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A Review of Apparent 20th Century Changes in the Presence of Mussels (*Mytilus trossulus*) and Macroalgae in Arctic Alaska, and of Historical and Paleontological Evidence Used to Relate Mollusc Distributions to Climate Change

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ABSTRACT. Live mussels attached to fresh laminarioid brown algae, all fastened to clusters of pebbles and small cobbles, were repeatedly cast ashore by autumn storms at Barrow, Alaska, in the 1990s. Specimens of *Laminaria saccharina* and *L. solidungula* shorten by 100 km a 500 km gap (Peard Bay to Stefansson Sound) between previously known concentrations of these kelp species. For the genus *Mytilus*, a 1600 km gap in fully documented locations existed between Kivalina in the southern Chukchi Sea and the Mackenzie River delta. Barrow specimens were identified using a mitochondrial DNA marker as *M. trossulus*, an identity consistent with dispersal from the Pacific-Bering side of the Arctic. Live mussels and macroalgae were neither washed up by storms nor collected by active biological sampling during extensive benthic surveys at Barrow in 1948 – 50. We cannot interpret the current presence of these bivalves and macrophytes as Arctic range extensions due to warming, similar to those manifested by the tree line in terrestrial systems and by Pacific salmon in marine environments. Supplemental information and critical evaluation of survey strategies and rationales indicate that changes in sea temperatures are an unlikely cause. Alternative explanations focus on past seafloor disturbances, dispersal from marine or estuarine refugia, and effects of predators on colonists. This review suggests refining some interpretations of environmental change that are based on the extensive resource of Cenozoic fossils of Arctic molluscs.

Key words: Chukchi Sea, Beaufort Sea, Barrow, *Mytilus*, *Laminaria*, climate change, benthic substrates, marine predation, estuarine refugia, Cenozoic fossil molluscs, dispersal mechanisms

RÉSUMÉ. Durant les années 1990, des moules vivantes fixées sur des algues brunes laminaires, toutes attachées à des agrégats de galets et de petits cailloux, ont été rejetées par les tempêtes automnales sur les rivages de Barrow, Alaska. Des spécimens de *Laminaria saccharina* et de *L. solidungula* raccourcissent de 100 km la distance de 500 km (de Peard Bay à Stefansson Sound) qui sépare les concentrations précédemment connues de ces espèces de varech. Pour le genre *Mytilus*, il existait une distance de 1600 km séparant les emplacements très bien documentés allant de Kivalina dans la partie méridionale de la mer des Tchouktches au delta du Mackenzie. À l’aide d’un marqueur ADN mitochondrial, les spécimens de Barrow ont été identifiés comme appartenant à *M. trossulus*, ce qui s’accorde bien avec une dispersion depuis le côté Pacifique-Béring de l’Arctique. Lors d’un vaste progamme de relevés benthiques à Barrow dans les années 1948 – 1950, les moules vivantes et les macroalgues n’ont pas été rejetées par les tempêtes ni obtenues par échantillonnages biologiques actifs. On ne peut interpréter la présence actuelle de ces bivalves et macrophytes comme des extensions de leur aire de distribution arctique dues au réchauffement, comme cela est le cas pour la ligne des arbres dans les systèmes terrestres et pour les espèces de saumons du Pacifique dans les milieux marins. D’autres informations ainsi qu’une évaluation critique des stratégies et des justifications de relevés révèlent que les changements dans les températures de la mer sont une cause peu probable. Les autres explications concernent des perturbations antérieures du plancher océanique, la dispersion depuis des refuges marins ou estuariens et l’impact des prédateurs sur les espèces colonisatrices. Cette étude suggère que l’on repense certaines interprétations du changement environnemental fondées sur les vastes quantités de fossiles de mollusques arctiques datant du cénozoïque.

Mots clés: mer des Tchouktches, mer de Beaufort, Barrow, *Mytilus*, *Laminaria*, changement climatique, substratums benthiques, prédation marine, refuges estuariens, mollusques fossiles du cénozoïque, mécanismes de dispersion

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INTRODUCTION

Westerly winds and waves during autumnal storms in 1993, 1994, 1995, and 1997 allowed us to secure live specimens of mussels (*Mytilus*, Fig. 1) and two species of macroscopic brown algae (*Laminaria saccharina*, and *L. solidungula*) fastened to clusters of pebbles and small cobbles from windrows along Barrow's Chukchi Sea shoreline. By contrast, no live specimens of either *Mytilus* or *Laminaria* were collected there after fall storms by investigators conducting intensive surveys in 1948–50. The prospect that these discrepant observations might reflect long-term changes in benthic ecology near Barrow (71˚20′ N, 156˚35′ W) since the mid-20th century led us to evaluate the possibility of using them as indicators of local or more widespread changes.

George and Nettie MacGinitie conducted all-season surveys of Arctic marine environments at the confluence of the Beaufort and Chukchi Seas in the years 1948 to 1950. Results of their project (G. MacGinitie, 1955; N. MacGinitie, 1959) remain the most comprehensive accounts of the region's benthic biota (Feder, 2001). The only benthic organisms found abundantly in the 1990s that the MacGinities did not report to be living near Barrow were the two morphologically distinct species of *Laminaria* (K.H. Dunton, pers. comm. 1997) and the more taxonomically challenging *Mytilus* (Geller et al., 1993).

These discrepancies over time at first seemed explicable as range extensions (Feder, 2001) like those reported in distributions of other biota, which analysts have linked to climatic warming in the Arctic. Examples include advances of the tree line (Payette et al., 2002) and the presence at higher latitudes of Pacific salmon (*Onchorhynchus* spp., Babaluk et al., 2000). Closer examination of published and unpublished sources, however, raised doubts that any environmental factors constraining either *Laminaria* or *Mytilus* have relaxed since 1950. *Mytilus*, for example, has populated Arctic latitudes of western Canada at least since the Pacific connection to the Arctic Ocean opened at the Bering Strait, most recently in the Holocene between 10 500 and 10 300 years ago (Dyke et al., 1996:167). Modern *Mytilus* populations are found at Baffin Island (Lubinsky, 1980) and widely off western Greenland (Petersen, 1978) as far north as Thule (79˚ N, Thorson, 1951). Between 10 000 and 5000 years ago, the genus was also widespread in eastern Greenland (Ockelmann, 1958) and in Svalbard to about 80˚ N (Salvigsen et al., 1992; Salvigsen, 2002). Gametogenic development is initiated and continues throughout the winter in intertidal populations of *Mytilus trossulus* in Prince William Sound at temperatures down to at least 0˚C (Blanchard and Feder, 1997). Given suitable substrate, *Laminaria solidungula* is also capable of sustaining populations at high latitudes, under sea ice persisting nine months or more annually (Dunton, 1990; Dunton and Dayton, 1995).

Three alternative statements describe and explain the contrasts between the Barrow-based observations in 1948–50 and those in the 1990s. 1) *Laminaria*, *Mytilus*, or both have expanded their ranges in the northern Chukchi Sea since 1950; 2) No range expansion has taken place, but the MacGinities' sampling missed kelp and mussel populations that were present near Barrow 50 years ago much as they are today; 3) These taxa were absent near Barrow in 1948–50, but their presence in the 1990s is evidence of one of the many swings from absence or extreme scarcity to local abundance and back again that biota in marginal environments and habitats exhibit over decades in response to episodic physical perturbations. 3a) A variant of 3 is that *Mytilus* populations disappear locally from marginal Arctic habitats as a result of predation.

FIG. 1. Fresh *Mytilus* specimens from storm windrow near Barrow on 25 September 1993. Photo by John Blackman.

To distinguish among these alternatives, we pursue several lines of evidence: A) Evaluation and comparison of the circumstances under which kelp and mussels eluded the MacGinities in 1948–50 at Barrow, but were collected frequently by amateurs in the 1990s; B) Review and characterization of other regional *Mytilus* observations and sampling efforts made after the MacGinitie years, and extension of opportunistic observations in the Chukchi Sea and at a fossil site on the Colville River; C) Identification to species of the *Mytilus* specimens from Barrow as a contribution to clarifying the taxonomy and biogeography of the genus at high latitudes.

MATERIALS AND METHODS

Beach Sampling at Barrow in the 1990s

Qualitative beach collecting at Barrow during the 1990s (by D.W. Norton) was undertaken to supply living specimens for public and classroom displays in several refrigerated saltwater aquaria in the community. Collectors traveled the strand line by lightweight all-terrain vehicle, covering beaches from south of Barrow northeastward past Point Barrow to Eluitkak Pass on the Beaufort Sea side of Barrow in a few hours. During the open-water seasons over six years, 1992–97, beach collecting was conducted each autumn except in 1996.

