



***Gammarus* (Amphipoda) species competitive exclusion or coexistence as a result of climate change in the Arctic?**

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Abstract: The coexistence of two congeneric amphipods, boreal *Gammarus oceanicus*, and arctic *G. setosus*, was studied during the summer seasons of 2017–2019 in the region of Isfjorden, Forlandsundet, and Prins Karl Forland island in the west-central part of the Svalbard archipelago (Arctic). Across the study area species distribution often overlapped, but the domination patterns mirrored environmental conditions preferred by each species. Both species, however, were able to survive in suboptimal conditions. On a small spatial scale (in one sample) the species were separated, which may suggest an antagonistic relationship between them. The ongoing changes in the environment of Svalbard will likely affect these two species differently. The increasing intrusion of Atlantic waters will probably favor the further expansion of *G. oceanicus* along the Svalbard coasts. This will be due to the gradual advance of the existing population, as an influx of individuals from the Nordic seas seems unlikely. *G. setosus* will remain the dominant species in cold-water areas such as the inner fjords and the northeastern coast of Svalbard and may find new suitable habitats in lagoons or estuaries fed by melting glaciers. Despite predicted changes in the distribution range of both species, their future coexistence should still be possible due to the wide range of environmental tolerance and the heterogeneity of the Svalbard coastal habitats.

Keywords: Arctic, Svalbard, Peracarida, congeneric species, sympatry, climate change.



Introduction

The warming of the European Arctic is considered exceptionally fast (ACIA 2005) and specific, as the local cold-water biota experiences not only temperature rise and sea-ice decay (as in Siberia and the Canadian Arctic) but also an increased influx of species-rich North Atlantic waters (Berge *et al.* 2005, 2015; Węśławski *et al.* 2011; Thyrring *et al.* 2017; Burrows *et al.* 2019). The west coast of the Svalbard archipelago is directly influenced by the relatively warm Atlantic waters carried by the West Spitsbergen Current (Willis *et al.* 2006; Piechura and Walczowski 2009; Walczowski *et al.* 2012) and its benthic fauna is poor in species and biomass compared to similar habitats in northern Europe (Kotta *et al.* 2016).

Gammarid amphipods represented by over 30 species are among the key species of the North Atlantic intertidal zone (Węśławski *et al.* 2020). Many of them are known for their wide tolerance to salinity, temperature, and habitat changes (Tzvetkova 1975; Węśławski *et al.* 2020). Gammarids are brooders, lacking pelagic larvae, though able to move swiftly over short distances between stones or algae, they are generally poor swimmers, dispersing slowly and not known to exhibit migratory behavior (Tzvetkova 1975). Changes in gammarid distribution are usually attributed to a man-assisted introduction *via* ships or debris (Grabowski *et al.* 2006) but may be also induced by coastal currents (Węśławski *et al.* 2018). The entire Spitsbergen coastline is inhabited by the circumarctic, cold-water species *Gammarus setosus* Dementieva, 1931, and, within a smaller area, by the recently expanding population of its boreal congener *Gammarus oceanicus* Segerstråle, 1947 (Węśławski *et al.* 2018). In Spitsbergen, both species are similar in size, exhibit roughly the same breeding seasonality, and have comparable food and habitat preferences (Węśławski 1994; Węśławski and Legeżyńska 2002). Genetic analysis of the Spitsbergen *Gammarus* populations showed that *G. setosus* has much longer evolutionary history in the Arctic than *G. oceanicus*, a species of boreal origin, which started its expansion around the end of the Last Glacial Maximum (Grabowski *et al.* 2019). In recent decades, *G. oceanicus* has gradually expanded its range along the Spitsbergen shores. Initially, it was recorded mainly on the Atlantic-influenced southwestern coasts (Węśławski 1994), later spread northward, and started to colonize the southern shores of the fjords tracking the pathway of warm shelf waters entering the fjords along their south coasts (Węśławski *et al.* 2018). Currently, the boreal *G. oceanicus* is also sporadically recorded in the northern part of Isfjorden, beyond the range of the direct influence of Atlantic waters (this study). Thus, the coastal area where the two species are observed to co-exist has increased significantly.

A stable co-occurrence of several closely related (congeneric) species is widespread among littoral amphipods, both on regional (sympatry) and habitat (syntopy) scale (Croker 1967; Ingólfsson 1977; Kolding and Fenchel 1979; Hill and Elmgren 1983; Lancelotti and Trucco 1993; Guerra-Garcia *et al.* 2010; Korpinen and Westerbom 2010; Beermann and Franke 2012; Vader and Tandberg

2019). Within genus *Gammarus* up to a dozen or so species may have overlapped regional distribution (Ingolfsson 1977; Vader and Tandberg 2019; Węśławski *et al.* 2020), and between two and five species are often found in the same habitat (Kolding and Fenchel 1979; Skadsheim 1983; Korpinen and Westerborn 2010). The co-existence of closely related, ecologically similar species may result in interspecific competition, leading to reduction or even local extinction of species that have weaker competitive abilities. To minimize competition congeneric gammarids often diverge by one or more traits when they share the same habitat (Kolding and Fenchel 1979). Coexistence is also facilitated by small-scale niche partitioning, for example, spatial segregation along environmental gradients such as wave exposure (Lancelotti and Trucco 1993), temperature, and salinity (Kolding and Fenchel 1979; Ikko and Luyubina 2010) or type of macroalgal cover (Korpinen and Westerborn 2010). Identifying the factors underlying species coexistence has been a major focus of theoretical ecological studies (*e.g.*, Boer 1980; Simberloff 1982), and the subject of experimental (*e.g.*, Skadsheim 1983; Jermacz *et al.* 2017) and field-based research on intertidal crustaceans (*e.g.*, Kolding and Fenchel 1979; Guerra-Garcia *et al.* 2010; Korpinen and Westerborn 2010; Beermann and Franke 2012).

