

Article

Confusing Invader: *Acanthocyclops americanus* (Copepoda: Cyclopoida) and Its Biological, Anthropogenic and Climate-Dependent Mechanisms of Rapid Distribution in Eurasia

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Abstract: *Acanthocyclops americanus* (Marsh, 1892), first described in Wisconsin (USA), was discovered shortly thereafter in Great Britain and then widely distributed in the Palearctic. Its current range includes Europe, North Africa, western and central Siberia with the largest number of findings along the migration tracks of aquatic birds. Until recently, the northern border was the 60th parallel, but in the last decade it has expanded further into the Arctic. The most rapid expansion of its range in Europe happened in the middle of the last century, which was partially hidden from scientists due to a taxonomic mistake caused by the merging of its name with the native Palearctic form *Acanthocyclops robustus* (Sars, 1863). This problem was solved only recently with the help of molecular genetic tools, allowing a return to the study of biological, anthropogenic and possible climate-dependent mechanisms of the successful rapid invasion of *A. americanus* into the Palearctic. This paper, along with a detailed description of the life cycle parameters, adaptive behavior of nauplii and population dynamics in *Acanthocyclops americanus* compared to those in two other native *Acanthocyclops* species (*Acanthocyclops vernalis* and *A. robustus*), provides a possible history of the biological invasion of *A. americanus* in the Palearctic. Special attention is paid to the climate-dependent mechanism of the expansion of its range into the north and far east of Asia. The introduction of the *A. americanus* into small lakes in Great Britain resulted in the dominance of this species in the summer plankton. In many high-trophic reservoirs in Belgium, France and Spain, as well as in newly built reservoirs in Europe, this species has become the only representative of crustacean zooplankton in the warm season. This has led to a significant transformation of the trophic webs of these reservoirs. The rapid dispersal of the invasive species, which was demonstrated by *A. americanus* in the last century, can make it difficult, and in some cases even impossible to study the historical reasons for the formation of the fauna of other invertebrates associated with such events including the movement of continents and the evolution of the Tethys Sea.



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Keywords: dormancy; reactivation; biogeography; climate change; biological invasion

1. Introduction

Acanthocyclops americanus (Marsh, 1892) was described in Wisconsin (USA), then found in England by Lowndes in 1926 [1,2] and in other European countries only thirty-five years later [3–6]. The main European freshwater cyclopoid identification keys written by Gurney [7], Rylov [8], Dussart [9] and Monchenko [10] recognized *A. americanus* as a distinct taxon. Kiefer [11], after comparing specimens from Marsh's collection and the related European form *A. robustus* (Sars, 1863), replaced the name *A. americanus* with *A. robustus* and merged the two taxa. Meanwhile, Kiefer used samples collected from Lake Mjosa near Oslo for his revision because the type material of Sars was lost. At that time, due to an invasion at that site by *A. americanus*, the figures and descriptions of *A. robustus* by Kiefer corresponded to *A. americanus* [12]. Besides morphology, both Kiefer [11] and

other authors [13,14] recognized differences in the ecology of *A. vernalis* and *A. robustus* sensu Kiefer (defined by the rounded shape of the female abdominal segment). The latter was considered pelagic or limnetic, while *A. vernalis* was considered littoral-benthic. Similar observations, but with a different nomenclature of species, were pointed out by Alekseev et al. [12], who indicated that *A. vernalis* and *A. robustus* inhabit the near-shore area and/or near-bottom zone in lakes and are very rarely mixed with truly pelagic species. *A. americanus*, on the other hand, is a pelagic species inhabiting eutrophic water bodies. Differences were also noted in behavior between the nauplii of *A. vernalis* and *A. americanus*, which reflect the ecological preferences of each species [15]. The nauplii of *A. vernalis* respond by sinking down and staying at the bottom when disturbed, but the nauplii of *A. americanus* continue wandering randomly.

The introduction of *A. americanus* into small lakes in Great Britain resulted in the dominance of this species in the summer plankton [16]. In many high-trophic reservoirs in Belgium, France and Spain, as well as in newly built reservoirs in Europe, this species has often become the dominative form of crustacean zooplankton in the warm season [10,12,17,18]. This has led to a significant transformation of the trophic webs of these reservoirs.

Kiefer's synonymy was meanwhile accepted by many authors, and *A. americanus* practically disappeared from most ecological studies and from subsequent identification keys [19]. This name, however, remained in the keys of several Russian and Ukrainian taxonomists who did not agree with this synonymization, which made it possible to trace the dispersal of the species in the 20th century [10,20]. There was too much variability within one species and *A. robustus* was recently split again. For related North American taxa, Dahms and Fernando [21] re-described *Acanthocyclops brevispinosus* (Herrick, 1884) and separated it from *A. robustus* and later confirmed its validity following Dodson's [22] earlier proposition. Alekseev et al. [12] confirmed that *A. robustus* sensu Sars exists—it was found in Belgium as well as *A. vernalis* and *A. americanus*—and that these three species could be easily separated one from one another. These authors raised the question of re-establishment of *A. americanus* as a valid species and its separation from *A. robustus*. On the other hand, Mirabdullaev and Defaye [23] redescribed *A. robustus* based on Kiefer's samples from Lake Mjosa, but since these samples contained only females, they used specimens from Lapland (Sweden) from the Kiefer collection to describe the male. However, the male they described corresponded to *A. americanus* according to the infallible character of the sixth leg. In the same work, a new species *Acanthocyclops trajani* was described, and among the listed synonyms for this species are *A. americanus* (Marsh, 1893) and *A. americanus* f. *spinosa* Monchenko, 1961. Another species of the same group, *Acanthocyclops einslei*, was also later described by the same authors [24]. Just recently, a molecular genetic approach was undertaken on this species complex, which showed that *A. americanus* exists separately from *A. robustus*; European populations of *A. americanus* are invasive and tightly related to the American population on the Atlantic coast; both newly described *A. trajani* and *A. einslei* are younger synonyms of *A. americanus* and *A. robustus*, so their names should be eliminated [25,26].

The rapid dispersal of the invasive species, which was demonstrated by *A. americanus* in the last century, can make it difficult, and in some cases even impossible to study the historical reasons for the formation of the fauna of other invertebrates associated with events such as the movement of continents and the evolution of the Tethys Sea. This may lead to the situation where a rapidly spreading invasive species is alternatively considered as a widespread native form (as in [27]).

This study opens a new page in the history of the biological invasion of *A. americanus* in Europe and its rapid spread over most of the Palearctic area in just one hundred years. In this paper, along with a description of life cycle parameters, adaptive behavior of nauplii and population dynamics of *A. americanus* in comparison with those of two other native species of the *Acanthocyclops* genus (*A. vernalis* and *A. robustus*), we reconstruct the history of the biological invasion of *A. americanus* in Eurasia. Special attention is paid to the

climate-dependent mechanism of following the expansion of its range to the north and far east of Asia.

2. Methods

Observations of the biological invasion of *A. americanus* in the Palearctic started in 1974 in the Volga Delta river and has continued until now during many field trips in Russia and 20 other countries (Figure 1). The total period of the author's observations so far is about 45 years. Partly because of its unstable taxonomical position and doubts about the validity, most of the biological features of this invasive species have never been published. Only recently, after molecular genetic confirmation of the species' existence and tracing of the place from which it migrated, some data have been reported on the distribution and morphological delineation between the two native Palearctic *Acanthocyclops* and the invasive Nearctic species [25,28,29]. For the first time, the parameters of the life cycle of all three species and new data on the presence or absence of invasive *A. americanus* in the Arctic and Far Eastern water bodies of the Palearctic are reported, and the role of climate warming in the future expansion of its range is discussed.