Review of Previous Surveys and Extension of Field Sampling beyond Barrow

To supplement examinations of published results, we reviewed results of sampling reported in refereed and fugitive literature, and we communicated with authors and investigators, as noted below, to verify their positive and negative findings for *Laminaria* and *Mytilus* in past and ongoing surveys. In June 2000 and July 2001, travel for other research projects enabled D.W. Norton to extend previous fieldwork by exploring the still-frozen Chukchi Sea strand line near Wainwright, Alaska, for remains of macroalgae and *Mytilus*. Participation in vertebrate paleontological investigations since 1991 also allowed D.W. Norton to examine mollusc shells found in marine sediments of the Cenozoic Gubik Formation, which overlies Cretaceous formations near Big Bend on Alaska's Colville River.

Mytilus *Identification to Species*

The three morphologically indistinguishable species that comprise the *Mytilus edulis* complex (*M. edulis*, *M. trossulus*, and *M. galloprovincialis*) can be distinguished using a variety of genetic markers (McDonald et al., 1991; Geller et al., 1994; Heath et al., 1995; Inoue et al., 1995; Rawson and Hilbish, 1995a, b). For dry tissue, mitochondrial markers are especially useful because they are typically present in high copy numbers in cells, and sufficient quantities of intact mtDNA can be obtained.

A small subsample of hundreds of viable mussels that had washed up on the beach in 1993 at Barrow, Alaska, was allowed to air dry. Two specimens that appeared to retain the whole dried animal were analyzed, following procedures described in detail in Geller (1999). Approximately 100 mg of dry tissue was cut from these specimens, homogenized in 500 μl CTAB extraction buffer and twice extracted with one volume of chloroform. DNA was precipitated with one volume of ice-cold 100% propanol and resuspended in 100 μl TE (10 mM Tris and 1 mM EDTA, pH = 8.0). Then 16S mitochondrial rDNA was amplified in two rounds of the polymerase chain reaction using previously described primers, negative controls, and reaction conditions (Geller and Powers, 1994; Geller et al., 1997; Geller, 1999). PCR products were cloned into pCR 2.1 (Invitrogen, Carlsbad, California). Purified plasmids were sequenced with a Sequitherm Excel II LC sequencing kit (Epicentre Technologies, Madison, Wisconsin) and electrophoresed on an automated sequencer (Licor 4200LR-2). One useful sequence was obtained and aligned, using Clustal X (Thompson et al., 1994), with 28 *Mytilus* spp. sequences (Rawson and Hilbish, 1995a, b, 1998) retrieved from GenBank. The computer program PAUP* 4.08 (Swofford, 1999) was then used to determine the phylogenetic affinity of the Alaskan mussel. We employed a bootstrapped neighbor-joining algorithm (Kimura two-parameter distance measure) with 1000 replicates.

RESULTS

*The Substrate-*Laminaria-Mytilus *Connection: Comparison of 1990s with 1948–50*

Yields of living specimens during beach collections in the 1990s reflected the strength and duration of onshore winds and waves accompanying fall storms. The most effective tactic for acquiring live *Mytilus* proved to be searching for fresh fronds of *Laminaria*, because mussels and other bivalves were predictably fastened to the bases of large algae that fast-moving observers could see from a distance. After prolonged storms, only a small fraction of the 10s to 100s of kelp fronds washed ashore with attached mussels were needed to replenish aquarium populations. No more than 50 individual *Mytilus* and 15 large *Laminaria* were taken after a productive storm. From the range of total lengths (10 to about 85 mm), the largest live *Mytilus* collected on the beach near Barrow appeared from annular ridge counts to exceed 13 years of age. Empty *Mytilus* valves in storm windrows at Barrow commonly bore characteristic drill holes, indicating that some local mussel mortality is caused by the predatory snails, *Natica* or *Polinices* (MacGinitie, 1955:90–92; Feder, 2001:55). Mussels and macroalgae were the only unexpected additions to benthic biota over what the MacGinities (1955, 1959) reported as living at Barrow. Thus, for example, live representatives of the same genera of sea stars reported in the earlier studies (MacGinitie, 1955:145)—*Crossaster*, *Solaster*, *Henricia* and *Leptasterias*—were collected from windrows on the beach in the 1990s.

Despite their focus on benthic fauna, George MacGinitie and his associates were vigilant for kelp during their field surveys. On a single occasion in 1949, for example, a windrow of unidentifiable algal material was recorded on the shore (H.M. Feder, unpubl. field notes). Moreover, their interpretations emphasized the "total absence of macroscopic algae," which they ascribed to a scarcity of rocky benthic habitats. In turn, MacGinitie (1955:189) asserted that the lack of macroalgae "excludes certain animals from the Point Barrow region."

In their treatment of habitats, macrophytes, and epibenthic fauna, the MacGinities emphasized the interdependence of rocky substrates, macroalgae, and epifauna in the Arctic. The direct physical attachments between macroalgae and mussels that we observed add weight to the MacGinities' characterizations of epibenthic biota crowding onto scarce suitable surfaces (MacGinitie, 1955:34–35). Stable attachment points in benthic communities, as the MacGinities pointed out, are at a premium near Barrow (cf. Norton, 2001a:12–13, illustration), where fine-grained sediments dominate a seafloor that is only occasionally punctuated by rocks or large cobbles. We

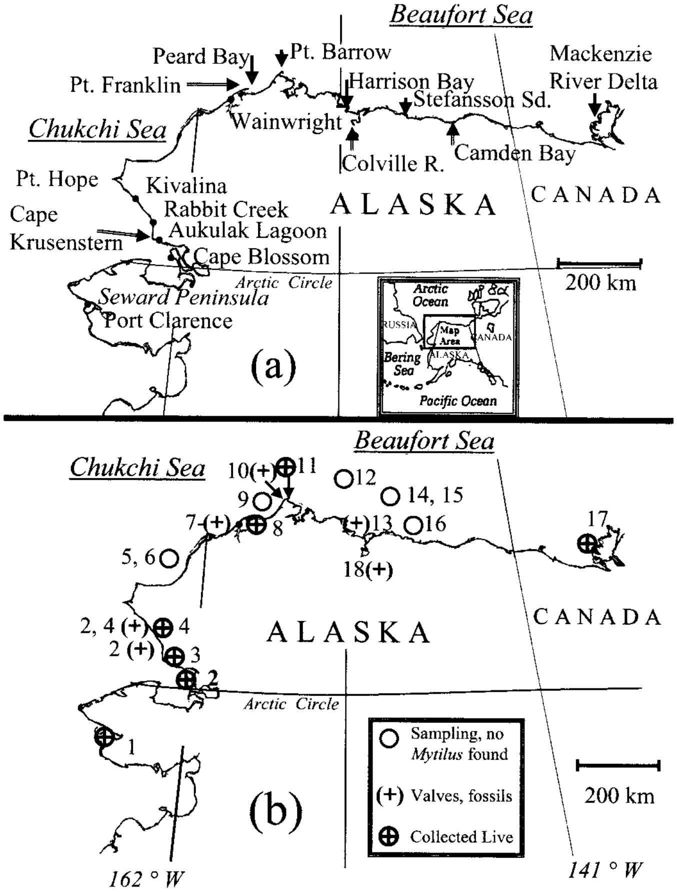

FIG. 2. *Mytilus* in Arctic Alaska, 1948–2002. a) Location map. b) Results of *Mytilus* collecting efforts, and number keys to authorities, corresponding to text entries in Table 1.

found that as it grows, whichever plant or animal first gains a hold on bits of hard substrate becomes an increasingly attractive target itself for attachment by smaller, later-arriving colonists. Masses of kelp and epifaunal animals in windrows showed instances in which small-bodied individual *Mytilus* had fastened themselves to the bases of more massive, already attached *Laminaria* plants by byssal threads, and instances of the reverse, in which young individual *Laminaria* had anchored themselves by holdfast to valves of attached *Mytilus*.

*The Substrate-*Laminaria-Mytilus *Connection: Field Studies Continuing the MacGinities' Work*

Mohr et al. (1957) reported finding occasional stranded pieces of algae on the Chukchi Sea shore, but they never found conspicuous masses of macroalgae on the strand line. After dredging at Barrow from 1951 to 1954 failed to find kelp, they commented, "Probably no…feature of the marine biota of the Point Barrow area is more striking than the absence of macroscopic benthic…[algae]" (Mohr et al., 1957:45). Their discovery of a few scattered kelp beds on rocky bottom, 60 km southwest of Barrow and just east of Peard Bay, showed that a few of these marine plants could be expected in the northeastern Chukchi Sea if appropriate substrate and other physical conditions were both present.

