

Will shrinking body size and increasing species diversity of crustaceans follow the Warming of the Arctic littoral ?

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Abstract

Over thirty species of littoral marine Gammaridea occur along the coasts of the North Atlantic. From one to several species can coexist in a single region. There is an evident, inverse relationship between egg incubation time and temperature (from 14 to > 120 days) and consequent trends in the size of the animals on reaching maturity (from 5 mm in warmer waters to 30 mm in the coldest ones) and in lifespan (from < 6 months to > 5 years). Littoral gammarids are a good example of the shrinking size effect of increasing temperatures and size-related species diversity. In large species the annual cohorts of the population (3 to 5 annual size groups) functionally replace the adults of smaller species. The ongoing warming of the European Arctic seas may extend the distribution limits of boreal species so that more *Gammarus* species may appear on northern coasts hitherto occupied by just one or at most two species.

Introduction

Temperature is widely regarded as a key factor both directly and indirectly responsible for the diversity of marine fauna. The usual patterns show species richness increasing from cold towards warmer regions among the majority of taxa, at least in the Palearctic and Nearctic (Gaston 1998, 2000). In poikilotherms, temperature directly controls metabolism and growth rates, and hence, the size of an organism. Species diversity is usually negatively correlated with the size of an organism, that was well documented on terrestrial insects (Siemann et al. 1996). That is why the temperature increase due to global warming is likely to cause a change in average individual size, or selection towards smaller species in communities (Atkinson & Sible 1997). Such a pattern has already been demonstrated in pelagic Copepoda (Beaugrand et al. 2000), but it is not yet universal in benthic communities (Mazurkiewicz et al. 2020). The blurred size pattern among soft-bottom benthos is due to the dominance of polychaete worms and bivalves – two groups in which linear growth is difficult to assess. Peracaridan crustaceans, on the other hand, are likely to be the best model taxon for studies of temperature-related size changes. Peracaridans have no larval stage, and juveniles grow throughout life, with the successive moults clearly demarcating the increments. Egg incubation time, egg size and gammarid female size are inversely related to temperature (see the review in Steele & Steele 1975). In addition, not only low temperatures but also oxygen levels are responsible for the large size of cold-water Crustacea, a phenomenon known as “polar gigantism” (Chapelle & Peck 1999).

Atlantic sector of the Arctic is warming very fast (ACIA 2005), mainly due to the increasing advection of Atlantic waters (Walczowski et al. 2012) that brings boreal species North of their previous limits of distribution (Berge et al 2005, Beuchel et al. 2006, Fleisher et al 2007, Weslawski et al. 2018).

Here, we hypothesize that a larger body size (associated with perennial longevity) in northern littoral *Gammarus* populations reduces the possibility of sibling species occurring sympatrically, as observed at present in warmer waters. We explore this by comparing diversity and size in *Gammarus* populations inhabiting

rocky North Atlantic coasts across latitudes from 45 to 81°N and water temperatures from -1.8 to 25°C. We expect that present-day patterns of distribution are likely to change, as the temperature increase will tend to shorten gammarid life cycles in the Subarctic. Such a phenomenon has already been observed in pelagic Crustacea, where the same species – *Calanus finmarchicus* – may produce from one generation in cold water to three in temperate seas per year, depending on the ambient temperature (Irigoien et al. 2000).

Material and methods

The original material comes from the unpublished archive of the first author, who sampled littoral *Gammarus* species in the Gulf of Gdańsk (Baltic Sea, 54°N) and Hornsund fjord (Svalbard Archipelago, 77°N) in 1979–1982. They were collected with a hand-net on the shore, at 0–1 m depth, from under stones and algae. The animals were measured from the tip of the head to the tip of telson, excluding spines. Formalin-preserved specimens were wet-weighed after having been blotted on filter paper. The temperatures for the different localities were obtained from the cited references or meteorological data currently available on the Internet. Some of the materials collected by the first author were presented in the form of an unpublished manuscript – an MSc thesis at the University of Gdańsk (Wolska 1983).