This article is the fourth in a series presenting *Gammarus* distribution in Svalbard. It was initiated by a publication describing the large-scale spatial distribution of *G. setosus* and *G. oceanicus* clearly related to the presence of Arctic and Atlantic water masses (Węśławski 1994). In the following work, Węśławski *et al.* (2018), described the gradual expansion of the boreal *G. oceanicus* along the coasts of Spitsbergen as a result of climate warming over the past 30 years. Finally, in the third study, it was showed that the population of *G. setosus* in Svalbard is genetically diverse, while *G. oceanicus* shows little genetic heterogeneity, which confirms the long history of the first species and the recent appearance of the second one (Grabowski *et al.* 2019). The purpose of this article is to discuss the phenomenon of coexistence of two species in the part of the west Spitsbergen coast, where the increasing impact of warm West Spitsbergen Current is observed, but the inner fjord basins contain local, glacier-impacted cold water and are periodically covered by fast-ice. Strong gradients of environmental conditions over small geographic scales make west Spitsbergen an ideal site for monitoring the impact of climate change on the Arctic marine ecosystem.

Using our distribution data, we discuss the following scenarios for the future fate of the two studied species in a warming Svalbard:

1. Gradual expansion of *G. oceanicus* caused by the intensification of warm Atlantic water supply and limitation of the range of *G. setosus* to typically arctic locations (such as inner glacial fjords).

2. The further coexistence of both species despite changing climatic conditions, possible due to their wide tolerance to environmental conditions and the diversity of habitats available in the fjords and on the coast of west Svalbard.

Study area

The Svalbard archipelago is situated between the Barents and Greenland Seas, expanding from 74° to 81°N and from 10° to 35°-E. The research was conducted in the central region of western Svalbard, in Isfjorden, the largest fjord complex (3084 km²) of Spitsbergen, on the Prins Karl Forland isle and in the 90 km long sound Forlandsundet, separating Prins Karls Forland and Spitsbergen (Fig. 1). Oceanographic conditions in this region are strongly related to the characteristics of the currents flowing northward along the west Spitsbergen coast: West Spitsbergen Current which carries relatively warm and salty Atlantic waters and weaker coastal Spitsbergen Polar Current transporting cold and fresh Arctic waters from the Barents Sea. Additionally, the fjord and Forlandsundet receive substantial amount of freshwater from: calving and ablation of glaciers (*c.a.* 1% of the entire fjord volume per year), melting of sea ice, precipitation, and rivers (Nielsen *et al.* 2008; Skogseth *et al.* 2020). In the fjord, the mean summer temperature of surface waters is 4–5°C and the total tidal amplitude is about 1 m (Skogseth *et al.* 2020). The sea-ice cover usually forms in January and may last up to five months in the side fjords of Isfjorden, while its central basin and outside coast generally remain ice-free during the whole year. The west coast of Spitsbergen is directly affected by global warming. Hydrographic data collected since 2002 in this area show an increase of 2°C over 20-year observations with the strongest increase in sea temperature in winter (Cottier *et al.* 2019). Since 2006, a significant reduction in the extent and thickness of sea ice has also been observed (Gerland *et al.* 2020).

Material and methods

Gammarids were sampled in the area between 77°43'N to 78°54'N during July–August 2017–2019 in Isfjorden, on its adjacent coasts, and the Prins Karls Forland (Fig. 1). The samples were collected by hand net at low tide from under loose stones, from a 20x20 cm area. In 2017 and 2018, samples were collected from approximately 100 meters long sections of the coast. At one site from one to several samples (squares) were collected depending on the presence of animals. One sample contained gammarids collected from under several small stones or from under one large stone. The samples taken in 2019 were used to investigate a small-scale distribution of the two species and each sample consisted of animals collected from a single large stone (of approximately 400 cm² area). The samples were collected only from typical gammarid habitat (loose flat stones in sheltered areas); the habitats with exposed gravel and sand beach, rocks, silty estuaries were omitted, so there are no 'absent' data. The animals were preserved in ethanol and subsequently identified in the laboratory according to the keys by

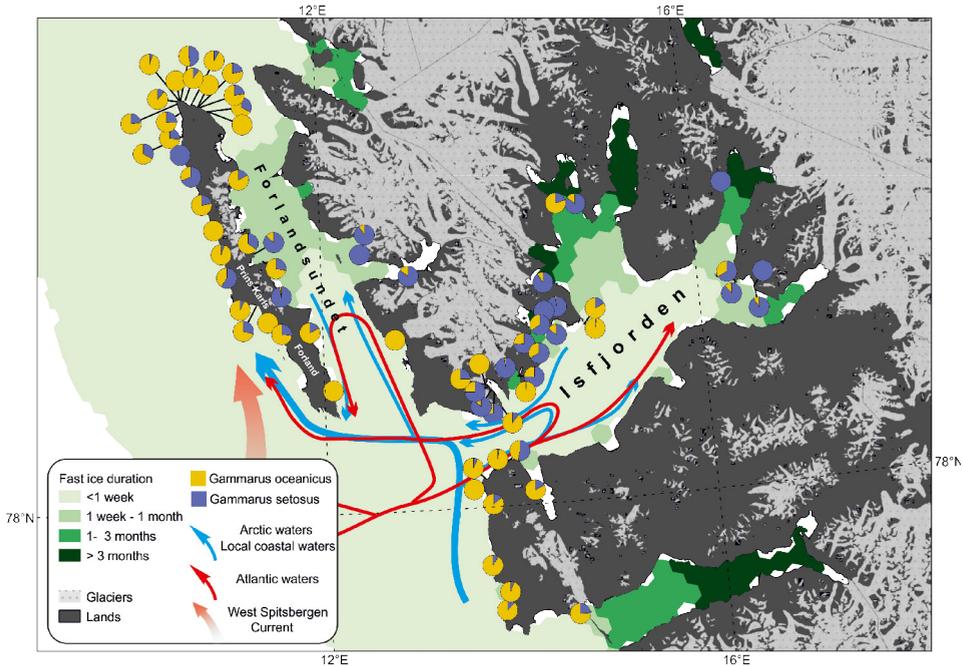


Fig. 1. Occurrence of *Gammarus oceanicus* (boreal species) and *Gammarus setosus* (Arctic species) in the West Svalbard region during the 2017–2019 summer seasons. An overview of the circulation pattern for the Arctic Water (ArW, blue arrow in the surface) and the AW (red arrow in deeper layers) in the Isfjorden Trough and the connection to Isfjorden and Forlandsundet (modified after Nielsen *et al.* 2016). Fast ice duration based on observational data from 2005–2018 provided in Urbański and Litwicka (2021).

