



High Arctic *Mytilus* spp.: occurrence, distribution and history of dispersal

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Abstract

Many marine species are known to change their distribution in response to changing climatic conditions. One such example is the blue mussel *Mytilus* spp., spreading northward coincident with an increase in ocean temperatures. On Svalbard, the first living specimens of *Mytilus* spp. were discovered in 2004. Here we present an analysis of the current distribution of *Mytilus* spp. on Svalbard, with a focus on the west coast of Spitsbergen where strong Atlantification has been documented over the last few decades. We conducted diver-based surveys to develop a distributional map and to compare the current distribution with that of the Holocene. Furthermore, we investigate the recent history of recruitment of mussels on Svalbard to help identify invasion pathways. Our results show that blue mussels have been present on the archipelago at least since 2000 and are widespread along the west coast today. We also present evidence of local reproduction in one of the sites explored.

Keywords Bivalves · Climate change · Arctic · Holocene *Mytilus* spp. · Range extension

Introduction

Blue mussels of the genus *Mytilus* are commonly found in intertidal and subtidal habitats in both hemispheres (Koehn 1991; Gosling 1992). They display an antitropical distributional pattern, occurring only in mid- and high-latitudes (Hubbs 1952). *Mytilus* spp. play important roles ecologically (as ecosystem engineers) and commercially (in the shellfish industry) and have the potential to dominate benthic

ecosystems in intertidal and shallow subtidal habitats (Seed 1969; Gosling 2003). Although they tolerate a broad spectrum of environmental conditions (e.g. temperature, salinity, predation and pollution), they are commonly used as climate indicators with winter air temperature being one of the main factors limiting their distribution (Salvigsen et al. 1992; Hjort et al. 1995; Dyke et al. 1996; Salvigsen 2002; Berge et al. 2005; Thyrring et al. 2015). Perhaps as a consequence of limiting winter temperatures, *Mytilus* rarely occur in the intertidal towards their northern distributional limit, but are generally subtidal at depths down to approximately 5 m (Thyrring et al. 2015; Mathiesen et al. 2017).

The *Mytilus* spp. complex in the Northern Hemisphere currently consists of four generally accepted and closely related species: *M. edulis*, *M. galloprovincialis*, *M. trossulus* and *M. californicus*. The last species is not known to occur in the North Atlantic and is, therefore, not considered in our study. Recent genetic work by Mathiesen et al. (2017) covered populations of *Mytilus* spp. from both the European Arctic and Greenland and found genetic markers from all three species to be present on both Svalbard and Greenland. Accordingly, we regard these three species as one complex and refer to them as '*Mytilus* spp.' hereafter.

Fossil and subfossil remains of blue mussels are found throughout the Arctic and sub-Arctic region, often in areas currently not inhabited by the species (Hjort and Funder

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1974; Hjort et al. 1995; Salvigsen 2002, Mangerud and Svendsen 2018). In the high Arctic archipelago of Svalbard, however, *Mytilus* spp. are starting to reoccupy their former range. In the last decade, the northern distribution limit *Mytilus* spp. has shifted northwards (e.g. Berge et al. 2005; Thyrring et al. 2015; Mathiesen et al. 2017). Their wide distribution and fossil evidence of successful settlement further north during warmer periods of the Holocene (Mangerud and Svendsen 2018) make the genus *Mytilus* useful for studying the impacts of environmental changes in the Arctic. Nevertheless, there are few studies regarding Arctic populations of *Mytilus* spp., and little is known about their distribution, life cycle, and reproduction, or the mechanisms behind the expansion and retreat of their populations in the North. The usefulness of *Mytilus* spp. as a sentinel for climate change, however, depends largely on our understanding of these autecological features.

Recently, a few live sightings of single *Mytilus* spp. individuals have been reported from Svalbard (see Berge et al. 2005 and references therein) with most individuals attached to flotsam. Only one small subtidal population consisting of young mussels has been reported (Berge et al. 2005, 2006). One reason for the low detection of living specimens may be that shipboard sampling typically avoids shallow areas where blue mussels occur cryptically among macroalgae within the hard bottom communities. Thus, we carried out a detailed field survey with scientific divers to map the *Mytilus* spp. distribution along the west coast of Svalbard, an area where blue mussels display long fossil records (Salvigsen 2002). Shells of the collected samples were examined to provide insight into the age distribution and recruitment frequency in Svalbard populations. We compare our results with findings from other living and fossil *Mytilus* spp. within the Atlantic–Arctic region to gain a fuller understanding of the population connectivity of Atlantic *Mytilus* spp. and to assess their potential for continued expansion on Svalbard.

