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Small details of big importance: Carbon mass determination in the invasive cladoceran *Cercopagis pengoi* (Ostroumov, 1891) by the high temperature combustion method

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Abstract

Carbon mass of the non-indigenous predatory fishhook water flea *Cercopagis pengoi* (Ostroumov, 1891) from the eastern Gulf of Finland, the Baltic Sea, was for the first time measured using the high temperature combustion method. Prior to the analysis, individual dry weight of *Cercopagis* was determined; altogether ca. 500 organisms were examined. Mean individual dry weight of *C. pengoi* for July-September was estimated as 34.0 µg; carbon mass averaged 15.8 µg; carbon content, calculated as percent of dry weight, averaged 43.4%. Those values varied over months, mainly because of different population structure of *C. pengoi* and variation in their diet due to seasonal dynamics of the food objects. However, relations between carbon mass and dry weight for different months did not differ statistically ($p<0.001$). Therefore, the general polynomial regressions (k=2), describing carbon mass-to-dry weight and carbon content-to-dry weight relationships, were calculated for the entire dataset of individual measurements of *C. pengoi* body metrics. These data will contribute to adequate evaluation of food web structure and ecosystem alterations in various water bodies invaded by *C. pengoi* which has got a strong potential to pelagic food web transformations that may impact the overall energy balance and decrease the size of fish stocks.

Keywords

Alien species, Baltic Sea, carbon content, *Cercopagis pengoi*, dry weight

Introduction

In invasion biology, ecosystems vulnerability to non-indigenous species introductions, biodiversity of native communities and competitive resource utilization depending on the size of organisms are pervasive and closely linked to environmental changes (Holopainen et al. 2016). For the adequate food web structure evaluation and the appropriate energy balance calculations in aquatic ecosystems, determination of carbon mass of organisms as a biomass measure is an important prerequisite. Since decades, individual carbon mass has been a routine parameter known for many zooplankton organisms (Hessen et al. 2013, Kiørboe 2013, Walve and Larsson 1999), even the smallest meso- and microzooplankters such as rotifers (Telesh et al. 1998b). For a limited number of zooplankters, the relations between carbon mass and other size metrics were established (Telesh et al. 1998b, Vasama and Kankaala 1990). Precise knowledge of the individual carbon mass and carbon content of aquatic organisms is of exceptional value when assessment of the impacts of alien species invasions on the ecosystems, food webs, competitive interactions, and composition of native communities is in the research focus.

Among such hotspot research fields is the estimation of ecosystem impact of the opportunistic generalist predator – the Ponto-Caspian onychopod cladoceran *Cercopagis pengoi* (Ostroumov, 1891), one of the recent invaders to the Baltic Sea (Ojaveer and Lumberg 1995, Krylov et al. 1999, Leppäkoski et al. 2002, Telesh et al. 1999, 2001, 2008, Rowe et al. 2016) and to the Laurentian Great Lakes (MacIsaac et al. 1999, Therriault et al. 2002). This invader has got a strong potential to cause alterations in plankton communities, including population shifts (Ojaveer et al. 2004, Telesh and Ojaveer 2002), resource competition (Holliland et al. 2012, Lehtiniemi and Lindén 2006), depletion of prey populations (Kotta et al. 2006), or changes in energy fluxes (Laxson et al. 2003, Litvinchuk and Telesh 2006, Naumenko and Telesh 2008).

However, despite the fact that much is known about population dynamics, feeding behavior and the diet of *C. pengoi* (Holliland et al. 2012, and references therein), as well as its role in fish diet (Gorokhova et al. 2004) and competition of *C. pengoi* with 0-group fish for small prey (Vanderploeg et al. 2002), such a routine parameter as biomass of *C. pengoi* can only be roughly estimated so far. Most often it is assumed that the individual dry weight of *C. pengoi* is 20 μg (Uitto et al. 1999), or carbon content is calculated assuming the carbon to dry weight relation of 44% which is available for other cladocerans (Hessen 1990). Until now, preliminary data on the direct carbon mass determination in *C. pengoi* from the eastern Gulf of Finland was only available as a brief abstract publication (Telesh et al. 1998a); correlation between those parameters has never been established.