Until the 1970s, the continental shelf of the Beaufort Sea off Alaska was also considered barren of rocky substrates and associated epibenthos. Although MacGinitie (1955:10) noted limited areas of scattered rocks offshore on the Chukchi Sea side of Point Barrow, Carsola (1952) assessed the substrate of the Beaufort Sea from western Arctic Alaska to the Mackenzie Delta in the east, and reported a bottom consisting of fine sediments devoid of rocks or boulders. Collins' (1927) earlier account of benthic algae of the Beaufort Sea states that no extensive stands of macroalgae were found between Point Barrow and the Mackenzie River. Over many years of beach surveys, occasional algal fragments were found from Point Barrow to the Canadian border, but entire plants were rarely observed in drift lines (Dunton et al., 1982). Because a hard substrate is required for attachment of algal species, ecologists continued to assume that algal beds along Alaska's Beaufort Sea coast are absent or rare.

In 1971, Erk Reimnitz discovered cobbles, rocks, and boulders with abundant attached kelp (primarily *Laminaria solidungula*: Dunton, 1985) in Stefansson Sound. The diverse invertebrate fauna associated with kelp in this boulder and cobble assemblage has been described by Dunton et al. (1982) and Dunton and Schonberg (1979, 2000). These investigations confirmed expectations that a rich flora and fauna can develop in the Arctic, given suitable and stable substrate. Stefansson Sound bridged a 1000 km gap in documented localities for *Laminaria* by being roughly equidistant from kelp beds described at Peard Bay (Mohr et al., 1957) and beds off the Mackenzie River delta of the Canadian Arctic (Lee, 1973).

Mytilus *Surveys and Findings Reviewed and Extended*

Nettie MacGinitie (1959) was sufficiently intrigued by *Mytilus* to attempt to explain the absence of living specimens from Barrow. Her list of 30 bivalve species collected at Barrow included *Mytilus* only because an empty valve of the taxon was taken by dredge at Eluitkak Pass in August 1948, and another partial valve washed ashore in September 1949. Her awareness that *Mytilus* inhabits high-latitude Atlantic sites prompted her to rationalize the absence of the genus from Barrow. She suggested that empty valves had been transported by currents or ice-rafted from distant "tidal-zone" habitats (MacGinitie, 1959: 157). The negligible celestial tides (e.g., 0.15–0.25 m) in northern Alaska (MacGinitie, 1955:24; Walker, 2001a:118) deprive Barrow of a zone periodically covered and uncovered at high and low water. Even if an intertidal zone existed, sea ice disturbance, as well as the unstable, gravelly substrate, would make it uninhabitable by intertidal benthos, epifauna, or epiphytes.

Table 1 summarizes positive and negative results of surveys, reviews, and collections in the Western North American Arctic that bear on the presence or absence of

TABLE 1. Summary of *Mytilus* observations and specimens from Arctic Alaska, 1948–2002.

Key	Location	Observation	Authority
1	N. Bering Sea: Port Clarence	Live *Mytilus* on rocky subtidal bottom, no kelp, depth of 3 m	North, 1972
2	Chukchi Sea: Cape Blossom	Cluster of 3 live juvenile *Mytilus*, 17–20 mm, aged 2–3 y, recovered from dredging offshore in 20 m of water	S. Jewett, pers. comm. 2001, 2002
	Rabbit Creek; Kivalina	Valves on beach; single live mussel being eaten by sea star *Asterias* in marine environment off lagoon; no mussel beds seen by divers; windrows of valves on beaches bordering lagoon	
3	Aukulak Lagoon, Krusenstern	Live *Mytilus*, lagoon habitat; (no substrate or depth information)	O'Clair et al., 1992
4	Kivalina	Live *Mytilus* in brackish lagoonal environments; valves onshore nearby; no specimens in marine environment offshore of the lagoon	Sparks and Pereyra, 1966:822
5	Pt. Hope to Pt. Franklin	No *Mytilus* specimens taken by trawls or grab sampling, 18–50 m	Feder et al., 1994a, b
6	Pt. Hope to Pt. Barrow	WEBSEC, 14 van Veen grab stations ≥19 m: No *Mytilus*	Naidu and Sharma, 1972
7	5 km SW of Wainwright (Thomas Point)	Thousands of adult *Mytilus* valves along channel connecting Chukchi Sea and Wainwright Inlet (estuary)	This study (D.W.N. beachcombing in June 2000, July 2001)
8	Kugrua Bay, inside Peard Bay	A small number of living *Mytilus* reported without comment.	Kinney, 1985:355
9	E of Peard Bay, NE Chukchi Sea	No *Mytilus* specimens taken by dredge from kelp beds at 13 m	Mohr et al., 1957; J.L. Mohr, pers. comm. 2000
10	Chukchi and Beaufort Seas, Barrow	Trawls, dredges, littoral surveys: two empty adult *Mytilus* valves in 1948–50;	G. MacGinitie, 1955; N. MacGinitie, 1959;
		5 articulated juvenile valves, 7–13 mm dated 1952–53 (LACM); additional single adult valves in undocumented Barrow collections at UA Museum	LACM, coll. by Mohr? (L. Groves, pers. comm. 2003)
11	Barrow, beach surveys, Chukchi, Beaufort coasts	Live *Mytilus* common following fall storms, 1993–97, most attached to *Laminaria*, 15–85 mm, max. age 14 y	This study, Barrow beachcombing, 1990s
12	NE Chukchi and W Beaufort Seas	No *Mytilus* specimens taken or noted in several seasons of littoral zone surveys in the 1970s	A. Carter Broad and S. Schonberg, pers. comm. 2000
13	Beaufort Sea: Harrison Bay, W. of Colville River Delta	*Mytilus* noted, but without details; authors of survey report do not recall circumstances (shown in Fig. 2b as empty valve)	Alexander et al., 1975; D.M. Schell, pers. comm. 2001
	W. Harrison Bay, Kogru Estuary to Fish Creek	Fresh-looking empty *Mytilus* valves photographed in 2001(?)	J.W. Helmericks, pers. comm. 2003
14	W. Beaufort Sea	No *Mytilus* taken by ship-based grab or otter trawls over survey area	Carey et al., 1974, 1981
15	W. Beaufort Sea	*Mytilus* specimens not taken by extensive grab and otter trawls	Bernard, 1979; Dunton and Schonberg, 2000
16	Beaufort Sea: Stefansson Sound Boulder Patch	*Mytilus* neither observed nor collected during thousands of SCUBA dives in 30 years since discovery of the *Laminaria* beds and rocky substrate community.	Dunton et al., 1982; Dunton and Schonberg, 2000; pers. comm. 2000
17	Mackenzie River Delta	Accepted western limit of modern *Mytilus* distribution in Canada's Beaufort Sea	Lubinsky, 1980; N. Foster, pers. comm. 2001
18	Fossil: Colville R., 40 km upriver of Nuiqsut, 50 km from mouth	Single adult *Mytilus* valve found in marine gravels of Bigbendian Transgression, in which other bivalves and gastropods, including naticids, are common	This study (D.W. Norton, pers. obs. 2002)

Mytilus. Figure 2 updates key localities, the geographic patterns of modern occurrence, and one case of a pre-Holocene specimen in northern Alaska. With reference to published accounts, our finding of live mussels at Barrow shrinks an apparent "*Mytilus* gap" of 1600 km between Kivalina, 700 km to the southwest of Barrow, and the Mackenzie River delta region, 900 km to the east (Fig. 2a). Rescuing some observations from fugitive literature shrinks the distance over which the genus can be regarded as currently absent. Until this review, however, biologists have continued N. MacGinitie's (1959) reluctance to regard empty *Mytilus* valves as evidence for populations living nearby in an a-tidal marine environment. Articulated juvenile *Mytilus* shells (and probably their living contents) were collected by dredge at Barrow in 1952–53, but the unknown collector may have doubted that they were of local origin (L. Groves, pers. comm. 2003).

