



The re-appearance of the *Mytilus* spp. complex in Svalbard, Arctic, during the Holocene: The case for an arrival by anthropogenic flotsam

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ARTICLE INFO

Keywords:

Global change
Arctic
Mytilus spp.
Plastic litter
Genetics
Vectors
Re-introduction

ABSTRACT

The blue mussel *Mytilus* spp. complex has re-appeared in the high Arctic in Svalbard after a thousand years, with the first recent indication of its appearance in 2002 at the mouth of Isfjorden on the west coast. We examine its genetic affinity to selected North Atlantic populations and the modes of spread that may be responsible for its recent re-colonisation. We record here its distribution on Svalbard archipelago along the north-western coastline and within Isfjorden collected over a seven years period. We record for the first time the intertidal occurrence that includes a presence close to a glacier front. Genetic composition of mussels *Mytilus* spp. from different Svalbard locations reveal similarities mainly with populations of *M. edulis*, *M. trossulus* and their hybrid from Western Europe, Faroe Island, Scotland and Norway. The re-introduction to Svalbard most probably involved shipping and natural or anthropogenic flotsam. It seems that a new transport vector - large plastic debris - plays a significant role in this process.

1. Introduction

A prerequisite for successful colonisation is an environment that should be suitable for survival, growth and propagation. The arrival of a species to new regions can involve different natural and anthropogenic spreading mechanisms by overcoming natural barriers. One of the relatively new vectors of species spreading is macroplastic litter (Barnes, 2002; Lewis et al., 2005). Plastic flotsam has increased manifold in recent decades and has become a vector of spread even in the remote ocean regions (Barnes et al., 2009). Characteristic organisms for this distribution mode are the blue mussels *Mytilus* spp. (Cárdenas et al., 2020; Miller et al., 2018).

The blue mussel *Mytilus* complex is widely distributed in coastal areas showing a bipolar or antitropical distribution pattern (Hilbish et al., 2000; McDonald et al., 1991). *Mytilus* taxa are morphologically similar and a number of genetic methods have been used for their identification (Kijewski et al., 2011; Śmietanka et al., 2014, 2013). Recently, molecular markers have been constructed, which allowed more precise identification of *Mytilus* taxa to the level of species and populations in both hemispheres. Among them, sets of Single Nucleotide

Polymorphisms (SNPs) are most feasible and sensitive (Simon et al., 2019; Zbawicka et al., 2014). Their application in population genetic studies enabled confirmation and discovery of invasive or introduced settlements and populations of *Mytilus* spp. among indigenous populations in northern and southern hemispheres and their hybridization (Gardner et al., 2016; Zbawicka et al., 2018, 2012).

Three sibling *Mytilus* species occur in the North Atlantic: *M. edulis*, *M. trossulus* and *M. galloprovincialis*. Populations of *M. trossulus* from North America and North Russia can be distinguished from introgressed *M. trossulus*/*M. edulis* from the Baltic Sea and from other European (Russia, Norway, Scotland) and Greenland populations as based on results of SNP research (Wenne et al., 2020). *M. edulis* populations form 4 main groups: pure American, American and European admixed (Scandinavia and Arctic), pure European and admixed Scotland *M. edulis*/*M. galloprovincialis* (Fraïsse et al., 2016; Wenne et al., 2020). Two main groups of *M. galloprovincialis* populations: Atlantic and Mediterranean are traditionally recognised (Zbawicka et al., 2012). According to Mathiesen et al. (2017), *M. edulis*, pure *M. galloprovincialis* and hybrids are present in recently re-established populations on Svalbard.

Past occurrence of *Mytilus edulis* (Linnaeus, 1758) in the Arctic has

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<https://doi.org/10.1016/j.gloplacha.2021.103502>

Received 26 May 2020; Received in revised form 30 March 2021; Accepted 1 May 2021

Available online 4 May 2021

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been documented by shell remains and the entire Svalbard archipelago was inhabited by this species in great abundance during the last Holocene warming 9–7 thousand YBP (Hjort et al., 1995; Mangerud and Svendsen, 2018). Subsequently during the cooling, the *Mytilus* disappeared from Svalbard. However, the youngest (single) *Mytilus* subfossil from Isfjorden dates from around 1 ky BP (Salvingsen et al., 1992). The first specimens in this region of the Arctic were collected on the island of Bjornoya, the southernmost island of the Svalbard archipelago (Weslawski et al., 1997a, 1997b). It was later recovered from the Isfjorden (Berge et al., 2005) the most visited and busiest fjord of western Spitsbergen. The *Mytilus* spp. are capable of tolerating cold polar conditions as they occur in the other regions of High Arctic (north-west Greenland and Baffin Island) (Blicher et al., 2013).

The recent reappearance of *Mytilus* in the Svalbard archipelago has been regarded as one of the signs of the shifting of boreal species to the Arctic attributed to the episodic larvae transport by the unusually high northward advection of warm Atlantic water (Berge et al., 2015a, 2015b, Berge et al., 2006; Kortsch et al., 2012; Ware et al., 2014). The recent report by Leopold et al. (2019) shows a very slow advance of *Mytilus* from the site of its first observation in western Spitsbergen (Berge et al., 2005). This is surprising as *Mytilus* with its pelagic mode of dispersal could be expected to reach wider areas within 15 years of the first record. For example, one of the best documented cases of recent spread of a boreal species, a littoral crustacean *Gammarus oceanicus*, devoid of pelagic larvae, shows that the species has moved over several hundred km along the Svalbard shores in the last 20 years (Weslawski et al., 2018).

Hitherto, *Mytilus* spp. have been recorded in Svalbard waters only in the subtidal. Here, we present the current status of the distribution of *Mytilus* spp. in this region with the first observation of its intertidal occurrence. We examine its possible origin and the way it spreads on the basis of genetic analysis, field observations and possible links to anthropogenic activities.

2. Material and methods

2.1. *Mytilus* spp. sampling and single nucleotide polymorphisms (SNP) genotyping

Samples of *Mytilus* spp. consisting of 43 individuals of mixed age and size were collected from eight sites on Svalbard and Faroe Islands coasts between 2014 and 2019 (Fig. 1, Table 1). Whole specimens or tissue samples were stored in 96% ethanol. DNA was isolated from the mantle tissue, using the modified CTAB method (Hoarau et al., 2002).

