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Research Article

Distribution of the invasive calanoid copepod *Pseudodiaptomus marinus* (Sato, 1913) in the Belgian part of the North Sea

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Abstract

The population structure of the non-indigenous calanoid copepod *Pseudodiaptomus marinus* (Sato, 1913) in the Belgian part of the North Sea (BPNS) is reported for the first time. Detailed *P. marinus* abundance data including sex and age class of the individuals was gathered on a monthly basis from February 2015 to February 2016 at six sites within the BPNS and Belgian harbors. Relevant environmental variables were analysed to identify potential drivers explaining the population structure of *P. marinus* within the BPNS. The abundances found were unexpectedly high, with peak densities of up to 560 ± 163 ind.m^{-3}. Even though *P. marinus* was found in all stations sampled, large spatial and temporal differences were found in the abundance of this species. *P. marinus* population structure was best explained by water temperature and chlorophyll *a* concentrations, while salinity and concentrations of dissolved inorganic nitrogen did not influence the distribution. The reported high abundances of the species, especially in the harbor of Zeebrugge, together with the high relative abundances of copepodites indicate that the species is able to reproduce within the BPNS and Belgian harbors, possibly leading to an established, permanent population. It is crucial to study the distribution of this species for a longer period in order to determine the possible establishment of this species in the BPNS and consequences for local planktonic populations.

Key words: non-native species, population structure, environmental drivers

Introduction

Maritime transport across the oceans is leading to the spread and establishment of an ever increasing number of alien species in coastal and brackish environments (Reise et al. 1999; Sabia et al. 2015). Ballast water is a major vector of non-native planktonic species dispersion on a global scale (Williamson 1996; Gray et al. 2007). Some of these species manage to establish permanent populations in different environments away from their indigenous range as well as to expand their distribution through colonization or migration. The calanoid copepod *Pseudodiaptomus marinus* (Sato, 1913) is known as a serial invader, and it is seen as a potential pest species all over the world due to its resistance to unfavorable conditions and its tolerance of a wide range of salinities (2.5–38) and temperatures (5–28 °C) (Sabia et al. 2015).

Pseudodiaptomus marinus is found in tropical and temperate coastal zones, typically inhabiting transitional areas from fresh to hypersaline waters (De Olazabal and Tirelli 2011; Brylinski et al. 2012; Sabia et al. 2014; Lučić et al. 2015). *Pseudodiaptomus marinus* is an indigenous species of the Northwestern Pacific Ocean (Walter 1986), occurring in Japan, Russia, China, Thailand, Australia, South Korea and Mauritius. Nowadays the species is spreading fast, mostly by means of ballast water transport and trans-coastal currents, resulting in an almost worldwide distribution (Sabia et al. 2015). The first record of *P. marinus* outside its indigenous region was described

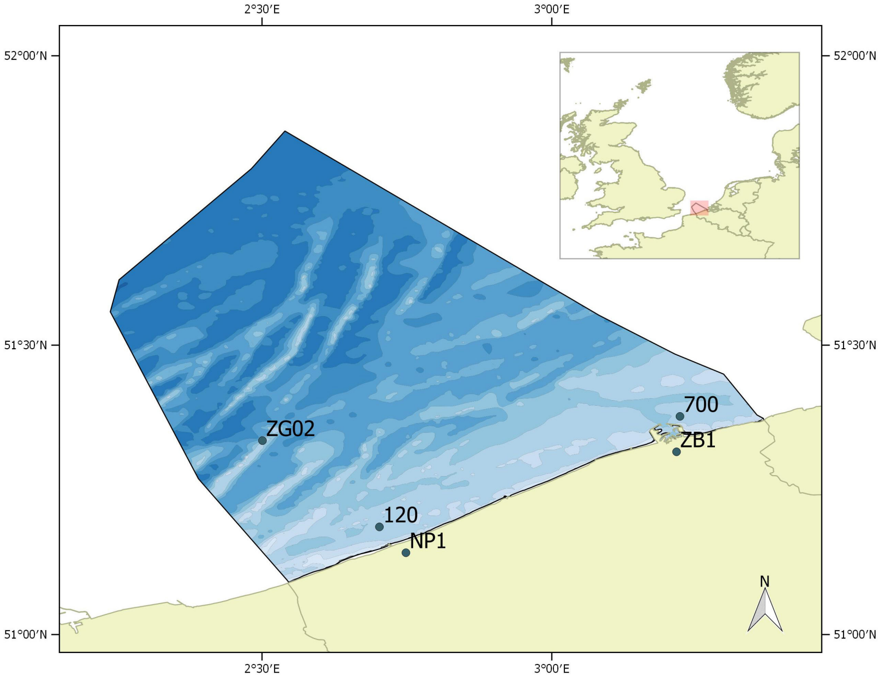

Figure 1. Location of stations sampled during the survey carried out in the Belgian part of the North Sea (BPNS). Harbors: Nieuwpoort (NP1) and Zeebrugge (ZB1); nearshore zone: station 120 and station 700; midshore zone: station ZG02 (geographic coordinates: Supplementary material Table S1).

by Jones (1966) in Hawaii, later extending its distribution towards the western coast of North America (Fleminger and Kramer 1988) and Baja California (Jiménez-Pérez and Castro-Longoria 2006). In Europe, this species has been recorded in the Adriatic Sea (De Olazabal and Tirelli 2011; Lučić et al. 2015), the French coast (Brylinski et al. 2012), the German Bight (Jha et al. 2013), the Netherlands (Rijkswaterstaat 2017; Jha et al. 2013) and the Iberian Peninsula (Albaina et al. 2016).

