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 toward 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, Tilman, & Haarstad, 1996). That is why the temperature increase due to global warming is likely to cause a change in average individual size, or selection toward smaller species in communities (Atkinson & Sibly, 1997). Such a pattern has already been demonstrated in pelagic Copepoda (Beaugrand, Ibanez, & Reid, 2000), but it is not yet universal in benthic communities (Mazurkiewicz, Górska, Renaud, & Włodarska-Kowalczuk, 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).

The Atlantic sector of the Arctic is warming very fast (ACIA, 2005), mainly due to the increasing advection of Atlantic waters (Walczowski, Piechura, Goszczko, & Wieczorek, 2012) that brings boreal species north of their previous limits of distribution (Berge, Johnsen, Nilsen, Gulliksen, & Slagstad, 2005; Beuchel, Gulliksen, & Carroll, 2006; Fleischer, Schaber, & Piepenburg, 2007; Węsławski, Dragańska-Deja, Legeżyńska, & Walczowski, 2018).
| Species/population | Region considered | Minimal female length (mm) | Max. length adult (mm) | Min. summer water temp. (°C) | Max. summer water temp. (°C) | Life span (years) | Sympatric species in region (nr) | Eggs incubation (days) | Reference |
|--------------------|-------------------|-----------------------------|------------------------|-----------------------------|-----------------------------|-------------------|-------------------------------|-------------------------|-----------|
| Chaetogammarus olivii (H. Milne Edwards, 1830) | Black, Medit. | 6 | 12 | 15 | 20 | 1 | 14 | Greze (1985) |
| Chaetogammarus warpacowskyi Sars, 1897 | Baltic | 5 | 7 | 10 | 10 | 1 | 6 | Zettler and Zettler (2017) |
| Dikerogammarus haemobaphes (Eichwald, 1841) | Azov, Black | 8 | 20 | 15 | 20 | 1 | 9 | Dobrzycka-Krahel, Kendzierska, and Szaniawskas (2013), Zettler and Zettler (2017), http://www.iop.krakow.pl/gatunkiobce/ |
| Dikerogammarus haemobaphes (Eichwald, 1841) | Baltic | 10 | 22 | 10 | 20 | 1 | 6 | Zettler and Zettler (2017), http://www.iop.krakow.pl/gatunkiobce/ |
| Dikerogammarus villosus (Sowinsky, 1894) | Baltic | 8 | 30 | 10 | 15 | 2 | 6 | Dobrzycka-Krahel et al. (2013), Zettler and Zettler (2017), http://www.iop.krakow.pl/gatunkiobce/ |
| Echinogammarus finnarchicus (Dahl, 1938) | White | 10 | 21 | 5 | 15 | 1 | 3 | 15–30 | Gurjanova (1951), Tzvetkova (1975), Lincoln (1979), Zettler and Zettler (2017) |
| Echinogammarus foxi (Schellenberg, 1928) | Mediterr. | 6 | 8 | 15 | 25 | 1 | 14 | Grinstov (2016) |
| Echinogammarus ischnus (Stebbing, 1899) | Baltic | 6 | 15 | 10 | 20 | 1 | 6 | https://nas.er.usgs.gov/queries/great_lakes/FactSheet.aspx?SpeciesID=23 |
| Echinogammarus ischnus (Stebbing, 1899) | Black | 5 | 10 | 15 | 20 | 1 | 9 | Greze (1985) |
| Echinogammarus karadagiensis Grintsov, 2009 | Black | 4 | 6 | 15 | 25 | 0.5 | 9 | Grinstov (2009, 2016) |
| Echinogammarus marinus (Leach, 1815) | North, W Atl. | 15 | 25 | 5 | 15 | 1 | 10 | 15–30 | Gurjanova (1951), Tzvetkova (1975), Lincoln (1979), Zettler and Zettler (2017) |
| Echinogammarus obtusatus (Dahl, 1938) | North, W Atl. | 9. | 20. | 5 | 15 | 1 | 10 | 15–116 | Gurjanova (1951), Tzvetkova (1975), Lincoln (1979), Steele and Steele (1975) |
| Echinogammarus pirloti (Sexton & Spooner, 1940) | North | 11 | 14 | 10 | 15 | 0.5 | 10 | 15 | Lincoln (1979) |
| Echinogammarus planicurus (Reid, 1940) | North | 5 | 9 | 10 | 20 | 1 | 11 | https://www.marlin.ac.uk/species/detail/1776 |
| Species/population   | Region considered | Minimal female length (mm) | Max. length adult (mm) | Min. summer water temp. (°C) | Max. summer water temp. (°C) | Life span (years) | Sympatric species in region (nr) | Eggs incubation (days) | Reference                                                                 |
|----------------------|-------------------|-----------------------------|------------------------|-----------------------------|-----------------------------|-------------------|-------------------------------|------------------------|--------------------------------------------------------------------------|
| Echinogammarus stoerensis (Reid, 1938) | North, W Atl. | 4                           | 8                      | 10                          | 20                          | 0.5               | 10                           | 16                    | Gurjanova (1951), Tzvetkova (1975), Lincoln (1979), Zettler and Zettler (2017), Steele and Steele (1975) |