All reference samples of the pure *Mytilus* taxa and their hybrids originated from already published works. Individuals from Canada, Halifax (KKAT), identified in Bach et al. (2019), provided a reference sample of *M. trossulus*. Populations from the Atlantic coast of North America - Indian River, Delaware (IRD), Lough Foyle (LGF), and from the Atlantic coast of North Europe - Oosterschelde (NLOO) - provided reference samples of *M. edulis* (Wenne et al., 2016, 2020). Reference specimens of *M. galloprovincialis* originated from the Mediterranean at Oristano (ORI). Additionally, mixed populations of *M. edulis* / *M. trossulus* from Barents Sea (BAR), Norway, Bergen (BRN) and Great Britain, Scotland, Loch Etive (LET), and population of *M. edulis* / *M. galloprovincialis* from Kerrera (KRR) were used to determine the potential source of mussels on Svalbard (Wenne et al., 2020). Seventy-nine SNPs differentiating *Mytilus* taxa and potential hybridisation were used (Gardner et al., 2016; Zbawicka et al., 2019, 2018, 2012). Samples were genotyped using the Sequenom MassARRAY iPLEX platform (Gabriel et al., 2009).

2.2. Littoral surveys and collection of stranded materials

Forty-seven coastal sites were inspected along the western shores of Svalbard and in Isfjorden in the summers of 2017 to 2019 for macroplastic, biofouling on debris, empty mussel shells and live bivalves. The

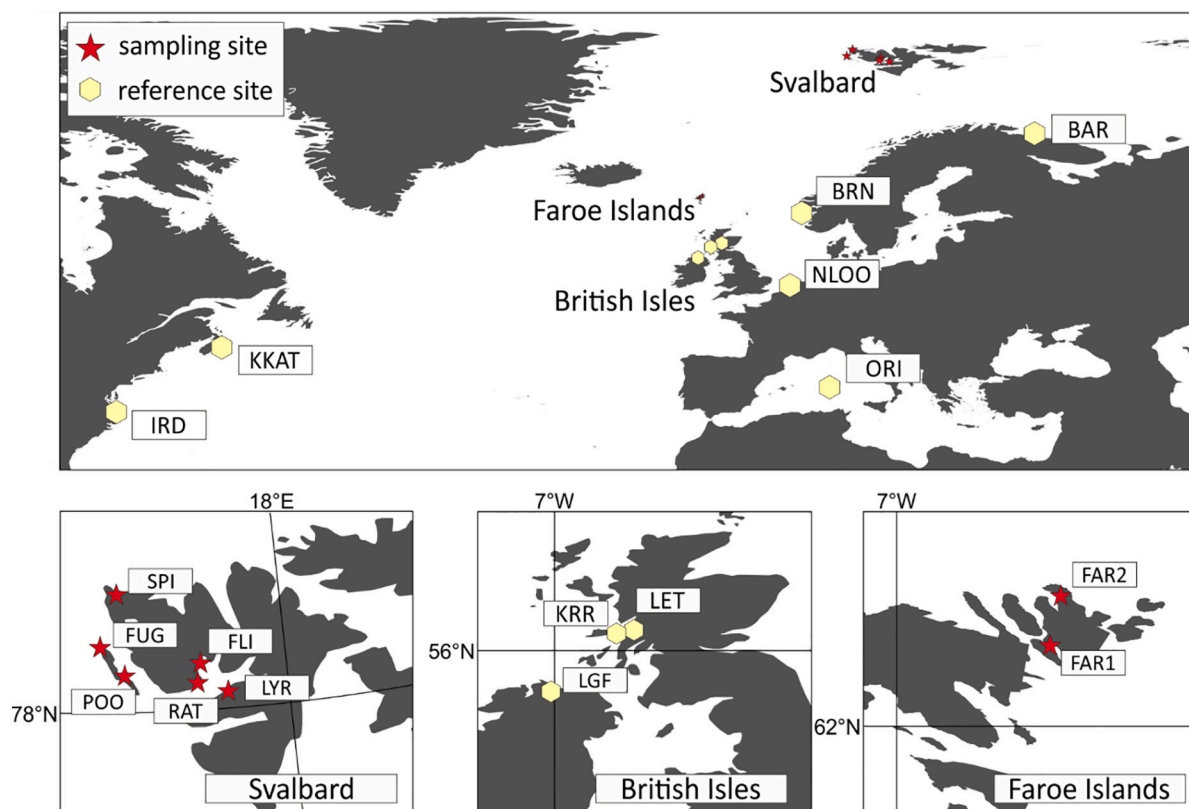


Fig. 1. Location of sampling sites on the Svalbard and Faroe Islands coast and reference sites for *Mytilus* spp.

Table 1
Detail information on mussel sampling and reference sites.

Sampling sites	Location	Country/area	Ocean region /Sea	No. of individuals	Latitude	Longitude	Sample collection
SPI	Smeerenburg	Svalbard	Arctic	4	79°38'46.94"N	11°04'10.38"E	2017
LYR	Longyearbyen	Svalbard	Arctic	7	78°13'46.20"N	15°36'05.39"E	2017
FUG	Fuglehuken	Svalbard	Arctic	18	78°53'45.92"N	10°32'40.90"E	2018
PKF	Poolepynten	Svalbard	Arctic	2	78°28'16.92"N	11°34'17.76"E	2019
FLI	Flintholmen, Isfjorden	Svalbard	Arctic	4	78°38'25.16"N	14°33'42.35"E	2019
RAT	Ratangen, Isfjorden	Svalbard	Arctic	1	78°22'04.83"N	14°24'37.51"E	2019
FAR1	Arnafjordur	Faroe Island	North Atlantic	3	62°13'20.97"N	06°34'20.84"W	2019
FAR2	Vidaroy	Faroe Island	North Atlantic	4	62°21'38.34"N	06°32'52.08"W	2019
Reference sites							
LGF	Lough Foyle	Ireland	Northeast Atlantic	20	55° 5'35.50"N	7° 4'48.92"W	2006
NLOO	Oosterschelde	Netherlands	East Atlantic	17	51°50'7.10"N	3°49'18.21"E	2000
IRD	Indian River Inlet, Delaware,	USA	West Atlantic	20	36°52'6.19"N	75°58'2.16"W	2012
KKAT	Halifax, Nova Scotia	Canada	Northwest Atlantic	20	44°30'33.79"N	63°29'24.91"W	1996
ORI	Oristano/Torre Grande port	Italy	Mediterranean Sea	20	39°47'59.88"N	8°31'9.72"E	2006
BAR	Barents Sea	Russia	Barents Sea	10	69°47'36.00"N	32°45'59.68"E	2004
BRN	Bergen	Norway	East Atlantic	20	60°23'25.65"N	5°12'27.08"E	2012
LET	Loch Etive, Scotland	Great Britain	East Atlantic	20	56°27'21.35"N	5°18'26.62"W	2008
KRR	Kerrera, Inner Hebrides, Scotland	Great Britain	East Atlantic	20	56°22'42.56"N	5°33'17.14"W	2014