Summer minimal temperature for the geographic region was taken as a critical value for marine poikilotherms (Golikov et al. 1990). The occurrence of the sympatric species was assessed for the region (sea) from the literature cited, species names were checked after Bellan-Santini and Costello (2001).

Results and discussion

At least thirty sibling species from *Gammarus* and other species from closely related genera (*Marinogammarus*, *Pontogammarus*, *Dikerogammarus* etc.) occur in the intertidal of both the eastern and western North Atlantic (Table 1). Their size at maturity ranges from 4 to 52 mm and is related to lifespan and ambient temperature (Fig. 1). Length frequencies in the summer samples of the Arctic population of two sympatric sibling *Gammarus* species indicate that there are three annual cohorts, or fourteen size groups (2 mm intervals) (Fig. 2). Compared to the Arctic, the temperate water population (Baltic) of the same species in summer (after the death of the winter cohort and juvenile release in spring) has a cohort of one age (length 6–15 mm) that corresponds to five size groups (2 mm intervals). The summer length frequency of the large (40 mm) species in the Arctic gives up to twenty size groups (2 mm intervals).

The growth in two very different populations of the same species (*G. oceanicus* from the Baltic and Arctic, summer temperatures plus 20 °C and 4 °C respectively) is similar, although the cold water population lives longer and grows to greater lengths (Fig. 3). A cold water individual may not reach maturity in the first year of its life, but will grow continuously for the next one or two years, ultimately attaining a large size.

If the life cycle is to be completed within a year or less, the critical phenomenon is the egg incubation time (Table 1). The relationship of this time to ambient temperature has been studied many times in poikilotherms like fish and crustaceans, as well as specifically in the genus *Gammarus* (Steele and Steele 1975, Whiteley et al. 2011). Incubation in *Gammarus setosus* or *G. wilkitzkii* lasts 120 and more days in cold, Subarctic – Arctic waters, at year round temperatures < 2°C (Steele & Steele 1974, Weslawski & Legeżyńska 2002). In the Black Sea or southern Baltic, by contrast, summer generations of *Gammarus inaequicauda* and *G. salinus* incubate eggs at temperatures > 20°C in less than 20 days (Jażdżewski 1970). The ability to shorten the egg incubation period is probably governed by temperature only (as observed in *Calanus* copepods – Irigoien et al. 2000 or pelagic hyperids – Koszteyn et al. 1995). Other factors controlling the size of these invertebrates are the availability and quality of food and/or oxygen saturation (Chapelle & Peck 1999). Adults of *Gammarus* species are omnivores (Tzvetkova 1975) and food availability is not a limiting factor in the littoral (plant detritus, meiofauna and microorganisms are plentiful; Weslawski et al. 1993). The oxygen concentration in coastal waters is always high, or even supersaturated, as there the water dynamics is the highest. *Gammarus* species have adequate food resources, a high level of oxygen and an appropriate range of salinity. The only limiting factor is suitable microhabitat, i.e. stones or crevices under which they can hide from predators. Gammarids are a preferred dietary constituent of coastal fish in the Baltic (MacNeil et al. 1999), and of fish, seabirds and seals on Svalbard (Weslawski & Kulinski 1989, Lydersen et al. 1994). The

interstices among loose stones, providing adequate shelter, are quickly filled when some hundreds of animals are trying to hide beneath one of them (Weslawski 1994). It is the occupation of this microhabitat by large, local species that is the likely factor preventing boreal, eurytopic species from successfully colonizing the North. Ca 300 large specimens (mean length 20 mm) or 2000 small ones (mean length 5 mm) can conceal themselves under a stone 400 cm² in area; this corresponds with the average densities reported for Arctic localities (300-500/m²) (Weslawski 1994) and for temperate sites, where the number of small gammarid species can exceed 10 000/m² (Tzvetkova 1975).

Niche selection and competition was described as a critical factor for the new species colonisation in littoral amphipods (Piscart et al. 2008, Kotta et al. 2013).