| Gammarus aequicauda (Martynov, 1931) | Black, Medit. | 10                          | 20                     | 15                          | 25                          | 1                 | 14                           |                       | Greze (1985)                                                            |
| Gammarus annulatus Smith, 1873 | W Atl. | 10                          | 20                     | 5                           | 15                          | 1                 | 5                            |                       | Bousfield (1969)                                                        |
| Gammarus chevreuxi Sexton, 1913 | North, E Atl. | 6                           | 13                     | 10                          | 20                          | 0.5               | 10                           | 15–30                  | Lincoln (1979)                                                          |
| Gammarus crinicornis Stock, 1966 | Mediterr. | 8                           | 20                     | 15                          | 25                          | 1                 | 14                           |                       | Lincoln (1979)                                                          |
| Gammarus crinicornis Stock, 1966 | Black | 10                          | 20                     | 15                          | 25                          | 1                 | 9                            |                       | Greze (1985)                                                            |
| Gammarus daiberi Bousfield, 1969 | W Atl. | 8                           | 12.5                   | 5                           | 20                          | 1                 | 5                            |                       | Bousfield (1969)                                                        |
| Gammarus duebeni Liljeborg, 1852 | North, Baltic | 8                           | 22                     | 10                          | 20                          | 1                 | 6                            | 30                    | Jazdżewski (1970a, 1970b), Lincoln (1979), Tzvetkova (1975), Steele and Steele (1975) |
| Gammarus duebeni Liljeborg, 1852 | White | 12                          | 25                     | 5                           | 15                          | 1                 | 3                            | 30–150                 | Gurjanova (1951), Tzvetkova (1975)                                      |
| Gammarus inaequicauda Stock, 1966 | North, Baltic | 8                           | 10                     | 10                          | 20                          | 1                 | 6                            |                       | Zettler and Zettler (2017)                                              |
| Gammarus insensibilis Stock, 1966 | E Atl., Med., Black | 5                           | 21                     | 15                          | 25                          | 1                 | 14                           |                       | Lincoln (1979), Greze (1985), Zettler and Zettler (2017)               |
| Gammarus lacustris G.O. Sars, 1863 | E Atl., Baltic | 10                          | 25                     | 10                          | 15                          | 1                 | 6                            |                       | Zettler and Zettler (2017)                                              |
| Gammarus lawrencianus Bousfield, 1956 | W Atl. | 5                           | 10                     | 5                           | 15                          | 0.5               | 5                            | 17–82                  | Steele and Steele (1970a, 1970b, 1975)                                  |
| Gammarus locusta (Linnaeus, 1758) | E. Atl., North | 15                          | 33                     | 10                          | 20                          | 2                 | 10                           |                       | Gurjanova (1951), Lincoln (1979), Zettler and Zettler (2017)            |
| Gammarus locusta (Linnaeus, 1758) | Baltic | 12                          | 18                     | 10                          | 20                          | 2                 | 6                            | 30–60                  | Jazdżewski (1970a, 1970b)                                               |
| Gammarus mucronatus Say, 1818 | W Atl. | 1                           | 4                      | 5                           | 30                          | 0.5               | 5                            | 12–15                  | Bousfield (1969), Fredette and Diaz (1986)                              |

