

COMMENT

Mytilus thermophily?

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Berge et al. (2005) conclude that their finding of live *Mytilus edulis* in 2004 at Sagaskjæret, Isfjorden, Svalbard is due to upward excursions in sea-surface temperatures (SST) enabling the blue mussel to settle that far north (78° N) for the first time in 1000 yr. This interpretation appeared in popular press stories (Reuters, CNN websites, September 2004) surprisingly soon after the discovery and more than a year before we could evaluate detailed scientific evidence for their conclusions in *Marine Ecology Progress Series*. The authors' responses to our cautionary comments below should help illuminate either contrasting physiological adaptations and phylogeography of different high-latitude populations of *Mytilus* sp., contrasting thresholds for scientific evidence that investigators on opposite sides of the Arctic accept, or perhaps both types of contrast.

The following comments stem from our review of *Mytilus* distribution in sub-Arctic and Arctic Alaska (Feder et al. 2003) and from other recent literature. For most of the decade following our first collections of live *Mytilus* near Barrow, Alaska, in 1993, we did not question the supposition voiced by some colleagues that *Mytilus* populations had moved northward in recent decades, in response to rising SST. Biological surveys failed to find living mussel specimens at the northern tip of Alaska close to Barrow (71 to 72° N) during the First International Polar Year (Ray 1885) and again in 1949 to 1950 (G. MacGinitie 1955, N. MacGinitie 1959). Upon closer examination, however, these and more recent surveys reported in published and fugitive literature, and biogeographic patterns in fossil evidence, convinced us that Pacific *Mytilus* populations have not shifted northward, but have lived patchily in marine environments near Barrow and elsewhere in the western Arctic throughout the Holocene. Although some of the surveys that we reviewed appeared to coincide with intervals of genuine local mussel scarcity (Feder 2001), investigators' generally inadequate sampling strategies have tended to

perpetuate scientific assumptions that living *Mytilus* are absent from Barrow, and from the entire region of northern and western Alaska.

By using the term 'relict' to characterise modern *Mytilus* populations in Arctic Alaska, Berge et al. (2005, p. 173–174) imply that they are static and isolated, hence non-interactive with congeners elsewhere in the circumpolar regions. We point out that our review supports the opposite conclusion: Alaska's *Mytilus* are physiologically hardy, their populations resilient, and their capabilities for long-distance dispersal noteworthy. Fully marine populations (living in salinities >28 psu) of this bivalve in northern Alaska consist of scattered aggregations, whole patches of which may be eliminated episodically by any of a variety of harsh physical conditions, or by any of a variety of highly effective predators inhabiting this region. *Mytilus* nevertheless recolonise those suboptimal marine habitats from estuarine and perhaps other brackish coastal habitats in the western Arctic. They thus persist in both brackish and marine subpopulations. These potential colonists live under selective pressures that continually favour the most dispersive and opportunistic individuals. Opportunism, combined with fossil evidence of their trans-Arctic movements, reveal western Arctic *Mytilus* to be vagile for a significant portion of their life cycle, undeterred by either low sea temperatures or low salinities. In terrestrial ecosystems, analogs to the *Mytilus* of northern Alaska are termed 'weeds'. This suite of weedy characteristics is consistent with evidence that Pacific representatives of the genus have repeatedly spread rapidly through the Arctic toward the Atlantic, most recently soon after the Holocene opening of the Bering Strait. *Mytilus* and the similarly 'weedy' *Macoma balthica* appear to have colonised newly available nearshore habitats during periods of accelerated freshwater runoff from shrinking glaciers and ice sheets (e.g. Dyke et al. 1996, cf. Luttikhuisen et al. 2003).

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We envy our Svalbard colleagues the certainty of their convictions. By comparison with their certainty that *Mytilus edulis* is the taxon to have settled in Isfjorden, we remain less certain of the identity or purity of *Mytilus trossulus* inhabiting Arctic Alaska, given the extensive hybridization zones elsewhere among members of the *Mytilus edulis* species complex (e.g. Riginos & Cunningham 2005). A second lack of certainty is our inability to identify a single, unidirectional current regime that explains convincingly the source of marine mussel beds near Barrow. One current tends to flow northeasterly (Alaska Coastal Water) along the Chukchi Sea coast, until it meets a weaker westerly current of brackish water that hugs the shore along the Beaufort Sea coast east of Point Barrow. Pelagic larvae from either direction could thus settle in beds near Barrow. Another possibility is that storm currents redistribute clusters of adult mussels attached to marine macroalgae, from kelp and mussel beds no closer than Hanna Shoal, 160 km west of Barrow, the shallowest portion of which reaches to within 30 m of the sea surface.