faunal samples for the *Mytilus* presence were collected during low tide, both in the intertidal zone and among the debris washed to the high shore. Plastic items were counted within sectors 100 m long and 10 m wide to include the drift line (report on the number, weight and categories) as well as data on mussel observation (presence/absence, coordinates, living and dry material) are presented in details on the web page <https://www.iopan.pl/projects/Adamant/>. Bivalves containing tissue were regarded as fresh and collected, assigned as sublittoral (washed up with macroalgae), intertidal (found attached in the tidal zone) and those species attached to stranded plastics (containers, nets, buoys).

2.3. Testing of genetic assignment and analysis of hybridisation and introgression

Clustering and genetic assignment testing for the individuals found on Svalbard and Faroe Islands were performed using two methods. The Bayesian-based method was implemented in STRUCTURE v. 2.3.4 software with no prior information about the origin of individuals (Pritchard et al., 2000). Values of genetic clusters (K) captures the main STRUCTURE of the populations (Evanno et al., 2005). Individuals with q-values from 0.2 to 0.8 were considered to be potentially admixed (Lecis et al., 2006). Additionally, software GeneClass 2.0 (Piry, 2004) that computes various genetic assignment criteria to assign or exclude reference populations as possible origins of individuals, on the basis of multilocus genotypes was used. This program uses frequency criteria of multilocus genotype data (Paetkau et al., 1995) and the Bayesian method of Rannala and Mountain (1997).

Individuals were considered to be correctly assigned to their location of origin if the assignment probability to that group was higher than any other assignment probability to any other group.

The software NewHybrids v1 (Anderson and Thompson, 2002) was used to identify *M. edulis* and *M. trossulus* hybrids based on genotypic information and is able to assign individuals to specific hybrid classes (e.g. F1, F2). The set of 16 SNP markers with allele characteristic for pure *M. trossulus* (about 90–100%) was used in hybrid index (HI) analysis (Wenne et al., 2020). These alleles distinguish *M. trossulus* from *M. edulis*. A score of zero is a 'pure' *M. edulis*, whereas a score of one is a 'pure' *M. trossulus*. HI was calculated for all individuals and averages for each population to assess the degree of introgression between *M. edulis* and *M. trossulus*.

3. Results

3.1. Coastal distribution of *Mytilus* spp. in Svalbard waters (2013–2019)

A general overview of the data on the presence of mussels in littoral surveys of Svalbard coasts is presented in Fig. 2. The living *Mytilus* spp. in the intertidal zone were spotted in three areas on the northern side of Isfjorden: Ekmanfjorden, Borebukta and Trygghamna only in 2019.

In Trygghamna, most living mussels were found half-immersed in silty sand and attached with byssus threads to small pebbles and gravel, which served as anchors (Fig. 3). Only a few specimens were fixed to small boulders in the *Fucus* sp. belt. Clusters of mussels were not found; single individuals were distributed over a length of approximately 1000 m. Their size varied from 21 to 57 mm, the size structure clearly indicated the presence of two generations (Fig. 3).

Based on the growth curves of blue mussels from different intertidal locations in the North Atlantic (Blicher et al., 2013) we estimate that the age of the largest specimen found in Trygghamna may be between 6 and 12 years, while the smallest one between 1+ and 6 years. The empty shells of mussels were found in the intertidal zone in nearly 20 sites visited in 2016–2019, and shells attached to plastic or among the debris washed to the high shore in 6 places, visited in 2013, 2018 and 2019 (Fig. 4).

3.2. Genetic STRUCTURE of *Mytilus* spp. from Svalbard and Faroe Islands

STRUCTURE analysis of eight samples from Svalbard and Faroe Islands for SNP variation along with reference populations from the northern hemisphere revealed the presence of 4 main clusters (Fig. 5).

Two samples from Faroe Islands and two from Svalbard (FLI, RAT) were identified mainly as pure European *M. edulis* by both STRUCTURE (*q* value greater than 0.76%) and NewHybrids. In three other samples from Svalbard (LYR, PKF, SPI), in addition to individuals of pure European *M. edulis* taxon and characteristic for North Europe American and European admixed, STRUCTURE reveals single hybrids: *M. edulis* and *M. galloprovincialis*, and *M. edulis* and *M. trossulus*. A completely different situation was observed in population from Fuglehuken (FUG), where STRUCTURE and NewHybrids analysis showed pure *M. trossulus* and pure *M. edulis* taxa and above 50% of hybrids (Fig. 6).

Frequency distribution of the hybrid index (HI) in the studied populations is presented on Fig. 7. Most samples from Svalbard and Faroe Islands were "pure" *M. edulis* (HI near 0, below 0.04). Contrary to this, in population from Fuglehuken (FUG), where HI reaches a value 0.4 (and range from 0.0 to 0.84), pure *M. edulis*, *M. trossulus* and hybrids were detected. In Fuglehuken the percentages of hybrids reaches 0.5 and the