Tzvetkova (1975) and Vader and Tanberg (2019). Only specimens longer than 6 mm were identified, as the species-specific features in smaller ones are not fully distinguishable. A set of basic environmental parameters and the percentage share of the boreal species in the total number of collected *Gammarus* spp. were determined for each sampling site. Hydrographic data were collected during the summer cruises of r/v *Oceania* and data on fast-ice extension and duration were taken from Urbański and Litwicka (2021). The presence or absence of Atlantic and local cold waters in summer was coded as 1 or 0, respectively. Ice conditions were coded according to the following scale: 0 – fast-ice occurrence <1 week a year; 1 – fast-ice occurrence < 1 month per year, 2 – occurrence of fast-ice from 1 to 3 months, 3 – fast ice occurrence > 3 months. Data regarding present (2017–2019) and archival (2008–2016) *Gammarus* sampling are available at https://adamant.iopan.pl/adamant/taxa_observations/.

The impact of environmental conditions (presence of Atlantic water, local cold water, and fast ice duration) on the *Gammarus oceanicus* contribution to the total *Gammarus* abundance was tested with type II permutation analysis of variance (Permanova) based on Euclidean distance among samples and 9999 permutations (*adonis.II()* function from *RVAideMemoire* package (Hervé 2021)).

Pairwise *post hoc* comparisons were performed with rank sums Dunn's test with Bonferroni correction for multiple comparisons. All the calculations were performed in R 4.0.4 (R Core Team 2021).

Results

A total of 123 samples were collected from 71 sites, which resulted in 3662 identifiable individuals (Table 1; Fig. 1). The distribution of *G. oceanicus* and *G. setosus* was largely related to environmental conditions. The relative proportion of the two species was influenced by the presence of the Atlantic water (Permanova $F(1, 65) = 8.34$, $p < 0.01$) and presence of the fast ice ($F(3, 65) = 4.66$, $p < 0.01$), but not by the presence of local cold water ($F(1, 65) = 0.01$, $p = 0.91$). The median of *G. oceanicus* contribution to the total *Gammarus* abundance at sites influenced by Atlantic waters was 87%, while 15% at no influenced sites. In the case of fast-ice presence, areas with fast-ice duration <1 week had statistically significant (Dunn's test <0.05) higher contribution of *G. oceanicus* (median = 89%) compared to stations with longer fast ice duration (median from 9 to 26%). The majority of the samples were dominated by one species and only at a few sites an equal share of both species was noted. At the small scale (sample under single stones) the two species tended to avoid each other (Fig. 2). The highest domination of one of the species characterized the most abundant samples (Fig. 3).

Discussion

Many factors may govern the distribution and co-occurrence patterns of the two species inhabiting in the Spitsbergen littoral. It is known that the arctic *G. setosus* is better adapted to low salinity and low temperatures than the boreal *G. oceanicus* what affects their large-scale distribution in the Arctic (Tzvetkova 1975; Węśławski 1994; Ikko and Luyubina 2010) and sub-Arctic localities (Steele and Steele 1970, 1972; Vader and Tandberg 2019). Both species, however, can tolerate a wide range of temperatures and salinity (Tzvetkova 1975), therefore these factors do not always determine species occurrence in the coastal waters of the Arctic and sub-Arctic. It is worth mentioning that *G. setosus* occurs also on Bjørnøya, the isolated, southernmost island of the archipelago situated at 74°N, at present in very mild Atlantic climate (Węśławski *et al.* 1997; confirmed by samples collected in 2018 on courtesy of Hallvard Strøm, Norsk Polarinstitutt). As documented by our data, *G. oceanicus* presence is not restricted to Atlantic waters, however, it performs worse in cold-water areas with long-lasting fast-ice, for example on the north coast of Isfjorden or the east coast of Prins Karls Forland. Progressive warming may differently affect the two

Table 1

List of sampling sites 2017-2019.

sampling site	N _s	Lat. N	Lon. E	date	FI	LCW	AW	N _i		% of total N _i	
								G. o	G. s	G. o	G. s
Knivodden	1	78.452	11.301	04.08.17	1	0	1	46	19	71	29
Ravlodden	1	78.434	11.365	04.08.17	1	0	1	4	0	100	0
Storkoben	1	78.39	11.567	04.08.17	1	0	1	35	13	73	27
Tistelodden	1	78.392	11.841	04.08.17	1	0	1	5	1	83	17
NE_Fuglehuken 1	1	78.898	10.506	05.08.17	1	0	1	12	0	100	0
Kaldneset	1	78.45	11.181	05.08.17	1	0	1	26	2	93	7
Ossianbekken	1	78.514	10.994	05.08.17	1	0	1	21	30	41	59
Havnes	1	78.564	10.938	06.08.17	1	0	1	37	2	95	5
Skjernes	1	78.616	10.86	06.08.17	1	0	1	48	0	100	0
NE_Fuglehuken 2	1	78.897	10.517	07.08.17	1	0	1	8	7	53	47
NE_Fuglehuken 3	1	78.897	10.567	07.08.17	1	0	1	9	1	90	10
NE_Fuglehuken 4	1	78.887	10.633	07.08.17	1	0	1	12	1	92	8
NE_Fuglehuken 5	1	78.870	10.846	07.08.17	1	0	1	15	0	100	0
NE_Fuglehuken 6	1	78.872	10.807	07.08.17	1	0	1	10	5	67	33
NE_Fuglehuken 7	1	78.882	10.735	07.08.17	1	0	1	10	3	77	23
NE_Fuglehuken 8	1	78.883	10.706	07.08.17	1	0	1	16	0	100	0
N of Skjernes	1	78.671	10.735	07.08.17	1	0	1	14	4	78	22
Skurvodden	1	78.732	10.621	07.08.17	1	0	1	8	18	31	69
Hornflya	1	78.82	10.535	08.08.17	1	0	1	34	12	74	26
Kapp Sietoe	1	78.779	10.506	08.08.17	1	0	1	0	27	0	100
Mossenhjellen	1	78.87	10.513	08.08.17	1	0	1	37	13	74	26
Fuglehuken	1	78.895	10.464	09.08.17	1	0	1	39	5	89	11
Mykrepnyten	1	78.884	10.72	10.08.17	1	0	1	36	10	78	22