The majority of marine littoral gammarids display a very wide tolerance to salinity and temperature (Tzvetkova 1975). In the North Atlantic intertidal, many different species occur in the temperature range between 0°C in winter to > 20°C in summer. Consequently, most of the species listed in Table 1, have a potentially very wide geographical distribution. If temperature were the only factor limiting their occurrence, the North Atlantic coast would be divided into a narrow zone with cold stenothermic *Gammarus* species (*Gammarus wilkitzkii* and *G. setosus*), with the rest of the area supporting the other, eurytopic species. In actual fact, however, the littoral gammarids are spatially more limited, and the number of species corresponds inversely to their size and life length (Table 1, Fig. 1). In the Arctic, where the two large, cold-water species (*G. wilkitzkii* and *G. setosus*) co-occur, there is almost no sympatric occurrence, as *G. wilkitzkii* is an ice-associated species and *G. setosus* is a littoral species. However, when the ice melts in coastal waters, *G. wilkitzkii* seeks the same shelter as its littoral congener (Weslawski 1994, Polterman 1997). Another example of regions where two large species occur together is Canada and Svalbard, where the local cold-water *G. setosus* is confronted with the boreal *G. oceanicus*. On Newfoundland, the coasts of which have an extensive tidal range from three to twelve metres, *G. setosus* was recorded higher up on the shore and *G. oceanicus* lower down (Steele & Steele 1974). On Spitsbergen, the two species co-exist recently, as the *G. oceanicus* is colonising the area after the glacial retreat (Grabowski et al. 2019).

In the littoral, when a species is large, there are many size groups that act as separate ecological units: size variations in gammarids lead to differences in mobility, food and behaviour (see Weslawski et al. 2010). All the available space is occupied and the number of true species is limited – to two, according to published observations. In areas where species are small, there are fewer size groups and more species can co-exist (up to fourteen in a region like the Mediterranean Sea, Table 1).

The sympatric occurrence discussed here is considering the regional scale (gamma diversity). The co-occurrence on a small scale of one sample, alpha diversity is difficult to assess, as there are very few data. In the Baltic, where 9 local plus four alien (man introduced) species occur, the actual occurrence of three to five species in one spot was confirmed (Jażdżewski 1970, own observations).

As the size of gammarids is so closely related to ambient temperature, we may speculate that with increasing coastal temperatures in the Arctic, littoral gammarids will complete their life cycle at a smaller size, which will create opportunities for the area's colonization by southern species. This will be a direct effect not of temperature (those eurytopic species are already capable of living there) but of the favourable size structure of competitors.

In summary, two phenomena are well documented in littoral *Gammarus* species. One is the direct relationship of temperature to lifespan and the size of an adult animal: at warmer temperatures, all known species grow faster and reach maturity at a smaller size. The other is the low number of sympatric species in areas where large species occur, and the high number of such species where the animals are small. From these two observations we can infer that climate change may shift the boreal species northwards, where competition from large species will be reduced as the temperature rises.

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Data availability statement

All data presented in this paper are available through the project web page ACCES <https://www.iopan.pl/projects/Acces/> (operational since June 2020).