Materials and methods

Examination of the mussels was carried out in the laboratory and included biometric analysis and age determination (based on winter growth checks on the external shell surface see Blicher et al. 2013). To test whether external growth lines are deposited annually in the Svalbard area, we placed marked individuals back in the field for 1 year. Twenty-one *Mytilus* spp. individuals were collected at Mitraskjæret (Kongsfjorden). The mussels were kept for 10 days in seawater onboard the research vessel *Helmer Hanssen*. During this period, they were stained with calcein dye for 20 h (see Gillikin et al. 2006 for further details) before being placed in cages on ocean observatories. Eleven individuals were placed in Kongsfjorden (primarily an Atlantic Water fjord),

and 10 individuals were placed in Rijpfjorden (primarily an Arctic Water fjord) at 15 m depth in September 2011 (see Cottier et al. 2005; Berge et al. 2009). The mussels were retrieved from the moorings in August 2012. The right valve of each individual was embedded in epoxy, cut from the umbo to the ventral margin, and polished. Cross sections were imaged using a Nikon Compound Episcopic Microscope capable of fluorescent imaging with wavelengths of 460–500 nm. Images were used to determine the number of growth increments visible in the cross section that occurred after the calcein stain line.

Diving surveys were conducted by groups of scientific divers during research cruises around Svalbard between 2011 and 2016. We focussed on two types of habitats: (1) shallow subtidal hard substrate areas, preferably in fjord-mouth locations with little sedimentation, but high current exposure, and (2) harbour areas as we considered ship traffic a possible vector of introduction of blue mussels. At each site, divers carefully examined the sublittoral between 0 and 5 m depth. Any *Mytilus* spp. specimens present were documented and photographed. Subsamples were collected at each locality by removing single individuals from the substratum with a knife and carefully placing them into a mesh bag.

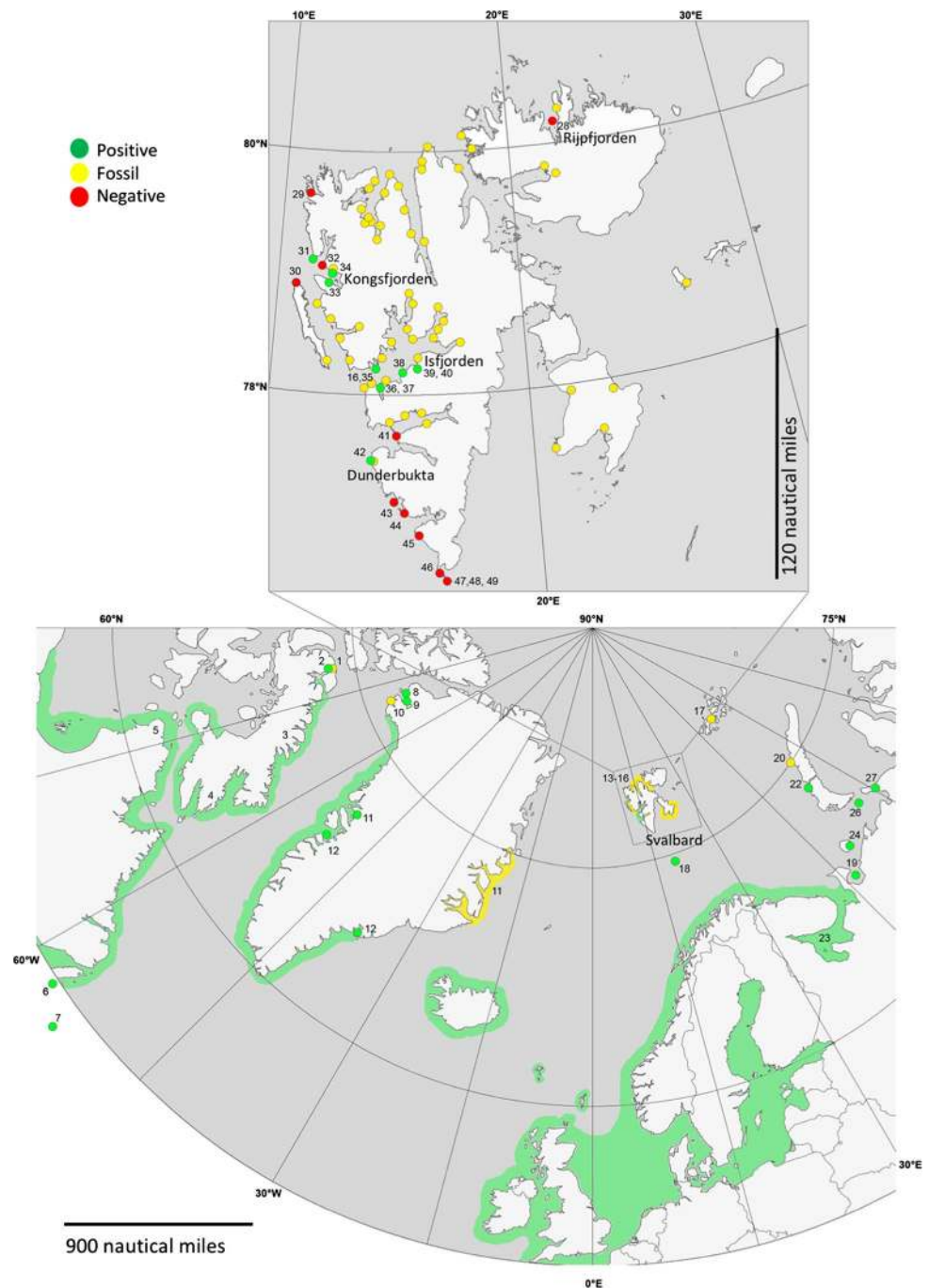
We used the literature of both fossil and living *Mytilus* spp. around the Atlantic–Arctic region, from the Eastern Canadian Arctic to Northern European Russia to determine the extent and former ranges of *Mytilus* spp. Where possible, we extracted geographical coordinates and habitat information (Fig. 1; Online Resource 1).