sampling site	N _s	Lat. N	Lon. E	date	FI	LCW	AW	N _i		% of total N _i	
								G. o	G. s	G. o	G. s
Pyramiden harbor	1	78.654	16.366	13.08.17	4	0	1	0	67	0	100
Gordonpynten	1	78.471	11.572	05.08.18	2	0	0	1	31	3	97
Sandbukta	1	78.264	12.061	05.08.18	1	0	1	16	0	100	0
Innerodden	1	78.587	11.231	06.08.18	2	0	0	36	19	65	35
Selvagflya	1	78.548	11.383	06.08.18	2	0	0	31	12	72	28
Sessflya	1	78.565	11.293	06.08.18	2	0	0	5	33	13	87
Hornflya	1	78.82	10.535	08.08.18	1	0	1	6	3	67	33
Murraypynten	1	78.724	11.14	09.08.18	2	0	1	29	6	83	17
Moschjellen	1	78.889	10.474	10.08.18	1	0	1	34	10	77	23
Fuglehuken	1	78.898	10.494	11.08.18	1	0	1	21	1	95	5
Kapp Linne	1	78.061	13.626	14.07.18	1	0	1	41	3	93	7
Osodden	1	77.874	13.641	01.08.19	1	0	1	100	10	91	9
Isforflya S	1	78.023	13.625	02.08.19	1	0	1	68	11	86	14
Isforflya N	1	78.044	13.597	03.08.19	1	0	1	89	0	100	0
Lewinodden	1	78.08	13.719	03.08.19	1	0	1	111	2	98	2
Minervaodden	1	78.03	14.124	04.08.19	2	0	1	81	17	83	17
Vestre Twillingodden	1	78.097	13.87	04.08.19	1	0	1	39	44	47	53
Gipshukodden 1	1	78.438	16.395	23.07.19	2	0	0	20	39	34	66
Gipshukodden 2	1	78.437	16.397	23.07.19	2	0	0	3	24	11	89
Gipsvika 1	3	78.414	16.599	23.07.19	2	0	0	4	39	9	91
Gipsvika 2	1	78.423	16.591	23.07.19	2	0	0	0	5	0	100
BlonaslettaCamp 1	1	78.636	14.773	26.07.19	4	0	0	8	45	15	85
Flintholmen	7	78.641	14.564	26.07.19	3	0	0	156	39	80	20
Yoldiabukta	1	78.472	14.366	26.07.19	4	1	0	1	10	9	91
Borebukten 1	1	78.376	14.394	27.07.19	2	0	0	0	30	0	100
Borebukten 2	1	78.368	14.411	27.07.19	2	0	0	6	33	15	85

sampling site	N _s	Lat. N	Lon. E	date	FI	LCW	AW	N _i		% of total N _i	
								G. o	G. s	G. o	G. s
Alkepynten	8	78.211	13.843	28.07.19	1	0	1	88	10	90	10
Bohemanflya watt	1	78.402	14.513	28.07.19	2	0	0	1	57	2	98
Bohemanneset E	11	78.378	14.763	28.07.19	1	0	0	80	16	83	17
Bohemanneset W	1	78.378	14.763	28.07.19	1	0	0	50	1	98	2
Eidembukta	1	78.369	12.759	28.07.19	1	0	1	26	0	100	0
Frontholmen	8	78.246	13.768	28.07.19	3	1	0	40	119	25	75
Ymerbukta 1	3	78.277	14.026	28.07.19	3	1	0	21	63	25	75
Ymerbukta 2	3	78.25	14.055	28.07.19	1	1	1	141	2	99	1
Ymerbukta 3	3	78.287	13.916	28.07.19	3	1	0	2	91	2	98
Dahlbreen 1	1	78.562	12.394	29.07.19	2	1	0	0	19	0	100
Dahlbreen 2	1	78.566	12.442	29.07.19	2	1	0	1	10	9	91
Ratangen	8	78.368	14.411	29.07.19	2	0	0	66	130	34	66
St. Johnfjord	1	78.505	12.93	29.07.19	2	0	0	4	23	15	85
Tundraodden N	5	78.344	14.233	29.07.19	3	0	0	20	54	27	73
Tundraodden S	4	78.34	14.244	29.07.19	3	0	0	32	66	33	67
Diabasbukta	1	77.758	14.486	29.08.19	2	0	1	34	11	76	24
Trygghamna 1	1	78.252	13.738	30.07.19	3	0	0	6	38	14	86
Trygghamna 2	1	78.259	13.715	30.07.19	3	1	0	4	12	25	75
Trygghamna 3	1	78.262	13.681	30.07.19	3	1	0	1	0	100	0
Trygghamna 4	1	78.263	13.684	30.07.19	3	1	0	12	4	75	25
Marvagen 1	1	77.776	13.761	31.07.19	1	0	1	119	16	88	12
Marvagen 2	1	77.815	13.802	31.07.19	2	0	1	74	4	95	5

N_i – number of individuals; N_s – number of samples collected, G.o – *G. oceanicus*, G.s – *G. setosus*; FI – fast ice, LCW – local cold water and AW – Atlantic water

species. The thermophilic *G. oceanicus* will likely continue its spread and gradually strengthen its dominance in already occupied areas, while cold-water *G. setosus* will simultaneously retreat toward the northeast coasts of Svalbard or the innermost parts of glacial bays where arctic conditions still prevail. On the other hand, the temperature rise will result in more intensive fresh-water runoff from the retreating glaciers and glacier-fed rivers and streams (Węśławski *et al.* 2011). The *G. setosus* population will likely benefit from a freshening of coastal waters and may increase in habitats in proximity to brackish lagoons and estuaries.