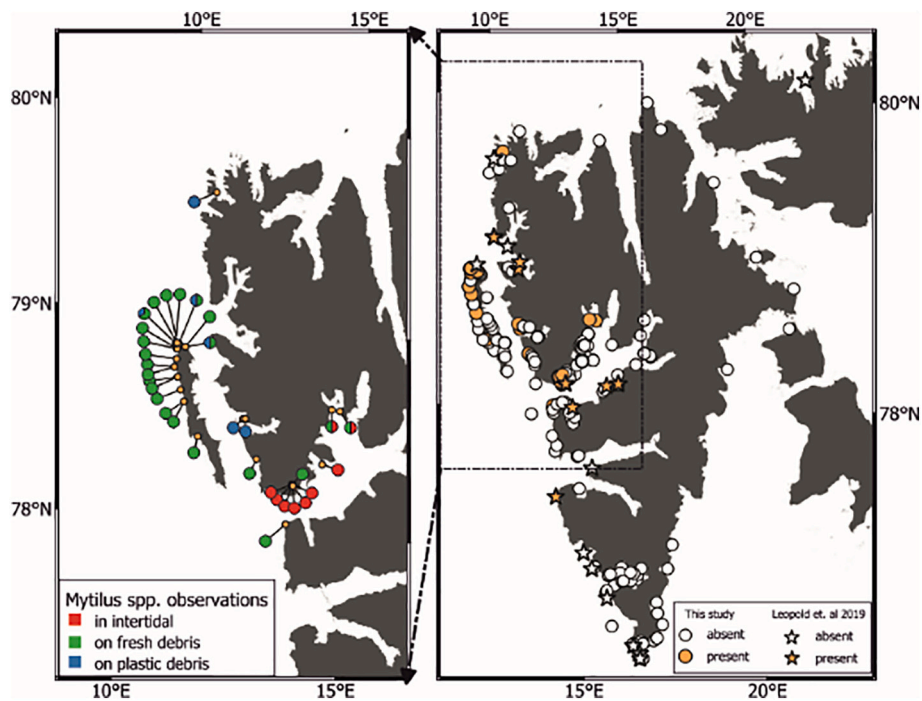


Fig. 2. Observations of *Mytilus* spp. on Svalbard shores 2013–2019.

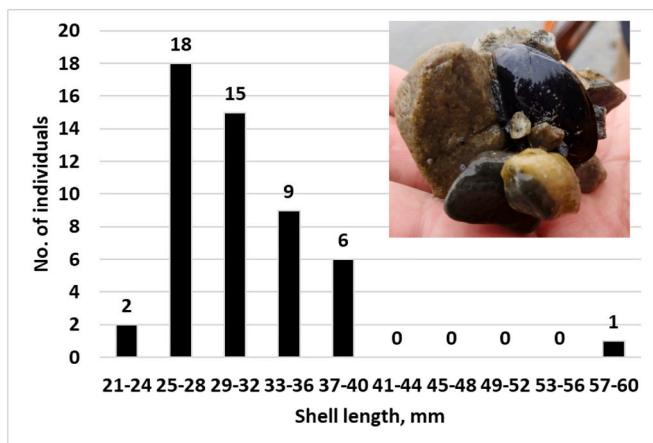


Fig. 3. Size structure of the mussel *Mytilus* spp. settlement in Trygghamna; photo: mussel attachment to pebbles and gravel, mechanism of settling in soft sediments on the littoral (photo: S. Olenin).

greatest HI range values was observed. However, NewHybrid analysis with high probability reveals all hybrid categories except F1 hybrid. Single *M. trossulus* and *M. edulis* hybrids with a probability over 0.9 were also observed in LYR (F2) and PKF (*M. edulis* backcross). No individual from Svalbard and Faroe Islands has been assigned to *M. galloprovincialis* cluster. Only one individual from Smeerenburg (SPI) was considered potentially admixed *M. edulis* x *M. galloprovincialis*. The difference in the presence of *M. trossulus* alleles in the PKF sample is associated with different method (STRUCTURE and NewHybrid) and the admixture on the border of statistical significance of each method.

The GeneClass analyses places *M. edulis* samples from Svalbard mainly in populations from Scotland, Hebrides (KRR) and Faroe Islands (FAR) (Table 1). Sample from Fuglehuken (FUG) containing *M. trossulus* and hybrid individuals found on the beach was assigned to populations from Norway (Bergen - BRN), as well as one individual from the Longyearbyen harbour (LYR). However, single individuals from Fuglehuken

(FUG) showed also similarity to samples from Barents Sea, Russia (BAR) and Loch Etive, Scotland (LET). However, the presence of a large number of different *M. edulis* x *M. trossulus* hybrids (F2 and backcrosses) in sample from Fuglehuken (FUG) indicates the potential origin of the sample from the coast of Norway rather than Russia were only F1 hybrids were observed. Four individuals from Smeerenburg (SPI) found in 2014 in a barrel thrown to the beach were assigned to very distant areas like North America, Scotland and The Netherlands. This indicates a non-simultaneous settlement of mussels on the rafting barrel. This applies especially to hybrid *M. edulis* x *M. galloprovincialis*. All reference populations were assigned correctly to the taxa and region of origin.

3.3. Distribution of stranded macroplastic and attached organisms

Based on the observations carried out on the surveyed transects, the amount of plastic rubbish ranged from a few to several dozen pieces per 100 m of the coastline. (Fig. 8) The most frequent plastic objects were household items such as PET bottles, lightweight containers, plastic bags and textiles, which were often high on the shore, followed by fragments of fishing equipment, buoys, lines and fragments of nets.

The largest plastic objects - fishing boxes, barrels, liquid containers - were often colonized by the encrusted organisms i.e. barnacles, blue mussels, bryozoans and marine brown and red macro-algae. Observed taxa include both widely dispersed species found previously in the coastal waters of Svalbard (*Electra* spp., *Eucratea loricata*, *Semibalanus balanoides*) as well as widely distributed species, but never recorded in the Svalbard waters (*Lepas anatifera*) (Fig. 9).

We hypothesize that accumulation of plastic debris can be considered as an indicator of places where larvae of benthic animals should first enter if they are carried over such distances by currents.

4. Discussion

All species are limited in their geographical distribution. In some cases, geographic ranges are restricted to small areas and are stable over long periods of time, while in others, they include large territories and shift very frequently (Gaston, 2009). A number of hypotheses have been proposed to explain the boundaries of the geographical range of the

