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# A potential barrier to the spread of the invasive cladoceran *Cercopagis pengoi* (Ostroumov 1891) in the Northern Baltic Sea



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## HIGHLIGHTS

- *C. pengoi* is present in the Bothnian Sea, yet absent/transient in the Bothnian Bay.
- Coastal zones appear to be important, with one record in the northerly Bothnian Bay.
- Peak abundances recorded in 2006/2007 are the highest reported in the Baltic Sea.
- Low biomass of potential prey may contribute to the current *C. pengoi* distribution.
- Climate change factors could modify barriers restricting the spread of *C. pengoi*.

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## ABSTRACT

The spread of the invasive cladoceran *Cercopagis pengoi* has been well documented in southern areas of the Baltic Sea, however, little research on this invasive species (nor the zooplankton community) has focused on the Gulf of Bothnia (Bothnian Sea and Bay). We analysed data collected over a 12–13 year period at two main stations, one coastal and one offshore, to examine the occurrence of *C. pengoi*, invasion dynamics, effects on natural zooplankton communities and associated environmental factors. Nine other stations in the Gulf of Bothnia were also examined and the contribution to three-spined stickleback (*Gasterosteus aculeatus*) diet was quantified. The zooplankton community response apparently differed between coastal and offshore stations with *Bosmina*, *Eurytemora*, and *Acartia* populations being influenced during peak abundances of *C. pengoi*. It appears that the native zooplankton community has some resilience, returning to its prior structure outside of peak invasion periods. *C. pengoi*, where present, contributed significantly to stickleback diet. We explored possible barriers for *C. pengoi* in the Bothnian Bay, suggesting that the low productive Bothnian Bay ecosystem may be incapable of supporting such a predator. This highlights the need for further studies, especially in the light of global climate change.

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## 1. Introduction

The Baltic Sea is a vast brackish water body characterised by gradients in salinity and temperature. The large latitudinal expanse, the topography and hydrology of this water body and the strong seasonality result in basin specific physico-chemical conditions. The relatively slow water exchange via the Danish Strait and

the net influx of freshwater from northerly rivers are significant players in the formation of conditions that strongly favour neither marine nor freshwater species (see [Ojaveer et al., 2010](#) for a short review). The physico-chemical conditions that constrain overall species richness may however be highly favourable for invasive species that are capable of coping with such conditions ([Paavola et al., 2005](#)).

*Cercopagis pengoi* is known to have rapidly colonised extensive aquatic systems and can have a potentially serious negative commercial impact (e.g. fouling of fishing gear, [Birnbaum, 2011](#) and [Ojaveer and Lumberg, 1995](#)). It can also alter colonised ecosystems and several recent studies have classified it as a highly

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bioinvasive species (Jazdzewski and Grabowski, 2011; Lehtiniemi and Gorokhova, 2008; Zaiko et al., 2011). The invasion and spread of *C. pengoi* has been well documented in the Baltic Proper (Kotta et al., 2006; Krylov et al., 1999; Leppäkoski and Olenin, 2000; Panov et al., 2007), including a significant amount of research on the Gulf of Finland, the Gulf of Riga and the northerly Baltic Proper. In addition, the invasion of the North American Great Lakes (MacIsaac et al., 1999), likely a secondary transfer from the Baltic Sea, and various ecological consequences have been well documented. In the Baltic Proper detailed documentation exists on: occurrence, dynamics (Krylov et al., 1999; Ojaveer et al., 1998), effects on the food web, persistence of populations and potential for competition with native zooplanktivorous fish (Gorokhova et al., 2005; Lehtiniemi and Gorokhova, 2008). Furthermore, incorporation into fish diet and apparent selective feeding on *C. pengoi* have been reported (Ojaveer and Lumberg, 1995; Gorokhova et al., 2004; Peltonen et al., 2004). In contrast, references to its presence in more northerly basins (the Gulf of Bothnia) are comparatively few and significantly less detailed (ICES, 2005; Katajisto et al., 2013; Leppäkoski and Olenin, 2000). They rarely quantify *C. pengoi* abundances, do not examine the zooplankton community as a whole, and mainly cite a warm summer in 1999 as the reason for the presence of this aggressive Ponto-Caspian intruder (Leppäkoski et al., 2002).

*C. pengoi* has evidently become integrated into the food web in certain areas of the Baltic Sea and is considered to have formed permanent populations (Gorokhova et al., 2000; Ojaveer et al., 1998; Telesh et al., 2001). It is an opportunistic generalist predator capable of capturing both small and large prey, including the cladoceran *Bosmina* (Kotta et al., 2006; Ojaveer et al., 2004) and copepods such as *Acartia* and *Eurytemora* (Lehtiniemi and Gorokhova, 2008; Orlova et al., 2006), despite their antipredator response (Viitasalo et al., 2001). Hence, the ecosystem effects of *C. pengoi* invasion have been suggested to include population shifts (Ojaveer et al., 2004), potential resource competition (e.g. with mysids or fish, Holliland et al., 2012 and Lehtiniemi and Lindén, 2006), lasting depletion of prey or competitor species (Kotta et al., 2006; Ojaveer et al., 2004) and different energy and nutrient routing (Holliland et al., 2012; Lehtiniemi and Lindén, 2006).

This study examines the occurrence of *C. pengoi* in the Gulf of Bothnia over a 12–13 year period, its apparent persistence, its potential impact on the native zooplankton community and the contribution of it to three-spined stickleback diet. The stations sampled traverse the current northerly extent of the *C. pengoi* invasion. We describe (1) the zooplankton community in the Gulf of Bothnia, (2) determine the apparent current northerly extent of this invasive species, (3) explore possible implications high abundances of *Cercopagis* have for the native zooplankton community, (4) explore if lasting alterations in the native zooplankton have occurred during this period, and (5) explore potential barriers that may explain the apparent distribution of *C. pengoi* in the northern Baltic Sea. Our study highlights the importance of present and future ecological impacts of this invasive predatory cladoceran, especially in the face of predicted global climate change, a factor that could alter some of the barriers seemingly responsible for maintaining the apparent low long-term impact or absence of *C. pengoi* in the Gulf of Bothnia.

## 2. Materials and methods

We used zooplankton community composition data at a number of stations in the northerly basins of the Baltic Sea (Gulf of Bothnia, including the Bothnian Sea and Bothnian Bay) (Fig. 1) from a long-running monitoring program based at Umeå Marine Sciences Centre (UMF). In addition, during July and August 2011 and 2012 we conducted a more detailed sampling program to study the food web structure, which also included fish collection.

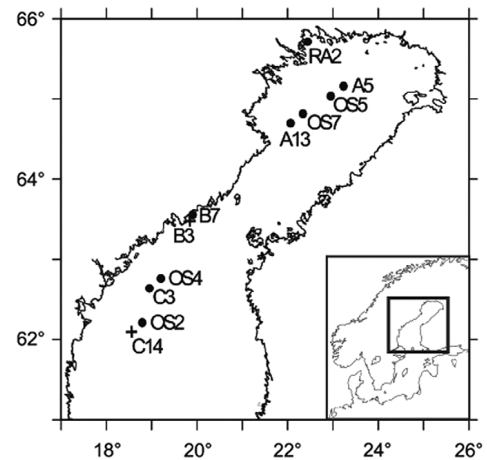


Fig. 1. Map of stations sampled in the Bothnian Sea and Bothnian Bay. Station C14 and B3, the two most heavily discussed in the paper, are marked with + symbols.