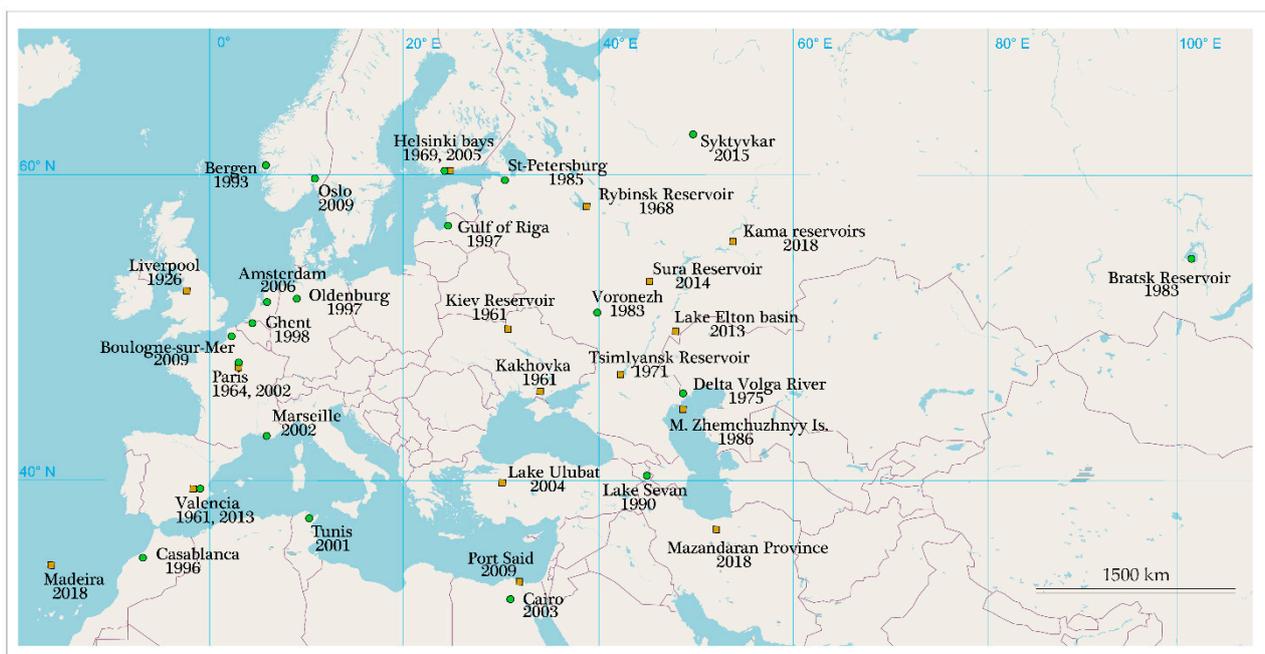


Figure 1. Sites of findings of *Acanthocyclops americanus* in Eurasia and North Africa. Green circles: personally examined by the author; orange squares: based on the literature ([1–3,10,25,30–35]; [36–38] as *A. robustus*; [39] as *A. trajani*).

2.1. Site Description

Populations of three *Acanthocyclops* species successfully living together in comparable population density were found in the period from 1974–1978 in the Volga Delta river in shallow temporal water bodies that are filled with river water every spring. These water bodies exist for one to three months (May–July), depending on water flooding conditions in different years [40]. They are intensively used by fish populations migrating from the Caspian Sea to reproduce. Fish fry feed in the naturally very productive ponds for one to two months, then young fish leave their nesting places and return to the sea. In July, the water bodies almost dry up, so all zooplankton organisms living there must produce resting stages to overcome the nine to eleven month period of desiccation. Summer diapause is thus a key adaptation for most invertebrate species living there. Despite the extreme environmental conditions, including harsh predation by fry, short time of existence, broad range of temperature, etc., the zooplankton fauna remain stable, rich and diverse. More than 450 species, including about 100 copepods, have been reported here [41].

Sites where *A. americanus* was also found during field trips in 1974–2019 include over 20 countries in Europe and North Africa, as well as about 40 locations in Russia, Ukraine, Kazakhstan and Armenia.

In deep lakes, rivers, and reservoirs, a towing net with an open hole of 25 cm and a mesh size of 100 µm was used for sampling. In shallow lakes and temporary pools, about 100 liters of water was filtered with a handle net (cell size 70 µm). Samples were preserved with 4% formalin or 85% alcohol solution.

A modified identification key for the *robustus* group as well as a molecular genetic based barcode confirmation were used for species identification [25].

2.2. Experiments on the Reactivation of Dormant Stages

Experiments and field observations were carried out in the laboratory of the Astrakhan Biosphere Reservation in 1974 by two methods.

1. Zooplankton samples (100 L, filtered through a handle net, 70 µm mesh) were collected and observed every day from the very beginning of the temporary water body filling with river water. Reactivated cyclopoids at 4–5 copepodid stages were immediately identified with preliminary prepared keys that were published later [42] or cultivated until they became adults.
2. In early April, before flooding with water, about 75 cm² of dried sediment (5 cm of surface ground), collected in three replicates in the lowest parts of the temporary water body, was delivered to the laboratory. About half a liter of river water filtered through a 1 µm membrane filter was added to each sample. The samples were then exposed to temperatures in the range of 8–18 °C for 10 days with the same duration of each temperature exposure. Water was carefully removed twice a day. Copepods were collected and reactivated by being filtered through a 70 µm mesh, counted and identified using special keys for major copepodid stages [42] or cultivated until maturation and then identified as adults.

2.3. Species Identification

Despite long-term confusion over the separation of *A. robustus* and *A. americanus*, a number of morphological differences can be found between these very closely related *Acanthocyclops* species [25]. For adults and C4–C5 copepodid stages, which are the first to recover from dormancy and always begin and finish seasonal development in their populations, different keys or signs should be used. The clearest differences in adults are provided in Figure 2, while for the copepodid stages, special illustrated keys are available [42].

2.4. Cultivation

Nearly 150 newly born nauplii of the same age obtained from 3–5 females of *A. americanus*, *A. vernalis* and *A. robustus* hatched from eggs at the same time of day (usually close to midnight) were separated from females to avoid cannibalism, divided into three groups and placed in glass tubes (200 ml volume) and covered on both sides with double 70 µm mesh. These tubes were placed directly in a water body for field control and observed in the lab once per week or when the maturation time of adults was registered in the lab.

A minimum of 30 nauplii of each species were picked randomly for individual cultivation in the laboratory in 20–100 mL glasses (20 mL for nauplii, then 100 mL for copepodid stages). Changes of water and length measurements under a compound microscope with 7 µm resolution were done every day in the morning hours. The growth rate in 22–28 individuals was traced from the orthonauplius to the adult stage in each species. Food for nauplii (a natural mixture of protists and algae), copepodites and adults (crustaceans freshly killed by heating) was refreshed after daily measurements, and the temperature in the lab was maintained within a narrow range (18–22 °C) and controlled/registered automatically. The development time for each stage was first converted to 20 °C and then estimated as an average (%) of female development time. Length–weight relationships

were estimated separately for nauplii (via an estimation of the volume of three-dimensional plasticine figures multiplied by 1.05) and for copepods/adults based on the evaluation of the length and body mass relationship for cyclopoids [43].