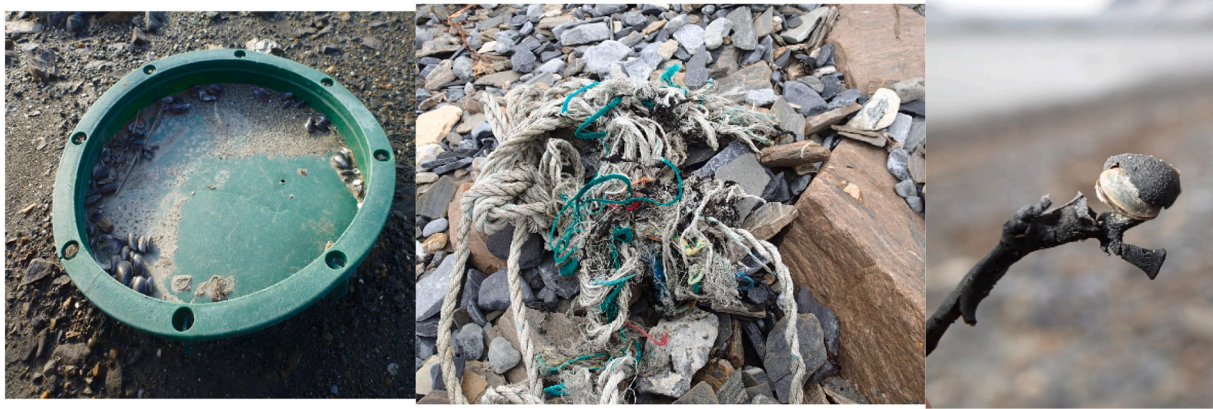


Fig. 4. (left) dried mussels attached to macroplastic, Prins Karl Forland 2019 (photo: L. Kotwicki); (middle) tangled ropes and a piece of fishing net with entwined *Ascophyllum* and (right) dried *Mytilus* attached to *Ascophyllum*, Dahlbrevbukta, 2019 (photo: S. Olenin).

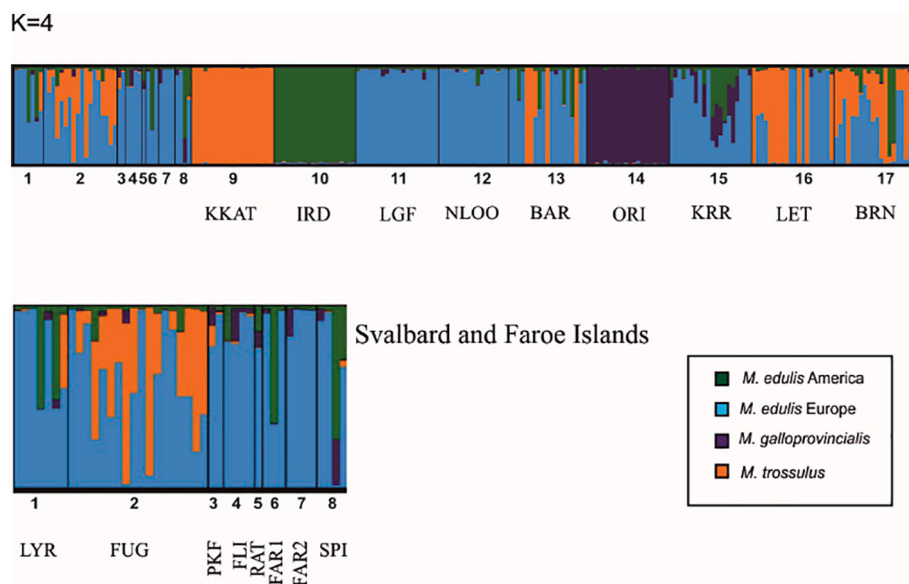


Fig. 5. STRUCTURE plots for the 8 samples from Svalbard and Faroe Islands and 9 references samples ($K = 4$). Each individual is represented by a single vertical line broken into 4 coloured segments, with lengths proportional to each of the K inferred clusters. Abbreviation of the samples is provided in Table 1. Vertical black lines separate the populations.

species and their diversity, with particular emphasis on the spreading. Moreover, the genetics of the population at the edge of a species remain poorly understood. Blue mussel *Mytilus* complex that is widely distributed and relatively well recognised genetically is an interesting model to study the mechanisms of distribution shifts. It occupies both coasts of the North Atlantic (including the Mediterranean) and the North Pacific in temperate to polar waters, as well as coasts of similar nature in the southern hemisphere. For a species to successfully colonize, conditions within a receptor area should be suitable for survival and growth and with an opportunity for reproduction. *Mytilus* is a broadcast spawner with a seasonal reproductive period and so larvae are likely to become dispersed from source according to local currents, whereas detached mussels are more likely to be clustered, and so the propagule pressure being more likely to be sufficient for recruitment. However, many arrivals may not attain such density dependent conditions.

4.1. Genetics and distribution

Population genetic analysis of *Mytilus* specimens sampled from Svalbard revealed their similarities with populations from several

localities within the North Atlantic. According to our data the Faroe Islands and the Svalbard in a major part are dominantly inhabited by European *M. edulis*, American and European admixed *M. edulis*, and much less by hybrids of *M. edulis* with *M. galloprovincialis*, and *M. trossulus* taxa. Contrary, in the Fuglehuken (FUG) on the west coast of Svalbard, a substantial number of *M. trossulus* individuals and their hybrids have been observed. So far no such large number of individuals with *M. trossulus* genes has been found on Svalbard. Only single hybrids were observed in Kongsfjorden and Adventfjorden (Mathiesen et al., 2017). Mathiesen et al. (2017) have reported erroneously occurrence of pure *M. galloprovincialis* in their samples from Svalbard (Kongsfjorden and Adventfjorden) due to methodological reasons (Simon et al., 2019). Despite that, Simon et al. (2019) stated that admixed mussels in Svalbard have lower proportions of Atlantic *M. galloprovincialis* ancestry than admixed mussels from Norway: Lofoten and Gaseid. According to our data only minor contribution of *M. galloprovincialis* genes to the genetic composition of Svalbard samples (FLI, SPI) was confirmed, but no *M. galloprovincialis* as a taxon was observed in this study.

European *M. edulis*, found in the studied samples, is characteristic for Western European populations, while the admixture of American and European *M. edulis* is typical for North European populations (Iceland,

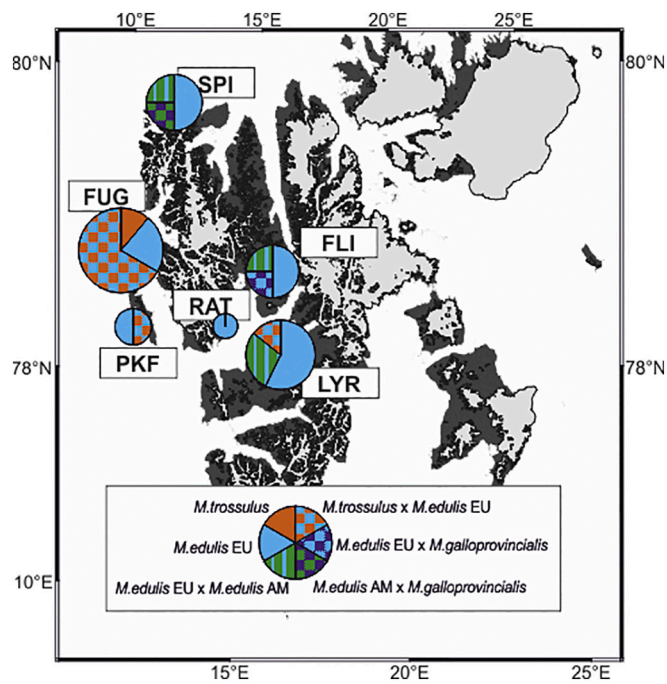


Fig. 6. *Mytilus* taxa and hybrids identified with SNPs ($K = 4$ computed with STRUCTURE) (pie charts visualize the quantity proportions) in west Spitsbergen localities: LYR - Longyearbyen, FUG - Fuglehuken, PKF - Prins Karls Forland, FLI - Flinholmen (Isfjorden), RAT - Ratangen (Isfjorden), SPI - Smeerenburg.