Stations sampled, frequency of the sampling and occurrence of sampling during the summer months (defined here as June–September) are shown in Table 1. The main data presented here are from two stations (one coastal, B3, and one offshore, C14) in the Bothnian Sea and concentrate on the summer months during the period 2000–2011/12. Our initial search was to recover all records of *C. pengoi* at the sampled stations during the sampling period. All the records are presented in this paper. Two details should be noted here. Firstly, data presented in Figs. 2 and 3 are from single sampling events each year (Table 2) and seasonal and detailed annual trends are not possible to define with this data. Secondly, during the sampling period two individual experts analysed the zooplankton samples taken from the monitoring database and a third expert analysed the samples collected in 2011 and 2012. To ensure comparable data to the highest degree possible current HELCOM guidelines were adhered to (HELCOM, 1988).

Sample collection was carried out using a 90  $\mu\text{m}$  zooplankton net in a single haul from the bottom (5 m up from sediment) of the water column to the surface, approximately 20 m and 80 m for station B3 and C14, respectively. Zooplankton samples were preserved with formaldehyde or Lugol's solution and the analysis was carried out in the laboratory using a stereomicroscope (Leica). A sub-sample was taken and all specimens were determined in the categories described below. Zooplankton counts (abundances) were converted into wet biomass ( $\text{g m}^{-3}$ ) using standard wet weights (Hernroth, 1985) where available. Data presented here are either abundances, wet biomasses, or relative values of these at a single sampling event. Abundant zooplankton members were classified at the genus level and those that were irregular members or represented relatively small biomasses were classified as 'other' for the purpose of this paper. The abundant genera were of the phylum Rotifera (*Keratella* and *Synchaeta*) and the subphylum Crustacea (copepods *Acartia*, *Eurytemora* and *Limnocalanus*, and cladocerans *Bosmina*, *Cercopagis* and *Daphnia*). Those grouped together as 'other' included: other members of the subphylum Crustacea (copepods: including Cyclopoida, Harpacticoida and unclassified specimens; and cladocerans: *Evadne*, *Pleopsis*, and *Podon*). It also includes members of the phyla Mollusca (*Bivalvia* and *Gastropoda*), Protozoa (*Radiosperma* and *Tintinnopsis*) and Rotifera (*Euchlanis* and *Polyarthra*). Since our sample hauls started at approximately 5 m above the bottom sediment surface some of the infrequent or low biomass members include meroplankton (*Bivalvia* and *Gastropoda*) and near-bottom (Harpacticoida) species.

Canonical analysis of correspondence (CCA) was used to link community composition to environmental factors. Environmental

**Table 1**

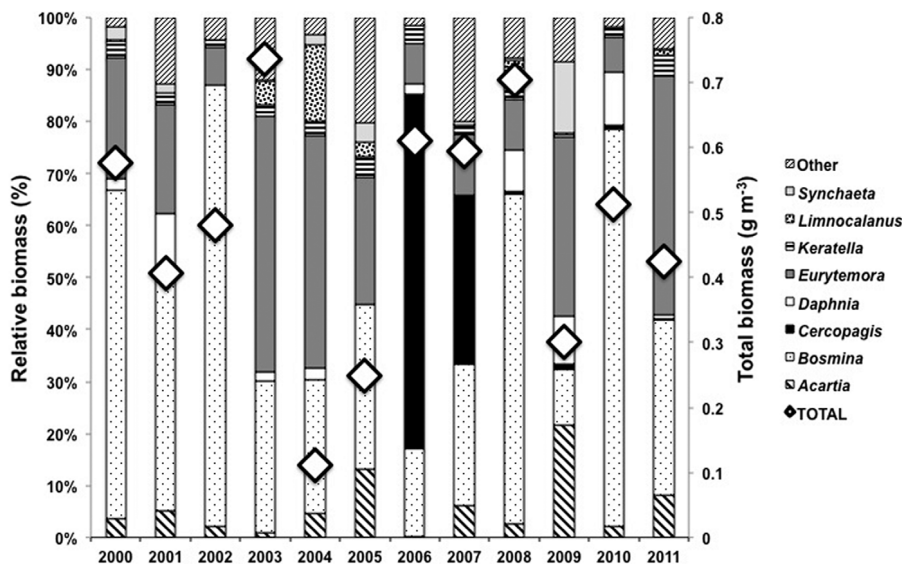
Bothnian Bay and Bothnian Sea stations sampled in this study, number of yearly sampling events and percentage of sampling events during 'summer months' (June–September). Percentage wet biomass of *C. pengoi* at stations other than C14 and B3 is indicated.

Station	Sampling period	Coordinates	Sampling events (mean per year)	Sampling events during 'summer months' (%)	Records of <i>C. pengoi</i>		
					Year	Month	Wet biomass (%)
C14 <sup>a,c</sup>	2000–2012	62° 05.99' 18° 32.91'	4	64	Multiple occurrences, Table 2 and Fig. 3		
OS 2 <sup>c</sup>	2011–2012	62° 13.01' 18° 47.95'	2	100	2011	August	1.20
					2012	August	2.26
C3 <sup>a,c</sup>	2000–2011	62° 39.17' 18° 57.14'	4	71	2008	August	1.14
					2012	August	2.42
OS 4 <sup>c</sup>	2011–2012	62° 46.22' 19° 12.56'	2	100	2011	August	0.00
					2012	August	1.18
B3 <sup>a</sup>	2000–2011	63° 29.95' 19° 49.10'	5	66	Multiple occurrences, Table 2 and Fig. 2		
B7 <sup>a</sup>	2000–2011	63° 31.50' 19° 48.50'	5	62	2006	September (5th)	30.57
					2011	August	4.56
A13 <sup>a,c</sup>	2000–2012	64° 42.50' 22° 04.00'	4	66	None detected		
OS7 <sup>c</sup>	2011–2012	64° 49.50' 22° 20.49'	2	100	None detected		
OS5 <sup>c</sup>	2011–2012	65° 02.94' 22° 57.31'	2	100	None detected		
A5 <sup>a,c</sup>	2000–2012	65° 10.00' 23° 14.00'	4	72	None detected		
RA2 <sup>b</sup>	2007–2011	65° 43.80' 22° 26.80'	6	63	2010	June (9th)	0.39

<sup>a</sup> Stations sampled in UMF-based monitoring program 2000–2011.

<sup>b</sup> Stations sampled in UMF-based monitoring program 2007–2011.

<sup>c</sup> Detailed sampling program in 2011 and 2012 only, or in addition to UMF-based monitoring program.