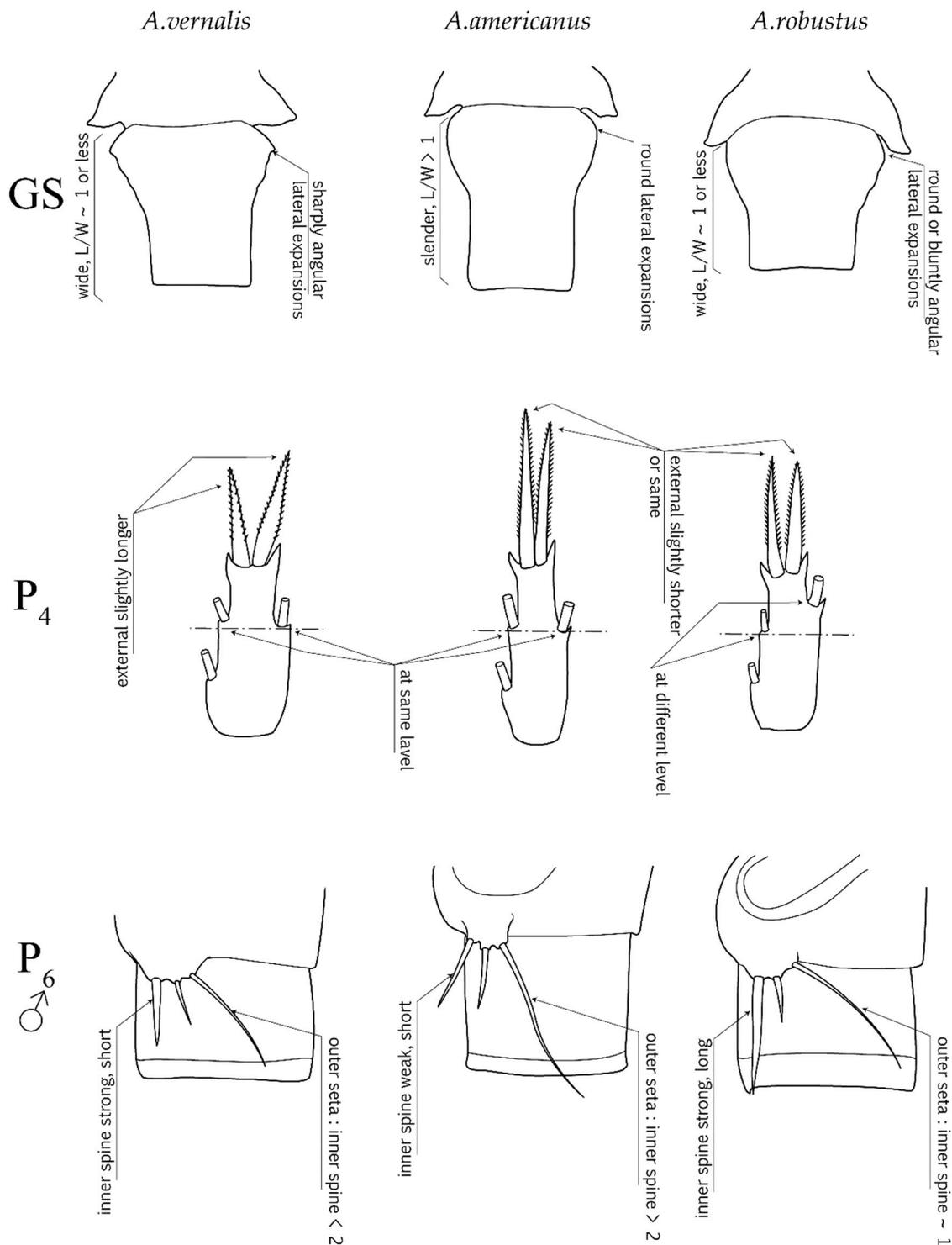


Figure 2. Scheme of the main differences between adults of *Acanthocyclops vernalis*, *Acanthocyclops americanus* and *Acanthocyclops robustus*.

Fecundity (number of eggs in both sacks) was calculated under the microscope by destroying the egg sack with a needle. This was estimated as the average per season in about 100 females randomly selected from field samples. Embryonic development time

was estimated in the lab at a controlled temperature. The observation of egg hatching time was carried out in 10–15 females by observation of the process in the lab with a frequency of about one hour.

The rest of the nauplii were grown together in 200 mL glass vials and used for the study of nauplii behavior and movement. Observations were made under a binocular microscope equipped with a photo camera and ocular micrometer with 25 μm resolution. The following parameters were estimated: length and stage of nauplii, length of jump in calm and in agitation; direction of movement in agitation (to bottom, surface or walls of vial); number of jumps in 10 s under different conditions (food provision, presence of a predator, water disturbance). These experiments are described in more detail in previous publications [15,44].

2.5. Calculations and Statistics

Metabolic rate, productivity and food consumption at each stage of development were calculated according to the manual of Winberg [45] and also converted to 20 °C following Crog's estimation. All experimental data were first tested for normality via the Kolmogorov test, and then a comparison among species was performed using Student's *t*-test or the Mann–Whitney test in the STATISTICA-6 packet of programs.

3. Results

In most of the observed sites, *A. americanus* was found as the single or at least highly dominant *Acanthocyclops* species, suggesting possible competition by the invader as was suggested for 40 localities in Spain [29]. To evaluate the competitive abilities in these species, they must be studied under very similar environmental conditions as those found in the single locality of the Volga Delta river, where *A. vernalis*, *A. robustus* and *A. americanus* coexist in comparable population densities. Extreme environmental conditions (fish predation, short time of the existence of the water phase, high temperature in the end of water body existence) should slow down or practically block interspecies competition. This unique situation allowed us to evaluate the competitive abilities in all three *Acanthocyclops* species without real competition and following species exclusion. The life cycle parameters in all three species were tested as described below (Tables 1 and 2).

Table 1. Development, growth and productivity parameters of *A. americanus* (Marsh, 1893) in the Volga Delta river (Russia). Adult female duration of development at 20 °C = 15.7 days \pm 1.5.

Stages of Development	Average Length, mcm	Mass, mg $\times 10^{-3}$	Duration of Development, in Percent of Adult Female	Daily Productivity Rate, mg $\times 10^{-3} \times \text{day}^{-1}$	Daily P/B Coefficient	Daily Metabolic Rate, Calorie $\times \text{Individual}^{-1} \times \text{day}^{-1} \times 10^{-3}$	Evlev's Coefficient Assimilation (K_2)
Orthonauplius	110	0.25	2.4	0.14	0.38	0.235	0.24
Metanauplius 1	125	0.37	4.2	0.26	0.54	0.290	0.32
-«»- 2	158	0.49	4.5	0.30	0.41	0.400	0.28
-«»- 3	178	0.73	4.5	0.53	0.53	0.510	0.36
-«»- 4	205	1.0	5.2	1.05	0.68	0.715	0.44
-«»- 5	250	1.55	6.4	2.30	0.79	1.140	0.52
Copepodite 1	400	2.90	5.3	3.38	0.63	1.900	0.49
-«»- 2	500	5.40	6.2	3.93	0.41	2.950	0.41
-«»- 3	613	9.60	7.5	5.02	0.32	4.310	0.38
-«»- 4 σ°	675	12.00	6.5	2.04	0.07	7.100	0.13
-«»- 4 ϱ	775	19.00	20.9				
-«»- 4 ($\sigma^{\circ} + \varrho$)/2	825	15.50	13.7				
-«»- 5 σ°	987	22.00	9.7				
-«»- 5 ϱ	850	36.50	32.9				
-«»- 5 ($\sigma^{\circ} + \varrho$)/2	1138	29.25	21.3				
Imago σ°		24.00					
-«»- ϱ		52.00					
-«»- ($\sigma^{\circ} + \varrho$)/2		38.00					

Table 2. Development, growth and productivity parameters of *A. vernalis* (Fischer, 1853) in the Volga Delta river (Russia). Adult female duration of development at 20 °C = 17.8 days ± 1.5.

Stages of Development	Average Length, mcm	Mass, mg × 10 ⁻³	Duration of Development, in Percent of Adult Female	Daily Productivity Rate, mg × 10 ⁻³ × day ⁻¹	Daily P/B Coefficient	Daily Metabolic Rate, Calorie × Individual ⁻¹ × Day ⁻¹ × 10 ⁻³	Evlev's Coefficient Assimilation (K ₂)
Orthonauplius		0.20					
Metanauplius 1	100	0.29	4.2	0.14	0.48		
-«»- 2	118	0.50	8.4	0.09	0.18		
-«»- 3	150	0.61	7.3	0.32	0.52	0.195	0.78
-«»- 4	163	0.96	6.2	0.32	0.34	0.295	0.14
-«»- 5	200	1.55	6.2	1.13	0.73	0.345	0.33
Copepodite 1	250	2.90	6.7	2.08	0.83	0.490	0.26
-«»- 2	400	9.10	6.7	3.89	0.72	0.715	0.46
-«»- 3	500	13.30	5.3	5.93	0.65	1.170	0.49
-«»- 4 ♂	600	19.00	6.7	3.35	0.25	1.900	0.52
-«»- 4 ♀	687	16.15	11.2	4.70	0.25	2.850	0.53
-«»- 4 (♂+♀)/2	797	17.00	16.9	3.60	0.25	4.450	0.30
-«»- 5 ♂	750	33.10	14.0	0.80	0.05	6.250	0.15
-«»- 5 ♀	950	25.05	14.0	3.70	0.11		
-«»- 5 (♂+♀)/2	775	19.00	25.3	2.25	0.08		
Imago ♂	1075	47.00	19.6				
-«»- ♀		33.00					
-«»- (♂+♀)/2							

3.1. Reactivation after Dormancy from a Desiccated State

In experiments with sediments exposed in a range of rising temperatures, the three species revealed the following sequence in reactivation: *A. vernalis*, *A. robustus* and *A. americanus*. In temperature-controlled experiments, the bulk of reactivated *A. vernalis* were first observed when the water temperature was low (8–10 °C) (see Figure 3).