Potentially, the already established population of *G. oceanicus* may be further fed by specimens advected with Atlantic waters from the Nordic Seas. The poleward distribution shifts of boreal species due to the increasing influx of Atlantic waters into the Arctic (Polyakov *et al.* 2020) were observed for biota including pelagic amphipods (Kraft *et al.* 2013), and benthic mollusc *Mytilus edulis* (Berge *et al.* 2005). For the species that lack a pelagic life-stage such as *G. oceanicus*, rafting on floating objects may be an important way of dispersal. Detached macroalgae seem to be a particularly suitable floating substrate for *Gammarus* due to their structural complexity and high nutritional value for grazers (Kießling *et al.* 2015). Observations made around Iceland suggested that many species of intertidal crustaceans, including *Gammarus* spp., may use floating seaweed as a means of dispersal (Ingólfsson 1995). On the other

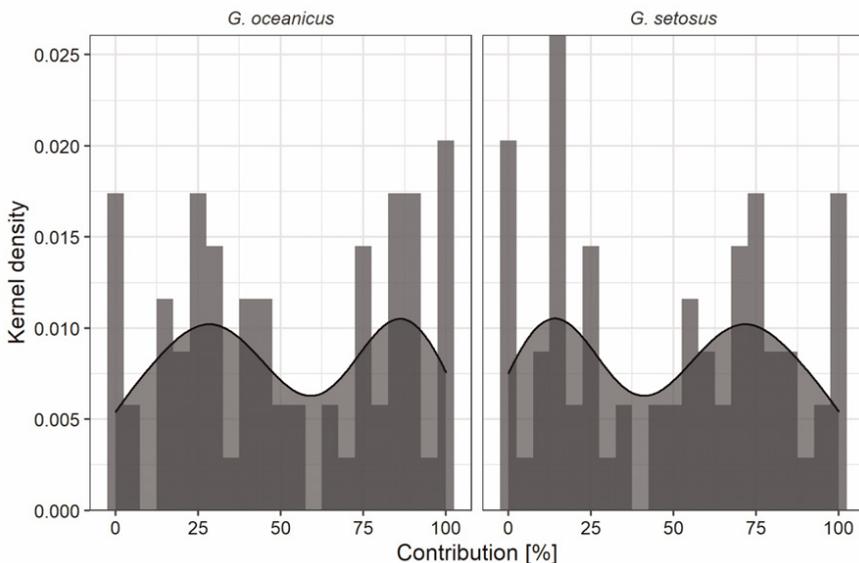


Fig. 2. Histogram and kernel density curve of the contribution of *Gammarus* species in the same microhabitat in 2019 (data from single sample, average area 400 cm², one large stone). Contribution – $(N / (N_{G.o} + N_{G.s})) * 100\%$, where N – number of individuals species, G.o – *Gammarus oceanicus*, G.s – *Gammarus setosus*.

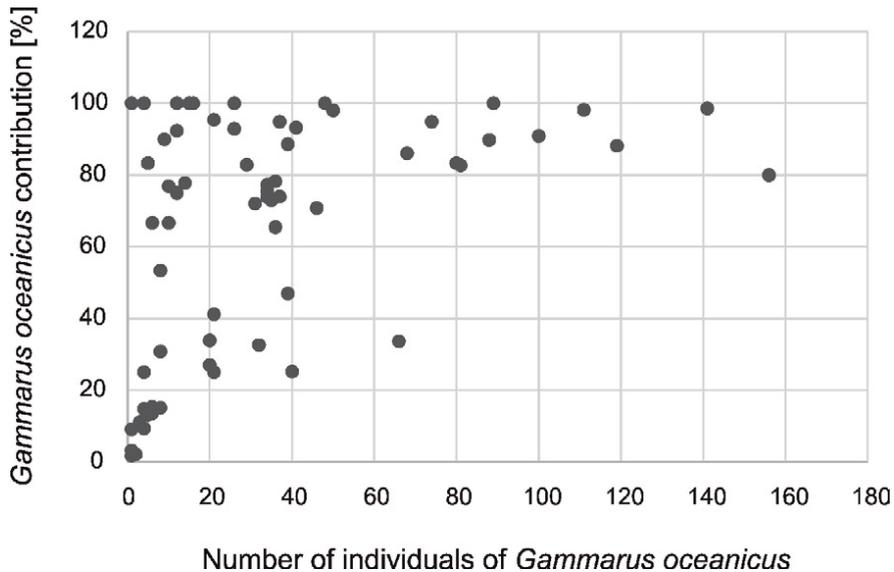


Fig. 3. The relation between density and species co-occurrence based on single sample. Contribution – $(N_{G.o} / (n_{G.o} + n_{G.s})) * 100\%$, where N – number of individuals, $G.o$ – *Gammarus oceanicus*, $G.s$ – *Gammarus setosus*.

hand, a strong decrease in the abundance of rafting organisms with increasing distance from the shore was reported (Ingólfsson 1995). Taking into consideration the distance between North Norway and Spitsbergen (>900 km) and challenging sea conditions in this region that may accelerate the disintegration of floating algal clumps, effective mass transport of *G. oceanicus* with drifting macroalgae seems low probable. It is known that the transport of boreal taxa may also occur with the vast amount of plastic litter transported by ocean currents to the Arctic (Csapó *et al.* 2021). Plastics are particularly persistent, remain positively buoyant for long periods, and may transport associated organisms over extensive distances (Kiessling *et al.* 2015; Węśławski and Kotwicki 2018; Kotwicki *et al.* 2021). This type of raft, however, suits organisms that can survive on plastic firmly attached to its smooth surface and acquire food from surrounding waters (such as sessile suspension-feeding barnacles or mollusc), while it may be of limited use for species that are unable to settle on this kind of substrate and are macrophagous, such as *G. oceanicus* (Kiessling *et al.* 2015). Indeed, a recent (2017–2019) inspection of plastic litter beached on the West Spitsbergen coast and in Isfjorden did not reveal the presence of *Gammarus* spp. (Kotwicki *et al.* 2021). Better knowledge on abundance and dispersal trajectories of biotic and abiotic floating items and the species capacity to survive on a different type of substrate is required to correctly assess the efficiency of long-distance rafting dispersal of *G. oceanicus*. However, considering the issues described above it appears that advection from the south likely occurs only sporadically. This is also supported by the fact that

G. oceanicus was not found on Bjornøya, an island halfway between Svalbard and the Norwegian mainland (Węśławski *et al.* 1997).