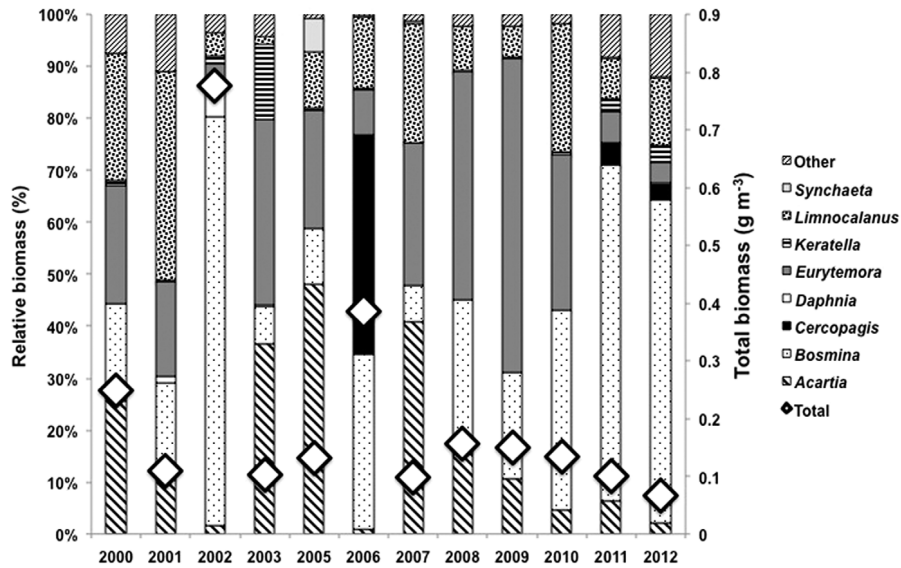


**Fig. 2.** Relative wet biomass (%) of major zooplankton groups and total biomass (large diamonds on secondary axis) during the years 2000–2011 at coastal station B3. The samples presented here represent all records of *Cercopagis* at this station during this period and were almost exclusively collected in August (Table 2). Comparative years without *Cercopagis* occurrence were selected in August of the given year. A single sampling event per year is shown.

data from stations B3 and C14 (temperature, salinity and chlorophyll *a*) were included as well as biomass of the main zooplankton contributors (*Acartia*, *Bosmina*, *Cercopagis*, *Eurytemora*, *Limnocalanus* and *Synchaeta*). Biomasses were fourth root transformed. Two temperature factors were included in the analysis; firstly those water temperatures at the specific sampling event (Table 1), and secondly mean air temperatures from the region that were available as daily mean values for the sampling period. The analyses were performed with PAST 3.1 (PALaeontological Statistics, Oslo, Norway<sup>o</sup>).

An analysis of similarities (ANOSIM) was applied to test the difference between community composition in pre-invasion, invasion and post-invasion phases (defined in our data set by the major invasion years of 2006/2007, further detail below). A matrix based on Bray–Curtis similarity of fourth-root transformed and standardised biomasses from stations B3 and C14 was used.

A comparison of the zooplankton community across the Bothnian Bay and Bothnian Sea was carried out using an analysis of similarity (ANOSIM) to test differences between stations and a SIMPER procedure was used to identify the major contributors



**Fig. 3.** Relative wet biomass (%) of major zooplankton groups and total biomass (large diamonds on secondary axis) during the years 2000–2012 (excluding 2004) at offshore station C14. The samples presented here represent all records of *Cercopagis* at this station during this period and were collected in August and September (Table 2). Comparative years without *Cercopagis* occurrence were selected from August or September, where possible. A single sampling event per year is shown.

**Table 2**

Summer sample collection at stations B3 and C14 (Y indicates sampling carried out). Recordings of *C. pengoi* in the collected sample (\*) and **bold text** indicates samples used in annual comparisons. Samples in which <sup>2</sup> is indicated represent two independent sampling events, usually at opposite extremes of the month, with environmental data for the later sampling occasion shown. Temperature (°C), salinity (recorded as practical salinity units) and chlorophyll *a* (mg m<sup>-3</sup>) are given for sampling occasions used in annual comparisons and correspond to averages over the top 10 m.

	B3	00	01	02	03	04	05	06	07	08	09	10	11	12
June		Y		Y		Y		Y <sup>2</sup>	Y	Y	Y	Y <sup>2</sup>		Y <sup>2</sup>
Temp.		6.2		10.8		10.5		13.0	12.2	12.0	10.3	8.7		11.8
Salinity		4.0		3.5		3.6		3.6	3.6	3.4	3.8	4.3		3.5
Chl.		1.3		2.2		1.4		3.0	1.8	2.2	2.7	4.7		2.3
July		Y	Y <sup>2</sup>		Y				Y*	Y	Y			
Temp.		14.0	12.0		14.7				<b>16.0</b>	17.5	16.3			
Salinity		3.4	3.4		3.3				<b>3.8</b>	3.6	3.1			
Chl.		ND	2.1		1.4				<b>1.8</b>	2.0	1.4			
August		Y <sup>2</sup>	Y	Y	Y	Y	Y	Y*		Y*	Y*	Y*	Y*	Y*
Temp.		<b>16.0</b>	<b>14.4</b>	<b>16.9</b>	ND	<b>9.6</b>	<b>16.3</b>	<b>16.8</b>		<b>14.6</b>	<b>13.4</b>	<b>15.7</b>	<b>18.2</b>	<b>18.2</b>
Salinity		<b>2.8</b>	<b>3.3</b>	<b>3.6</b>	ND	<b>4.6</b>	<b>3.4</b>	<b>4.0</b>		<b>3.6</b>	<b>4.0</b>	<b>3.4</b>	<b>3.6</b>	<b>3.6</b>
Chl.		<b>1.5</b>	<b>1.0</b>	<b>2.5</b>	<b>1.2</b>	<b>0.8</b>	<b>1.9</b>	<b>1.4</b>		<b>4.8</b>	<b>3.3</b>	<b>2.6</b>	<b>1.3</b>	<b>1.3</b>
September			Y	Y			Y		Y		Y	Y	Y	Y
Temp.			13.3	14.1			11.7		9.6		10.2	11.5	15.4	
Salinity			2.7	4.0			3.9		4.4		5.2	3.8	3.5	
Chl.			ND	2.6			2.5		3.1		1.9	3.1	3.9	
C14		00	01	02	03	04	05	06	07	08	09	10	11	12
June				Y	Y		Y	Y	Y	Y <sup>2</sup>	Y	Y <sup>2</sup>		Y
Temp.				9.4	10.6		8.7	14.0	12.0	14.0	8.7	11.6		8.9
Salinity				5.2	5.4		5.1	4.7	5.1	5.2	5.4	5.1		5.2
Chl.				1.1	0.8		2.3	1.9	0.7	1.4	1.3	1.1		1.2
July		Y	Y	Y		Y				Y	Y		Y	Y
Temp.		11.5	13.7	19.8		16.6				17.1	13.8		14.7	12.9
Salinity		5.2	4.7	4.7		5.1				5.1	5.3		5.3	4.2
Chl.		1.1	0.7	0.8		1.5				2.5	2.0		1.9	1.9
August		Y	Y		Y					Y	Y	Y <sup>2</sup>	Y*	Y*
Temp.		<b>12.8</b>	<b>15.3</b>		<b>18.8</b>					<b>15.2</b>	<b>14.9</b>	<b>13.9</b>	<b>16.8</b>	<b>16.9</b>
Salinity		<b>5.2</b>	<b>4.4</b>		<b>5.3</b>					<b>4.9</b>	<b>5.0</b>	<b>5.2</b>	<b>5.2</b>	<b>3.7</b>
Chl.		<b>1.2</b>	<b>0.7</b>		<b>0.7</b>					<b>2.0</b>	<b>2.3</b>	<b>1.2</b>	<b>0.4</b>	<b>1.9</b>
September				Y			Y	Y*	Y				Y	
Temp.				<b>17.5</b>			<b>13.5</b>	<b>18.7</b>	<b>10.7</b>				16.4	
Salinity				<b>4.8</b>			<b>5.0</b>	<b>5.0</b>	<b>5.0</b>				4.8	
Chl.				<b>0.9</b>			<b>2.1</b>	<b>1.2</b>	<b>1.8</b>				2.6	