Many of the valves found near Wainwright (entry 7 in Table 1 and Fig. 2b) in 2000 and 2001 were still in articulated pairs, suggesting mortality and deposition ashore during the most recent ice-free seasons (1999 and 2000, respectively). Besides consisting entirely of empty valves, the Wainwright specimens were distinguished from those found at Barrow by three other characteristics: 1) absolute numbers and densities were at least an order of magnitude greater at Wainwright than ever seen at one time at Barrow; 2) no *Laminaria* or other macroalgae were attached to any of the valves at Wainwright; 3) of 118 valves saved from two seasons of beachcombing, none bore the distinctive drill holes made by the marine predatory snails, *Polinices* or *Natica*, found at Barrow (MacGinitie 1955:90–92; Feder 2001:55; cf. Coan et al., 2000:158). When shown a collection of mussel shells, a lifelong senior resident of Wainwright recalled eating bivalves "like these" that his mother gathered (H. Tazruk, pers. comm. 2000).

Table 1 includes two additions of *Mytilus* occurrence in Arctic Alaska that came to light in mid-2002. First, Stephen C. Jewett (pers. comm. 2002) found clusters of juvenile mussels (17–20 mm, ages 2–3 yr) while dredging for benthos offshore at Cape Blossom. The puzzlement we expressed over distributional gaps alerted Dr. Jewett to *Mytilus* specimens at several locations in the Chukchi Sea during his fieldwork there. Second, a single *Mytilus* valve was found among marine mollusc shells examined in the Gubik Formation along the west bank at Big Bend on the Colville River, 50 km inland from the Beaufort Sea. Molluscs have long been collected from this and other locations comprising the several "Gubik" marine transgressions (intervals of higher sea level associated with non-glacial or interglacial warmer climates and with raised marine deposits containing fossils). The *Mytilus* valve from Big Bend was examined and found not to bear a drill hole made by predatory naticid snails (although other bivalves from this location do, and shells of naticids themselves are found there, cf. Peacock, 1989) before the specimen was lost in transit between the field and the University of Alaska Museum.

Mytilus *Identification to Species*

Degraded DNA from the two 1993 Barrow specimens was visualized on ethidium bromide stained gels. A first round of PCR with primers D16SAR and D16SBR yielded faint products. A second round of PCR, using first-round products as template, produced strong bands. For second-round PCR, primer combination D16SAR /MYT16SB produced stronger amplification for specimen two; this product was cloned and sequenced, and we refer to this sequence as the Barrow mussel. Negative controls did not produce amplification products. This sequence has been deposited in GenBank (Accession number AY099472). A neighbor-joining tree placed the Barrow mussel in a cluster with female *Mytilus trossulus*. Both male and female *M. trossulus* carry the female lineage of mtDNA in somatic tissues (Geller, 1994), so we conclude only that this mussel was likely *M. trossulus*. One hundred percent of 1000 bootstrap replicates placed the Barrow mussel in this cluster, providing us high confidence in this result (Fig. 3).

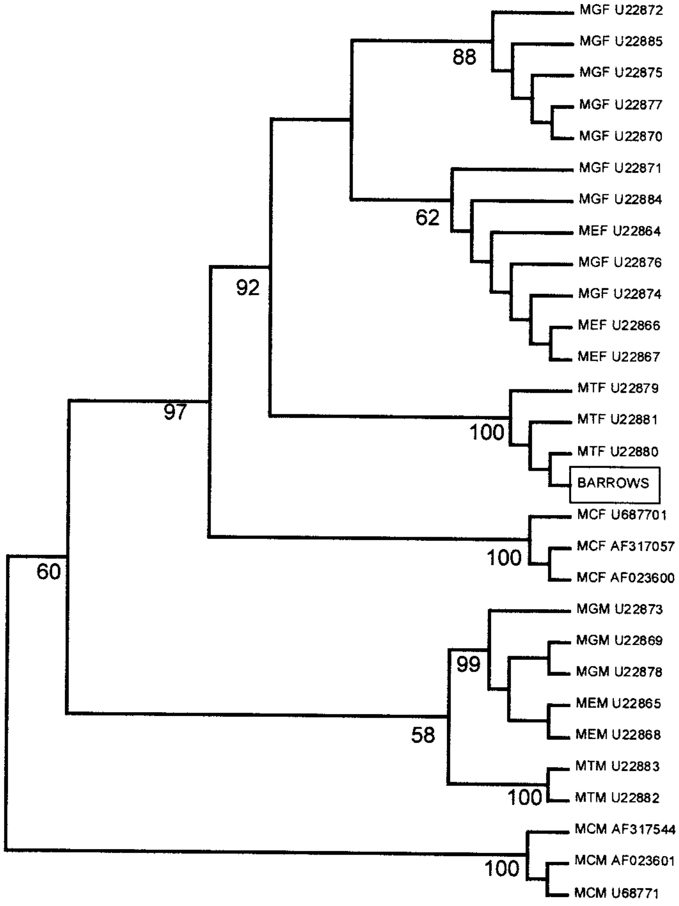

FIG. 3. Neighbor-joining phylogenetic tree of *Mytilus* spp. using partial rRNA gene sequences from Rawson and Hilbish (1995a, 1998). MCM/F = *M. californianus* male/female, MGM/F = *M. galloprovincialis* male/female, and MTM/F = *M. trossulus* male/female. The Barrow mussel is boxed and labeled "Barrows." GenBank accession numbers follow taxonomic labels. Numbers under nodes are some bootstrap support values (1000 replicates). The Barrow mussel is identified with high certainty as *Mytilus trossulus*. Male mussels carry female mtDNA in somatic tissues; therefore, the sex of specimens is uncertain.

DISCUSSION

Biogeographic Implications of Mytilus trossulus

The MacGinities regarded *Mytilus* as an obligate intertidal organism, as many biologists continue to do today, on the basis of their experience with the genus at lower latitudes. Subtidal populations are known, for example, from the Gulf of St. Lawrence (Gaymer et al., 2001; Gaymer and Himmelman, 2002) and the Baltic Sea (Littorin and Gilek, 1999; Westerbom et al., 2002). Because tides are negligible, the condition under which *Mytilus* lives near Barrow should be considered "a-tidal" rather than subtidal.

Mussels of the genus *Mytilus* are found in all oceans and major seas of the world (Morris et al., 1980; Seed and Suchanek, 1992). Despite the scientific and commercial importance of *Mytilus* and an extensive literature on the genus, the taxonomy of the group is still unsettled (Lobel et al., 1990; McDonald et al., 1991; Seed, 1992; Geller et al., 1993). Aside from *Mytilus californianus* (adults of which are morphologically distinct from congeners), three morphologically similar species of *Mytilus* are recognized: *M. edulis*, *M. galloprovincialis*, and *M. trossulus*. In this group of three species, referred to as the *Mytilus edulis* complex, morphological similarity combined with environmental variation, hybridization, and frequent unintentional transport of larvae have confused the understanding of biogeographic relationships. McDonald et al. (1991) summarized the biogeographic evidence for separation of the three species resulting from analysis of frequency and distribution of allozymes. *Mytilus edulis* occurs on the Atlantic coasts of Europe and North America, *M. galloprovincialis* is found on the coast of southern Europe, and *M. trossulus* within the Baltic Sea and on the coasts of the Pacific Ocean in North America and Siberia in the Chukchi Sea. Prior to this review, *Mytilus trossulus* had been described along Alaskan shores as far north as Prince William Sound (Geller, unpubl. data) and the Shumagin Islands (Gosling, 1992; Geller et al., 1994).

Taxonomy of the *M. edulis* species-complex in the past was largely based on morphology, particularly of the shell. But variations in shell shape result from environmental differences that affect shell growth (Seed, 1968), and hybridization between several species of the genus produces confusion over mussel taxonomy. Recent investigations based on genetic methods have clarified much of this confusion (Varvio et al., 1988; Lobel et al., 1990; McDonald et al., 1991; Geller et al., 1994; Suchanek et al., 1997; Hummel et al., 2001). Three species are now usually recognized: *Mytilus edulis*, *M. galloprovincialis*, and *M. trossulus*. In Europe and North America, the distribution of each species is characterized by a number of investigators (e.g., Koehn, 1991; Vainola and Hvilsom, 1991). All mussel populations studied in the northern European Arctic (the White Sea and Tromsø, Norway) are assigned to *Mytilus edulis* (Hummel et al., 2001). *Mytilus* populations on the east coast of Newfoundland, Canada, consist of two genetically distinct forms, *M. edulis* and *M. trossulus*, living sympatrically at some locations (Comesaña et al., 1999). These investigators report limited hybridization between the two species in these populations. *Mytilus galloprovincialis* has been introduced to the western United States, but its distribution has been mostly limited to California (McDonald and Koehn, 1988; Geller, 1994; Rawson and Hilbish, 1995a; Suchanek et al., 1997), with occasional appearances associated with aquaculture efforts in Washington State (Heath et al., 1995).