Norway, North Russia) (Fraïsse et al., 2016; Simon et al., 2019; Wenne et al., 2020). According to our results, *M. edulis* samples from Svalbard show greatest affinity to the mussels populations from Scotland Hebrides (KRR) and Faroe Islands (FAR). While the individual *M. edulis* x *M. galloprovincialis* hybrid, which we identified, was assigned mainly to Scotland Hebrides. The Hebrides, exposed to the warm Gulf Stream of the Atlantic Ocean are characterized by large *M. galloprovincialis* introgression (Wenne et al., 2020). They are inhabited by mussels of different genetic composition: pure European *M. edulis*, American and European admixed *M. edulis* and admixed *M. edulis*/*M. galloprovincialis* hybrids.

Sample from Fuglehuken (FUG), composed of *M. trossulus* and European *M. edulis* x *M. trossulus* hybrid, was assigned to population from

Norway (BRN), characterized by large number of *M. edulis* x *M. trossulus* hybrids. Although single individuals show affinity to samples from Russia (BAR) or Scotland (Loch Eive - LET), the presence of a large number of different type of hybrids (F2 and backcrosses) characteristic of Norway, does not support their origin from Russia or Scotland, where mainly F1 hybrids were observed (Wenne et al., 2020).

Mussels found in Smeerenburg (SPI) on the barrel, GeneClass assigned to populations of mussels *Mytilus* from distant areas in Europe and North America. Three individuals were assigned to the European or admixed *M. edulis*, whereas one was classified as American *M. edulis* and *M. galloprovincialis* hybrid. This type of hybrid is very rare. Only single hybrids of this type were reported in populations from Atlantic coast of North America: Nova Scotia Ship Harbour and in Norway (Simon et al., 2019; Wenne et al., 2020). GeneClass assigned this individual to the North America, but its Norwegian origin should also be taken into account, since the other “passengers” of the barrel came from Europe.

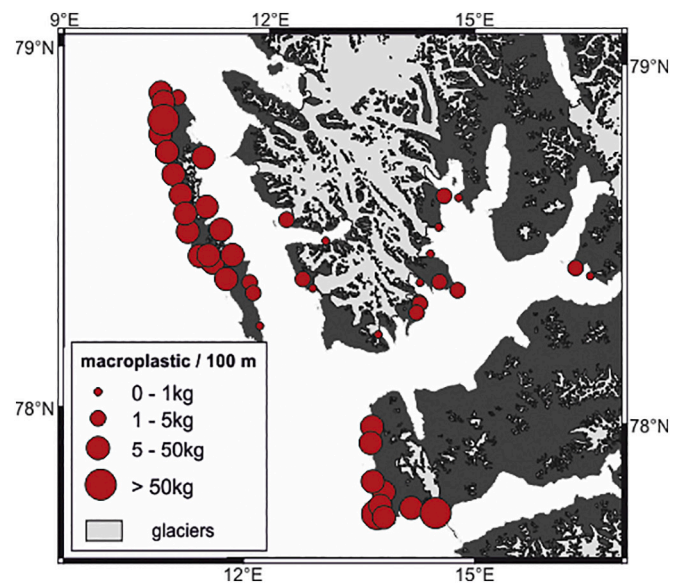


Fig. 8. Assessment of the macroplastic debris distribution based on the 2017–2019 littoral surveys. The same sites were examined for the presence of living mussels, their vacant shells and fouling organisms.

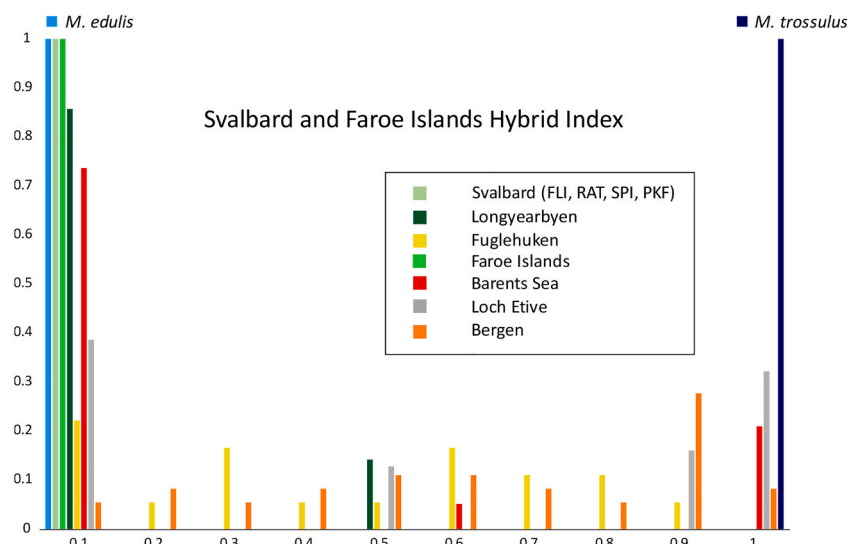


Fig. 7. The frequency distribution of the score for a hybrid index (HI) analysis giving the percentage of *M. trossulus* characteristic alleles for Svalbard and Faroe Islands samples with references. A score of zero is a pure *M. edulis*, whereas a score of one is a pure *M. trossulus*.



Fig. 9. (left) Fragmented frond of *Ascophyllum nodosum*, (Adventfjorden, 2013) (right) Empty shell of *Mytilus edulis* and *Lepas anatifera* remains (Prins Karls Forland, 2018).