to any dissimilarity. Data from 2007 onwards were used in order to include station RA2 in the analysis (sampling at RA2 was only initiated in 2007, Table 1). The input was a matrix based on Bray–Curtis similarity of fourth-root transformed and standardised biomasses.

ANOSIM and SIMPER analyses were run with the program Primer 5.0 (Plymouth Marine Laboratory).

Total biomasses at different stations were compared using an ANOVA. Tukey tests for unequal  $n$  were performed for subsequent multiple comparisons. The analyses were performed with Statistica 6.0. Comparison over the whole period, excluding station RA2, which was only sampled from 2007 onwards, was carried out and an identical analysis was applied on data post-2007 in order to include comparable information from station RA2.

To determine if *C. pengoi* was utilised as a food resource by pelagic planktivorous fish in the Gulf of Bothnia three-spined sticklebacks (*Gasterosteus aculeatus*) were collected in August 2011 and 2012. A night-time (22.00–04.00) surface trawl haul with a head-rope height of 15 m was taken between neighbouring stations. This procedure produced four independent fish samples, two representative of each basin (Bothnian Sea and Bothnian Bay). The following trawls were performed: trawl 1 (trawl between C14 and OS2, Fig. 1), trawl 2 (C3–OS4), trawl 3 (A13–OS7) and trawl 4 (OS5–A5). All four trawls were carried out during 2011 but only trawl 1 and trawl 4 were repeated in 2012. The collected fish were stored on ice prior to freezing in the laboratory. The stomach contents of 20–22 individuals from each sampling location were individually analysed and individual fish size was recorded. Prey items comprised of the following taxonomic groups: *Bosmina* sp, cyclopoid copepods, calanoid copepods, Ostracoda, and *C. pengoi*. In addition, terrestrial winged insects were found in some stomachs and these were classified as surface insects. Where abundant enough, the length of 10 prey from each category were measured. The lengths of the prey were transformed to dry weight using weight–length relationships (Bottrell et al., 1976; Dumont et al., 1975; Persson et al., 1996) and data are reported as relative percentages of total stomach content biomass. For *C. pengoi* a standard individual dry weight of 20  $\mu\text{g}$  was used (Gorokhova et al., 2004). Since there is a great variation in *C. pengoi* size and biomass in different environments it should be noted that using 20  $\mu\text{g}$  could represent an underestimation of relative *C. pengoi* contribution to stickleback diet. However, this standard value was used, despite a mean value of 43  $\mu\text{g}$  being determined in our 2011/2012 samplings. Because our studies were not targeted directly towards *C. pengoi*, the stage and sex identification of *C. pengoi* was not carried out and therefore the sample number on which this value was calculated was extremely low.

Although presence of *C. pengoi* was first reported in the Bothnian Sea as early as 1999 (Leppäkoski et al., 2002) it was not until 2006 (and 2007 at B3) that it was first detected for these specific stations. In the data we present here we describe this as our 'invasion peak'. Any data collected pre-2006 is described as 'pre-invasion' and data collected post-2006 is described as 'post-invasion'.

### 3. Results

#### 3.1. Occurrence of *C. pengoi* at sampled stations within the Gulf of Bothnia

*C. pengoi* were regularly found at stations B3 and C14 (Bothnian Sea), whereas only fleeting presence of *C. pengoi*, or a complete absence, was detected at the other sampled stations (Table 1). Thus only stations B3 and C14 are presented in detail. *C. pengoi* was first detected at stations B3 and C14 in 2006 and with the exception of the B3 sampling event in July 2007 (July 31st) and the C14 sampling event in 2006 (September 3rd) all other encounters with *C. pengoi*

were during the month of August. Where available, data from August has been used in all of the following community composition comparisons (to standardise seasonal effects as much as possible) and the presented data only represent a single sampling event each year (Table 2, Figs. 1 and 3). Interestingly, in 2010 *C. pengoi* was recorded at the extremely northerly Bothnian Bay coastal station RA2 (Table 1), although not at any other Bothnian Bay station.

#### 3.2. Potential impact of *C. pengoi* in Bothnian Sea coastal waters

The coastal station (B3) zooplankton community was dominated by *Bosmina* and *Eurytemora* between the years 2000 and 2005 (pre-invasion), jointly making up 56%–92% of the relative wet biomass. However, during 2006 and 2007 (invasion peak) *C. pengoi* became an abundant member of the zooplankton community (32%–68% relative wet biomass) and *Bosmina* and *Eurytemora* were depleted to 25%–39% relative wet biomass (Figs. 2 and S1). Despite the detection of *C. pengoi* in subsequent years (2008–2011, post-invasion) it was only recorded at low relatively percentages of the overall zooplankton wet biomass ( $\sim 1\%$ ) and *Bosmina* and *Eurytemora* were again the dominant members of the community, representing 45%–83% relative wet biomass (Figs. 2 and S1). The number of individual *C. pengoi* encountered ranged between 6–59  $\text{m}^{-3}$  during years with relatively minor abundances and 4006–7030  $\text{m}^{-3}$  during the peak invasion period (Table S1, see Appendix A). Furthermore, the 2004 and 2005 sampling occasions (those directly prior to the invasion period) had the lowest recorded total zooplankton biomasses of all examined years. The years of major *C. pengoi* invasion (2006 and 2007) had larger total zooplankton biomasses, however the years of invasion were on the whole not above average in total biomass when compared to data for the whole period examined (Fig. 2).

#### 3.3. Potential impact of *C. pengoi* in Bothnian Sea offshore waters

Offshore station (C14) also showed a peak *C. pengoi* biomass during 2006. With the exception of 2002 (a warm August, similar to 2006), the invasion peak showed the highest total zooplankton biomass, an increase somewhat representative of the *C. pengoi* biomass alone. Station C14 zooplankton community was generally dominated by *Acartia*, *Bosmina*, *Eurytemora* and *Limnocalanus* during non-invasion years (Fig. 3).