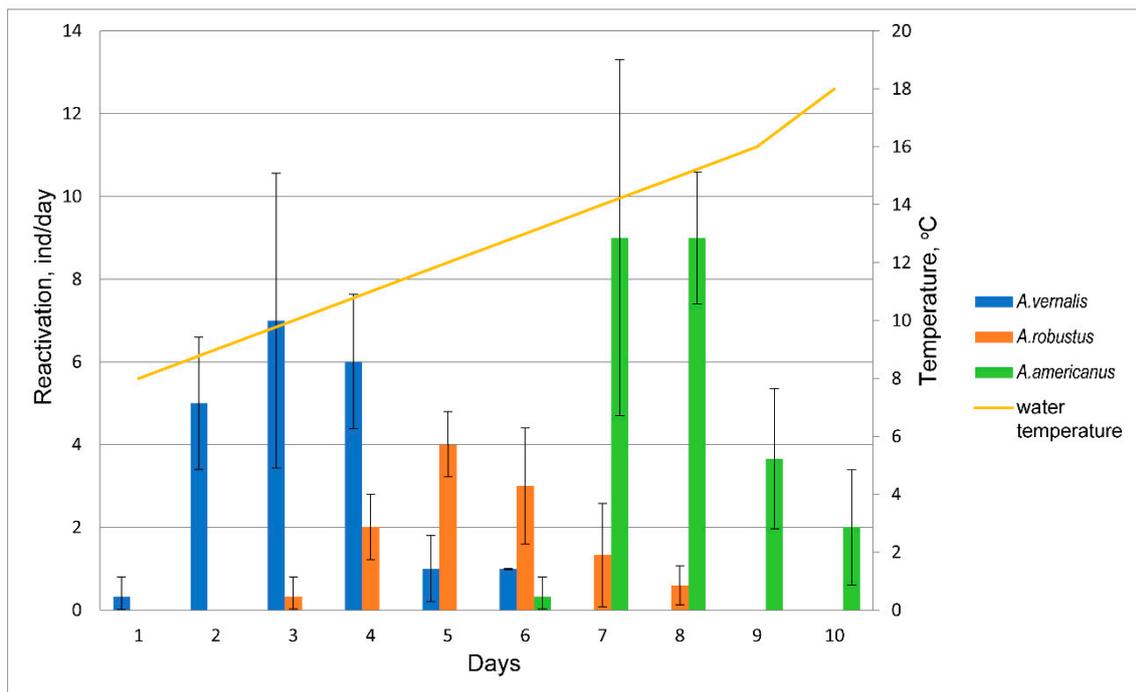


Figure 3. Dependence of the reactivation rate on temperature in *Acanthocyclops vernalis*, *Acanthocyclops americanus* and *Acanthocyclops robustus*.

Field observations for the appearance of this species in zooplankton samples showed the same: *A. vernalis* copepods and adults were found on the first days of water body appearance, then females started reproduction and produced a peak of nauplii stages. In a few days, C4–5 and adults of *A. robustus* appeared and began reproduction. Finally, when the water temperature was 17–18 °C, adults of *A. americanus* were found in plankton samples. Soon thereafter, almost all adult copepods were eliminated by fish fry, and

cyclopoids were represented mainly by small sized juveniles. The temperature of water in our experiments and in the field was relatively high (starting from 8–10 °C on the first days and increasing to 20–24 °C later on).

Even though differences in reactivation were small, *Acanthocyclops* species showed a clear separation in maximal density in adults and their breeding periods. This may have an adaptive role in reducing feeding competition between their offspring.

It is important to note that the adults of each species were eliminated from plankton by the fish fry quite soon after offspring appearance, so the cyclopoids were able to release only one or two clutches of eggs. According to our observations, only when the youngest fish fry consumed females could the eggs in the egg sack develop after leaving the fish's digestive gut. In large size fish, in which the digestive tract has developed into a loop, the egg sacs of cyclopoids lose this ability. It seems that fish fry predation on adults reduces competition between these very closely related species, which explains their coexistence and high biodiversity in the zooplankton of water bodies.

3.2. Following Population Dynamics

After consuming adults by fish fry, all three of these species disappeared from plankton samples, which happened due to the impossibility of identifying their nauplii and young copepodid stages. In 3–4 weeks after the maximum of reactivation, copepod stage 4 of *Acanthocyclops* was observed in zooplankton again, which correlated with the duration of this stage development observed in the growth experiments. The subsequent dynamics of both species depended on the duration of spring water flooding. In years with a short period (30–45 days) of the water phase, cyclopoids of different species stopped their development at stage 4 and entered diapause. When the level of flooding was higher and the water phase lasted longer (60–75 days), many small sized species like *Microcyclops* terminated diapause at an early stage (within 2–3 weeks) and then produced a second cycle of breeding [46]. In *Acanthocyclops*, this second peak of reproduction was not observed, indicating that the species entered dormancy at a non-protective stage of development.

3.3. Growth Rates in *A. vernalis/robustus* and *A. americanus*

Development time and body length at comparable developmental stages in laboratory experiments and in field control groups in two native *Acanthocyclops* species were similar and analyzed together. Females of *A. vernalis* and *A. robustus* became adults at a temperature of 20 °C, which confirms the equivalence of experimental laboratory conditions to natural ones. Both species revealed similar rates of growth at the same temperature/food conditions.

The invasive species grew faster and reached maturity under the same conditions in a shorter time with a larger body length and weight (see Figure 4). As a result, the rates of feeding, metabolism and productivity, which in many respects determine the competitiveness of invasive species, were higher than those of the native congeners.

3.4. Fecundity

Reactivated crustaceans usually have higher fecundity than in following generations due to lipids accumulated in the body at the end of the previous season [47,48]. *A. vernalis*, *A. robustus* and *A. americanus* revealed fecundity close to maximal for these species [10]. Average fecundity in the invasive species (113 ± 7 eggs per female) was slightly higher than in *A. vernalis* (106 ± 11) and *A. robustus* (97 ± 14), but the differences were not statistically confirmed.

3.5. Nauplia Behaviour

In calm conditions, nauplii behavior and movement in *A. vernalis*, *A. robustus* and *A. americanus* were similar. When they were distributed in the vial center, the length of jumps in metanauplius 3 was about 100 µm with a frequency of 8–10 jumps per 10 s. When vials were shaken or another disturbance was imitated with a pipette tip or needle, the

response in these two species was totally different. Following agitation, the nauplii of *A. americanus* stayed in the vial center without any movement until the agitation ceased. In contrast, *A. vernalis* and *A. robustus* nauplii in the stress situation increased the length and frequency of their jumps by 2–3 times and moved to the bottom or vial walls in an attempt to escape danger.