Molecular studies generally suggest a North Pacific distribution for *M. trossulus* with a history of occasional trans-Arctic dispersal to the North Atlantic, where it may overlap and hybridize with *M. edulis*. Studies in circumarctic waters are few, however, and the ranges of *M. trossulus* and *M. edulis* in this region remain uncertain. Mussels to the northwest of Tromsø on the subarctic island of Bjørnøya (midway between Norway and Spitsbergen) are considered *M. edulis* (Weslawski et al., 1997) but were not genetically analyzed. No mussels are currently found on Spitsbergen, although some (currently named *M. edulis*) were present on raised coastlines 5300–9400 years old (Salvigsen et al., 1992; Hjort, 1995; Salvigsen, 2002). Both Theisen (1973) and Petersen (1978) describe populations of mussels identified as *M. edulis* on the Arctic shores of Greenland. Mussels (also identified as *M. edulis*) are present widely in the Canadian Arctic, although Dyke et al. (1996) consider the western Canadian Arctic *Mytilus* population separate from the eastern, or Atlantic, population. The western Canadian population extends from the mouth of the Mackenzie River (Lubinsky, 1980) in the west, north at least to Walker Bay (71˚35′ N) on western Victoria Island (A. Dyke, pers. comm. 2003) and to Bathurst Inlet in the east. Dyke et al. (1996:175) assume uninterrupted distribution of the genus through the Alaskan Beaufort Sea and Chukchi Sea and continuing southward to Bering-Pacific populations. They use radiocarbon dates to argue that this western Arctic population was established from the Pacific by 10 300 years ago, soon after the Bering Strait opened (Dyke et al., 1996:167). Failure by a number of investigators to collect *Mytilus* in the Alaskan Beaufort Sea for so many years (Table 1) imparts unusual biogeographic interest to our finding *M. trossulus* at the junction of the Chukchi and Beaufort Seas. Further mtDNA studies of modern Canadian specimens should clarify their affinities.

Assessment of the Bjørnøya, Greenland, and Canadian Arctic *Mytilus* using molecular methods may show that they comprise mixed populations of *M. edulis* and *M. trossulus*, or some proportion of the hybrids described for these species on the east coast of Newfoundland (Varvio et al., 1988; Koehn, 1991). Because of limited sample size, and because mtDNA analysis does not readily identify hybrid animals, our data are currently not sufficient to exclude the possibility that hybrids are present in the Barrow region.

Our tentative assignment of Barrow mussels to *M. trossulus* is consistent with founder populations of this Pacific taxon having moved northward through the Bering Strait into the Chukchi Sea. If populations from Bathurst Inlet west and southward are homogeneous but distinct from eastern Arctic populations, Dyke et al. (1996) may be vindicated in their assumed *Mytilus* connection through Alaska and assumed affinity of western Canadian populations with Pacific forms. Physical oceanographers recognize a shallow current regime that moves identifiable water masses (Bering Sea Water [BSW] and Alaska Coastal Water [ACW]) and presumably dispersive larval stages through the modern Bering Strait northward past Barrow and eastward in ACW almost to Stefansson Sound before the ACW identity weakens and disappears (cf. Moore et al., 2000:433). (The Boulder Patch in Stefansson Sound seems equally likely to receive dispersive life stages in some years from the Mackenzie Delta, as discussed below.) *Mytilus* grows slowly in subarctic and arctic conditions (Theisen, 1973; Blanchard and Feder, 2000). The largest windrowed live mussels are evidence of suitable substrates near Barrow that remain stable enough to sustain reproducing populations of mussels for at least 13 years. Mussels in subarctic Alaska are reproductively active by three years of age (Feder and Keiser, 1980).

Dispersal Mechanisms and Capabilities

Mytilus life cycles include stages sufficiently dispersive to account for natural colonization of suitable habitats hundreds of kilometres distant from source populations. Veliger larvae of *Mytilus* remain dispersive for relatively long periods (Gosling, 1992). Veligers can persist in the water column for up to 28 days. Pediveligers (larvae that have developed a pedal organ and are capable of settlement) may delay metamorphosis and settlement for 40 days or more (Bayne, 1965), and they may move to sites far from their first place of attachment via secondary settlement from temporary attachments (Bayne, 1964). This secondary pelagic phase, bysso-pelagic migration or byssus drifting, is facilitated by formation of long byssus threads (Sigurdsson et al., 1976; Lane et al., 1985). Post-larval mussels can continue to drift up to a size of 2–2.5 mm. They may take several months to reach this size, and much of this time could be spent in repeated bysso-pelagic migration (Seed and Suchanek, 1992). Thus, larval and post-larval juvenile stages of *Mytilus* can remain viable while being transported over considerable distances. The absence of *Mytilus* from rocks and boulders in Stefansson Sound (Table 1, Fig. 2) is striking, given the presence of populations of these highly dispersive bivalves to the west near Barrow and to the east in the Mackenzie River delta.

A mechanism for establishment of mussel beds by post-larval stages is suggested by the observations of Feder and Bryson-Schwafel (1988) on a sediment shore in Port Valdez, Prince William Sound, Alaska. Surges and tsunamis caused by the Alaska earthquake of 1964 swept shores within the Sound clear of flora and fauna. Subsequently, small rocks were deposited on the barren mudflat by a fast-flowing adjacent stream. Macroalgae (*Fucus distichus*) recruited to the small rocks, and strong tidal currents lifted ('parachuted') the rocks and attached algae, gradually dispersing them over the entire beach. The small rocks were eventually colonized by mussels, which soon weighted the rocks sufficiently to fix them to the bottom. Adjacent clumps of mussels coalesced to form extensive beds, which then served as a secondary substrate for other algal species and associated fauna. A similar series of events in the presence of the strong currents off Barrow could account for establishment or reestablishment of algal stands and mussel beds. Unlike Prince William Sound, the region near Barrow ultimately depends on rafting by continental freshwater ice to renew supplies of cobbles and boulders on the seafloor (see Norton, 2001b:340 for illustration of boulders on a natural freshwater ice island). Once released as dropstones to the seafloor, cobbles and rocks may be buried in sediments and episodically re-excavated by currents. Macroalgae may be instrumental in redistributing small stones in the shallows, as they do in Port Valdez. Suitable physical conditions for settlement by *Mytilus* are obviously more limited in time and space in the waters near Barrow than in Prince William Sound. Salvigsen et al. (1992:8) cite several observations of fresh *Mytilus* on seaweed at Spitsbergen as evidence of the capability of the two organisms together to disperse over considerable distances.

Dispersal of young mussels by storms may represent another way the bivalves can be transported to a new area. Unlike *M. californianus,* which remains permanently fixed to rocky substrate by its byssus threads, *M. trossulus* can change its position on the substrate. This behavior enables the mollusc to avoid suffocation during periods of extreme sediment deposition (Morris et al., 1980). Such loosely attached or moving mussels could be removed from the substrate by extreme turbulence during storms and transported elsewhere by currents. Dispersal by this mechanism was observed for *M. trossulus* on a rocky shore in Port Valdez, Alaska (Feder and Keiser, 1980; Feder, pers. obs.). Wave scour and redistribution of bivalves by storms are also described for bivalves in shallow-water benthic associations (Rees et al., 1976).

Another possible mechanism for bringing propagules to mussel beds near Barrow is human facilitation. Hulls or ballast water of ships that visit northern Alaska may have introduced *Mytilus* larvae (e.g., see discussions of marine invasions of non-indigenous species in Carlton, 1985, 1992; Geller et al., 1994). Dyke et al. (1996:146) suggest that Pond Inlet (72–77˚ N), an outpost site for Atlantic-Arctic *Mytilus,* could have been repopulated by whaling vessels in the 19th century. Population genetic analysis of larger samples in northern Alaska and at sites throughout the more southern range of *M. trossulus* could distinguish this possible repopulation from natural processes of larval and adult dispersal.