To fill in this gap, the present research aimed at direct measurement of carbon mass and dry weight of the invasive water flea *Cercopagis pengoi* from the eastern Gulf of Finland (the Baltic Sea), for (i) evaluating its average individual carbon mass, dry weight and carbon content, and (ii) for calculating the carbon mass-to-dry weight relationship during the period of maximum population development when the impact of *C. pengoi* on the native pelagic community is the greatest.

Materials and methods

Zooplankton samples were collected in July, August and September 1997 at three sampling stations in the eastern Gulf of Finland (EGF), the Baltic Sea: station P (St. P, sampling dates 22 August and 11 September) in the coastal zone near Primorsk, station F-2 (St. F-2, sampling date 22 July) in the open waters of the EGF, and station 21 (St. 21, sampling date 10 September) in the coastal waters of the EGF in the vicinity of Zelenogorsk (Fig. 1). All stations were located in the oligohaline waters with salinity 4-6 psu at the depth of 12 m (St. 21 and St. P) and 23 m (St. F-2).

Zooplankton at each station was sampled by several vertical tows from 1.5 m above the bottom to the surface using the Juday plankton net with the opening diameter 0.2 m and mesh size 138 µm. The composite samples from each location were preserved with formaldehyde (final concentration 4%) and frozen at -18 °C. This method is known to provide superior preservation for the purpose of carbon mass determination for many zooplankton species (Salonen and Sarvala 1980, Telesh et al. 1998b).

On the date of the analysis, samples were defrosted, ca. 120 individuals of *C. pengoi* were picked from each sample, rinsed 5 times in distilled water in Petri dishes and kept on ice at about -5 °C until processing. Prior to carbon mass determination, *Cercopagis* were placed in pre-weighed tin capsules individually and dried at 60 °C for 36 h. Dried organisms were kept in desiccator until carbon mass determination. Individual dry weight (DW) of each cladoceran was registered using Sartorius microbalance (± 0.0001 mg) immediately before carbon measurement. Altogether, ca. 500 individuals of *Cercopagis* were analyzed.

Carbon mass (CM) of each individual *Cercopagis* with the known dry weight was measured using the high temperature (+950 °C) combustion method (Salonen 1979) in the Universal Carbon Analyzer (UNICARB) at the Department of Biology, Faculty of Science and Forestry, University of Eastern Finland (Joensuu, Finland). The results of carbon mass determination and dry weight measurements of *C. pengoi* obtained in 1997 were statistically analyzed at the Zoological Institute of the Russian Academy of Sciences (St. Petersburg, Russia) in 2015-2016.

Carbon content (CC) was calculated as percent of dry weight for each individual. Mean dry weight, carbon mass, carbon content of *C. pengoi* and regressions for these parameters were calculated separately for each month (July, August and September) and for the entire study period using the complete dataset.

Variations in dry weight and carbon mass of *C. pengoi* at three stations during different months were compared statistically using the method of Multiple Comparisons (2-tailed) that allowed to assess the impacts of categorical independent variables, controlling for the effects of the continuous predictor variable, CM. The non-parametric Kruskal-Wallis ANOVA by Ranks test was also used for comparison of multiple independent samples (groups) to determine whether DW- and CM-frequency distribution varied over months. Dry weight dependency of carbon mass and carbon content was examined using the linear and polynomial (k=2) regressions based on individual measurements of body metrics and calculated CC-values. Statistical analyses were carried out using the program package Statistica 7.0.