REFERENCES

- ACIA (2005). Impacts of a warming Arctic: Arctic Climate Impact Assessment. Cambridge University Press, New York.
- Atkinson D., Sibly R.M. (1997). Why are organisms usually bigger in colder environments ? Making sense of life history puzzle. *TREE*12, 235- 239
- Beaugrand G., Ibanez F., Reid PC (2000). Spatial seasonal and long term fluctuations of plankton in relation to hydroclimatic features in the English Channel, Celtic Sea and Bay of Biscay. *Marine Ecology Progress Series* 200, 93-102
- Bellan-Santini, D., & Costello, M.J. (2001). Amphipoda. in: Costello, M.J. et al. (Ed.) (2001). *European register of marine species: a check-list of the marine species in Europe and a bibliography of guides to their identification. Collection Patrimoines Naturels* 50: pp. 295-308.
- Berge J., Johnsen G., Nilsen F., Gulliksen B., & 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.
- Beuchel F., Gulliksen B., & Carroll M.L. (2006). Long-term patterns of rocky bottom macrobenthic community structure in an Arctic fjord (Kongsfjorden, Svalbard) in relation to climate variability (1980–2003). *Journal of Marine Systems* , 63, 35–48.
- Bousfield E.L. (1969). New records of Gammarus (Crustacea: Amphipoda) from the Middle Atlantic Region, *Chesapeake Science* 10 (1):1-17.
- Chapelle G., Peck L.S. (1999). Polar gigantism dictated by oxygen availability. *Nature* 399, 114-115
- Dobrzycka-Krahel, A. Kendzierska, H. Szaniawska, A. (2013). Ponto-Caspian gammarids – new species in the Gulf of Gdańsk (Southern Baltic Sea), *Journal of Ecology and Health* 17(3), 110-114.
- Fleischer D., Schaber M., & Piepenburg D. (2007). Atlantic snake pipefish (*Entelurus aequoreus*) extends its northward distribution range to Svalbard (Arctic Ocean). *Polar Biology* , 30, 1359–1362.
- Fredette T.J., R. J. Diaz. (1986). Life history of *Gammarus mucronatus* Say (Amphipoda: Gammaridae) in warm temperate estuarine habitats, York River, Virginia, *Journal of Crustacean Biology*6(1): 57-78.
- Gable M.F., R. A. Croker, (1977). The Salt Marsh Amphipod, *Gammarus palustris* Bousfield, 1969 at the Northern Limit of its Distribution I. Ecology and Life Cycle. *Estuarine and Coastal Marine Sciences* 5: 123-134.
- Gaston K.J. (1998). Species- range size distributions: products of speciation, extinction and transformation. *Pr. Trans. Royal Soc.B*, 353
- Gaston K.J. (2000). Global patterns of biodiversity. *Nature* 405, 220-227
- Golikov A.N., Dolgolenko M.A., Maximovich N.N., Scarlato O.A. (1990). Theoretical approaches to marine biogeography. *Marine Ecology Progress Series* 63; 289- 301
- Grabowski M., Jabłońska A., Weydmann-Zwolicka A., Gantsevich M., Strelkov P., Skazina M., Węślawski J.M. (2019). Contrasting molecular diversity and demography patterns in two intertidal amphipod crustaceans reflect Atlantification of High Arctic. *Marine Biology* 166, 155