Results

One single growth band was discernible distal to the calcein stain line in each of the 21 mussels deployed on the observatories in the two fjords (Fig. 2). The growth line was visible as an internal line that extended to the external shell surface where it manifested as a ridge. Consequently, we conclude that the growth lines are annual and will herein regard using the number of external lines on the shell as a good approximation of the age of each individual.

Our field survey recorded live *Mytilus* spp. at 21 locations along the west coast of Svalbard from Kongsfjorden (79°N) in the north, to Dunderbukta (77°30'N), just south of Bellsund in the south (Fig. 1, Online Resource 1). Densities were generally very low (<0.5 individuals (ind.) m⁻²), but considerably higher at the two harbour sites examined in Ny-Ålesund and Longyearbyen, where densities reached 10 ind. m⁻² (Table 1). In general, all individuals lived well hidden in cracks in the substrate or were otherwise densely overgrown with macroalgae (kelp, red algae) and sessile invertebrates (bryozoans, hydrozoans, cirripedians, and

Fig. 1 Geographic location of subfossil (yellow) and living (green) *Mytilus* spp. in the Atlantic-Arctic region based on literature data. Enlargement showing Svalbard locations with subfossil, recent living and negative findings of *Mytilus* spp. (yellow, green, and red dots, respectively). Numbering is in accordance with Online Resource 1 and Table 1. Subfossil findings are based on Salvigsen (2002) and Mangerud and Svendsen (2018), whereas recent observations were made by the authors in the period of 2004–2016. Negative findings (red) are dive sites specifically surveyed for blue mussels during this period that revealed no encounter