(Continues)
### Table 1 (Continued)

| Species/population | Region considered | Minimal female length (mm) | Max. length adult (mm) | Min. summer water temp. (°C) | Max. summer water temp. (°C) | Life span (years) | Sympatric species in region (nr) | Eggs incubation (days) | Reference |
|---------------------|-------------------|-----------------------------|------------------------|-----------------------------|-------------------------------|-------------------|---------------------------------|------------------------|-----------|
| *Gammarus oceanicus* Segerstråle, 1947 | Atlantic | 11 | 38 | 5 | 20 | 2 | 10 | 60–150 | Lincoln (1979), Steele and Steele (1972), Tzvetkova (1975), Steele and Steele (1975) |
| *Gammarus oceanicus* Segerstråle, 1947 | Baltic | 10 | 30 | 10 | 20 | 2 | 6 | 25–94 | Jazdżewski (1970a, 1970b), Zettler and Zettler (2017) |
| *Gammarus pulex* (Linnaeus, 1758) | Baltic | 12 | 23 | 10 | 15 | 1 | 6 | | Zettler and Zettler (2017) |
| *Gammarus salinus* Spooner, 1947 | E Atl. | 12 | 24 | 10 | 20 | 1 | 10 | | Lincoln (1979), Tzvetkova (1975) |
| *Gammarus s.婆 difference* | Baltic | 10 | 24 | 10 | 25 | 2 | 6 | 30–60 | Jazdżewski (1970a, 1970b), Zettler and Zettler (2017) |
| *Gammarus setosus* Dementieva, 1931 | Arctic | 13 | 44 | 0 | 15 | 3 | 1 | 35–150 | Gurjanova (1951), Steele and Steele (1970a, 1970b), Tzvetkova (1975), Steele and Steele (1975) |
| *Gammarus subtypicus* Stock, 1966 | Black | 6 | 20 | 15 | 25 | 1 | 9 | | Greze (1985) |
| *Gammarus tigrinus* Sexton, 1939 | North, Baltic | 4 | 14 | 10 | 25 | 1 | 6 | 30 | Bousfield (1969), Lincoln (1979), Zettler and Zettler (2017) |
| *Gammarus wilkitzkii* Birula, 1897 | Arctic | 20 | 52 | 0 | 5 | 5 | 0 | 37–180 | Tzvetkova (1975), Poltemann (1997) |
| *Gammarus zaddachi* Sexton, 1912 | E Atl. | 10 | 20 | 10 | 25 | 1 | 6 | 30–60 | Jazdżewski (1970a, 1970b), Lincoln (1979), Tzvetkova (1975), Steele and Steele (1975) |
| *Gammarus zaddachi* Sexton, 1912 | Baltic | 7 | 30 | 10 | 30 | 1 | 6 | | Gurjanova (1951), Tzvetkova (1975), Zettler and Zettler (2017) |
| *Obesogammarus crassus* (G.O. Sars, 1894) | Baltic | 7 | 15 | 10 | 15 | 1 | 6 | | Grabowski, Jazdżewski, and Konopacka (2007), Dobrzycka-Krahel et al. (2013), http://www.iop.krakow.pl/gatunkiobce/default2436.htm?nazwa=ops&id=356&je=pl |
| *Pontogammarus robustoides* (G.O. Sars, 1894) | Baltic, North | 12 | 22 | 10 | 20 | 1 | 6 | | Zettler and Zettler (2017) |
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, Head, Cummings, & Harbour, 2000).