Considerations of Substrate, Community and Environment

The MacGinitie investigations were witness to strong storms at the end of the open-water period (mid-October) in 1949. MacGinitie (1955:56–57) blamed erosion accompanying those storms for burying seafloor pebbles and cobbles ("rubble bottoms") out to 50 km from shore under as much as 8 cm of fine sediments, which he believed came from Elson Lagoon. Benthic epifaunal species that were collected in 1948 and the summer of 1949 were absent for the remainder of the MacGinitie investigations in 1950. The 1949 storms and consequent burial by sediment may have affected any mussel and kelp beds so severely that years were required for these local biota to recover fully. Such episodic disturbances of the sea bottom make the benthic environment off Barrow unstable and may periodically extirpate benthic biota. Re-establishment may take place once conditions stabilize and substrate becomes available. The articulated juvenile *Mytilus* shells collected at Barrow (Table 1, #10), now in the Los Angeles County Museum collections, suggest that recruitment had begun by 1952 or 1953 on substrates re-emerging after burial by sediment in 1949. Shallow-water Arctic regions elsewhere may be similarly unstable if the seafloor is subject to natural disturbances, including ice scour and storms, that result in periodic burial and excavation of benthic organisms (Dunton et al., 1982; Dayton, 1990; Jewett et al., 1999).

There can be little doubt that the proximate sources of mussels and kelp reaching the beach together at Barrow are fully marine Chukchi Sea locations. *Laminaria* (to which a number of our *Mytilus* specimens were attached) is not known to tolerate low salinities. Drill holes in many empty *Mytilus* valves on the shore at Barrow in the 1990s are further evidence that these specimens were from marine rather than lagoonal or estuarine beds. Relatively abundant populations of bivalve-predatory snails (*Polinices* spp. and *Natica* spp.) are found in strictly marine waters off Barrow (MacGinitie, 1959:90–91; Norton pers. obs.).

Candidate marine sites must be shallow enough in the photic zone for photosynthesis by *Laminaria*, yet deep enough and relatively sheltered—such as by surrounding islands, spits, or bars—for plants and invertebrates to be protected from frequent bottom scour by keels of moving sea ice. Mussel beds that are the sources of live adults washed onto beaches in the Barrow region might be sought on slopes of the Barrow Canyon, either near Barrow or closer to Peard Bay, where Mohr et al. (1957) found scattered kelp beds (Fig. 4). Reduced gouging by ice along the sloping walls and side arms of the Barrow Canyon may improve the chances for isolated mussels to reach maturity. Compared to ice-covered waters, the open-water flaw lead that tends to form alongshore beyond shorefast ice in late winter and spring over the Barrow Canyon (Norton, 2002) admits more light to the water column, thus favoring *Laminaria* growth. Strong upslope and downslope currents in the canyon (Weingartner and George, 2001) could displace predators and remove fine-grained sediment from patches of cobbles and rocks, which could then serve as substrates for epibenthic recruits. Episodically, stronger storm currents could dislodge rocks with attached algae, mussels, and other epifauna, exposing them to transport ashore by storm waves.

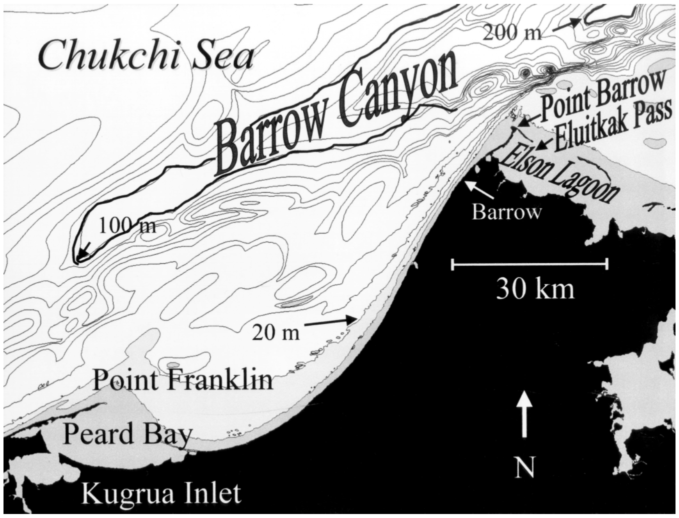

FIG. 4. The Barrow Peninsula in greater detail, from Kugrua Inlet on the Chukchi Sea coast to Elson Lagoon region at the western end of the Beaufort Sea. Bathymetry is shown to illustrate the NE–SW orientation of Barrow Canyon. Isobaths are superimposed on a RADARSAT image of sea ice from 21 May 2001 at 10 m intervals, with 20 m, 100 m, and 200 m isobaths emphasized.

An intriguing clue to another marine source for mussel beds came to our attention in the last stages of manuscript revision. Although Fay (1982) did not list *Mytilus* among the prey of Pacific walrus (*Odobenus rosmarus*), his collaboration with Soviet Russian scientists led to his receipt of new, unpublished data from a U.S.-USSR cooperative oceanographic cruise to the northern Chukchi Sea in September 1987 (G. Sheffield, pers. comm. 2003; S.C. Jewett, pers. comm. 2003). Two of 44 walrus collected for dietary analysis that month contained single specimens each of "*Mytilus* sp." The coordinates for specimens secured on 20 and 21 September 1987 were 71˚21′ N, 161˚44′ W and 71˚19′ N, 161˚37′ W, respectively. These walrus collecting locations are about 70 and 75 km (38–41 nautical miles) to the south of Hanna Shoal, a feature which rises to within 20–30 m of the sea surface about 160 km WNW of Barrow. This shoal regularly produces a grounded ice feature that lasts for most of the annual cycle, occasionally year-round. The shallowest part of the shoal can be detected in satellite images as a combination of grounded ice and semipermanent open-water flaw zone (polynya) on the lee, or southwest, side of the stationary grounded ice (Barrett and Stringer, 1978). Although we believe Hanna Shoal is too far away for most storms to deliver live kelp and mussels from there to Barrow, Hanna Shoal does meet the photic depth and protection-from-ice-scour criteria that we stipulate above for associated macroalgae and mussels.

Postulating a proximate marine source population for adult *Mytilus* falls short of explaining all of the taxon's natural history in Arctic Alaska, however. After replacing our view of *Mytilus* as an obligate intertidal organism with a perception that *Mytilus* takes advantage of tides as one of several forms of refuge from predators (e.g., Gaymer et al., 2001; Gaymer and Himmelman, 2002), we shifted our emphasis from direct physical determinants to factors that might constrain mussel predators. Bivalve predators such as sea otters (*Enhydra lutris*) in Prince William Sound episodically eliminate *Mytilus* from beds over wide areas

(VanBlaricom, 1987). Other predators, including the several genera of sea stars—*Crossaster*, *Solaster*, and *Leptasterias*—and moon snails (*Polinices* [Feder, 2001:55; MacGinitie, 1959:91–92] and *Natica* [MacGinitie, 1959:90]), have been prominent in benthic communities near Barrow throughout the time spanned by investigations reviewed here. Mussels seem to establish beds in environments where one or more physical parameters fall outside their predators' tolerance. *Mytilus* populations are able to withstand desiccation and the dislodging forces of waves, which reduce the effectiveness of sea stars and other predators in intertidal zones elsewhere (e.g., Ricketts et al., 1985). Low salinities also deter mussel predators (Westerbom et al., 2002). In the absence of tides and habitable intertidal zones, tolerance for euryhaline conditions may afford *Mytilus* the only effective predator-avoidance shield in many Arctic locales. In Alaska's Prince William Sound, for illustration, intertidal *Mytilus* populations are immersed for up to seven months annually (April to October) in a freshwater or low-salinity lens produced by runoff from glaciers and snowfields. The lens, which is maintained from April–May until autumn and winter storms and falling water temperatures mix the Sound's stratified water, keeps predators below the depth of mussel beds. The final stages of gametogenic development, spawning activity, and major shell growth also take place during this low-salinity period (Feder and Bryson-Schwafel, 1988; Blanchard and Feder, 1997, 2000). Dense mussel beds in the Sound are found within or adjacent to intertidal outfalls and small deltas of freshwater streams, in which low salinities extend predator deterrence year-round (Feder, pers. obs.; Norton, pers. obs.). Inlets and barrier island-lagoon systems in the Chukchi Sea collect river and stream inputs of freshwater near locations where mussel valves have been found (Table 1, Fig. 2). Such lagoons offer protection from sea ice scour, and where water is too deep (> 2 m) for annual ice to freeze to the bottom, lagoons and estuaries may furnish suitably stable habitats for persistent *Mytilus* beds—in effect, serving as refugia. Few systematic examinations of estuaries have been conducted north of the Bering Strait.