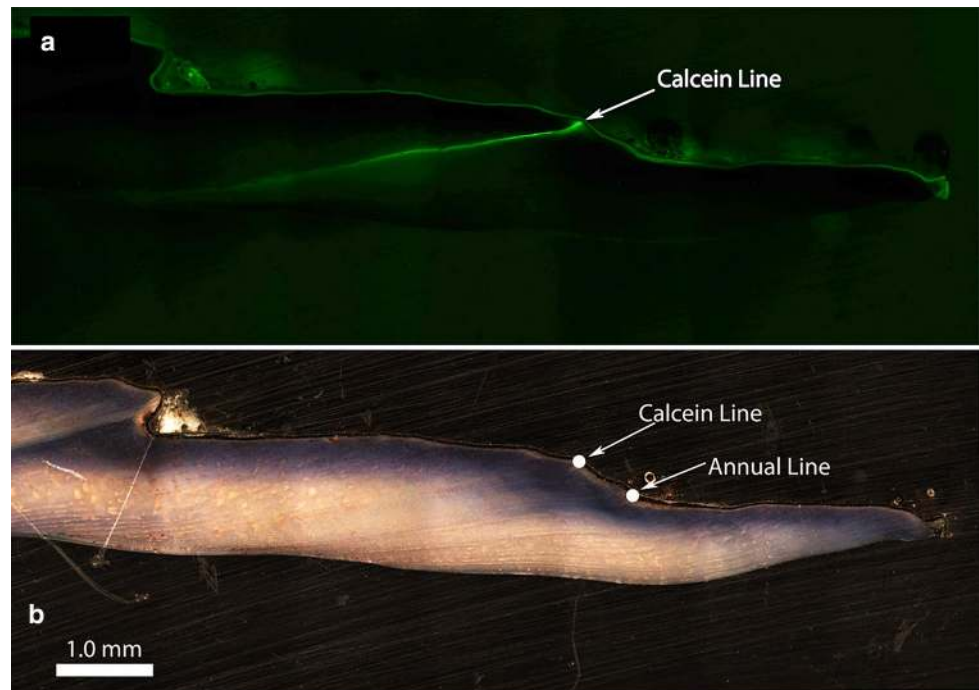


tunicates). In total, we recorded ~600 blue mussels ≥ 2 year old during surveys conducted from 2011 to 2016, of which 328 were collected. In addition, one diver reported a single living blue mussel on the rocky slope at Fuglefjellet (just outside Adventfjorden) (P. Kuklinski pers com, see Online Resource 1). The collected individuals showed a broad range of size and age (8 to 88 mm length, 1–14 years). The reconstructed settlement year of individual mussels was estimated by subtracting the number of external (annual) growth lines from the year of collection for mussels collected inside

Adventfjorden and Kongsfjorden. This indicated recruitment every year since 2000 (Fig. 3). Although the numbers of individuals we encountered varied for the two fjords, our results clearly indicate an annual and continuous recruitment in both areas.

At one site (Longyearbyen harbour), we documented a dense patch (> 400 ind. m^{-2}) of 1-year-old *Mytilus* spp. attached to the hull of a local charter boat (M/S Ulla Rinman). The vessel's itinerary indicated that she had not left the coastal waters of the archipelago during the past

Fig. 2 Ventral margin of *Mytilus* sp. from Kongsfjorden, 11 months after staining with calcein. **a** Calcein line under fluorescence at $\times 5$ magnification. **b** Ventral margin in dark field at $\times 5$ magnification. Arrows indicate location of calcein/annual line



year, spending considerable time in both Adventfjorden and Hornsund (further south at around 77°N).

Discussion

Based on the wide range of locations where we found *Mytilus* spp., we argue that blue mussels are widespread along the western Svalbard coast (Fig. 1, Table 1). So far, only Berge et al. (2005, 2006) has reported the existence of resident *Mytilus* spp. on Svalbard and only at one site (Sagasjkæret, Isfjorden). They postulated that blue mussel larvae had settled on Svalbard in 2002 and that the larvae had been transported from a source population on mainland Norway by the North Atlantic Current and West Spitsbergen Current (WSC). This was suggested to be a one-time event as all mussels found were of similar age. The oldest mussel collected in our study, however, settled around the year 2000 in Adventfjorden, right outside Longyearbyen. Despite the low densities at all sites, our data clearly show that settlement of blue mussels is a recurring event, with evidence of recruitment every year since 2000 (Fig. 3).

Mytilus spp. is often considered to be a reliable climate indicator (Salvigsen et al. 1992; Hjort et al. 1995; Dyke et al. 1996; Salvigsen 2002; Berge et al. 2005; Thyrring et al. 2015). This foundation species' wide distribution and role in structuring benthic communities render it a prime model organism for geologists and palaeontologists to reconstruct paleoclimate and for biologists to predict future marine community composition. The genus once occurred farther

north than today during the warmer periods of the Holocene (roughly 9–6.5 ky BP) and died out, presumably due to direct and indirect effects of the cooling climate (Salvigsen 2002).