In the pelagic realm, the warming results in less diversified size structure of plankton (northern species mature at smaller size and small southern species arrive north). However, in the three dimensional pelagial, the competition for space or microhabitat is not crucial. In contrary, the coastal gammarids compete for the limited space on the seabed and here the size comes as an important factor.

### 2 | 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. In gammarids, males use to be larger than females. As mature females those with setosed oostegites were considered, and as adult males the specimens with developed palpi pennealae on 7th segment. Two values were taken from the literature for the calculations: the maximal size of the specimen from the given population and the minimal size of adult female (that indicates ability to mature at low size).

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 unpublished).

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

### 3 | 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 (Figure 1, Table 1). Number of sibling gammarid species in given temperature/region corresponds inversely with the size of specimens. In low temperature, where the large species occurs, number of sympatric similar species is low, and in warmer temperatures, high number of small species coexist (Figure 2). 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) (Figure 3). Compared to the Arctic, the temperature 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 spans up to twenty such size groups (*G. setosus* or *G. wilkitzkii*).

The growth in two very different populations of *Gammarus 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 (Figure 4). 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 & Steele, 1975; Whiteley, Rastrick, Lunt, & Rock, 2011). Incubation in *G. setosus* or *G. wilkitzkii* lasts 120 and more days in cold, Subarctic—Arctic waters, at year round temperatures <2°C (Steele & Steele, 1974; Węsławski & Legeżyńska, 2002). In the Black Sea or southern Baltic, by contrast, *Gammarus inaequicauda* and *G. salinus* incubate eggs at temperatures >20°C in less than 20 days (Jażdżewski, 1970a). 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—Kostzytn, Timofeev, Węsławski, & Malinga, 1995). Other factors controlling the size of these invertebrates are the availability and quality of food and 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; Węsławski,Wiktor, Zajączkowski, & Swerpel, 1993). The oxygen concentration in coastal waters is always high, or even supersaturated, as there the water dynamics are 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, that is, stones or crevices under which they can hide from predators. Gammarids are a preferred dietary constituent of coastal fish in the Baltic (MacNeil, Dick, & Elwood, 1999), and of fish, seabirds, and seals on Svalbard (Lydersen, Gjertz, & Węsławski, 1989; Węsławski & Kulinski, 1989). The interstices among loose stones, providing adequate shelter, are
quickly filled when some hundreds of animals are trying to hide beneath one of them (Węsławski, 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 2,000 small ones (mean length 5 mm) can conceal themselves under a stone 400 cm$^2$ in area; this corresponds with the average densities reported for Arctic localities (300–500/m$^2$) (Węsławski, 1994) and for temperate sites, where the number of small gammarid species can exceed 10,000/m$^2$ (Tzvetkova, 1975).

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

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 and >20°C in summer. Consequently, most of the species, listed in Table 1, have a potentially very wide geographical distribution. If temperature was 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, Figure 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 (Poltermann, 1997, 1998; Węsławski, 1994). 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 meters, *G. setosus* was recorded higher up on the shore and *G. oceanicus* lower down (Steele & Steele, 1974). On Spitsbergen, the two species coexist recently, as the *G. oceanicus* is colonizing 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 behavior (see Węsławski 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 coexist (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, 1970a, 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 favorable 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 and the cold-water species will lose the competitive advantage of their large size.

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CONFLICT OF INTEREST
None declared.

AUTHOR CONTRIBUTION
Jan M. Węsławski: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal). Joanna Legeżyńska: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal). Maria Włodarska-Kowalczyk: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal).

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) or direct email to the first author <weslaw@iopan.gda.pl>.

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