- Greze I. 1985, , Higher Crustacea, Fauna Ukrainy, 26, Naukova Dumka, Kijev,
- Grintsov V.A. (2009). A New Amphipod Species *Echinogammarus Karadagiensis* Sp. N. (Amphipoda, Gammaridae) From Crimean Coasts (Black Sea, Ukraine), *Vestnik Zoologii*, 43(2): 23-26
- Grintsov, V.A. (2016). Dynamics of population structure of two species of Echinogammarus genus (Gammaridae, Amphipoda) from Laspi Bay (Crimea, Black Sea), *Marine Biological Journal* 1 No 3: 22-26.
- Gurjanova E.P. (1951). Amphipoda Gammaridea from the seas of the USSR and vicinity. *Opredeliteli Faune SSSR* pp. 1–1029. Zoologicheskii Institut Akademii Nauk SSSR.
- Irgoien X., Head R.M., Cummings D., Harbour D. (2000). Feeding selectivity and egg production of *Calanus helgolandicus* in the English Chanel. *Limnology and Oceanography* 45, 44-54
- Jażdżewski K. (1970). Biology of Crustacea Malacostraca in the Bay of Puck, Polish Baltic Sea. *Zoological Poloniae* 20, 423–480.
- Koszteyn J., Timofeev S., Weslawski J.M., Malinga B. (1995). Size structure of *Themisto abyssorum* Boeck and *T. libellula* Mandt populations in European-Arctic Seas. *Polar Biology* 15, 85-92
- Kotta J., Pärnoja M., Katajisto T., Lehtiniemi M., Malavin S. A., Reialu G., & Panov V. E. (2013). Is a rapid expansion of the invasive amphipod *Gammarus tigrinus* Sexton, 1939 associated with its niche selection: a case study in the Gulf of Finland, the Baltic Sea.
- Lincoln R. J. (1979). British marine Amphipoda: Gammaridea. British Museum of Natural History, London, 658pp.
- MacNeil C., Dick J.T.A., & Elwood R.W. (2007). The dynamics of predation on *Gammarus* spp. (Crustacea: Amphipoda). *Biological Reviews* 74, 375–395.
- Mazurkiewicz M., Górska B., Renaud P., Włodarska-Kowalczyk M. (2020). Latitudinal consistency of biomass size spectra - benthic resilience despite environmental, taxonomic and functional trait variability. *Scientific Reports* 10:4164, <https://doi.org/10.1038/s41598-020-60889-4>
- Piscart C., Maazouzi C., & Marmonier P. (2008). Range expansion of the North American alien amphipod *Gammarus tigrinus* Sexton, 1939 (Crustacea: Gammaridae) in Brittany, France. *Aquatic Invasions* 3 (4), 449-453.
- Poltermann M. (1987). Franz Josef Land amphipods. *Berichte zum Polarforschung AWI*
- Siemann E., Tilman D., Haarstad J. (1996). Insect species diversity abundance and body size relationships. *Nature* 380, 704–706.
- Steele D. H., And V. J. Steele 1970 The Biology Of *Gammarus* (Crustacea, Amphipoda) In The Northwestern Atlantic. Iv. *Gammarus lawrencianus* Bousfield. *Can. J. Zool.* 48: 1261-1267.
- Steele D.H., & 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 D.H., & Steele V.J. (1975). The biology of *Gammarus* (Crustacea, Amphipoda) in the north-western Atlantic. XI. Comparison and discussion. *Canadian Journal of Zoology* 53, 1116–1126.
- Steele V.J., & Steele D.H. (1970). The biology of *Gammarus* (Crustacea, Amphipoda) in the north-western Atlantic. II. *Gammarus setosus* Dementieva. *Canadian Journal of Zoology* 48, 659–671.
- Steele V.J., & 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.
- Tzvetkova N.L. (1975). Coastal waters gammarids from the North and Far East seas of the USSR and adjacent waters, Nauka, Leningrad, pp 258.

Walczowski W., Piechura J., Goszczko I., & 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.

Węśławski J.M. & Legeżyńska J. (2002). Life cycles of some Arctic amphipods. *Polish Polar Research* 23, 253–264.

Węśławski J.M. (1994). *Gammarus* (Crustacea, Amphipoda) from Svalbard and Franz Josef Land. Distribution and density. *Sarsia* 79, 145–150.

Węśławski J.M., Kuliński W. (1989). Notes on fishes in Hornsund fjord area (Spitsbergen). *Polish Polar Research* 10, 241-250.

Węśławski J.M., Opanowski A., Legeżyńska J., Maciejewska B., Włodarska-Kowalczyk M, Kędra M. (2010). How many roles can a species play? Hidden diversity in Arctic crustaceans. *Pol. Polar Research* 31, 205-216.

Węśławski J.M., Wiktor J., Zajączkowski M., & Swerpel S. (1993). Intertidal zone of Svalbard: Macroorganism distribution and biomass. *Polar Biology* 13, 73–79.

Węśławski JM, Dragańska-Deja K, Legeżyńska J, Walczowski W (2018). Range extension of a boreal amphipod *Gammarus oceanicus* in the warming Arctic. *Ecol Evol* 8(15):7624-7632.doi:10.1002/ece3.4281

Whiteley N.M., Rastrick S.P.S., Lunt D.H., & Rock J. (2011). Latitudinal variations in the physiology of marine gammarid amphipods. *Journal of Experimental Marine Biology and Ecology* 400, 70–77.