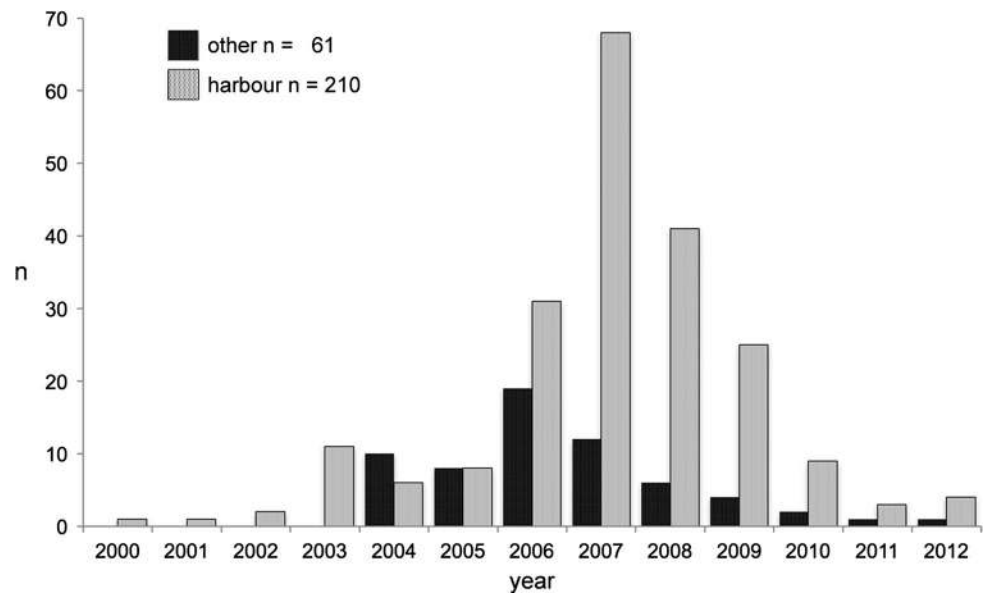
Shifts in species ranges and community composition of Svalbard/Barents Sea benthos have even been observed to fluctuate over the past 100 years (Renaud et al. 2007). Sea surface temperatures (SST) and sub-surface temperatures around Svalbard and off the western Barents shelf have varied during the Holocene, mostly due to the advected Atlantic Water (AW) and a northward shift in the sea ice margin. The warmest phase, referred to as the 'Holocene thermal optimum', occurred around 10.7–7.7 kyr. BP, peaking at 10.2–9.2 kyr. BP (Mangerud and Svendsen 2018). Reconstructed summer SSTs were as high as 8°C during this period and later dropped to around 4°C where they stabilized and persisted for ~ 5 kyr. (Sarnthein et al. 2003). Werner et al. (2013) showed the same trend for sub-surface water temperatures of the Atlantic Water core (50–200 m depth) at the western Barents shelf. This water mass feeds the WSC directly and is therefore responsible for the transport of warm AW to western Svalbard. Ultimately, some branches of the WSC may reach into the west-facing fjords to various extents in different years (Cottier et al. 2007). Werner et al. (2011) also showed mild warming for the last 3 kyr. and a more drastic temperature increase during the last 1 kyr. Modern (since 1900), summer sub-surface temperature ranges (50–100 m depth) equal the values of the Holocene thermal optimum for the western Barents shelf area. Even though the summer SSTs today around Svalbard are

Table 1 Location, date, and brief description of *Mytilus* spp. sampling sites on Svalbard