The overlapping occurrence of the two *Gammarus* species dwelling in Spitsbergen littoral is probably forced by and limited availability of preferred habitat and predation pressure. Predation pressure on *Gammarus* species is usually very strong. Because of their size, poor mobility, density, and energetic value they are preyed upon by a variety of animals (Macneil *et al.* 1999; Gerhardt *et al.* 2011), in the Arctic mainly by seals, seabirds (Lydersen 1989), and numerous species of small and medium-sized coastal fish (Węśławski and Kuliński 1989). In consequence, *G. setosus* and *G. oceanicus* inhabit Arctic intertidal zone living, almost exclusively, under loose stones, which offer protection from carnivores (Steele and Steele 1974; Tzvetkova 1975; Węśławski 1994). Strong predation pressure may result in the coexistence of closely related species (Simberloff 1982). Experiments on freshwater amphipods showed that the predator presence increases the aggregation level of prey gammarids (Jermacz *et al.* 2017). Habitats preferred by *Gammarus* on Svalbard are sheltered skjerra, covered with large clumps of *Fucus* L. and loose stones, which conceal hiding places (Węśławski 1994; Ikko and Luyubina 2010). Such habitats have limited range (*c.a.* 16% of the whole coastline) and may be separated by the kilometre-long stretches of ‘unusable’ shores: gravel and stony beaches (dynamic and unstable), muddy tidal flats (turbid and very dynamic), and rocky coasts, which provide little shelter as they are mostly barren or covered by tiny filamentous algae (Węśławski *et al.* 1993). Moreover, the available space is also vertically limited by the low amplitude of tides on Svalbard (1–1.5 m). In the extensive intertidal zones of Newfoundland or Iceland (with tides of several meters) *G. oceanicus* and *G. setosus* are known to be spatially segregated by the tide levels, the former being usually noted in low intertidal and shallow subtidal, and the latter occurring generally above the zone populated by *G. oceanicus* in intertidal (Ingólfsson 1977).

Both species are similar in size, feeding behaviour, and reproduction time (Węśławski and Legeżyńska 2002), which suggests strong competitive tensions between them in a spatially limited habitat of the Spitsbergen coast. Indeed, our data document a clear separation of the two species on the scale of a single sample. Only at three sampling locations, both species were equally abundant. Partly, it can be explained by environmental patchiness and preferences of each species, but it also strongly suggests an antagonistic relationship between the species. Our field observations agree with the results of experiments performed on two species of freshwater gammarids *Dikerogammarus villosus* (Sovinsky, 1894) and *Pontogammarus robustoides* (G.O. Sars, 1894) (Jermacz *et al.* 2017). Both species, when choosing shelters, preferred those already occupied by conspecific and avoided aggregating with heterospecific. The authors commented that antagonistic reaction toward the other species may contribute to their separation at a scale of microhabitat natural environment and in consequence

decrease the risk of competition between them. Further experimental studies are needed to better understand mechanisms regulating interspecific relations at a microhabitat scale.

In conclusion, the distribution of the two species reflects their environmental preferences. Both species, however, can persist in suboptimal due to the wide range of environmental tolerance. The ongoing warming will likely enable further expansion of the boreal species of *G. oceanicus* in the Arctic. In Svalbard, this will result from a gradual advance of the existing population, since an influx of specimens from the Nordic seas seems unlikely. The local, arctic species *G. setosus* will remain a dominant species in cold-water areas such as the inner fjords and the northeast coast of Svalbard. This species may benefit from the freshening of coastal waters and find suitable habitats in lagoons and outlets of rivers and streams fed by glacier meltwater. It seems that the two species, due to their wide range of environmental tolerance and the patchiness of littoral habitats, will continue their sympatric occurrence on the West Spitsbergen coast. To understand mechanisms regulating co-occurrence of the two species on a small spatial scale further field studies and laboratory experiments are required. The observations so far indicate that on the microhabitat scale the two congeners tend to avoid each other.

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References

- ACIA. 2005. *Impacts of a warming Arctic: Arctic Climate Impact Assessment*. Cambridge University Press, New York.
- BEERMANN J. and FRANKE H.D. 2012. Differences in resource utilization and behaviour between coexisting *Jassa* species (Crustacea, Amphipoda). *Marine Biology* 159: 951–957.
- BERGE J., HEGGLAND K., LØNNE O.J., COTTIER F., HOP H., GABRIELSEN G.W., NØTTESTAD L. and MISUND O.A. 2015. First records of Atlantic Mackerel (*Scomber scombrus*) from the Svalbard Archipelago, Norway, with possible explanations for the extension of its distribution. *Arctic* 68: 54–61.
- BERGE J., JOHNSEN G., NILSEN F., GULLIKSEN B. and SLAGSTAD D. 2005. Ocean temperature oscillations enable reappearance of blue mussels *Mytilus edulis* in Svalbard after a 1000 year absence. *Marine Ecology Progress Series* 303: 167–175.
- BOER den P.J. 1980. Exclusion or coexistence and the taxonomic or ecological relationship between species. *Netherlands Journal of Zoology* 30: 278–306.
- BURROWS M.T., BATES A.E., COSTELLO M.J., EDWARDS M., EDGAR G.J., FOX C.J., HALPERN B. S., HIDDINK J.G., PINSKY M.L., BATT R.D., MOLINOS J.G., PAYNE B.L., SCHOEMAN D.S.,