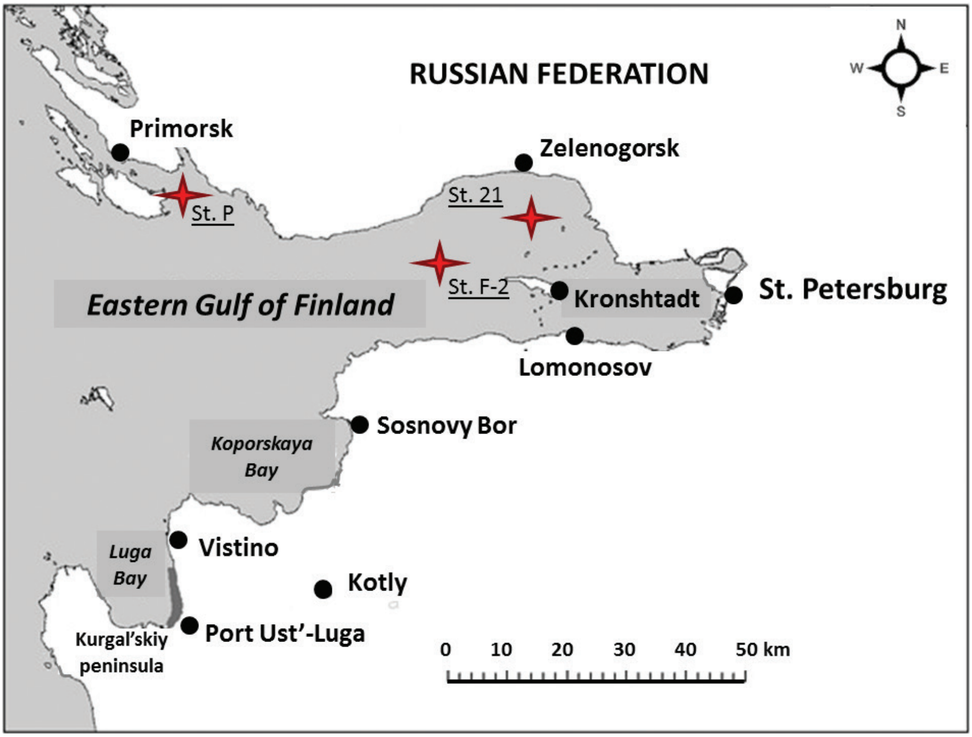

Figure 1. Scheme of the eastern Gulf of Finland (the Baltic Sea) showing the location of sampling stations: St. P, St. F-2 and St. 21 (asterisks).

Results

Dry weight of *C. pengoi* individuals collected in the eastern Gulf of Finland in July–September 1997 ranged one order of magnitude: from 9 to 94 µg; variation in carbon mass exceeded two orders of magnitude and ranged from 0.21 µg to 46.09 µg. The exceptionally low values of CM (< 1.0 µg) and the relevant DW and CC values were excluded from the analyses as possible results of methodological bias during CM-measurements in the smallest individuals of *C. pengoi*. The overall number of CM/DW measurements used for the further analyses was 432.

In July, the population of *C. pengoi* consisted mainly of rather small individuals with DW from 13 to 35 µg, while the organisms larger than 52 µg DW were absent, except for one individual of 88 µg (Fig. 2A). In August and September, the population of these cladocerans in the study area was represented by organisms with a broader DW range, and larger individuals of 53-73 µg DW were common in all sampling locations, particularly in September (Fig. 2B–D).

Mean DW of *C. pengoi* in the study area in July–September was 34.0 ± 14.2 µg, CM averaged 15.8 ± 8.8 µg; these parameters, however, varied between months; the highest average DW (39.6 µg) and CM (18.5 µg) values were registered in August (Table 1).

Table 1. Carbon mass, dry weight and carbon content (mean ± SD) of *Cercopagis pengoi* in the eastern Gulf of Finland (the Baltic Sea).

Parameter	July	August	September*	Average for July – September
Carbon mass (CM, µg)	10.8 ± 7.7	18.5 ± 8.4	17.1 ± 8.5	15.8 ± 8.8
Dry weight (DW, µg)	26.3 ± 11.4	39.6 ± 14.9	35.2 ± 13.4	34.0 ± 14.2
Carbon content (CC, %)	37.0 ± 12.3	44.9 ± 7.1	45.9 ± 10.7	43.4 ± 11.0
Number of individuals analyzed (*n*)	112	111	209	432

* Data from samples collected in September at two stations (St. 21 and St. P) were pooled because preliminary tests revealed high similarity of both data sets (*p*<0.001).