No.	Location	Latitude/longitude	Sampling date	n	Length range (mm)	Age range (years)	Density (ind/m ²)	Habitat/comment	Depth (m)
<i>Nordautland</i>									
28	Rijpfjorden	80°11'N 22°14'E	03.10.2014	–	–	–	–	Exposed kelp forest	–
<i>Smeerenburg</i>									
29	Moseøya	79°39'N 10°55'E	14.09.2015	–	–	–	–	Exposed kelp forest	–
<i>Prins Karls Forland</i>									
30	Fuglehuken	78°54'N 10°28'E	15.05.2014	–	–	–	–	Exposed kelp forest	–
<i>Kongsfjorden</i>									
31	Mitraskjæret	79°07'N 11°08'E	30.09.2012	21	n.d.	2–8	<1	Exposed kelp forest	2–6
			03.09.2013	13	14.5–36.5	4–9	<1	Exposed kelp forest	2–6
			14.05.2014	23	45.5–85.9	6–10	<1	Exposed kelp forest	2–6
32	Guissezholmen	79°04'N 11°38'E	14.05.2014	–	–	–	Exposed kelp forest	–	
33	Ny Ålesund harbour	78°56'N 11°56'E	24.09.2014	2	31.1, 63.7	2, 6	<5	Vertical pile wall	1–6
34	Bloomstrand-halvøya	78°59'N 11°58'E	29.09.2014	1	46.3	7	single ind.	Bare rock	2
<i>Isfjorden</i>									
35	Sagaskjæret	78°13'N 13°56'E	08.2004	11	27–55	2–3	<1	Exposed kelp forest	4–7
36	Grønnfjorden	78°06'N 14°E	2010	2	≤43	≤6	n.d.	n.d.	n.d.
37	Grønnfjorden	78°04'N 14°12'E	09.07.2016	1	33.5	4	single ind.	Vertical pile wall	1
38	Fuglefjellet	78°13'N 15°14'E	26.07.2012	1	n.d.	n.d.	single ind.	Dense kelp forest	6
39	Longyearbyen harbour	78°14'N 15°36'E	18.05.2014	197	19.3–87.5	2–14	<25	Vertical pile wall	1–7
40	M/S Ulla Rinman	78°14'N 15°36'E	10.2014	120	7–23	1–2	<200	Rudder stock	1–2
<i>Bellsund</i>									
41	Akseløya	77°41'N 14°55'E	10.07.2016	–	–	–	–	Exposed kelp forest	–
42	Dunderbukta	77°29'N 13°53'E	11.07.2016	5	36.0–60.2	4–10	<1	Exposed kelp forest	2–4
<i>Hornsund</i>									
43	Isøyane	77°08'N 14°48'E	12.07.2016	–	–	–	–	Bare rock	–
44	Dunøya	77°02'N 15°04'E	13.07.2016	–	–	–	–	Exposed kelp forest	–
45	Vestvika	76°51'N 15°32'E	15.07.2016	–	–	–	–	Exposed kelp forest	–
<i>Sørkapp</i>									
46	Tokrossøya	76°33'N 16°19'E	14.07.2016	–	–	–	–	Bare rock	–
47	Sørkappøya	76°30'N 16°28'E	14.07.2016	–	–	–	–	Bare rock	–
48	Sørkappøya	76°30'N 16°30'E	14.07.2016	–	–	–	–	Exposed kelp forest	–
49	Sørkappøya	76°28'N 16°31'E	14.07.2016	–	–	–	–	Exposed kelp forest	–

Numbers correspond to locations in Fig. 1

Fig. 3 Recruitment years, estimated by number of winter growth lines on the external shell surface, and number of individuals settled for 271 *Mytilus* spp. individuals collected during the years 2012–2014 on Svalbard. Samples are separated by collection sites



some 5–8 °C lower than during the thermal peak of the early Holocene, they are well within the temperature range when *Mytilus* spp. previously occupied the archipelago. The Holocene occurrence of *Mytilus* spp. was most likely a recurring event during intermittent warm periods (see Mangerud and Svendsen 2018, results and discussion). In summary, advection of AW and temperatures in the area around Svalbard and farther north favour the arrival, settlement, and survival of boreal species, including *Mytilus* spp. This is consistent with fluctuations in species distributions over at least the past 10 kyr. and has recently been shown by many authors for both pelagic and benthic species over the past 4 decades (Kortsch et al. 2012; Berge et al. 2015; Renaud et al. 2015).

There are three non-mutually exclusive scenarios that could explain the occurrence and distribution of Svalbard blue mussels today. First, they might be a relict population that descended from Holocene blue mussels. Second, they may be closely related to the Northern Atlantic *M. edulis* population, as proposed by Berge et al. (2005, 2006). Third, mussels could be introduced by human activity, e.g. in the form of ballast water transport (Ware et al. 2014) or attached to hulls of visiting ships. Each of these possibilities is examined separately.