Wet biomasses of *Acartia* were most strongly reduced at peak *C. pengoi* occurrence (Fig. S2, see Appendix A). During the invasion peak of 2006 *Acartia* (and to a lesser extent *Limnocalanus*) abundances were reduced, however *Eurytemora* abundances appeared unaffected and *Bosmina* abundances increased (Fig. S3, see Appendix A). Interestingly this trend was not apparent in the biomass data (Fig. S2, see Appendix A), suggesting that fewer but larger *Limnocalanus* and more but smaller *Bosmina* individuals were present during this invasion period. The number of individual *C. pengoi* encountered ranged between 6–17  $\text{m}^{-3}$  during years with relatively minor abundances and 2717  $\text{m}^{-3}$  during the invasion peak (Table S1, see Appendix A). No data is presented for station C14 in 2004 as no comparable sampling was carried out.

#### 3.4. Environmental drivers of zooplankton community.

Canonical analyses of correspondence indicated that the first axis accounted for most of the variance and was driven by temperature and salinity (Table 3). The analysis indicated that *Cercopagis* was strongly favoured by higher temperature and lower salinity, *Bosmina* was positively influenced by higher temperature, *Limnocalanus* was positively affected by higher salinity and *Synchaeta* by lower salinity (Table 3). Water temperature at individual sampling events, albeit few in number, showed no significant trends and the more detailed air temperature values are referred to here.

**Table 3**

Summary of CCA analysis on environmental variables and zooplankton genera for stations B3 and C14 (2000–2012) and scores of environmental and biological variable on the two first axes.

	Axis 1 (88.6%)	Axis 2 (11.4%)
Temperature	0.588	0.209
Salinity	−0.426	0.371
Chlorophyll <i>a</i>	0.180	−0.339
<i>Acartia</i>	−0.298	−0.949
<i>Bosmina</i>	1.351	0.307
<i>Cercopagis</i>	3.323	1.640
<i>Eurytemora</i>	0.147	−0.084
<i>Limnocalanus</i>	−1.224	1.433
<i>Synchaeta</i>	−0.497	−1.543

### 3.5. Zooplankton biomass in pre-, during and post-invasion periods

The comparison between zooplankton biomasses during pre-invasion, invasion and post-invasion periods did not show any clear distinctions. The global ANOSIM was significant but there was only weak distinction between the three periods (B3: global  $R = 0.399$  and  $p = 0.008$ ; C14: global  $R = 0.233$  and  $p = 0.058$ ; B3 and C14 pooled together global  $R = 0.222$ ,  $p = 0.01$ ).

### 3.6. Similarities and differences in zooplankton community between basins and habitat type

Stations showed between 67% and 80% similarity in zooplankton community composition across the summer sampling events (Table S2, see Appendix A). The similarity at offshore Bothnian Bay stations was slightly lower than at offshore Bothnian Sea stations and *Limnocalanus* and *Eurytemora* were mainly responsible for observed similarities in offshore waters (Table S2, see Appendix A). At the two coastal stations examined more diverse genera were responsible for the similarities (Table S2, see Appendix A). *Acartia*, *Bosmina* and *Evadne* were the major drivers of differences in offshore waters, although *Daphnia* was a major contributor at the most northerly station A5. In coastal waters the major drivers were *Daphnia*, *Acartia* and *Synchaeta*.

The comparison between stations showed clear distinctions. The global ANOSIM was significant showing that zooplankton community composition at offshore stations in the Bothnian Sea differed most strongly from the stations in the Bothnian Bay. The same trend was observed between the two coastal stations in these basins (Table S3, see Appendix A).

### 3.7. Spatial and habitat variation in total zooplankton biomass

Comparisons of total biomass showed significant differences between stations (ANOVA  $p < 0.001$ ). Throughout the whole period, total biomass was higher at station C14 compared to C3, A13 and A5 ( $p < 0.05$ ), and the highest at station B3 compared to all other stations ( $p < 0.05$ ). From 2007 onwards, where station RA2 was included in the analysis, station RA2 was the only station showing significantly different (higher) total biomass ( $p < 0.001$ ).

### 3.8. Contribution of *C. pengoi* to stickleback diet in the Gulf of Bothnia

Sticklebacks from more southerly trawls were on average slightly larger than those collected in more northerly trawls and empty stomachs were only encountered at relatively low frequency at one station, and discarded from further analysis (Table S4, see Appendix A). *C. pengoi* were recorded in the stomachs of sticklebacks from our two most southerly sites in the Bothnian Sea (Trawl 1 and 2). At trawl 1 site, *C. pengoi* was recorded in 95% and 86% of the stickleback stomachs examined in 2011 and 2012,

respectively, whereas corresponding occurrence was 33% at the trawl 2 site (2011). At the more northerly sites in the Bothnian Bay *C. pengoi* was not found in stickleback stomachs. At sites where *C. pengoi* was found in diets, it contributed an average of 12%–17% of relative stomach content (Table S4, see Appendix A).

## 4. Discussion

The results presented here represent data collected during the summer months (June–September) over a 12–13 year period directly following the year in which *C. pengoi* was first reported in the Bothnian Sea region (1999) (Leppäkoski et al., 2002). However, in the data we present here, for these specific stations, the earliest detection of *C. pengoi* was in 2006 and we describe this as our ‘invasion peak’; with data collected pre-2006 described as ‘pre-invasion’ and data collected post-2006 described as ‘post-invasion’. In total the two main stations examined were each sampled 72 times during this period and on 11 of these occasions *C. pengoi* was detected. The abundance of *C. pengoi*, and thus its relative biomass contribution varied greatly on the occasions it was detected. At its peak of invasion (2006), abundances represent the highest records currently presented in the literature for the Baltic Sea (Table S1, see Appendix A). While *C. pengoi* was detected in all post-invasion years at Bothnian Sea coastal station B3 it was only detected in 2011 and 2012 in post-invasion offshore waters (C14). With one exception (coastal station RA2), *C. pengoi* appeared completely absent in the Bothnian Bay.

The majority of the data is extracted from a long-term monitoring program and supplemented with more extensive sampling, examining whole food webs, during 2011 and 2012. The data we present here are the most detailed up to date information available on the invasive cladoceran *C. pengoi* in the two most northerly basins of the Baltic Sea (Bothnian Sea and Bothnian Bay). It is also an important contribution to the relatively limited pool of information available on the zooplankton community in this region. Furthermore, the data presented traverse the current invasion limit of *C. pengoi*, an invasion that has arguably stalled or encountered a significant barrier within the geographical region of this study.

Although the data presented here are important certain issues must be considered when interpreting them. Firstly, data collected in the monitoring program and in the additional sampling (2011 and 2012) were not targeted specifically towards *C. pengoi*, having the primary purpose of detailing the zooplankton community. Secondly, the data in the monitoring database has been produced by two individuals and the extensive sampling during 2011/12 by a third. Thirdly, the population development of *C. pengoi* has been shown to exhibit pronounced seasonal dynamics (Bielecka et al., 2000; Gorokhova et al., 2000; Telesh et al., 2001) and distribution is often patchy (Svensson and Gorokhova, 2007). The relatively limited number of sampling events each year and the specific timing of them (determined by other factors than the monitoring of *C. pengoi*) may have resulted in community snapshots that are not representative of the entire season/year. Thus the sampling regularity does not allow detailed description of *C. pengoi* development and reproductive cycles, may not account for any potential clump formation of *C. pengoi*, and the graphical comparisons made between years (Figs. 2 and 3) are from single sampling events at the peak of summer each year (Table 2). It is therefore not possible to elaborate on the mechanisms behind the observed high *C. pengoi* abundances, is impossible to discuss *C. pengoi* population dynamics and caution should be exercised when exploring any detailed temporal patterns within this data. However, our sampling procedure is constant across all sampling events, all experts carrying out zooplankton analysis adhered to the current HELCOM guidelines, thus ensuring the best possible comparative data, our discussion of potential zooplankton

community change is strongly based on pre-, during and post-invasion periods that encompass multiple years, and the regular appearance of *C. pengoi* at certain stations (e.g. B3) and clear absence at other stations (e.g. A5) over such an extensive time period is in itself extremely informative.