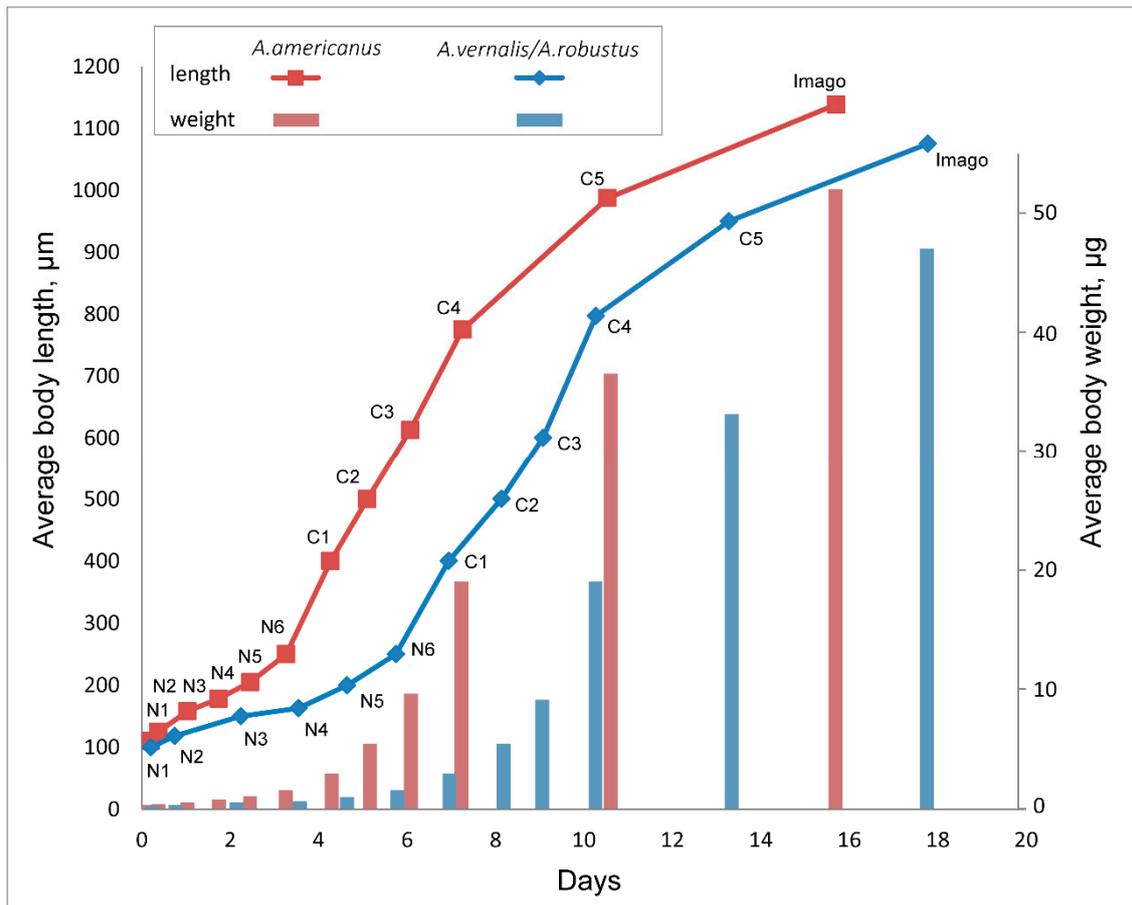


Figure 4. Development time and body length/weight of invasive *Acanthocyclops americanus* and two native *Acanthocyclops* species.

4. Discussion

A comparison of the modern ranges of three closely related species—*A. americanus*, *A. vernalis* and *A. robustus*—shows that the invader has spread widely in Eurasia since the first finding in Great Britain in 1926, occupying a niche as a planktonic predator in limnic systems in the summer season. The distribution of *A. americanus* covers the entire area of Europe, from approximately 60° N (Oslo, Helsinki, St. Petersburg) to the extreme south, and has also been noted in North Africa, i.e., in Tunisia [49] (as *A. robustus*) and Egypt [29,31]. In Asia, this species has been found in large quantities in newly created reservoirs and shallow water bodies north of 36° N, i.e., the Mazandaran Province of Iran [39] (identified as *A. trajani*). The eastern part of the range is currently limited by the Bratsk reservoir [29]. The species has not been encountered in water bodies located in the high-latitude polar Arctic (Arkhangelsk vicinity, the River Ob estuary, the River Lena delta) and in the Pacific region east of Lake Baikal. In recent years, there have been tendencies for some expansion of this area to the north. In northeastern Europe, *A. americanus* has apparently begun to move north of the 60th parallel (temporary pools in the area of the city of Syktyvkar, personal observation).

It should be noted that the closely related species *A. vernalis* and especially *A. robustus*, which until recently was considered its older synonym, live practically throughout the Palearctic from the coast of the Arctic Ocean (Arkhangelsk, Murmansk, the Ob river delta, the Lena river delta, the Kolyma river delta) to the south of Europe (Spain, Italy, Macedonia, Greece). The species are also known in the reservoirs of Asia Minor, Central Asia and the Far East [8,10]. All findings of the twin *Acanthocyclops* species since 2011 were checked by profound identification based on the abovementioned ecological, molecular genetics and morphological criteria [25].

Experiments done in the Volga Delta river showed that the main characters of the life cycle, i.e., the growth rate, the number of offspring produced, adult sizes and population density after reactivation in all three *Acanthocyclops* species were similar, but higher in *A. americanus*. Along with naupliar adaptations of behavior to avoid cannibalism, this may explain the competitive substitution of other cyclopoid species observed in many other places where they could live together [29].

At the same time, the currently observed difference in their ranges is most likely determined by the temperature preference at which these species develop. Indeed, the appearance of Eurasian species in spring is noted shortly after the ice melts, which is associated with their early reactivation after diapause in spring at temperatures close to 4–5 °C [50]. The appearance of the American species was observed in our experiments at temperatures above 14 °C, which coincides well with the summer cycle of its development in plankton. Although these three species require approximately the same number of degree days before reaching sexual maturity, the onset of population development occurs at different times. As a result, the native species from Eurasia are able to reach sexual maturity at lower average seasonal temperatures than *A. americanus*, usually in spring [10]. By starting development at a temperature of 4–5 °C, *A. vernalis* and *A. robustus* can complete the development cycle in water bodies of high latitudes, such as tundra lakes and permafrost lying on a lens of ice, where water temperatures rarely exceed 10 °C. For the American species, such temperature conditions may be insufficient, even if the water warms up above the temperature of their reactivation (14–15 °C) at the peak of summer. The brevity of the Arctic summer does not allow this species at present to gain the required number of degree days to reach the stage of the fourth copepodite, at which this species tolerates unfavorable conditions in a state of diapause.

At the same time, in accordance to the Russian Hydrometeorological Centre, in all regions and federal districts of Russia for the period from 1976 to 2018, there has been a steady increase in the average annual air temperature [51]. The growth rate of the mean annual temperature averaged over Russia was 0.47 °C/10 years (Figure 5), with the fastest growth observed in spring (0.61 °C/10 years) where most intense warming is observed in western Siberia (+0.65 °C/10 years), central Siberia (+0.79 °C/10 years), and eastern Siberia (+0.77 °C/10 years). The warming of the climate noted in recent decades has apparently shifted the border of temperature limits for this species and will possibly allow it to move northward. In particular, this has been confirmed by the author's recent finding of this species in the city of Syktyvkar (61° N).

The peculiarities of late reactivation of the invasive species seems favorable to its rapid distribution in the Palearctic with spring migrating aquatic birds. Waterfowl, migrating north to nesting sites in the high-latitude Arctic, reach the temperate climate zone for a rest on melted shallow water bodies and feed on the remains of the previous year's aquatic vegetation in which the resting stages of many cyclopoid species are encapsulated, so dispersal of *A. americanus* to the north by a constant migration route can occur very quickly, as soon as the water bodies warm sufficiently to allow this species to complete its life cycle. Late recovery requires a higher water temperature to keep them in dormancy up to the moment of passing through the bird gut. Survivorship is significantly increased due to existing in a gel-like cyst known in many American species.

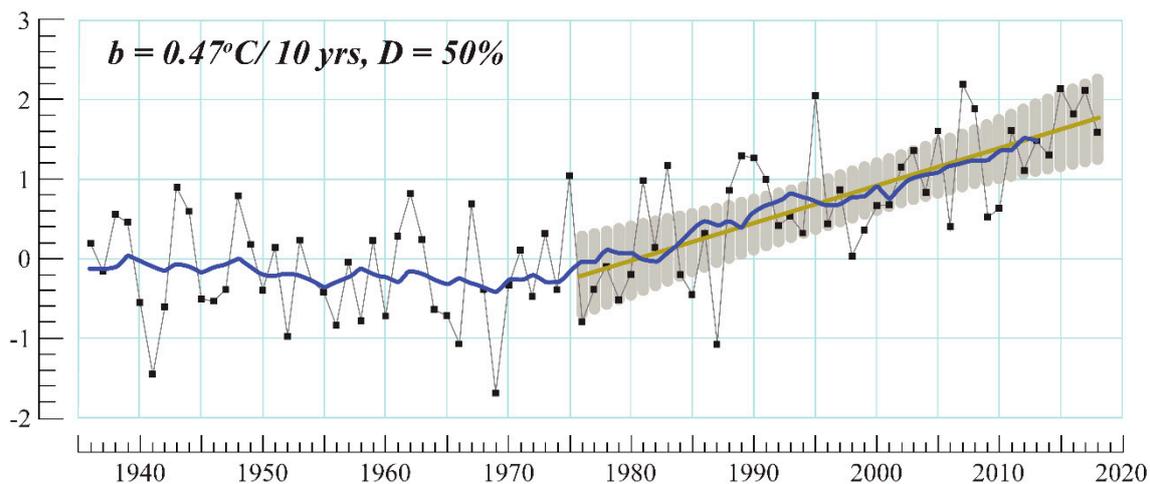


Figure 5. Average annual surface air temperature anomalies ($^{\circ}\text{C}$), averaged over the territory of Russia, 1936–2018. Anomalies are calculated as deviations from the 1961–1990 mean. Also shown is the 11 year moving average and linear trend for 1976–2018 with 95% confidence band, where b is the trend coefficient ($^{\circ}\text{C}/10$ years) and $D\%$ is the trend contribution to the total dispersion [51].