Otherwise it would mean a non-simultaneous settlement of mussels on the rafting barrel. Different genetic composition of the samples, observed in most locations on Svalbard, indicates various sources of

mussel origin, but mostly from European North Atlantic.



Fig. 10. Physical barriers for the *Mytilus* distribution on Svalbard (fast ice data: Urbanski et al. 2020 modified).

4.2. Possible modes of spread of the *Mytilus* complex to Svalbard

Well-known natural and anthropogenic vectors that can transport marine species over relatively long distances are currents, driftwood, birds, ship hulls and ballast water (Barnes, 2002; Barnes et al., 2009; Minchin et al., 2009). There is far less information on marine debris as a transoceanic transport vector for potentially invasive species (Audr ezet et al., 2021). Here, we discuss the possible pathways of spread and the role that plastic flotsam may play.

4.2.1. Sea currents - natural dispersal mechanisms

The dispersal of *Mytilus* larvae (seasonal from April till June, (Mileikovsky, 1968)) is strongly controlled by the sea currents and tides. Spitsbergen fjords off the west coast are exposed to the coastal current of local waters, that enters the fjord from the south and leaves along the northern shore (Fig. 10). Atlantic water from the shelf (West Spitsbergen Current) enters occasionally into deeper and wider west Spitsbergen fjords (Goszczo et al., 2018). Hence, the larvae from the colony of *Mytilus* that settled on NW shore of Isfjorden (Berge et al., 2005) may easily travel further NW, and unlikely towards the fjords inner basins. Dominant wind pattern in Isfjorden is from the eastern sector – from the glacier along the fjord (Fraser et al., 2018). This would prohibit the spreading of larvae towards inner fjord basins.

The arrival of the *Mytilus* complex to Svalbard, as proposed by Berge et al. (2005), resulted from larval drifting, from the Lofoten region of Northern Norway, by means of the North Cape Current and West Spitzbergen Current. It occurred in 2002 with unusual temperatures ranging from $\sim 12^{\circ}\text{C}$ to $\sim 4^{\circ}\text{C}$ on this route with a transport time of 32 to 38 days (calculated based on a flow rate of 0.30 to 0.35 m^{s}). This drift measurement was eventually pass to the north side of Isfjorden where eleven individuals were obtained at Sagaskj eret by divers (Berge et al., 2005). The direct sea distance from Lofoten is ~ 950 km. A larval plume released in north Lofoten would be expected to become considerably dispersed over such a distance and it is unclear whether larval mussels would have frequented such depths for such a long time. The duration of *Mytilus* in the plankton, the pediveliger stage could be extended by postponing metamorphosis by up to 40 days at 10°C in the absence of a suitable settlement surface (Bayne, 1965). According to Beaumont and Budd (1982) larvae might extend their existence in the plankton beyond two months at a low temperature, with such a duration Svalbard might be in range; but probably at a high cost of larval mortality. There is also the possibility that an existence in the plankton may be lengthened by passive byssal drifting (Lane et al., 1985; Sigurdsson et al., 1976); although it would appear this state is rare offshore (Shanks and Shearman, 2011). While larval drift might be possible, it is unlikely to explain the levels of hybridization on the western coast of Svalbard. Furthermore studies on the local larval dispersal in Isfjorden do not reveal any data on *Mytilus* larvae occurrence (Ronowicz et al., 2018; Weydmann et al., 2018). The first comprehensive study on the subarctic - arctic species larval drift was that of Mileikovsky (1968), who suggested that the duration of the pelagic stage in this species does not allow to drift for more than a few weeks. Consequently it is unlikely that mussel larvae would reach Svalbard from Norway.

Leopold et al., 2019 provided a detailed biogeographic review of the distribution of *Mytilus* spp. on Svalbard, including new discoveries of live blue mussels along the west coast of Spitsbergen, and compared the patterns with fossil distributions from the area. In addition, based on finding a dense assemblage of annual *Mytilus* spp. (> 400 ind. m^{-2}) in Isfjorden suggest that local reproduction may occur on Svalbard. As they point out, although this is only circumstantial, the sheer density of sedentary individuals suggests that the larvae have not been transported long distances.

Furthermore, for the *Mytilus*, which is predominantly a coastal species ice may be an obstacle due to the physical scouring of animals from the hard substrate, or by freezing the organisms into the ice. Fast ice (seasonal ice that is attached to the shore) distribution indicates

permanently ice-free areas on west and northwest coasts of Spitsbergen and rapid retreat of ice from the inner basins of Isfjorden (Fig. 10). Drifting ice (pack ice) from the Barents Sea rarely reach the W and NW of Spitsbergen, and when this does happen it is in late spring for a few days, when loose ice floes are passing with the coastal current. The observed sector of the Svalbard archipelago (W-NW) may be regarded as having mild ice conditions, when compared with the Greenland coast where *Mytilus* occurs (Bl icher et al., 2013). Summer sea-surface temperatures on the NW-W of Spitsbergen are the highest in the archipelago (Piskozub, 2017; Promińska et al., 2017). Both the presence of ice and the sea temperatures do not prevent colonisation of *Mytilus* on the NW-W coast of Svalbard.

4.2.2. Flotsam

In pre-historic times flotsam will have provided and opportunity for the spread of biota world-wide, for example, the long distant transport from Chile to New Zealand of the oyster *O. chilensis* (O' Foighil et al., 1999). It is unclear what the transport substrate was but might involve floating baulks of timber, such as what is found on Svalbard shores today transporting tereidenid mollusks and stalked cirripedes (Weslawski and Kotwicki, 2018). Flotsam has changed over the last century from natural to synthetic materials (Minchin, 1996) and these are now widely distributed by ocean and wind vectors within the world's oceans and seas (Thiel and Gutow, 2005), much of this being cast ashore (Browne et al., 2011). Approximately 50% of plastic debris is buoyant (Andrady, 2011) forming rafts available for colonisation (Engler, 2012; Kiessling et al., 2015). Many plastics have been spread to Arctic seas with local environmental impacts (C ozar et al., 2017; Trevail et al., 2015). Plastics arriving on Svalbard shores have distant origins (Weslawski and Kotwicki, 2018) and have been arriving over several decades. The appearance of plastics elsewhere (Barnes et al., 2009; Bergmann et al., 2017; Browne et al., 2010; Convey et al., 2002; Merrell Jr., 1980; Wenne et al., 2016) and in remote and uninhabited areas (Barnes, 2002) indicate this is a worldwide litter problem. Barnes and Milner (2005) reported that 5.5% of the plastic items on Spitsbergen were colonized by encrusting fauna such as barnacles. Adult organisms rafting on plastic debris are more likely to survive long-distance travel on a powerful transmission vector (Barnes et al., 2009; Winston et al., 1997). Whereas, natural flotsam, can rot and develop a reduced buoyancy over time, or the organisms grow sufficiently to overwhelm the ability to raft and so such materials may be more important for local spread (Ing olfsson, 1995). A compromised buoyancy may happen with plastics but the abundance of plastics may provide a greater transmission threat today which can be enhanced with tectonic events (Bryan et al., 2004; Miller et al., 2018; Risso et al., 2002). With some biota capable of reproducing on route, such as brooders (Gall and Thompson, 2015).