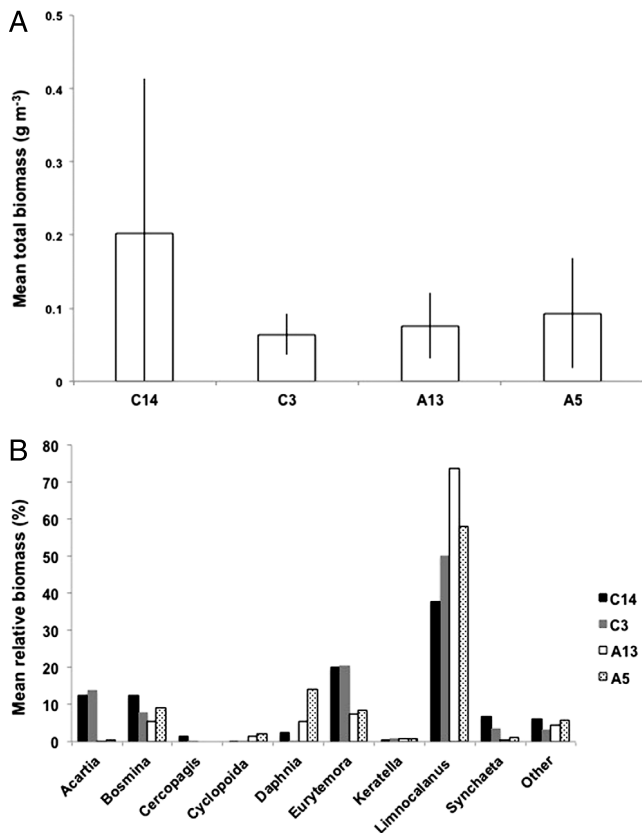
*C. pengoi* was detected regularly at sampling stations in the Bothnian Sea. It was detected in all post-invasion years at Bothnian Sea coastal station B3, indicating it has become a permanent member of the zooplankton community. Considering other records (Katajisto et al., 2013; Leppäkoski et al., 2002) and our own data at Bothnian Sea offshore station C14 it is also likely that *C. pengoi* is a permanent member of the community, however our data alone lack the sampling regularity to confirm this with absolute certainty. *C. pengoi* was also detected irregularly at more northerly offshore Bothnian Sea station C3 (2008 and 2012) in addition to OS4 in 2012, suggesting it is present but indicating that more detailed studies of the region are required, with particular focus on determining the current invasion limit.

The abundances of *C. pengoi* at Bothnian Sea coastal (B3) and offshore (C14) stations during the invasion-peak were extremely high, higher than reports from more southerly sites (Svensson and Gorokhova, 2007; Telesh and Ojaveer, 2002); sites where clear impacts on the zooplankton community were recorded (e.g. Ojaveer et al., 1998 and Ojaveer et al., 2004). Abundances found during our invasion-peak would undoubtedly have had an ecological impact and it is quite possible that during the invasion-peak prey abundance would have been depleted to an extent that limited further growth of the *C. pengoi* population. Unfortunately, such impacts and any carryover effects cannot be determined from this data since; for example, subsequent zooplankton monitoring was carried out two and eight months after the peak invasion reported in 2006 for B3 and C14, respectively. A targeted sampling strategy would be required and should be carried out. Weekly sampling during the warm summer period in which population development of *C. pengoi* (e.g. Ojaveer et al., 2004), and other predatory cladocerans (e.g. Lesutienė et al., 2012), takes place would be necessary. Such studies have been carried out in more southerly regions of the Baltic Sea and would be extremely valuable in this region, in particular traversing the current invasion front. This would determine factors such as prey abundances and/or temperature that may control *C. pengoi* populations. It would also determine the direct impact this invasive species has on the zooplankton community and possible food web effects. Furthermore this information would assist monitoring programs in the region, which currently potentially underestimate or omit the presence of this invasive species. Thus it could be helpful in defining clearer sampling strategies that could best incorporate this invasive species.

Despite regular sampling at the Bothnian Bay offshore stations (A5 and A13) *C. pengoi* was never detected during this thirteen-year period, neither was it detected in three-spined stickleback diet during our 2011 and 2012 studies. Our data suggest that *C. pengoi* is not present in Bothnian Bay offshore waters, at least not at the stations sampled in this study. In a recent study it was however reported in two of nine sampling years in the Bothnian Bay at a slightly more southerly location than our own stations (but not further north), with the authors concluding it probably occurs irregularly in this basin (Katajisto et al., 2013). Such conclusions were supported (although not exclusively) by the relatively low abundance, or absence, of eggs in sediments of the Bothnian Bay (Katajisto et al., 2013). Our data on the current distribution of *C. pengoi* are in general agreement with this recent study. The single record we report here of *C. pengoi* at Bothnian Bay coastal station RA2 (<1% total wet biomass, 16 individuals), an extremely northerly station (water temperature 10.6 °C and salinity 1.3), is however intriguing, especially in light of the apparent importance of coastal regions for *C. pengoi* recruitment (Katajisto et al., 2013).

Where *C. pengoi* was detected in the Bothnian Sea, maximum abundances were recorded during August 2006 (Table S1, see Appendix A), a warm month (mean monthly air temperature being above 18 °C, based on records from Holmön SMHI monitoring station) and an overall warm summer. Despite the August mean monthly temperature in 2007 being lower than other years *C. pengoi* was still abundant at coastal station B3, possibly as a result of the high population density in the previous year, although clearly conditions were also suitable for hatching and development. This however was not the case at offshore station C14. This difference between the stations could be due to the water at the coastal station (16.1 °C) being warmer than the offshore station (10.7 °C) at the 2007 sampling events. Furthermore, our analysis of environmental data indicate that temperature, and to a lesser extent low salinity, have a strong positive effect on *C. pengoi* biomass, a finding that is in keeping with seasonal studies in more southerly locations. Temperature alone however cannot be the only controlling factor for *C. pengoi*. In 2002 although the mean August air temperature (Holmön SMHI) was higher even than 2006, *C. pengoi* was apparently not detected during any sampling event that year (although the sampling regularity may also play a part in this). However, such anomalies have been recorded previously where high abundances of *C. pengoi* have been detected at apparently unfavourable temperatures (Ojaveer et al., 2004). It is clear though that the peak abundance of *C. pengoi* is somewhat temperature dependent, with highest abundances generally falling in August when the local mean monthly air temperatures peak (mean of 15.5 °C across the studied years). Considering the warmer climate in its native Ponto-Caspian region it is somewhat unsurprising that temperature has an important role in the invasion success of *C. pengoi*, especially at such northerly latitudes. This in itself is an important area of research considering the northern regions of the Baltic Sea are predicted to increase in summer surface water temperature by as much as 4 °C due to global climate change (e.g. Viitasalo, 2012 and Andersson et al., 2015). This would alter the available growth period for *C. pengoi* (e.g. altering diapause, reproductive cycles and egg hatching success), influence its metabolic needs and the abundances and composition of prey species; while other concurrent changes (such as increased freshwater inflow, Viitasalo, 2012 and Andersson et al., 2015) are unlikely to be potent deterrents (Panov et al., 2007). Other factors such as the development of suitable prey species Ojaveer et al. (2004) are also important, and potentially interlinked. In our study the statistical analysis of environmental factors indicated that the biomass of *Bosmina* (on which *C. pengoi* has been shown to feed) was also very much dependent on temperature and reliance on an abundance of this prey species may also be occurring.