If *Mytilus* spp. were present on Svalbard since the Holocene, the population would have had to reproduce successfully and survive throughout the notably colder (than today) temperatures of the late Holocene. The youngest (single) *Mytilus* subfossil from Isfjorden (Kapp Thordsen) dates from around 1 ky BP and there is a gap of almost 3 ky to the next youngest deposits (found in Billefjorden) (Salvigsen et al. 1992). Genotypes of isolated (relict) species will diverge over time from their nearest relatives and can eventually lead to species segregation (Vermeij 1991). Also, if the

Svalbard population of mussels were isolated for at least 1 ky, we would expect its genome to be different from their closest ancestors, northern Norwegian mussels. This aspect was addressed in a study by Mathiesen et al. (2017) who investigated the genetic diversity and connectivity between Arctic and sub-Arctic *Mytilus* populations. Different populations of mussels from Greenland, Iceland, Russia, Norway, and some of the Svalbard specimens from this study were compared using genetic markers. *Mytilus* spp. from Svalbard were mainly *M. edulis*; however, some samples were classified as *M. galloprovincialis* and hybrids of both, *M. edulis*/*M. galloprovincialis* and *M. edulis*/*M. trossolus*. One has to keep in mind that results of genetic studies only reflect what was sampled. The absence of certain taxa or hybrids, therefore, has to be considered carefully as it may just represent undersampling. The Svalbard samples, however, clustered closest with Norwegian and White Sea samples, indicating that a colonization of Svalbard from the south is the most likely scenario for present day *Mytilus* spp. on Svalbard. We suggest the scenario of *Mytilus* being present throughout the Holocene as rather unlikely due to the lack of both fossil and recent evidence. In addition, the presence of some hybrids in our samples (Mathiesen et al. 2017) suggests a recent establishment of *Mytilus* spp. on Svalbard. It is unlikely that hybrids would have survived since or even been present during the Holocene warm periods. Mangerud and Svendsen (2018) conclude that *Mytilus* spp. likely became locally extinct on Svalbard around 3.7 ky BP and that the youngest fossil deposit is from a Medieval warm period reimmigration that may be comparable with its recent arrival described by Berge et al. (2005). Both authors postulate that advection of larvae or transport of individuals on flotsam has initially and repetitively seeded the blue mussel stock on

Svalbard. Our finding of scattered mussel patches along the outer western coast and inside the mouth of the west-facing fjords coincides with likely drift patterns and reinforces this hypothesis. Also, the same area was subject to an intensive intertidal survey in the early 1990 (Weslawski et al. 1993, 1997) without any records of living *Mytilus* spp, providing at least circumstantial evidence that they were not living in the area at that time.

The fact that we also find *Mytilus* deep inside the fjords, especially on artificial harbour structures, points towards a second vector of dispersal: ship traffic. Ware et al. (2014, 2016) did not find *Mytilus* spp. larvae in ballast water samples on Svalbard taken from bulk carriers originating from non-Norwegian ports. They did, however, detect several other non-indigenous species in the ballast water samples. Ware et al. (2016) point out the insufficiency of the ballast water management practices on Svalbard and that required protocols are often not followed by vessels. They conclude, therefore, that Svalbard ports are at high risk of ballast water and biofouling introductions, where currently no management regulations exist. Blue mussels are important contributors to fouling assemblages (Gosling 2003) and have been introduced to several parts of the world far beyond its native range, often through long-range maritime transport (see Beyer et al. 2017 and references herein). Adult mussels are able to detach themselves from ship hulls or spawn when inside ‘foreign harbours’. We consider it likely that *Mytilus* spp. has been introduced by ship traffic in addition to natural advection from the Norwegian mainland.

We provide a detailed biogeographic overview of the distribution of *Mytilus* spp. on Svalbard, including new findings of living blue mussels along the west coast of Spitsbergen, and compare the patterns with fossil distributions from the area. Also, the finding of a dense aggregation of one-year-old *Mytilus* spp. ($> 400 \text{ ind. m}^{-2}$) in Isfjorden suggests that there is local reproduction on Svalbard. Although circumstantial, the mere density of settled individuals suggests that the larvae have not been transported over long distances. The occurrence of blue mussels on Svalbard is most likely the result of at least two distinct dispersal vectors: natural larval advection by ocean currents and human introduction by ship traffic. Based on the estimated year of settlement of specimens found in non-harbour locations (Fig. 3), we conclude that the settlement of *Mytilus* spp. is an annual, rather than unique, event as suggested by Berge et al. (2005). Combined with the circumstantial evidence of local reproduction, this implies that current environmental conditions are favourable for continued persistence of Svalbard’s *Mytilus* spp. populations.

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Compliance with ethical standards

Conflict of interest There are no identified conflicts of interest regarding the work presented herein.

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