Zettler M.L., Zettler A. (2017). Marine And Freshwater Amphipoda From The Baltic Sea And Adjacent Territories. Conchbooks, Harxheim, Germany Pp. 846

Table 1 Gammaridae from Atlantic region	region	minimal	max.	min.	max.	life
	considered	female length	length adult	summer water temp.	summer water temp.	span
species/population		mm	mm	°C	°C	yrs
Chaetogammarus olivii (H. Milne Edwards, 1830)	Black, Medit.	6	12	15	20	1
Chaetogammarus warpachowskyi Sars, 1897	Baltic	5	7	10	10	1
Dikerogammarus haemobaphes (Eichwald, 1841)	Azov, Black	8	20	15	20	1
Dikerogammarus haemobaphes (Eichwald, 1841)	Baltic	10	22	10	20	1
Dikerogammarus villosus (Sowinsky, 1894)	Baltic	8	30	10	15	2
Echinogammarus finmarchicus (Dahl, 1938)	White	10	21	5	15	1
Echinogammarus foxi (Schellenberg, 1928)	Mediterr.	6	8	15	25	1
Echinogammarus ischnus (Stebbing, 1899)	Baltic	6	15	10	20	1
Echinogammarus ischnus (Stebbing, 1899)	Black	5	10	15	20	1
Echinogammarus karadagiensis Grintsov, 2009	Black	4	6	15	25	0,5
Echinogammarus marinus (Leach, 1815)	North, W Atl.	15	25	5	15	1
Echinogammarus obtusatus (Dahl, 1938)	North, W Atl.	9.	20.	5	15	1
Echinogammarus pirloti (Sexton & Spooner, 1940)	North	11	14	10	15	0,5
Echinogammarus planicrurus (Reid, 1940)	North	5	9	10	20	1
Echinogammarus stoerensis (Reid, 1938)	North, W Atl.	4	8	10	20	0,5
Gammarus aequicauda (Martynov, 1931)	Black, Medit.	10	20	15	25	1
Gammarus annulatus Smith, 1873	W Atl.	10	20	5	15	1
Gammarus chevreuxi Sexton, 1913	North, E Atl.	6	13	10	20	0,5
Gammarus crinicornis Stock, 1966	Mediterr.	8	20	15	25	1
Gammarus crinicornis Stock, 1966	Black	10	20	15	25	1
Gammarus daiberi Bousfield, 1969	W Atl.	8	12,5	5	20	1
Gammarus duebeni Lilljeborg, 1852	North, Baltic	8	22	10	20	1

Table 1 Gammaridae from Atlantic region	region	minimal	max.	min.	max.	life
Gammarus duebeni Lilljeborg, 1852	White	12	25	5	15	1
Gammarus inaequicauda Stock, 1966	North, Baltic	8	10	10	20	1
Gammarus insensibilis Stock, 1966	E Atl., Med., Black	5	21	15	25	1
Gammarus lacustris G.O. Sars, 1863	E Atl., Baltic	10	25	10	15	1
Gammarus lawrencianus Bousfield, 1956	W Atl.	5	10	5	15	0,5
Gammarus locusta (Linnaeus, 1758)	E. Atl. , North	15	33	10	20	2
Gammarus locusta (Linnaeus, 1758)	Baltic	12	18	10	20	2
Gammarus mucronatus Say, 1818	W Atl.	1	4	5	30	0,5
Gammarus oceanicus Segerstråle, 1947	Atlantic	11	38	5	20	2
Gammarus oceanicus Segerstråle, 1947	Baltic	10	30	10	20	2
Gammarus palustris Bousfield, 1969	W Atl.	4	14	5	25	1
Gammarus pulex (Linnaeus, 1758)	Baltic	12	23	10	15	1
Gammarus salinus Spooner, 1947	E Atl.	12	24	10	20	1
Gammarus salinus Spooner, 1947	Baltic	10	24	10	25	2
Gammarus setosus Dementieva, 1931	Arctic	13	44	0	15	3
Gammarus subtypicus Stock, 1966	Black	6	20	15	25	1
Gammarus tigrinus Sexton, 1939	North, Baltic	4	14	10	25	1
Gammarus wilkitzkii Birula, 1897	Arcic	20	52	0	5	5
Gammarus zaddachi Sexton, 1912	E Atl.,	10	20	10	25	1
Gammarus zaddachi Sexton, 1912	Baltic	7	30	10	30	1
Obesogammarus crassus (G. O. Sars, 1894)	Baltic	7	15	10	15	1
Pontogammarus robustoides (G.O. Sars, 1894)	Baltic, North	12	22	10	20	1

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