When detected in high abundances, *C. pengoi* appeared to influence the zooplankton community, although any peak invasion associated changes in the community appear relatively temporary when examined over longer temporal periods (Figs. 2, 3, 4 and S3). We cannot exclude the possibility that variation in predation pressure from other forms of predators (e.g. fish or mysids) may also have contributed to the changes in the native zooplankton community. However, considering the high abundances of *C. pengoi* that coincided with recorded changes in the native zooplankton community it seems likely that *C. pengoi* had an impact, as suggested elsewhere (Gorokhova et al., 2005; Lehtiniemi and Gorokhova, 2008; Ojaveer et al., 2004). It also appears that the zooplankton communities at the studied stations have an element of resilience (e.g. Bernhardt and Leslie, 2013 and Ojaveer et al., 2011), returning to a similar pre-invasion structure once the main peak of invasion (2006/2007) had passed. This however could somewhat be an artefact of the sampling carried out and may also represent the strong importance of temperature in the development of *C. pengoi* populations. Although differences in the zooplankton community



**Fig. 4.** Comparison of zooplankton biomass and community at offshore stations in the Gulf of Bothnia (2000–2012). A. Mean total biomass ( $\text{g m}^{-3}$ ) at offshore stations in the Bothnian Sea and Bothnian Bay during summer months ( $n = 36, 34, 33$  and  $35$  for stations C14, C3, A13 and A5, respectively). B. Mean relative biomass (%) of major zooplankton community members at the above stations.

were apparent between pre-, during- and post-invasion periods, no clear separation could be assigned. This is most likely due to the sampling strategy having been devised for general zooplankton analysis and not for the specific purpose of monitoring *C. pengoi* population fluctuations. However, changes in the native zooplankton community during the invasion peak differed between the Bothnian Sea coastal and offshore stations. At the coastal station (B3), *Bosmina* was the dominant zooplankton with *Eurytemora* being the other most dominant member of the community prior to the 2006 invasion. Both were depleted during the peak invasion period, despite temperature also having a positive influence on *Bosmina* biomass (as well as *C. pengoi*). In contrast, at the offshore station (C14), where *Bosmina*, *Eurytemora*, *Acartia* and *Limnocalanus* constituted the dominant community members prior to the invasion, *Bosmina* was not depleted while *Acartia* was. Interestingly, our biomass data indicates that larger (adult) *Bosmina* may still have been depleted, with the apparent increase in abundance being constituted of high numbers of smaller (juvenile) individuals. This depletion of adult *Bosmina* may also offer explanation for the reduced biomass of *Bosmina* in offshore waters during the post-invasion period (Fig. S2, see Appendix A). Such trends offer support to published data that indicate *C. pengoi* to be an opportunist generalist predator capable of feeding on a wide range of zooplankton prey (e.g. Holliland et al., 2012 and Ojaveer et al., 2004).

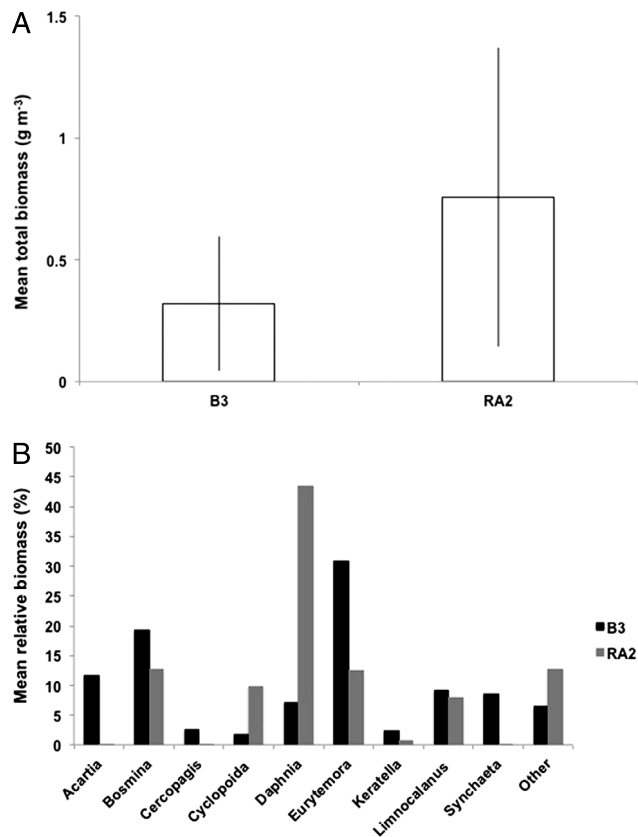
Changes in the food web structure forced by invasion will likely influence productivity at higher trophic levels, such as fish. Previous studies on *C. pengoi* have indicated that this invasive species may not only alter the food web structure (by predation) but may also induce competition for prey with mysids and fish (Holliland et al., 2012; Lehtiniemi and Lindén, 2006). While *C. pengoi* has been

shown to have a dietary overlap with zooplanktivorous fish in the Baltic Sea the potentially negative effects may be counterbalanced by the opportunistic predatory nature of *C. pengoi* (Holliland et al., 2012; Kotta et al., 2006). By feeding on other food sources, energy and nutrients previously unavailable to higher trophic levels may be accessed by predators capable of capturing and ingesting *C. pengoi* (e.g. zooplanktivorous fish). In our study it is clear that where *C. pengoi* exists, as in our southerly sampling areas, it was frequently ingested by three-spined sticklebacks (33%–95% frequency occurrence). Sticklebacks appear to preferentially feed on *C. pengoi* as they are present at a higher relative biomass in the stomachs (12%–17%) than in the water column (4.5%) at concurrent sampling events, as seen elsewhere (Kotta et al., 2006; Peltonen et al., 2004). Such changes in resource use by the zooplankton community and for higher trophic levels, plus the consequent alterations in the flow of energy in the food web could be especially important considering climate change predictions for the Gulf of Bothnia (Andersson et al., 2015).