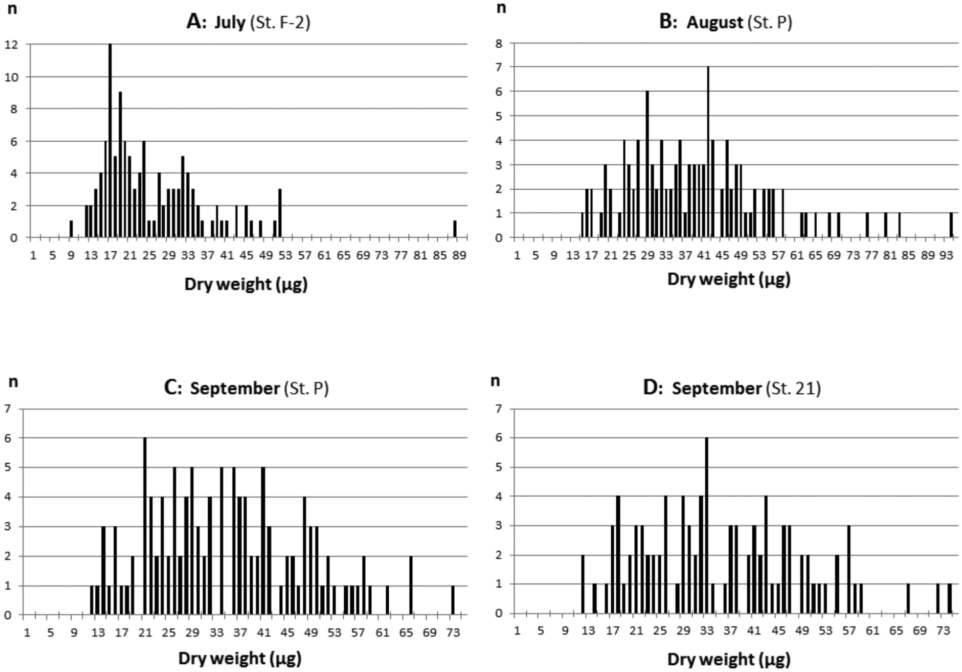

Figure 2. Frequency distribution (*n*) of *Cercopagis pengoi* individuals with different dry weight (µg) at three stations in the eastern Gulf of Finland in July (**A**), August (**B**) and September (**C, D**).

Variation in the data on *C. pengoi* DW- and CM-frequency distribution during three months was statistically significant (Kruskal-Wallis ANOVA by Ranks test for DW: H (3, N=432) =59.908; *p*<0.001; test for CM: H (3, N=432) =50.830; *p*<0.001). However, the Multiple Comparison (2-tailed) *p* values witnessed for the fact that only data for July were statistically different from the rest of the dataset (*p*<0.001), while the differences in data for August and September were statistically insignificant. Univariate test of significance for CM allowed concluding that DW was the major contributor to standard deviation of CM-values while the input of the factor "Month" was negligible (*p*<0.001).

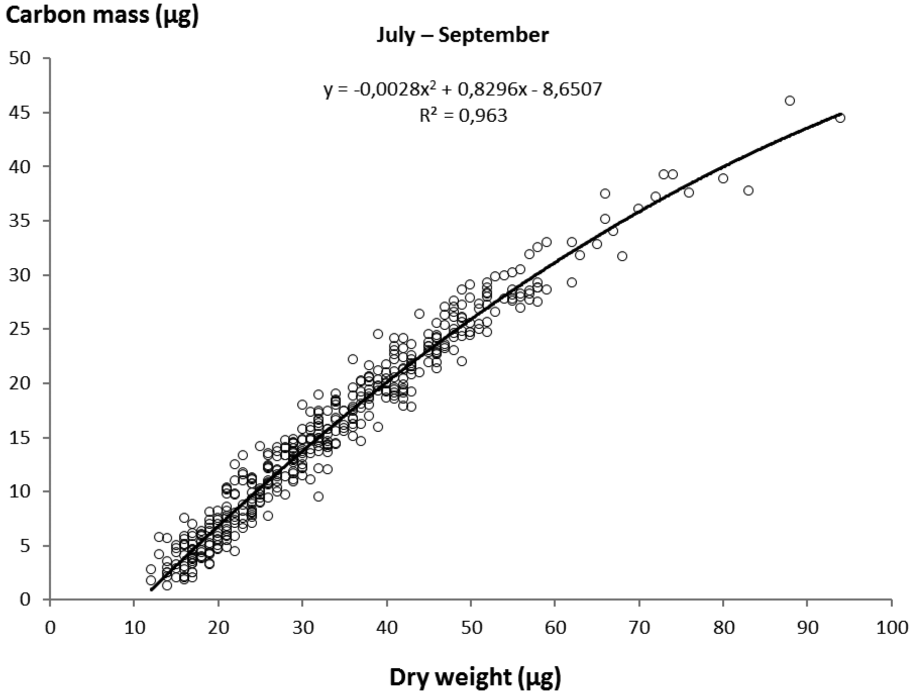

Figure 3. Relationship between carbon mass (µg) and dry weight (µg) of *Cercopagis pengoi* for July–September.