The scenario of the *A. americanus* invasion into the Palearctic can be presented in several time-steps:

1. Crossing of the Atlantic Ocean between USA and Europe at the end of the 19th to the beginning of the 20th century, likely in ship ballast compartments that were part of ship construction in American oceanic ships starting in 1880.
2. Widespread and increased population densities in water bodies in Great Britain in 1920–1930 when this species was first found by Lowndes [1] in the vicinity of Liverpool.
3. Penetration and widespread in continental Europe, possibly during the Second World War or soon after it, facilitated by intensive building of hydroelectric power stations and the creation of large new limnetic habitats, (i.e., chains of water reservoirs in Spain, France and Ukraine). In these countries, *A. americanus* was found in the late 1950s and 1960s [3,4]. At this step, the migration routes of aquatic birds likely became an important factor for the rapid distribution of *A. americanus* along the Baltic Sea, North Sea and Atlantic coast of France and Spain to North Africa (Figure 6).
4. Created in 1941–1962, a large chain of water reservoirs along the Volga Delta river opened up an easy way for invasive species to reach a second aquatic bird migration route via the Caspian Sea (Figure 7). In 1968, this species was found as new summer planktonic cyclopoid in the Saratov and Volgograd water reservoirs [52], and in 1974 it was identified as a mass species in the Volga Delta river [6] and soon after in the northern Caspian Sea [30].
5. Creation of shallow water-reservoirs on Siberian rivers along with *A. americanus* reaching the second most important aquatic bird migration route provided the invader with a new gateway to western and central Siberia as well as in Kazakhstan. In 1981, it was found in the Bratsk water reservoir (the Yenisei River, personal observation) and in the Lake Aral vicinity [53].

Next steps:

6. Invasion of the high Arctic.
7. Invasion into eastern Siberia and the far east of the Palearctic as well as into central Asian countries.

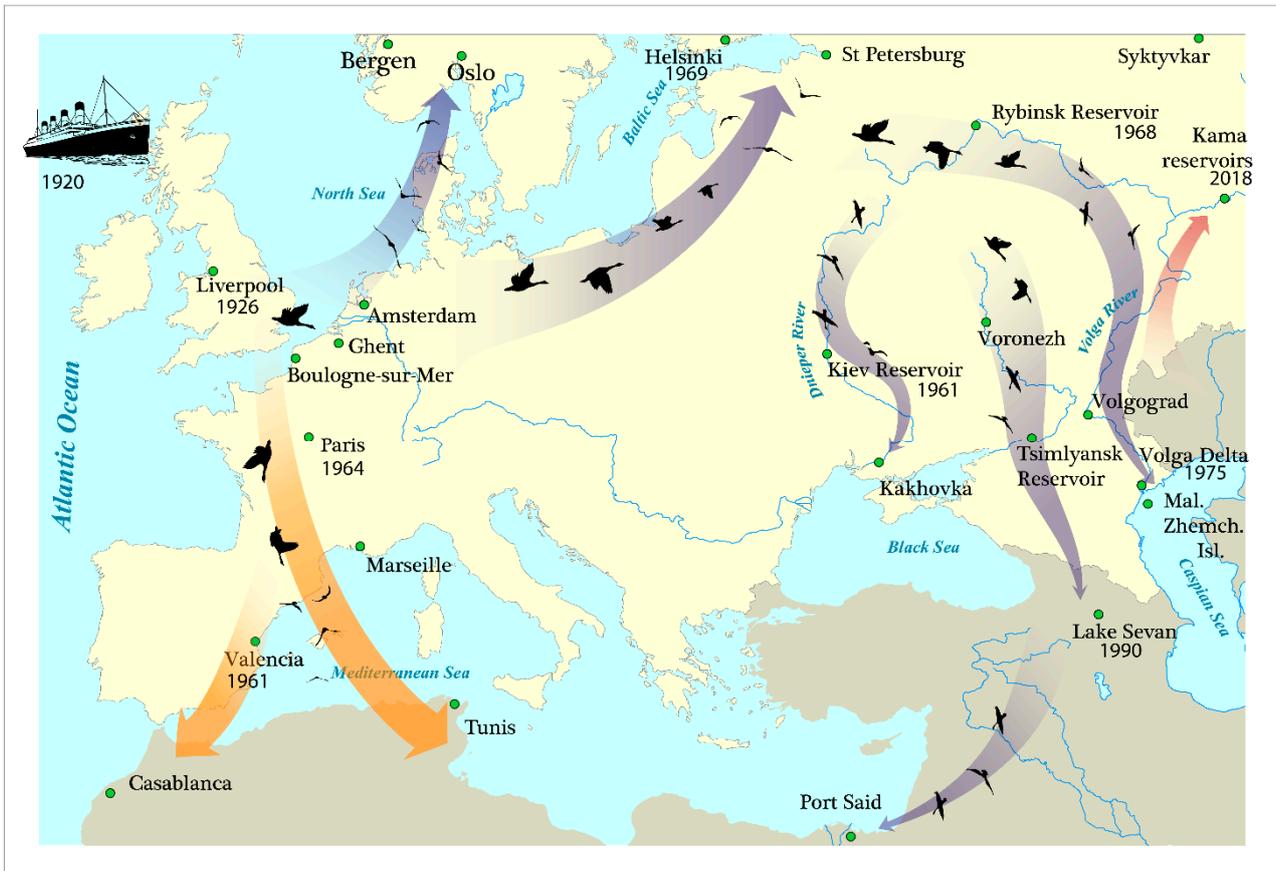


Figure 6. Illustration of the mechanism of distribution of *Acanthocyclops americanus* with waterfowl along the main routes of migration.



Figure 7. Water reservoirs along the Volga Delta river.

These events are tightly linked to climate warming. In my opinion, this is confirmed by the absence of this species in the material collected by the author in recent years in the Arctic zones of Eurasia: the European Arctic zone last year, the Arkhangelsk area and the northern Dvina delta in 2017, in the Asian Arctic zone and the River Lena delta (western Siberia) in 2016, in the Ob-Taz river estuary (western Siberia) in 2018, the Arctic zone of the far east in the Anadyr (Chukotka) in 2018, Kamchatka and Vladivostok (far east of Russia).

The dispersal of the American species further to the east of Asia is currently limited by the non-mixing of the migration routes of waterfowl flying into the Arctic through the Caspian Sea and the Dzungarian gates of Mongolia. The latter route contributes to the distribution and nesting of species inhabiting the Arctic to the east of the Yenisei River. It is possible that, in the Arctic region, birds of these two migration routes may meet in border areas. One can easily imagine that, as soon as this species gains the ability to successfully reproduce and create dense populations in the tundra lakes, which are simultaneously visited by birds that arrive from the Caspian and Dzungarian routes, further dispersal of this species to the east will only be a matter of time. An additional factor that could trigger the creation of such populations in the east may be the construction of new reservoirs on Arctic rivers east of the Yenisei (Lena, Indigirka, Kolyma). A similar scheme for capturing a planktonic niche was noted in the reservoirs of the European part of the former USSR, built on the Dniester, Dnieper, Don and Volga rivers, as well as during the creation of reservoirs and hydroelectric power plants on the Yenisei River.

Thus, further expansion of the range of *A. americanus* to the north and east is likely to be related or will depend on further warming of the climate. The potential for the rapid dispersal of this species has been demonstrated by its previous history, in which it crossed numerous territorial zoogeographic thresholds in less than one hundred years. Such an ability for rapid dispersal within this short period was the result of a combination of climatic and anthropogenic changes in this vast region with the biological qualities of the American species. These include the reactivation of diapause at higher temperatures in spring, along with a rapid growth rate, high fecundity, active predation and adaptation of juveniles, in which behavioral modification reduces cannibalism from adults.

The appearance of this species in some limnetic ecosystems of the Old World has led to a significant change caused by an increase in the proportion of carnivorous invertebrates in zooplankton, and in extreme cases has led to the monoculture of one species in this community. This can lead to significant changes in biological diversity and restructuring of food chains in water bodies of vast areas, especially in fragile Arctic ecosystems.