By contrast with their numbers in the Chukchi Sea, the scarcity of mussels along Alaska's Beaufort Sea coast invites explanation. Estuarine refugia, which we consider important in the Chukchi Sea distribution of *Mytilus*, are probably harder to colonize in the Beaufort Sea for two reasons. First is the widely noted absence of hard substrates (except for the Stefansson Sound Boulder Patch). Second, the low salinity of lagoons and inlets that deters predators may not be as seasonally reliable on the Beaufort Sea coast. Except during spring snowmelt and runoff, freshwater input to coastal lagoons is limited. Alaska's Colville River discharge completely ceases by midwinter (Walker, 2001b:18). Simpson Lagoon, just east of the Colville River delta, turns saline during the open-water months whenever westerly winds drive marine water through gaps in the chain of barrier islands that form its seaward boundary (Niedoroda and Colonell, 1990). More fully enclosed lagoons and inlets, like Peard Bay and Wainwright Inlet on the Chukchi Sea coast, are less susceptible to influxes of high-salinity water from offshore.

The Boulder Patch in Stefansson Sound seems to have almost all the prerequisites for establishment of *Mytilus* beds in an a-tidal locale. Its boulders and cobbles are an ideal rocky substrate. Pre-sessile larvae should reach Stefansson Sound from either the west or the east. Young-of-the-year Arctic cisco (*Coregonus autumnalis*), spawned in the Mackenzie River system, regularly drift through Stefansson Sound on their way to the Colville River. These small fish are carried along in a narrow, brackish plume of coast-hugging water that generally flows westward from the Mackenzie River (Gallaway et al., 1983; Fechhelm and Griffiths, 1990; Wilson and Gallaway, 1997). The Sound is protected from ice scour by a string of offshore islands. *Laminaria solidungula* is abundant in the Boulder Patch. The Boulder Patch is a natural experiment in the biogeography of colonizing isolated habitat islands, reminiscent of MacArthur and Wilson's (1967) equilibrium theory, and of subsequent manipulative experiments (Quammen, 1996:427–431). In view of the apparent failure of *Mytilus* to colonize at least the densely cobbled core of the Boulder Patch (Table 1), this natural experiment suggests several conclusions:

1) Ocean-like salinities in the Stefansson Sound Boulder Patch do not inhibit establishment by predatory sea stars, *Crossaster* and *Leptasterias*, and the predatory gastropod *Polinices* (Dunton et al., 1982:474);

2) The density of cobbles, boulders, and associated epiflora and fauna aggregated in Stefansson Sound is greater and more constant than in the scattered configuration of cobbles near Barrow. A "gatekeeping" array of predators that persist in the Boulder Patch can quickly locate and consume recently settled *Mytilus* recruits (cf. Gaymer and Himmelman, 2002);

3) Therefore, rocky substrate, protection from ice scour, and the presence of kelp may be necessary, but insufficient, preconditions for *Mytilus* establishment.

Marine populations of *Mytilus* in the Chukchi and Beaufort Seas are unlikely to approach the densities seen in more southerly intertidal mussel beds, owing to the limiting nature of the substrate and to the likelihood that predators would eliminate dense concentrations within a year or two of discovering them (cf. Robles, 1987; Gaymer et al., 2001). Instead, small, widely separated clusters of *Mytilus*-with-algae are more likely in the long term to foster survivorship to reproductive stages. Patchy distribution confers some protection. Even if predatory sea stars eliminate every patch of mussels they encounter, a few separated clusters can remain undiscovered long enough for individuals to reach reproductive size. The probability of predation may be influenced by epibionts attached to *Mytilus* shells (Laudien and Wahl, 1999). Where *Laminaria* and *Mytilus* occur together, turbulence and current-induced motion by algal fronds may keep sea stars from preying upon *Mytilus* (Gaymer et al., 2001; Saier, 2001). Kelp fronds may contribute to spreading of pebbles and cobbles, and to dispersal of adult *Mytilus*, through the mechanism of 'parachuting' described above for Prince William Sound. During especially severe storms, however, the buoyancy conferred by *Laminaria* fronds may become a lethal liability.

The Barrow and Stefansson Sound environments differ in sedimentation regimes, which may further explain why periodic re-establishments and eliminations of epifaunal populations are seen at Barrow but not in the Boulder Patch. Heavy, storm-induced sedimentation at Barrow like that observed in 1949 can bury benthic biota over a wide area (MacGinitie 1955:56–57). Sediment deposition during the annual open-water season in the Boulder Patch tends to be a thin film, which is generally re-suspended and exported during the fall (Dunton et al., 1982:472). We suggest that after extensive destruction of benthic fauna near Barrow, *Mytilus* recolonization of re-exposed rocky substrate is effected promptly by pelagic larvae released by populations in nearby refugia. By contrast, sea star and naticid re-establishment after extirpation off Barrow is likely to be slow. Most of these predators reproduce by direct development, which results in non-pelagic juvenile stages. The limited dispersal capabilities of the juveniles can delay re-establishment of these predators for years if the nearest marine source populations are hundreds of kilometres distant (Chia, 1970). In other words, *Mytilus* is an opportunistic form that benefits from episodic perturbations in shallow Arctic marine environments. Analogously to early-succession stage organisms such as fireweed (*Epilobium* sp.) and willows (*Salix* spp.) in terrestrial plant communities, *Mytilus* may become less dominant in later seral stages in marine communities.

Although *Mytilus trossulus* is absent from the Boulder Patch in Stefansson Sound, another mytilid, *Musculus discors*, is present in sizable numbers. Presence of this bivalve and absence of *M. trossulus* can be explained by differences in the behavior after settlement and the reproductive biology of the two species. Aggregates of *Musculus* after settlement cover themselves with compact byssal nets (MacGinitie, 1955; Coan et al., 2000), which probably offer some protection from predatory sea stars. *M. discors* has direct development (Bayne, 1976), and the byssal nets form nests in which large numbers of eggs are brooded during the reproductive period. Tiny replicas of adults emerge from the eggs and settle within the nest or immediately adjacent to the adults. This results in numerous scattered *Musculus* in aggregations with a reproductive potential that enables them to maintain their population in the Boulder Patch in the presence of sea star and naticid predation. Groups of *Mytilus* do not form byssal nets to cover and protect themselves at any age.

Had *Mytilus*, *Laminaria*, or both been deposited ashore at Barrow by the autumn storms of 1949, as they were in the 1990s, the MacGinities' sampling tactics would almost certainly have detected them. Although beach surveys on foot in 1948–50 were slow compared to today's motorized surveys, which cover 30–50 km of beach in hours, there are only a few productive collecting locations along the local extent of coastline. Nunavak Inlet southwest of Barrow, the curved Chukchi beach immediately southwest of Point Barrow, and Plover Point at Eluitkak Pass, 3 km east of Point Barrow (Fig. 4), are locations at which waves and currents concentrate organisms coming ashore. Both monographs (G. MacGinitie, 1955; N. MacGinitie, 1959) indicate by frequent mention of these localities that the earlier sampling team had mastered the same site-specific efficiencies that another generation re-learned decades later. Barrow residents' surprise at collection of the deep-water echinoderm *Gorgonocephalus* (sp.) with a baited shrimp trap at Barrow in 2002 vindicated our confidence in the thoroughness of the MacGinities' sampling. By contrast with other echinoderm species, basket stars are unknown in storm drift lines. Yet MacGinitie (1955:145) reported collecting *Gorgonocephalus* on three occasions at depths ranging from 40 to 200 m.

Failure of storms to deposit *Mytilus* and *Laminaria* onshore in 1948 or 1949 does not exclude the possibility that populations of each flourished offshore at the time. Fall storms differ in trajectories, duration, and intensity, so that not all storms produce windrows of benthic organisms near Barrow. The absence of beached organisms following the unusually violent storm of 10 August 2000, which produced destructive waves and winds from the west, drew comment from several puzzled observers. The intense depression moved eastward past Barrow so rapidly that currents and onshore waves apparently failed to build enough power to scour the bottom at depths from which benthic flora and fauna are dislodged. The absence of the priapulid *Halicryptus* from beached samples at Barrow (Shirley and Storch, 1999; Feder, 2001) spanned the same years (1950 to 1993) as elapsed between the MacGinities' field work and the finding of *Mytilus* and *Laminaria* after storms.