Mussels have been found attached to plastics at distance from shore in the cold waters of the Southern Ocean (Barnes, 2014). Those carried onto shores become desiccated (Weslawski and Kotwicki, 2018). In 1995, a heavily fouled net was retrieved from the sea at $74^{\circ} 45' \text{N}$ and 19°E , just 25 km due north of Bjornoya (Bear Island), part of the Svalbard archipelago. This net contained several invertebrates including amphipods, nudibranchs, polychaetes, hydroids and *M. edulis* (Đuriš and Weslawski, 1995). A further indication that macroplastics may be involved in transmissions was from a survey in 1994, on Bjornoya, mussels of 2 cm were obtained from the eastern and most sheltered part of the island (Weslawski et al., 1997a, 1997b). Nearby on the upper shore there were plastic fish boxes, floats, rope and net fragments had accumulated (Weslawski, unpublished observation). Furthermore, over a decade later a large plastic barrel with large numbers of attached mussels was stranded on the NW shore of Svalbard in 2013 (Weslawski and Kotwicki, 2018). Anthropogenic plastics carry *Mytilus* over wide regions, mussels can be present in large numbers on some floating anthropogenic materials. On arriving on a shore mussels may become rubbed off or perhaps undergo a spawning event. The rafting of groups of adult organisms favours their better biological dispersal compared to

larval transport, and is considered in this work as one of the causes for the reappearance of genus *Mytilus* on Svalbard.

4.2.3. Birds

Bennike and Wagner (2013) claim migrating geese may have introduced *Mytilus* spp. to Greenland and birds have been shown to transport other byssate species inland (Banha et al., 2016). Undoubtedly *Mytilus* being an important food for migrating ducks might, by association, be capable of being spread. Birds may transport mussels over short distances as food to their young 2 km (Leopold et al., 1996) so spread over greater distances becomes more unlikely. Should mussels be transported, the numbers of individuals carried are likely to be very low, nevertheless migrations of many birds might lead to a viable inoculation.

4.2.4. Vessels

We cannot overlook the role of ships, floating structures and other craft in the transmission. Byssate mollusks are widely distributed on the hulls of recreational craft, floating structures to large ships that include *Mytilus* spp. (Casoli et al., 2016; Gollasch, 2002; Lewis et al., 2003; Minchin and Nunn, 2013; Apte et al., 2000). Such are the numbers involved that a spawning event on the hull of a ship, with a short turnaround, may leave behind sufficient zygotes to form an inoculum (Minchin and Gollasch, 2003). We already know *Mytilus* can endure cold temperatures while attached to a hull having been found on a vessel visiting Antarctic waters (Lee and Chown, 2007) and in Svalbard a vessel, with a home port in Bremerhaven, Germany, and berthed in Longyearbyen, which had a mussel fouling burden of >400 m² of 1 year mussels (October 2014). It is unclear whether these had spawned within the Isfjorden or had a distant origin. Diver studies in areas of ports have reported mussels at densities of <5 m² (Ny-Ålesund) and < 25 m² (Longyearbyen) (Leopold et al., 2019). These too may have been as a result of a spawning; but the original inoculation in the port region, which shows a different signature to the mussels on the outer island coasts could have been as a result of a visiting vessel having its hull brushed by floating ice to result in a drop-off of mussels. The scraping of fouled hulls when drawn up on to the shore might be responsible for the *Mytilus* recovered from the intertidal area near the glacier.

Ballast water of ships arriving from different European ports, has and, is known to be discharged in Isfjorden at the port of Longyearbyen. Ware et al. (2014, 2016) recorded more than thirty non-native species in arriving ballast. Discharges occurred mainly during June to September involving a mean discharge of 21,000 m³, yet propagule pressure was considered to be low (Ware et al., 2014). Mytilid larvae have been frequently recorded within ballast water in studies 2002–2010 in the North and Baltic seas (Gollasch et al., 2015). Ships arriving included bulkers with large ballast volumes discharged in order to take on the bituminous coal mined on Svalbard. These exports were mainly to Norway consisting of >2 million tonnes in 2008 and exports to Russia from Barentsburg will have taken place up until 2007, when this activity ceased. Since the arrival of *Mytilus* will have taken place before these dates and before the implementation of the IMO Ballast Water Management Convention, even though guidelines existed, (IMO, 2004). Consequently, there is the possibility that ballast water could have introduced mussels. In particular since Leopold et al. (2019) have evidence of subtidal mussels having annual growth rings have recruited since 2000 with fourteen year classes.

5. Conclusion

We suggest that the colonisation of the Svalbard archipelago by the blue mussel *Mytilus* spp. is not only an effect of a single, favourable hydrological event, but also the result of other possible pathways including a massive plastic litter drift from southern regions. We contend that this is an overlooked pathway whereas the role of shipping in the spread of mussels is widely accepted. The arrival would appear to

be consistent with the warming of the west coast of Svalbard, conditions which may have been favourable for colonisation since the 1930s. While shipping will have been active in this area over some centuries the role of plastic flotsam as a recognised vector of transmission of biota to this region, since the 1960s, has not been fully recognised.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This project has received funding from the European Union's Horizon 2020 research and innovation programme (GA No 776617) under the BiodivScen call (research project no. 2018/28/Z/NZ8/00079, acronym: ACCES, research funding institution: National Science Centre, Poland) and funding from National Science Centre, Poland within research project no. 2017/27/L/NZ8/03331 (acronym: ADAMANT). The projects sponsored by Sysselmannen Miljøvernfond – Svalbard Intertidal Project RIS-ID 3423 and Aliens on the Beach were of great help in the field work realization.

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