- STUART-SMITH R.D. and POŁOZANSKA E.S. 2019. Ocean community warming responses explained by thermal affinities and temperature gradients. *Nature Climate Change* 9: 959–963.
- COTTIER F., SKOGSETH R., DAVID D. and BERGE J. 2019. Temperature time-series in Svalbard fjords. A contribution from the integrated marine observatory partnership (iMOP). In: E. Orr, G. Hansen, H. Lappalainen, C. Hübner and H. Lihavainen (eds) *Svalbard Integrated Arctic Earth Observing System*. SESS report 2018, Longyearbyen: 108–118.
- CROKER R.A. 1967. Niche diversity in five sympatric species of intertidal amphipods (Crustacea; Haustroidae). *Ecological Monograph* 37: 174–200.
- CSAPÓ H.K., GRABOWSKI M. and WĘŚLAWSKI J.M. 2021. Coming home — boreal ecosystem claims Atlantic sector of the Arctic. *Science of the Total Environment* 771: 144817.
- GERHARDT A., BLOOR M. and MILLS C.L. 2011. *Gammarus*: important taxon in freshwater and marine changing environments. *International Journal of Zoology* 2011: 524276.
- GERLAND S., PAVLOVA O., DIVINE D., NEGREL J., DAHLKE S., JOHANSSON A.M., MATURILLI M. and SEMMLING M. 2020. Long-term monitoring of landfast sea ice extent and thickness in Kongsfjorden, and related applications (FastIce). In: F. Van den Heuvel, C. Hübner, M. Błaszczuk, M. Heimann and H. Lihavainen (eds) *Svalbard Integrated Arctic Earth Observing System*. SESS report 2019, Longyearbyen: 160–167.
- GRABOWSKI M., JABŁOŃSKA A., WEYDMANN-ZWOLICKA A., GANTSEVICH M., STRELKOV P., SKAZINA M. and WĘŚLAWSKI J.M. 2019. Contrasting molecular diversity and demography patterns in two intertidal amphipod crustaceans reflect Atlantification of High Arctic. *Marine Biology* 166: 155.
- GRABOWSKI M., KONOPACKA A., JAŹDŻEWSKI, K. and JANOWSKA E. 2006. Invasions of alien gammarid species and retreat of natives in the Vistula Lagoon (Baltic Sea, Poland). *Helgoland Marine Research* 60: 90–97.
- GUERRA-GARCIA J.M., BAEZA-ROJANO E., CABEZAS M.P. and GARCIA-GOMEZ J.C. 2011. Vertical distribution and seasonality of peracarid crustaceans associated with intertidal macroalgae. *Journal Sea Research* 65: 256–264.
- HERVÉ M. 2021. RVAideMemoire: Testing and Plotting Procedures for Biostatistics. <https://cran.r-project.org/web/packages/RVAideMemoire/index.html>
- HILL C. and ELMGREN P. 1987. Vertical distribution in the sediment in the co-occurring benthic amphipods *Pontoporeia affinis* and *P. femorata*. *Oikos* 49: 221–229.
- IKKO N.V. and LYUBINA O.S. 2010. Distribution of the genus *Gammarus* (Crustacea, Amphipoda) along the coast of Arctic fjords as an indicator of prevailing environmental conditions. *Doklady Biological Sciences* 431: 149–15.
- INGÓLFSSON A. 1977. Distribution and habitat of some intertidal amphipods in Iceland. *Acta Naturalia Islandica* 25: 1–28.
- INGÓLFSSON A. 1995. Dynamics of macrofaunal communities of floating seaweed clumps off western Iceland: a study of patches on the surface of the sea. *Journal of Experimental Marine Biology and Ecology* 231: 119–137.
- JERMACZ Ł., ANDRZEJCZAK J., ARCZYŃSKA E., ZIELSKA J. and KOBAC J. 2017. An enemy of your enemy is your friend: Impact of predators on aggregation behavior of gammarids. *Ethology* 123: 627–639.
- KIESSLING T., GUTOW L. and THIEL M. 2015. Marine litter as habitat and dispersal vector. In: M. Bergmann, L. Gutow and M. Klages (eds) *Marine anthropogenic litter*. Springer, Cham.
- KOLDING S. and FENCHEL T.M. 1979. Coexistence and life cycle characteristics of five species of amphipod genus *Gammarus*. *Oikos* 33: 323–327.
- KORPINEN S. and WESWTERBOM M. 2010. Microhabitat segregation of the amphipod genus *Gammarus* (Crustacea, Amphipoda) in the Northern Baltic Sea. *Marine Biology* 157: 361–370.
- KOTTA J., ORAV-KOTTA H., JÄNES H., HUMMEL H., ARVANITIDIS C., VAN AVESAATH P., BACHELET G., BENEDETTI-CECCHI L., BOJANIĆ N., COMO S., COPPA S., COUGHLAN J.,

- CROWE T., DAL BELLO M., DEGRAER S., DE LA PENNA J.A.J., FERNANDES DE MATOS V.K., ESPINOSA F., FAULWETTER S., FROST M., GUINDA X., JANKOWSKA E., JOURDE J., KERCKHOF F., LAVESQUE N., LECLERC J.-C., MAGNI P., PAVLOUDI C., PEDROTTI M.L., PELEG O., PÉREZ-RUZAF A., PUENTE A., RIBEIRO P., RILOV G., ROUSOU M., RUGINIS T., SILVA T., SIMON N., SOUSA-PINTO I., TRONCOSO J., WARZOCCHA J. and WĘSŁAWSKI J.M. 2016. Essence of the patterns of cover and richness of intertidal hard bottom communities: a pan-European study. *Journal of the Marine Biological Association of the United Kingdom* 97: 525–538.
- KOTWICKI L., WĘSŁAWSKI J.M., WŁODARSKA-KOWALCZUK M., MAZURKIEWICZ M., WENNE R., ZBAWICKA M., MINCHIN D. and OLENIN S. 2021. The re-appearance of the *Mytilus* spp. complex in Svalbard, Arctic, during the Holocene: The case for an arrival by anthropogenic flotsam. *Global and Planetary Change* 202: 103502.
- KRAFT A., NÖTHIG E.M., BAUERFEIND E., WILDISH D.J., POHLE G.W., BATHMANN U.V., BESZCZYŃSKA-MÖLLER A. and KLAGES M. 2013. First evidence of reproductive success in a southern invader indicates possible community shifts among Arctic zooplankton. *Marine Ecology Progress Series* 493: 291–296.
- LANCELOTTI D.A. and TRUCCO R.G. 1993. Distribution patterns and coexistence of six species of the amphipod genus *Hyale*. *Marine Ecology Progress Series* 93: 131–141.
- LYDERSEN C., GJERTZ I. and WĘSŁAWSKI J.M. 1989. Stomach contents of autumn feeding marine invertebrates from Hornsund, Svalbard. *Polar Records* 25: 107–114.
- MACNEIL C., DICK J.T.A. and ELWOOD R.W. 1999. The dynamics of predation on *Gammarus* spp. (Crustacea: Amphipoda). *Biological Reviews* 74: 375–395.
- NILSEN F., COTTIER F., SKOGSETH R. and MATSSON S. 2008. Fjord–shelf exchanges controlled by ice and brine production: The interannual variation of Atlantic Water in Isfjorden, Svalbard. *Continental Shelf Research* 28: 1838–1853.
- PIECHURA J. and WALCZOWSKI W. 2009. Warming of the West Spitsbergen Current and sea ice north of Svalbard. *Oceanologia* 51: 147–164.
- POLYAKOV I.V., ALKIRE M.B., BLUHM B.A., BROWN K.A., CARMACK E.C., CHIERICI M., DANIELSON S.L., ELLINGSEN I., ERSHOVA E.A., GÅRDFELDT K., INGVALDSEN R. B., PNYUSHKOV A.V., SLAGSTAD D. and WASSMANN P. 2020. Borealization of the Arctic Ocean in response to anomalous advection from Sub-Arctic Seas. *Frontiers in Marine Science* 7: 491.
- R CORE TEAM. 2021. R: A language and environment for statistical computing. <https://www.r-project.org>
- SIMBERLOFF D. 1982. The status of competition theory in ecology. *Annales Zoologici Fennici* 19: 241–253.
- SKADSHEIM A. 1983. The ecology of intertidal amphipods in the Oslofjord. Distribution and responses to physical factors. *Crustaceana* 44: 225–244.
- SKOGSETH J., OLIVIER L.L.A., NILSEN F., FALCK E., RASER N., TVERBERG V., LEDANG A.B., VADER A., JONASSEN M.O., SØREIDE J., COTTIER F., BERGE J., IVANOV B.V. and FALK-PETERSEN S. 2020. Variability and decadal trends in the Isfjorden (Svalbard) ocean climate and circulation – An indicator for climate change in the European Arctic. *Progress in Oceanography* 187: 102394.
- SØREIDE J.E., PITUSI V., VADER A., DAMSGÅRD B., NILSEN F., SKOGSETH R., POSTE A., BAILEY A., KOVACS K. M., LYDERSEN C., GERLAND S., DESCAMPS S., STRØM H.; RENAUD P. E., CHRISTENSEN G., ARVENS M.P., MOISEEV D., SINGH R. K., BÉLANGER S., ELSTER J., URBAŃSKI J., MOSKALIK M., WIKTOR J. and WĘSŁAWSKI J.M. 2020. Environmental status of Svalbard coastal waters: coastscapes and focal ecosystem components (SvalCoast). In: M. Moreno-Ibáñez, J.O. Hagen, C. Hübner, H. Lihavainen and A. Zaborska (eds) *Svalbard Integrated Arctic Earth Observing System*. SESS report 2020, Longyearbyen: 142–175.
- STEELE D.H. and STEELE V.J. 1974. The biology of *Gammarus* (Crustacea, Amphipoda) in the north-western Atlantic. VIII. Geographic distribution of the northern species. *Canadian Journal of Zoology* 52: 1115–1120.