The CM-to-DW relationships for different months can be sufficiently well described by the linear regressions ($r^2 = 0.951–0.969$, $p<0.001$). However, the best approximation was achieved by applying the polynomial (quadratic) regression model ($r^2 = 0.975–0.984$, $p<0.001$); moreover, slopes and intercepts for these regressions for different months did not differ statistically ($p<0.001$). Therefore, the general polynomial regression (k=2), describing CM-to-DW relationship during July through September, was calculated for the entire dataset of individual measurements of *C. pengoi* body metrics (Fig. 3):

$$CM = -0.0028\ DW^2 + 0.8296\ DW - 8.6507 \qquad (1)$$

where CM is carbon mass (in µg), and DW is dry weight (in µg); $r^2=0.96$, $p<0.001$.

Average carbon content of *C. pengoi* in July-September was estimated as 43.4%. The highest mean CC (45.9%) was recorded in September; this value, however, was close to the one for August (44.9%); in July, CC of crustaceans was the lowest and averaged 37.0% (Table 1). Carbon content-to-DW relation was described by quadratic regression (Fig. 4):

$$CC = -0.0177\ DW^2 + 1.9507\ DW + 0.8942 \qquad (2)$$

where CC is carbon content (in percent of dry weight), and DW is dry weight (in µg); $r^2=0.66$, $p<0.001$.

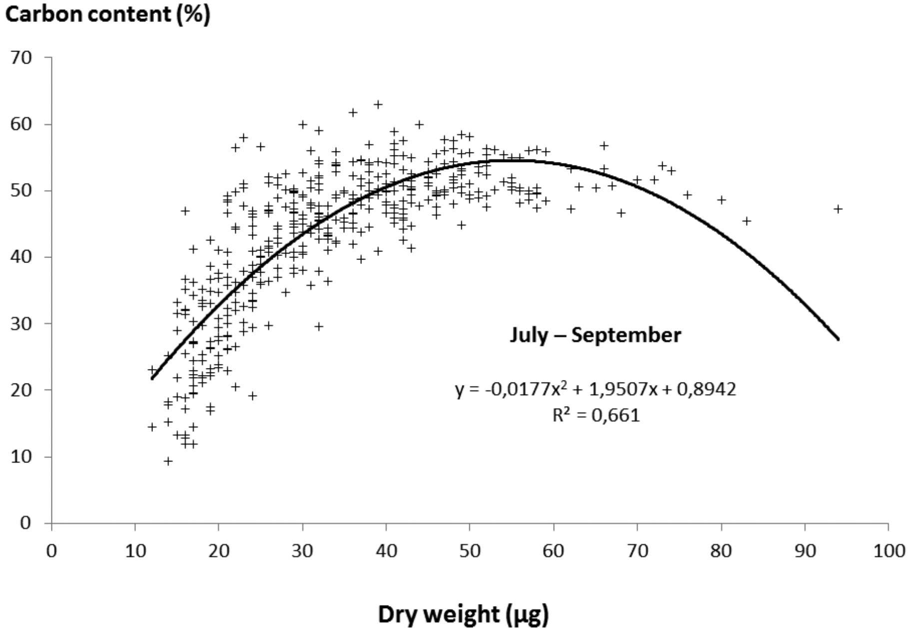

Figure 4. Relationship between carbon content (%) and dry weight (µg) of *Cercopagis pengoi* in July–September (*n*=432).

Discussion

The fishhook water flea *Cercopagis pengoi* (Ostroumov, 1891) has recently become an important component of the pelagic food web in the eastern Gulf of Finland. On the one hand, planktivorous pelagic fishes such as herring and sprat can feed on *Cercopagis* (Antsulevich and Välipakka 2000, Gorokhova et al. 2004); besides, these cladocerans are readily consumed by mysids (Gorokhova and Lehtiniemi 2007). On the other hand, *C. pengoi* significantly impacts the native zooplankton community by feeding on dominant native species such as podonid cladocerans and preferably copepods *Acartia* spp. and *Eurytemora affinis* (Lehtiniemi and Gorokhova 2008, Holliland et al. 2012). These water flees can also feed on *Bosmina* spp. (Gorokhova et al. 2005, Pollumäe and Väljataga 2004) and other planktonic filtrating crustaceans (Laxson et al. 2003) which are abundant during summer. These carnivorous planktonic invaders thus make the food chain longer by one level which allows additional energy losses during the energy flow through the pelagic ecosystem (Telesh et al. 2015b). This phenomenon can affect the overall energy balance and the size of pelagic fish stocks.