Paleontological Evidence Used to Relate Mollusc Distributions to Climate Change

Salvigsen et al. (1992) and Salvigsen (2002) use supposed *Mytilus* thermophily and the presence of valves in strata underlying raised Holocene beaches to explain *Mytilus* presence in Svalbard from ca. 9500 to 3500 years ago as evidence of higher summer surface temperatures earlier in the Holocene. Dyke et al. (1996) cite the appearance of *Mytilus*, followed by a decline in its numbers in Arctic Canada and Greenland during the interval 10 000 years ago to the present, as well as the appearance-disappearance of Arctic *Macoma balthica* between 10 000 and 5000 years ago, as evidence for an early Holocene period of elevated sea level and temperature, followed by falling water levels and temperatures. Doubts that marine biota are reliable indicators of temperature have been expressed repeatedly since at least 1970 (Peacock, 1989). Our assessment of distribution patterns of mussels over time and space in waters of northern Alaska suggests that water temperature cannot be the primary determinant of *Mytilus* persistence in the Arctic. Low water temperature is known to prolong dispersive life-cycle stages and to slow later development and growth, but it has not been shown to limit *Mytilus* survival or reproduction. We suggest that the presence of this bivalve during periods of higher sea level during the early Holocene is a response to lower and more variable salinity of coastal waters rather than to increased temperature.

Our single specimen of *Mytilus* from the Colville River (#18, Table 1) belongs to a fauna of the "Bigbendian" marine transgression, dated between 2.2 and 3 million years B.P. with a sea level between 35 and 60 m higher than at present (Rawlinson, 1990:43; Carter and Hillhouse, 1992). The age and level of this second of six marine transgressions comprising the widespread Gubik Formation (Black, 1964) in northern and northwestern Alaska would put *Mytilus* in the timeframe of another earlier Pacific-Arctic connection at the Bering Strait. The Bigbendian fauna is indeed Pacific: its fossils include *Astarte*, *Hiatella*, *Chlamys*, *Clinocardium*, *Mya*, *Macoma*, *Nuculana*, *Nucula*, various species of the predatory gastropods *Neptunea* and the naticids *Natica* and *Polinices*, *Buccinum* (another predatory gastropod, Nielsen, 1975), and a sea otter (*Enhydra*?).

Mytilus specimens from Cenozoic marine transgressions have been found elsewhere. MacNeil (1957:104; Plate 12) reports a valve of "*Mytilus*?" from Carter Creek, which drains into Camden Bay between the Colville River and the Alaska-Canada boundary (Fig. 2a). This specimen is part of a mollusc fauna in the Nuwok Member, which Rawlinson (1990) assigns to the late Oligocene. Fouch et al. (1990) re-interpret the Nuwok Member as late Pliocene, however, and its fauna as an entirely Atlantic Arctic assemblage. Some 20 million years younger than late Oligocene, Carter Creek nevertheless pre-dates an early Pleistocene Pacific-Arctic connection at the Bering Strait, hence ~ 3 million years B.P. Northern Alaska displays at least six Cenozoic marine transgressions, the most recent of which ("Simpsonian," Rawlinson, 1990), at ~ 57 000 years B.P., is older than either the Wisconsinan glaciation or any of the Holocene *Mytilus* and other Mollusca from Canada (Dyke et al., 1996; Gordillo and Aitken, 2000) and Svalbard (Salvigsen, 2002).

Since the late Pliocene, *Mytilus* has probably dispersed repeatedly into and around the Arctic. Whenever changing conditions provide this taxon with dispersal opportunities and some obstacle that could shield these colonists from predators, *Mytilus* spreads in shallow Arctic waters. Thus, the persistence of *Mytilus* in northern Svalbard from 9500 to 5300 years B.P. and elsewhere in the archipelago from ca. 9500 to 3500 years B.P., and its fleeting re-establishment at about 1000 years B.P. (Salvigsen et al., 1992; Salvigsen, 2002) suggest abundant freshwater runoff into fjords and other nearshore shallow waters during earlier millennia of the Holocene. The deterioration in numbers of *Mytilus* fossils, and the spottiness of more recent radiocarbon-dated *Mytilus* shells (Salvigsen et al., 1992:7) may reflect 1) the decreasing volumes of freshwater produced annually by glaciers after they shrank rapidly, then stabilized; and 2) the elimination of mussels by sea stars and gastropods once the water became more saline, as these predators discovered and exploited mussel beds.

Abundant opportunities for further interdisciplinary and inter-regional comparative analyses are suggested by our review. Dyke et al. (1996), Gordillo and Aitken (2000), Salvigsen et al. (1992), and Salvigsen (2002) base persuasive interpretations of Wisconsinan-Holocene climate change over the past 10 000 to 18 000 years on molluscan macrofossils in the Arctic to the east of Alaska. Reconstructions could be extended some 3–3.5 million years backward in time past the beginning of the Pleistocene by analyzing fossils in the series of marine transgressions in northern Alaska that were spared obliteration or inundation by more recent glacial maxima (Rawlinson, 1990). Expanded climate reconstructions, however, should make use of the synecological realities illustrated here. That is, inconvenient synecological truths prevented us from drawing an attractive (convenient) conclusion that *Mytilus* has filled gaps in its Western Arctic distribution since 1950 in an autecological (physiological) response to increasing water temperatures. Although their study areas did not yield *Mytilus* fossils, Gordillo and Aitken (2000) illustrate the thoughtful interdisciplinary approaches that can unite earth scientists and marine biologists in a common analysis. Their analysis of mollusc fauna of the Canadian Arctic Archipelago sets a standard for considering variables of taphonomy (post-mortem processes that determine the probability that fossils of a taxon will be preserved), habitat use, locomotion, and trophic relations. For analyses of both modern biogeography and reconstructed paleoecology, taxa like the *Mytilus edulis* complex should be evaluated in the multidimensional terms suggested by this review. We are impressed by the opportunistic behavior of mussels at high latitudes, in that juveniles and adults appear in the wake of disturbances and regime changes. *Mytilus* may continue to surprise investigators by appearing in unexpected locations, as they did at a depth of 180 m near Jan Mayen Island off eastern Greenland (Ockelmann, 1958). Besides the interaction of *Mytilus* with substrates, tides, water depths, and salinity, investigations should consider the dispersion-enhancing and settling-deterrent roles played respectively by macrophytes and predators, some of which leave little or no fossil trace (e.g., algae and sea stars).

Future dating techniques may prove sensitive enough to detect peaks in local populations where peak-to-peak periods of local abundance are in the range of 10–100 years, as suggested by discrepant observations at Barrow. If we apply the concept that *Mytilus* intermittently matures and reproduces in marginal marine environments (as at

Barrow), and if we further stipulate a steady state for this cyclic pattern over time within a region, geologists 10 000 years from now could date fossils to discern this cyclicity. If future analysts miss this point, however, they could interpret *Mytilus* as more evenly spread and abundant over space and time than we see the taxon's presence today. Adult-sized *Mytilus* valves left behind by 100–1000 cycles of intermittent presence could create an overall impression of widespread distribution, whereas instantaneous sampling of living specimens at any single coastal locality would be the same hit-or-miss experience as comparing observations in Arctic Alaska today with those of 50 years ago. Gordillo and Aitken (2000:308) term this problem "time-averaging." Our final observation concerns sampling methodology. We recommend cautious attribution of negative results to previous studies. Emphasis on climate change at high latitudes will continue to draw attention to organisms and populations that appear at localities from which they were previously unreported. Credible negative results in earlier observers' contributions therefore assume especial value. Training and current practices, however, do not prepare investigators to deal with their own or others' negative results. The negative results that the MacGinities (1955, 1959) report are made nearly unassailable by their comments on the absence of both macroalgae and *Mytilus* from their samples, but most subsequent regional studies—our own recent opportunistic collections at Barrow and Wainwright, for example—should not be trusted quantitatively for negative results useful to future investigators. Studies in this region since the 1950s generally fall short of the thoughtful natural history practiced by the MacGinities, while also failing to be thorough, probability-based surveys of nearshore biota or the coastline. Inferences of *Mytilus* absence from a researcher's failure to mention finding them are not statistically defensible. The 1971 discovery of the Boulder Patch in Stefansson Sound highlights the potential for unsampled regions to surprise us with long-unsuspected biological populations. Even the most intense and quantitative modern observations by divers in the Stefansson Sound Boulder Patch since 1971 are not probability-based ('random') surveys that support strong conclusions from negative findings. Outer fringes of Stefansson Sound may contain appropriate habitats sufficiently disjunct for scattered *Mytilus* populations to avoid notice by predators. Surveys that encompass suitable habitats and proposed refugia would address our hypothesis that *Mytilus* populations have long flourished intermittently in many isolated patches around the Arctic Basin.

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