- STEELE V.J. and STEELE D.H. 1970. The biology of *Gammarus* (Crustacea, Amphipoda) in the northwestern Atlantic. II. *Gammarus setosus* Dementieva. *Canadian Journal of Zoology* 48: 659–671.
- STEELE V.J. and STEELE D.H. 1972. The biology of *Gammarus* (Crustacea, Amphipoda) in the north-western Atlantic. V. *Gammarus oceanicus* Segerstråle. *Canadian Journal of Zoology* 50: 801–813.
- THYRRING J., BLICHER M.E., SØRENSEN J.G., WEGEBERG S. and SEJR M.K. 2017. Rising air temperatures will increase intertidal mussel abundance in the Arctic. *Marine Ecology Progress Series* 584: 91–104.
- TZVETKOVA N.L. 1975. *Pribejnye gammaridy severnyh i dal'nevostochnyh morei SSSR i sopredel'nyh vod*. Leningrad University, Leningrad.
- URBAŃSKI J.A. and LITWICKA D. 2021. Accelerated decline of Svalbard coasts fast ice as a result of climate change. *Cryosphere Discuss*: 1–15.
- VADER W. and TANDBERG A.H. 2019. Gammarid amphipods (Crustacea) in Norway, with a key to the species. *Fauna norvegica* 39: 12–25.
- WALCZOWSKI W., PIECHURA J., GOSZCZKO I. and WIECZOREK P. 2012. Changes in Atlantic water properties: an important factor in the European Arctic marine climate. *ICES Journal of Marine Science* 69: 864–869.
- WĘSŁAWSKI J.M. 1994. *Gammarus* (Crustacea, Amphipoda) from Svalbard and Franz Josef Land. Distribution and density. *Sarsia* 79: 145–150.
- WĘSŁAWSKI J.M. and KOTWICKI L. 2018. Macro-plastic litter, a new vector for boreal species dispersal on Svalbard. *Polish Polar Research* 39: 165–174.
- WĘSŁAWSKI J.M. and KULIŃSKI W. 1989. Notes on fishes in Hornsund fjord area (Spitsbergen). *Polish Polar Research* 10: 241–250.
- WĘSŁAWSKI J.M. and LEGEŻYŃSKA J. 2002. Life cycles of some Arctic amphipods. *Polish Polar Research* 23: 253–264.
- WĘSŁAWSKI J.M., DRAGAŃSKA-DEJA K., LEGEŻYŃSKA J. and WALCZOWSKI W. 2018. Range extension of a boreal amphipod *Gammarus oceanicus* in the warming Arctic. *Ecology and Evolution* 8: 7634–7632.
- WĘSŁAWSKI J.M., KENDALL M.A., WŁODARSKA-KOLWALCZUK M., IKEN K., KĘDRA M., LEGEŻYŃSKA J. and SEJR M.K. 2011. Climate change effects on Arctic fjord and coastal macrobenthic diversity—observations and predictions. *Marine Biodiversity* 41: 71–85.
- WĘSŁAWSKI J.M., LEGEŻYŃSKA J. and WŁODARSKA-KOWALCZUK M. 2020. Will shrinking body size and increasing species diversity of crustaceans follow the warming of the Arctic littoral? *Ecology and Evolution* 10: 10305–10313.
- WĘSŁAWSKI J.M., WIKTOR J., ZAJĄCZKOWSKI M. and SWERPEL S. 1993. Intertidal zone of Svalbard. Macroorganism distribution and biomass. *Polar Biology* 13: 73–79.
- WĘSŁAWSKI J.M., ZAJĄCZKOWSKI M., WIKTOR J. and SZYMELFENIG M. 1997. Intertidal zone of Svalbard 3. Littoral of a subarctic oceanic island, Bjornøya. *Polar Biology* 18: 45–52.
- WILLIS K., COTTIER F., KWASNIEWSKI S., WOLD A. and FALK PETERSEN S. 2006. The influence of advection on zooplankton community composition in an Arctic fjord (Kongsfjorden, Svalbard). *Journal of Marine Systems* 61: 39–54.

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