In general, the predator capture rates are known to scale positively with consumer mass (Barrios-O'Neill et al. 2016). Additionally, invasion success and spatial distribution of a planktonic predator can be restricted by a larger invasive competitor (Ptáčníková et al. 2015). Thus, body size of these organisms is recognized as a pivotal component of evolutionary fitness which provides a beneficial contribution to certain ecological patterns (Telesh et al. 2015a, 2016). Nevertheless, despite the long-recognized importance of body size in ecology, it is only recently that ecologists have begun to comprehensively resolve the body mass dependencies of consumer feeding rates, including the invasive predators (Barrios-O'Neill et al. 2016, and references therein). In particular, body mass of *C. pengoi* was accounted as part of the algorithm which allows evaluating its predation impact (Telesh et al. 2001, Laxson et al. 2003), and this assessment can be used for monitoring of the invasion range and its effect on the natural zooplankton community. However, exact knowledge of the body mass and particularly carbon content of the invader is essential for the precise calculations of matter turnover and energy balance, as well as for the consumer feeding rate evaluation.

Results of the current study for the first time allowed calculating the carbon mass-to-dry weight relationship based on the precise, direct carbon mass measurement by the high temperature combustion method (Salonen 1979) in a large number of *C. pengoi* individuals. In this research, the laboratory determination of carbon mass and dry weight of *C. pengoi* from the eastern Gulf of Finland were carried out and its average individual carbon mass, dry weight and carbon content were evaluated for July, August and September 1997 when *C. pengoi* was characterized by the maximum population density, as shown in our previous publications (Krylov et al. 1999, Litvinchuk and Telesh 2006, Telesh et al. 2001). The proposed polynomial (k=2) regression (Fig. 3) can describe perfectly well the carbon mass-to-dry weight relationship for *C. pengoi* individuals of 12-94 μg DW for the entire study area, which can be considered as a uniform shallow-water sampling site since it is characterized by the intensive wind-induced water mixing and the subsequent relative homogeneity of zooplankton community in the region (Telesh et al. 1999, 2008).

The discovered differences in averaged values of DW and CM of *C. pengoi* between July and August-September (Table 1) can be explained by several reasons. Firstly, they can be attributed to different population structure of these cladocerans in July and August-September: e.g., the changing abundance proportion of parthenogenetic and gametogenetic females and males (Litvinchuk and Telesh 2006). Moreover, major part of the *C. pengoi* population in July are often represented by the so-called 'spring form' (the first parthenogenetic generation, hatched from resting eggs) which are thereafter gradually substituted by the individuals of the 'summer form' – organisms with longer caudal spine, as shown for the Gulf of Riga of the Baltic Sea (Simm and Ojaveer 1999).

Other reasons can involve shifts in the diet of *C. pengoi* at different developmental stages (Holliland et al. 2012), also due to their diel vertical and spatial migrations (Krylov et al. 1999). Moreover, seasonal succession in dominant zooplankters from rotifers in spring to small cladocerans and juvenile copepods in summer to adult copepods in the fall in the eastern Gulf of Finland (Telesh et al. 1999, 2001) defines significant differences in composition of prey organisms for *C. pengoi*. Inputs of different carbon sources caused by varying stoichiometry of pelagic systems due to changing plankton community structure (Hessen et al. 2013) is largely responsible for the discovered variation in the carbon content of these crustaceans in different months, as well as for the lower CC in the smaller individuals of *C. pengoi*. This conclusion bases on the fact that the diet of the smaller *C. pengoi* differs substantially from the diet of the larger crustaceans, not only due to the inability of the smallest *C. pengoi* to catch larger prey but also due to different zooplankton community structure and, therefore, different elemental composition of food objects for the small vs. large individuals of *C. pengoi*.