Our most persistent uncertainty remains: how should we deal with observers' failures to report the presence of living specimens of an organism? What constitutes sufficient evidence to persuade science of the organism's absence? Collectively, the scarcity of hard substrates, frequent ice scour, high risk that storm-driven sediments will bury mussel beds, and the abundance of gastropod and echinoderm predators, make the shallow marine habitats within 100s of km in either direction from Barrow so marginal for blue mussel survival as to constitute a bottleneck for them. Despite physical and biotic adversities, evidence fails to convince us that mussels have ever been wholly absent from localities near Barrow—much less in Arctic Alaska and Arctic Canada generally—at any time since the beginning of the Holocene, 10 000 yr ago.

The claim that *Mytilus* has been absent from Svalbard appears based, in part, on the enviable availability of qualified observers over space and through time on the Atlantic side of the Arctic. Given the fitful scientific survey history in Alaska, we cannot match Berge et al.'s (2005, p. 173–174) certainty that 'intensive sampling along the western coast of Spitsbergen during the last 30 yr' ensures that observers would have detected small numbers of *Mytilus* living at densities similar to those in Arctic Alaska—had they been present. Lack of mention of *Mytilus* in published studies and surveys in the past 50 yr in Arctic Alaska is contradicted in some cases by physical evidence of their presence. Specimens of *Mytilus* collected from near Barrow in the mid-1950s were accessioned into at least 2 American museums' natural history collections with no known accompanying published comment. Photographs

(35 mm color positive transparencies) taken by the first scientific SCUBA team to operate near Barrow in 1970 to 1972 were made available to us after our review article went to press. Divers photographed live macroalgae (*Laminaria solidungula* and *L. saccharina*, unobserved in 1949 to 1950) attached to various types of hard substrates at several locations within 50 km of Barrow, and at depths of up to 30 m. They also collected and photographed at least one articulated set of *Mytilus* valves. Neither of these discrepancies between divers' biological observations and the 2 MacGinitie monographs on local biota were published. We further suspect that N. MacGinitie's (1959) extended discussion of *Mytilus* as a virtually obligate intertidal bivalve (hence, unsuited to living near Barrow, where celestial tides are negligible) dissuaded more recent investigators from reporting findings that directly challenged her assessment. Years before suspected environmental changes motivated investigators to search for distributional changes in 'indicator' species, natural history surveys steadily expanded the known range of *Mytilus* in the Arctic, to include localities that rival Barrow for adversity (cf. Ellis & Wilce 1961, Blake 1973). Arctic Alaska's nearest analog to Sagaskjæret is the Stefansson Sound Boulder Patch. In all respects, except for the presence of predatory echinoderms and gastropods, the Boulder Patch appears ideal for colonisation by *Mytilus*. SCUBA divers have spent hundreds of hours observing and collecting biota quantitatively in the central part of this formation over the past 35 yr. We trust their assurances that they have never seen *Mytilus* in this seafloor formation (all of which is within 20 m of the surface). Yet if divers could conduct probability-based surveys of the entire Boulder Patch formation, it would not surprise us to learn that 'outer fringes of Stefansson Sound ... contain appropriate habitats sufficiently disjunct for scattered *Mytilus* populations to avoid notice by predators' (Feder et al. 2003, p. 403).

Berge et al. (2005, p. 168–169) develop circumstantial evidence (a combination of modeling, satellite remote sensing data, and data from oceanographic stations) to argue that currents were capable of, and temperatures and salinities suitable for, transporting *Mytilus edulis* larvae from Andøya, mainland Norway, to Sagaskjæret, Isfjorden in the especially favourable summer of 2002. Given their careful marshalling of this evidence, we wonder why Berge and co-authors do not mention the possibility that larvae may have had to travel only half that distance, if there is a reproductively active *Mytilus* population on Bjørnøya, as suggested by Weslawski et al. (1997). Presumably, even an unconfirmed contribution of blue mussel larvae from a Bjørnøya population would strengthen their case for linking Isfjorden's *Mytilus* colonists to transport by the West Spitsbergen Current.

In overview, single autecological characteristics, such as thermophily or tolerance for low or varying salinities, seem inadequate to explain past or predict future changes in *Mytilus* distributions (cf. Kinne 1970, p. 502, quoted in Peacock 1989). Modern and fossil members of the *Mytilus edulis* species complex should ultimately yield more detailed and persuasive ecological information when investigators take time to synthesize the full context of paleontological, modern natural historical (synecological), physiological, isotopic, and genetic observations now accumulating at unprecedented rates.

Future studies on *Mytilus* spp. on both sides of the Arctic could do better at adhering to protocols for collecting and vouchering physical specimens in public repositories to ensure that future investigators will be able to verify taxonomic identities that we assign to our subjects. Radio- and stable isotope analyses should be routinely conducted on valves of *Mytilus* from modern, sub-fossil and fossil specimens to extend our understanding of both geological dates and environmental parameters such as the salinities in which bivalves grew (e.g. $\delta^{18}\text{O}$, Simstich et al. 2005).

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