A well-developed system for the identification of *A. americanus*, including both morphological and molecular genetic characters [25], along with a clearly observed ecological preference (as it is the only true pelagic *Acanthocyclops* species among congeners) make it possible to recommend *A. americanus* as a convenient marker of the rate of advancement of thermophilic fauna to the north as the climate changes. In this way, it can become an indicator of future changes in the biota of Arctic water bodies.

5. Conclusions

A. americanus, an invader from North America, seems to possess several features important for competition with native *Acanthocyclops* species and can substitute them in a historically short period of time. They include faster growth and development rates, higher fecundity under the same food conditions and nauplius behavioral adaptations to avoid female predation. Later reactivation after winter dormancy that starts at 14 °C facilitates the successful wide spreading of this species with aquatic bird spring migrations. This is how within one century *A. americanus* has overcome many biogeographic barriers and increased its areal in the Palearctic from Great Britain islands to Central Siberia in the east and North Africa in the south. Subsequent expansion to the north and to the far east of the Palearctic seems likely but depends on the climate warming process. As a summer zooplankton species recover after dormancy at a high spring temperature, *A. americanus* is limited based on the temperature that can be achieved in water bodies during summer at

the 60th parallel. Oncoming climate warming will move this limit border to the north. In some places such as the Syktyvkar vicinity (northeastern Europe, 61° N) we have found this species as a newcomer in temporary pools.

In experiments, the invasive species was a very effective predator, easily consuming both small sized prey (nauplii of other copepod species) and large-sized larvae of phyllopodids that hatched from resting eggs. In small water bodies in the summer, *A. americanus* very often become the only zooplankton species. When it arrives in the Arctic zone, where most tundra lakes are small and shallow, this may totally transform food webs, not only for fish, but also for birds that consume large arctic phyllopodids (*Artemiopsis*, *Chirocephalus*, etc.) as the main protein source available in polygonal tundra.

In this sense, it is easy to recognize that *A. americanus* is the only true pelagic *Acanthocyclops* species in the Eurasian continental hydro-fauna and that it could be a convenient biological indicator of southern fauna penetration to northern ecosystems caused by oncoming climate change.

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References

1. Lowndes, A.G. On *Cyclops americanus*, Marsh. *Ann. Mag. Nat. Hist.* **1926**, *17*, 616–619. [[CrossRef](#)]
2. Lowndes, A.G. *Cyclops americanus* Marsh. A discussion and description of its specific characteristics and its occurrence in Europe. *Int. Rev. Ges. Hydrobiol.* **1928**, *19*, 12–20. [[CrossRef](#)]
3. Monchenko, V.I. On species independence of *Acanthocyclops americanus* (Marsh) and on its finding in the Soviet Union. *Zool. Zhurnal* **1961**, *40*, 13–19. (In Russian)
4. Dussart, B.H. Contribution à l'étude des copépodes d'Espagne. *Publ. Inst. Biol. Appl.* **1967**, *42*, 87–105.
5. Dussart, B.H. *Acanthocyclops americanus* en France. *Bull. Muséum Natl. Hist. Nat.* **1971**, *42*, 725–729.
6. Alekseev, V.R.; Kosova, A.A. Finding of *Acanthocyclops americanus* (Copepoda) in the delta of the Volga River. *Zool. Zhurnal* **1976**, *5511*, 1726–1728. (In Russian)
7. Gurney, R. Br. *Fresh-Water Copepoda. III. The Classification of the Cyclopoida and the Parasitic Forms Derived from Them*; Ray Society: London, UK, 1933.
8. Rylov, V.M. *Freshwater Cyclopoida. Fauna of USSR*; Zoological Inst. Acad. Sci. USSR: Leningrad, Russia, 1948; Volume 3. (In Russian)
9. Dussart, B.H. *Les Copépodes des Eaux Continentales d'Europe Occidentale 2. Cyclopoïdes et Biologie Quantitative*; Boubée: Paris, France, 1969.
10. Monchenko, V.I. *Gnathostome cyclopoids (Cyclopidae). Fauna of the Ukraine*; Naukova Dumka: Kiev, Ukraine, 1974; Volume 27. (In Ukrainian)
11. Kiefer, F. Freilebende Copepoda. In *Die Binnengewässer Einzeldarstellungen aus der Limnologie und ihren Nachbargebieten. Das Zooplankton der Binnengewässer, 2. Teil*; Elster, H.J., Ohle, W., Eds.; Schweizerbart'sche Verlagsbuchhandlung: Stuttgart, Germany, 1978.
12. Alekseev, V.R.; Fefilova, E.; Dumont, H.J. Some noteworthy free-living copepods from surface freshwater in Belgium. *Belg. J. Zool.* **2002**, *132*, 133–139.
13. Petkovski, T.K. Revision von *Acanthocyclops*-formen der *vernalis*-Gruppe aus Jugoslawien (Crustacea, Copepoda). *Acta Musei Macedonici Sci. Nat.* **1975**, *14*, 93–142.
14. Fryer, G. An ecological validation of a taxonomic distinction: The ecology of *Acanthocyclops vernalis* and *A. robustus*. *Zool. J. Linn. Soc.* **1985**, *84*, 165–180. [[CrossRef](#)]