Meanwhile, the obtained values of carbon content, calculated as percent of dry weight, averaged 43.4% for July-September which is in good correspondence with the 44% value obtained earlier for other cladocerans (Hessen 1990), especially for *Evadne* sampled in the Baltic Sea in 1997 (42.5%, Walve and Larsson 1999), and close to 46-49% for copepods *Acartia* and *Eurytemora* (Kiørboe 2013, Walve and Larsson 1999). However, these data differ substantially from the 5.2% carbon content of copepods, cladocerans and rotifers suggested by Mullin (1969), the latter value being presumably a percentage of wet weight (compare: Table 1 in Kiørboe 2013).

Interestingly, the mean CC values for *C. pengoi* in July were significantly lower than in August-September (Table 1), and calculations showed that the smallest individuals contained less carbon (Fig. 4). These surprising results were possibly recorded due to substantial morphological differences between the 'spring forms' of *C. pengoi* in July and 'summer forms' in the following months. The rigid, chitinous caudal process of the summer individuals is usually twice as long as that of the 'spring forms': in July the caudal process is as long as 225% of the total body length while in the 'summer forms' it constitutes 474% of the total body length (Simm and Ojaveer 1999). Therefore, the longer caudal process in the larger individuals in August-September is likely responsible for the higher proportion of carbon in these organisms if compared with the July forms.

Besides, the brood pouch of the instar III parthenogenetic females of *C. pengoi* is known to be 236% larger than that of instar I individuals of the smaller size (Grigorovich et al. 2000) which, therefore, contain relatively less carbon compared to larger individuals. At the same time, the brood pouch of females is filled with body fluids and embryos that have lower proportion of chitin and, respectively, lower carbon content compared to the brood pouch itself. This fact was additionally supported by the discovery of lower carbon content of *Evadne* compared to *Bosmina*, since *Evadne* contains more water due to its large egg sac (Walve and Larsson 1999). Similarly, carbon content was increasing with growth of mysids *Nyctiphanes couchi*: 33.41% in calyptopis stage CI, 36.02% in stage CII, and 37.60% in CIII (Lindley et al. 1999). Winter forms of *Meganyctiphanes norvegica* contained less carbon (39.4%) than spring forms (46.5%) (Lindley et al. 1999). These and other examples support our findings on carbon content of *C. pengoi* from the Baltic Sea.

According to our results, the assumed individual dry weight of 20 µg (Uitto et al. 1999) which is commonly used for *C. pengoi* biomass calculations (e.g., Gorokhova et al. 2004), is apparently largely underestimated. In our study, the lowest mean *C. pengoi* individual dry weight of 26.3 µg was registered in July, while in August and September these values were significantly higher: 39.6 and 35.2 µg DW, respectively (Table 1).

These data along with equations (1) and (2) for calculation of carbon mass-to-dry weight and carbon content-to-dry weight regressions reported in this study will allow avoiding miscalculations of *C. pengoi* biomass and favor adequate assessment of the food web structure and energy fluxes. These results may be applied also to *C. pengoi* from the Laurentian Great Lakes, albeit regional variations in the diet of these cladocerans likely exist (Lehtiniemi and Gorokhova 2008, Laxson et al. 2003, Ptáčníková et al. 2015), due to specific features of zooplankton community composition, diversity and environmental characteristics.

Conclusion

The research presents new data on the average individual carbon mass (15.8 µg), dry weight (34.0 µg) and carbon content (43.4%) of the invasive cladoceran *Cercopagis pengoi* from the eastern Gulf of Finland (the Baltic Sea), and suggests the polynomial (k=2) regressions for describing carbon mass-to-dry weight and carbon content-to-dry weight relationships during the period of maximum population development of *C. pengoi* when the invader's impact on the native community and food web is the greatest. This impact jointly with ecosystem vulnerability to invasions, food web structure and biodiversity are closely interrelated and tightly linked with the on-going environmental alterations (Vuorinen et al. 2015, Holopainen et al. 2016). New experimentally derived knowledge on carbon mass of the alien fishhook water flea *C. pengoi* will contribute to future development of methods for assessment of the ecosystem impacts of non-indigenous species and refining the invasibility criteria for successful species coexistence in the changing environment which might significantly enhance predictive ecology.

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