (1), 54–60.
- Ray, G.C., Curtsinger, B., 1979. Learning the ways of the walrus. *National Geographic* 156 (4), 564–580.
- Ray, G.C., Hufford, G.L., 1989. Relationships among Beringian marine mammals and sea ice. *Rapports et Procès-verbal des Réunion-Conseil International pour l'Exploration de la Mer* 188, 22–39.
- Ray, G.C., McCormick-Ray, J., 2004. *Coastal-Marine Conservation: Science and Policy*. Blackwell Science, Oxford, UK, pp. 189–202. Chapter 6.
- Ray, G.C., Wartzok, D., 1980. Remote sensing of marine mammals of Beringia. Results of BESMEX: the Bering Sea marine mammal experiment. Report under NASA Contract NAS2-9300, pp. 1–77.
- Rhoads, D.C., 1974. Organism–sediment relations on the muddy sea floor. *Oceanography and Marine Biology Annual Review* 12, 263–300.
- Roseberry, L., Vincent, B., Lemaire, C., 1991. Croissance et reproduction de *Mya arenaria* dans la zone intertidale du Saint-Laurent. *Canadian Journal of Zoology* 69 (3), 724–732.
- Rowe, G.T., Phoel, W.C., 1992. Nutrient regeneration and oxygen demand in Bering Sea continental shelf sediments. *Continental Shelf Research* 12 (4), 439–449.
- Sarmiento, J.L., Slater, R., Barber, R., Bopp, L., Doney, S.C., Hirst, A. C., Kleypas, J., Matear, R., Mikolajewicz, U., Monfray, P., Soldatov, V., Spall, S.A., Stouffer, R., 2004. Response of ocean ecosystems to climate warming. *Global Biogeochemical Cycles* 18 (GB3003), 1–23.
- Seitzinger, S.B., Giblin, A.E., 1996. Estimating denitrification in North Atlantic continental shelf sediments. *Biogeochemistry* 35, 235–260.
- Sejr, M.K., Sand, M.K., Jensen, K.T., Petersen, J.K., Christensen, P.B., Rysgaard, S., 2002. Growth and production of *Hiatella arctica* (Bivalvia) in a high-Arctic fjord (Young Sound, Northeast Greenland). *Marine Ecology. Progress Series* 244, 163–169.
- Sheffield, G.G. 197. Walrus feeding: a re-examination. MS Thesis, University of Alaska: 1–55.
- Sheffield, G., Fay, F.H., Feder, H., Kelly, B.P., 2001. Laboratory digestion of prey and interpretation of walrus stomach contents. *Marine Mammal Science* 17 (2), 310–330.
- Shugart, H.H., 1984. *A Theory of Forest Dynamics: The Ecological Implications of Forest Succession Models*. Springer-Verlag, New York, NY.
- Simpkins, M.A., Hiruki-Raring, L.M., Sheffield, G., Grebmeier, J.M., Bengtson, J.L., 2003. Habitat selection by ice-associated pinnipeds near St. Lawrence Island, Alaska, in March 2001. *Polar Biology* 26, 577–586.
- Smetacek, V., Nicol, S., 2005. Polar ocean systems in a changing world. *Nature* 437, 362–368.
- Springer, A.M., McRoy, C.P., 1993. The paradox of pelagic food webs in the northern Bering Sea: III. Patterns of primary production. *Continental Shelf Research* 13 (5–6), 575–599.
- Springer, A.M., McRoy, C.P., Flint, M.V., 1996. The Bering Sea green belt: shelf-edge processes and ecosystem production. *Fisheries Oceanography* 5 (3–4), 205–223.
- Stoker, S. 1973. Under-ice studies of winter benthos on the continental shelf of the northeastern Bering Sea. Masters Thesis. University of Alaska, Fairbanks.
- Stoker, S., 1981. Benthic invertebrate macrofauna of the eastern Bering/Chukchi continental shelf. Pp. 1069–1090. In: Hood, D.W., Calder, J.A. (Eds.), *The Eastern Bering Sea Shelf: Oceanography and Resources*, vol. 2. Office Marine Pollution Assessment, NOAA, U.S Dept. Commerce, Washington, D.C., p. 455.
- Votrogov, L.M., Bogoslovskaya, L.S., 1980. Gray whale off the Chukotka Peninsula. Report of the International Whaling Commission 30, 435–438.
- Wartzok, D., Ray, G.C., 1980. The hauling-out behavior of the Pacific Walrus. U.S. Department of Commerce, National Technical Information Service PB80-192578: 1–46.
- Welch, H.E., Martin-Bergmann, K., 1990. Does the clam *Mya truncata* regenerate its siphon after predation by walrus? An experimental approach. *Arctic* 43 (2), 157–158.
- Weston, D.P., 1988. Macrobenthos–sediment relationships on the continental shelf off Cape Hatteras, North Carolina. *Continental Shelf Research* 8 (5), 267–286.
- Wheatcroft, R.A., Drake, D.E., 2003. Post-depositional alteration and preservation of sedimentary event layers on continental margins: I. The role of episodic sedimentation. *Marine Geology* 199, 123–137.