15. Alekseev, V.R. Species Dependent Characters of Naupliar Behavior in Freshwater Cyclopoids. In *Behavior of Aquatic Invertebrates, 4th All-Union Symposium, Borok, USSR, 18–20 October 1983*; Gagarin, V.G., Ed.; Academy of Sciences: Rybinsk, Russia, 1986; pp. 95–99. (In Russian)
16. Fryer, G. *The Freshwater Crustacea of Yorkshire: A Faunistic and Ecological Survey*; Yorkshire Naturalists' Union: York, UK; Leeds Philosophical and Literary Society: Leeds, UK, 1993.
17. Sahuquillo, M.; Miracle, M.R. The role of historic and climatic factors in the distribution of crustacean communities in Iberian Mediterranean ponds. *Freshw. Biol.* **2013**, *58*, 1251–1266. [[CrossRef](#)]
18. Armengol, X.; Antón-Pardo, M.; Ortells, R.; Olmo, C. The “malladas” of La Devesa de El Saler: The recovery of a set of coastal interdunal lagoons in the Albufera Natural Park. *Recerca Territ.* **2018**, *10*, 173–192.
19. Einsle, U. Copepoda: Cyclopoida. Genera *Cyclops*, *Megacyclops*, *Acanthocyclops*. In *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World*; Dumont, H.J.F., Ed.; SPB Academic Publishing: Amsterdam, The Netherlands, 1996; Volume 10, pp. 1–82.
20. Alekseev, V.R. Key to freshwater Cyclopidae of Russia and adjacent lands (Crustacea). *Zoosystematica Ross.* **1998**, *7*, 25–43.
21. Dahms, H.U.; Fernando, C.H. Redescription of *Acanthocyclops brevispinosus* (Herrick, 1884) from Ontario. *Crustaceana* **1997**, *70*, 129–144. [[CrossRef](#)]
22. Dodson, S.I. Morphological analysis of Wisconsin (USA) species of the *Acanthocyclops vernalis* group (Copepoda: Cyclopoida). *J. Crustacean Biol.* **1994**, *14*, 113–131. [[CrossRef](#)]
23. Mirabdullayev, I.M.; Defaye, D. On the taxonomy of the *Acanthocyclops robustus* species complex (Copepoda, Cyclopidae) 1. *Acanthocyclops robustus* (G.O. Sars, 1863) and *Acanthocyclops trajani* n. sp. *Selevinia* **2002**, *1–4*, 7–20.
24. Mirabdullayev, I.M.; Defaye, D. On the taxonomy of the *Acanthocyclops robustus* species complex (Copepoda, Cyclopidae): *Acanthocyclops brevispinosus* and *A. einslei* sp. n. *Vestnik Zoologii* **2004**, *38*, 27–37.
25. Miracle, M.R.; Alekseev, V.R.; Monchenko, V.; Sentandreu, V.; Vicente, E. Molecular-genetic-based contribution to the taxonomy of the *Acanthocyclops robustus* group. *J. Nat. Hist.* **2013**, *47*, 863–888. [[CrossRef](#)]
26. Bledzki, L.A.; Rybak, J.I. *Freshwater Crustacean Zooplankton of Europe: Cladocera & Copepoda (Calanoida, Cyclopoida) Key to Species Identification, with Notes on Ecology, Distribution, Methods and Introduction to Data Analysis*; Springer: New York, NY, USA, 2016.
27. Corgosinho, P.H.C.; Hołyńska, M.; Marrone, F.; de Oliveira Gerales-Primeiro, L.J.; dos Santos-Silva, E.N.; Perbiche-Neves, G.; López, C. An annotated checklist of freshwater Copepoda (Crustacea, Hexanauplia) from continental Ecuador and the Galapagos Archipelago. *ZooKeys* **2019**, *871*, 55. [[CrossRef](#)]
28. Alekseev, V.R.; Monchenko, V.I. Morphological and Molecular-Genetic Studies of Copepod-Sibling Species. In *Aquatic Invertebrate Biodiversity in Continental Water-Bodies*; Zoological Institute of Russian Academy of Sciences: St-Petersburg, Russia, 2011; pp. 7–14. (In Russian, with English abstract)
29. Alekseev, V.R.; Miracle, M.R.; Sahuquillo, M.; Vicente, E. Redescription of *Acanthocyclops vernalis* (Fischer, 1853) and *Acanthocyclops robustus* (Sars, 1863) from neotypes, with special reference to their distinction from *Acanthocyclops americanus* (Marsh, 1892) and its invasion of Eurasia. *Limnetica* **2021**, *40*, 57–78. [[CrossRef](#)]
30. Chuykov, Y.S. Fauna Planktonnykh Bespozvonochnykh Vodoyemov Severnogo Prikaspiya i Kaspiya. In *Gidrobiologicheskiiye Issledovaniya Estuariyev*; Zoological Institute of Russian Academy of Sciences: St. Petersburg, Russia, 1986; pp. 58–74. (In Russian)
31. Dumont, H.J. A Description of the Nile Basin, and a Synopsis of its History, Ecology, Biogeography, Hydrology, and Natural Resources. In *The Nile*; Dumont, H.J., Ed.; Springer: Dordrecht, The Netherlands, 2009; pp. 1–21. [[CrossRef](#)]
32. Lazareva, V.I.; Gusakov, V.A.; Zinchenko, T.D.; Golovatyuk, L.V. Zooplankton of saline rivers in the arid zone of southern Russia (Lake Elton basin). *Zoologicheskii Zhurnal* **2013**, *92*, 882–892. (In Russian) [[CrossRef](#)]
33. Lazareva, V.I.; Sabitova, R.Z.; Bykova, S.V.; Zhdanova, S.M.; Sokolova, E.A. Distribution of summer zooplankton in cascade of Volga and Kama reservoirs. *Proc. IBIW* **2018**, *83*, 62–84. (In Russian)
34. Senkevich, V.A.; Tsyganov, A.N.; Stojko, T.G. Zooplankton community in the Penza water storage basin. University proceedings. Volga region. *Nat. Sci.* **2016**, *1*, 35–49. (In Russian)
35. Vecchioni, L.; Sala, J.; Arculeo, M.; Marrone, F. On the occurrence of *Eudiaptomus gracilis* (GO Sars, 1863) (Copepoda: Diaptomidae) in Madeira (Portugal). *Limnetica* **2020**, *39*, 571–578. [[CrossRef](#)]
36. Alper, A. Ulubat Gölü Cladocera ve Copepoda (Crustacea) Türlerinin Tespiti ve Mevsimsel Dağılımlarının Belirlenmesi. Master's Thesis, Balıkesir Üniversitesi Fen Bilimleri Enstitüsü, Balıkesir, Turkey, 2004.
37. Monakov, A.V. *Fauna of Cyclopids in the Coastal Zone of the Rybinsk Reservoir. BIOLOGY and Trophic Connections of Freshwater Invertebrates and Fish*; Nauka: Moscow, Russia, 1968; pp. 33–40. (In Russian)
38. Purasjoki, K.; Viljamaa, H. *Acanthocyclops robustus* (Copepoda, Cyclopoida) in plankton of the Helsinki sea area, and a morphological comparison between *A. robustus* and *A. vernalis*. *Finn. Mar. Res.* **1984**, *250*, 33–44.
39. Rahmati, R.; Esmaili Fereidouni, A.; Rouhi, A.; Agh, N. Effects of different diets on population growth and fatty acids composition in cyclopoid copepod *Acanthocyclops trajani* (Mirabdullayev and Defaye, 2002): A potential supplementary live food for freshwater fish larvae. *Iran. J. Fish. Sci.* **2020**, *19*, 1447–1462.
40. Gorbunov, K.V. The main features of changes in the natural complex of reservoirs in the delta and avandelta of the Volga river. *Hydrobiol. Zhurnal* **1965**, *1*, 13–23. (In Russian)
41. Kosova, A.A. Zooplankton in the Western Part of the Lower Volga Delta During Flow Regulation. In *Changes in the Biological Complexes of the Caspian Sea over the Past Decades*; Nauka: Moscow, Russia, 1965; pp. 98–138. (In Russian)

42. Alekseev, V.R. *Key to Freshwater Cyclopinae of the European Part of the USSR. Major Copepodid Instars/Manus*. Depon; VINITI: Moscow, Russia, 1987; p. 98. (In Russian)
43. Balushkina, E.V.; Winberg, G.G. Dependence Between Length and Weight of Planktonic Crustaceans. In *Experimental and Field Studies of the Biological Foundations of Lake Productivity L.*; Zoological Institute of Russian Academy of Sciences: Saint Petersburg, Russia, 1979; pp. 58–80. (In Russian)
44. Alekseev, V.R. Peculiarities of the development of copepods in the temporary reservoirs of the Volga delta. *Inform. Bull. IBVV Acad. Sci. USSR* **1980**, *47*, 30–33. (In Russian)
45. Winberg, G.G. (Ed.) *Methods for Determining the Production of Aquatic Animals*; Vysshaja Shkola: Minsk, Belarus, 1968. (In Russian)
46. Alekseev, V.R. Growth of *Microcyclops gracilis* (Lill.) and *M. varicans* (Sarc) in temporary water bodies of the Volga delta. *Gidrobiol. Zhurnal* **1978**, *14*, 32–34. (In Russian)
47. Arbačiauskas, K. Does Timing of Emergence within a Season Affect the Evolution of Post-Diapause Traits? Post-Diapause and Directly Developing Phenotypes of *Daphnia*. In *Diapause in Aquatic Invertebrates. Theory and Human Use*; Alekseev, V.R., De Stasio, B., Gilbert, J.J., Eds.; Springer: Dordrecht, The Netherlands, 2007; pp. 167–175. [\[CrossRef\]](#)
48. Arbačiauskas, K. Seasonal Diphenism in *Daphnia* from Temperate Environments: Organismal Traits and Molecular Regulation. In *Dormancy in Aquatic Organisms. Theory, Human Use and Modeling*; Pinel-Alloul, B., Alekseev, V.R., Eds.; Springer: Cham, Switzerland, 2019; pp. 163–174. [\[CrossRef\]](#)
49. Turki, S.; Defaye, D.; Rezig, M.; El Abed, A. Le cycle biologique d'*Acanthocyclops robustus* (G. O. Sars, 1863) (Crustacea, Copepoda, Cyclopidae) en Tunisie. *Zoosystema* **2002**, *24*, 735–770.
50. Monchenko, V.I. The problem of induction and termination of diapause in cyclopoid copepods. *Hydrobiologia* **1996**, *320*, 119–122. [\[CrossRef\]](#)
51. Hydromet Report. 2018 Report on the Features of the Climate in the Territory of the Russian Federation. 2019. Available online: http://www.meteorf.ru/upload/pdf_download/o-klimat-rf-2018.pdf (accessed on 10 June 2020). (In Russian)
52. Vijushkova, V.P.; Kuznetsova, V.P. Distribution of *Acanthocyclops americanus* (Marsh.) Copepoda in USSR. *Zool. Zhurnal* **1974**, *53*, 1873–1875. (In Russian)
53. Kruppa, E.G. On the Morphological Deviations of *Acanthocyclops americanus* Marsh and *Cyclops vicinus* Uljanin (Crustacea, Copepoda) from the Polluted Water Bodies of Almaty Region (Southeastern Kazakhstan). *Russ. J. Aquat. Ecol.* **1998**, *7*, 11–16.