Records of *C. pengoi* at Bothnian Sea coastal (B3) and offshore (C14) stations generally occurred at the sampling occasion (8 out of 11) for which the highest level of total zooplankton community biomass (and usually abundance) for that year were detected. This trend could highlight an important factor controlling the spread of *C. pengoi*. Since first being detected in the Baltic Sea in 1992 (Gulf of Riga, Ojaveer and Lumberg, 1995) there has been a rapid geographical range expansion of *C. pengoi*, including records in the northern Bothnian Sea by 1999 (a seven year period). However, in the following circa 13 years the range of *C. pengoi* appears not to have increased markedly in a northerly direction. It also appears that the Bothnian Bay has remained somewhat impenetrable with the only currently published records representing occasional detection in the water column and relatively low numbers of eggs in the sediment in the southern Bothnian Bay (Katajisto et al., 2013), plus the single record in this paper itself (coastal station RA2). Nutrient status (carbon:nitrogen and nitrogen:phosphorus ratios) of bulk offshore zooplankton biomass (potential food resource for *C. pengoi*) did not differ between stations (extensive 2011/12 sampling, Carolyn Faithful, Umeå University, pers com), indicating that resource quality is not a limiting issue. However, one notable change was the general decline in mean total zooplankton abundance and biomass at more northerly Bothnian Bay stations. This limitation of food availability could be a significant factor controlling *C. pengoi* invasion success (Telesh and Ojaveer, 2002).

At offshore stations in the Bothnian Bay (A13 and A5), where *C. pengoi* was not detected in our study, mean total zooplankton biomass was much lower than at Bothnian Sea station C14 (Fig. 4(A)). In addition to this decrease in total potential food resource (total zooplankton biomass), changes in the relative community composition were also recorded. At the offshore Bothnian Bay stations the relative proportion of both *Acartia* and *Eurytemora*, known prey for *C. pengoi*, decreased compared with the offshore Bothnian Sea stations (each decreasing ~12%, to <0.5% and <9% mean total biomass, respectively; Fig. 4(B)). Moreover, the relative proportion of *Daphnia* and *Limnocalanus*, two species for which the suitability as prey for *C. pengoi* has been poorly determined in the Baltic Sea (especially in these northern reaches), increased by as much as 13% and 35%, respectively, to represent as much as 14% and 74% of the total zooplankton biomass (Fig. 4(B)). Considering literature from other aquatic ecosystems that have been invaded by *C. pengoi* it is likely that *Daphnia* would be a suitable food resource (Laxson et al., 2003), however, *Limnocalanus* can likely be discounted as a possible resource due to its general residence in the colder and more saline deeper waters of the Baltic Sea, as opposed to *C. pengoi* generally being most abundant in warmer and less saline surface waters.

At coastal stations the trend was somewhat different, with higher total mean biomass recorded at the northerly Bothnian Bay



**Fig. 5.** Comparison of zooplankton biomass and community at coastal stations in the Gulf of Bothnia (2000–2011 for B3 and 2007–2011 for RA2). A. Mean total biomass ( $\text{g m}^{-3}$ ) at coastal stations in the Bothnian Sea and Bothnian Bay during summer months ( $n = 38$  and  $18$  for stations B3 and RA2, respectively). B. Mean relative biomass (%) of major zooplankton community members at the above stations.

station (RA2). At station RA2, at which *C. pengoi* was detected on a single occasion, the total mean biomass was higher than Bothnian Sea coastal station B3 (Fig. 5(A)). It was also higher than any of the offshore stations, supporting the suggestion that coastal regions could be important for *C. pengoi* recruitment (Katajisto et al., 2013), and possibly more susceptible to invasion. At the Bothnian Bay coastal station (RA2) there was however a stark decline in the relative biomass of zooplankton on which *C. pengoi* has been reported to feed (in the Baltic Sea literature), as compared to the coastal Bothnian Sea station (B3). Mean relative biomass decreases of *Acartia* (~12%, to <0.005%), *Eurytemora* (~31%, to ~12%) and *Synchaeta* (~9%, to <0.1%) were all recorded, while relative biomass of zooplankton of currently uncertain edibility for *C. pengoi* increased (*Daphnia* by ~36% and *Cyclopoida* by ~8%) at the Bothnian Bay station RA2 (Fig. 5(B)). Detailed studies on the suitability of resident zooplankton as prey items for *C. pengoi* in this region are clearly required, as well as studies to determine if total biomass (potential prey resource) may contribute to controlling the current invasion limits. Such factors would not be at odds with the apparent current distribution of *C. pengoi* (Katajisto et al., 2013; and our data) and could determine, at least in part, the success of this voracious predator and the potential for future range expansion in northerly areas of the Gulf of Bothnia.

Although temperature clearly plays a significant role in controlling *C. pengoi* population development, abundance and distribution it is also possible that insufficient biomass (Telesh and Ojaveer, 2002), in particular the biomass of suitable prey, could be responsible, at least in part, for the stalled invasion front of *C. pengoi* in the southern Bothnian Bay region. The Bothnian Bay exhibits low basal (bacterial and phytoplankton) productivity (Andersson et al., 1996,

2015), the knock on effects of which will be transferred to higher trophic levels such as zooplankton, preventing large biomass production. Consequently, limited potential prey resources (zooplankton abundance and biomass) and thus sheer nutrient and energy resources for growth and development could prevent population development of *C. pengoi*. As a facultative parthenogen *C. pengoi* gains significant advantages when invading new habitat. However, it is likely that should such resource limitation exist it would inhibit any potential population boom (via parthenogenesis) and prevent the completion of a sexual life cycle and the laying of eggs. Such a barrier would be well matched with the currently described distribution of both *C. pengoi* in the water column and sediment situated eggs (Katajisto et al., 2013; and our data), although further research, including experimental systems, is clearly required to confirm the specific controlling factor(s) influencing the invasive success and distribution of *C. pengoi* in the region.

In conclusion *C. pengoi* appears to be incorporated into and be a permanent member of the zooplankton community in the Bothnian Sea, however, it appears to be transient or absent in the Bothnian Bay. This paper presents zooplankton community composition data over a 12/13 year period and important information on the current extent of the *C. pengoi* invasion in the Gulf of Bothnia, a geographical region of the Baltic Sea in which *C. pengoi* (and zooplankton as a whole) has been somewhat overlooked. We report a single record of *C. pengoi* at an extremely northerly Bothnian Bay coastal station (RA2) and suggest total zooplankton biomass, in particular potential prey, as a possible contributor to the barrier responsible for this apparent longstanding geographical range constraint. Our data highlight some future perspectives and knowledge gaps, including: supporting the need for future research on coastal zones (Katajisto et al., 2013), the need for the determination of the current invasion boundary and clarification of the factors maintaining this boundary. They also indicate that this northern region of the Baltic Sea, traversing the invasion front, requires further research directed specifically towards *C. pengoi*. This would include studies on *C. pengoi* diet (e.g. edibility of *Daphnia* from the region), studies on possible competition and studies to examine if zooplankton community biomass, in particular suitable prey biomass, contributes to controlling the success of *C. pengoi*. Furthermore, such information could be extremely pertinent considering climate change predictions for the region that may directly (e.g. increased temperature) and indirectly (e.g. altered prey biomass due to temperature increase) liberate *C. pengoi* from factors currently constraining its range.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.rsma.2015.12.004>.

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