From this overview, it is clear that its introduction and establishment in the coastal areas of Europe is a recent and ongoing process whose consequences are not yet predictable (Sabia et al. 2015). Further data on the abundance and relative importance of *P. marinus* in zooplankton assemblages in invaded sites will add to the growing amount of information on its ecological role. Hopefully these data will lead to a better understanding of the possible impacts on native species and factors that may sustain the invasion of other areas (Sabia et al. 2015). Invasive species may disturb interactions between species and can cause local species extinctions leading to a cascading effect throughout the food web potentially even altering ecosystem functioning (Mack et al. 2000). The North Sea is a highly invaded area, where over 60% of the invasive species are known to disrupt multiple species or even the wider ecosystem (Molnar et al. 2008). A regular monitoring effort to look for invasive species in European coastal waters has been highlighted as an adequate prevention policy to minimize alien species introductions (Boxshall et al. 2007; Zenetos et al. 2010).

This paper reports for the first time the occurrence and population structure of the non-indigenous calanoid copepod *P. marinus* in the Belgian part of the North Sea (BPNS). The BPNS (Figure 1) is a semi-enclosed system with a northwesterly connection to the Atlantic Ocean through the English Channel (Sündermann and Pohlmann 2011). The input of brackish water from the Scheldt estuary along the border between Belgium and The Netherlands is also an important factor in the hydrology of the region (Nihoul and Hecq 1984). The BPNS is a shallow shelf sea, with a maximum depth of 35 meters on the Belgian continental shelf. Coastal waters in the BPNS are characterized by the lack of a thermocline due to strong tidal mixing (Otto et al. 1990).

In order to understand the ecological role of this serial invader, it is important to have detailed information on its spatial and temporal distribution. Zooplankton samples and environmental variables were collected monthly to evaluate the seasonal demographic structure of the population and assess which variables were potentially driving the patterns in the population structure of *P. marinus* within the BPNS.

Table 1. Distance based linear modelling (DistLM, Primer 6, PERMANOVA) results of a sequential test based on AICc values for the environmental variables dissolved inorganic nitrogen (DIN), chlorophyll *a* (chl *a*), temperature (temp) and salinity (sal). Prop. = portion of the explained variation in total *P. marinus* densities.

MARGINAL TESTS(res.df: 46)

Variable	SS(trace)	Pseudo-F	P	Prop.
log(DIN)	0.079069	0.028055	0.8673	0.00060951
log(chl *a*)	0.56851	0.20248	0.6665	0.0043824
temp	22.656	9.7336	0.0027	0.17464
log(sal)	0.68856	0.24546	0.6141	0.0053078

BEST SOLUTIONS: best result for each number of variables

AICc	R^2	RSS	No. Vars	Selections
42.776	0.17464	107.07	1	temp
44.367	0.18639	105.55	2	temp, log(chl *a*)
46.444	0.19158	104.87	3	temp, log(chl *a*), log(sal)
48.926	0.19187	104.84	4	temp, log(chl *a*), log(sal), log(DIN)

Material and methods

Zooplankton sampling

Zooplankton sampling was conducted on a monthly basis for one year (February 2015 to February 2016) at five stations in the nearshore and midshore area of the BPNS and in the ports of Zeebrugge and Nieuwpoort (Figure 1, Table 1). Triplicate zooplankton samples were collected as in Van Ginderdeuren et al. (2014) with a WP2 zooplankton net (70 cm diameter, 200 µm mesh size) fitted with a flow meter that was towed in an oblique haul from the bottom to the surface at each station. Zooplankton samples were fixed and stored in a 4% (final concentration) formaldehyde solution and were transferred to the laboratory for species identification and enumeration. In each sample, successive subsamples were taken until at least 100 calanoid copepods had been identified; if the sample consisted of > 100 calanoid copepods, the entire sample was identified.

Zooplankton identification

All calanoid copepods were identified to species level, and, for each *P. marinus* individual, the developmental stage was determined. Only *P. marinus* individuals of copepodite stage IV or older were included in analyses, as younger (i.e., smaller) stages might not be successfully sampled with the 200 µm mesh size of the WP2 net. Adult individuals were sexed. Zooplankton identification was carried out under a stereoscopic microscope (Leica MZ 10), and a microscope (Leica Dialux 20) was used for identification confirmation of *P. marinus* (Sato 1913). This species was identified following the keys of Brylinski et al. (2012). *Pseudodiaptomus marinus* shows minor morphological differences among different populations, more specifically in the number of minor setae on the endopod of the right fifth leg of the males (Walter 1986; Brylinski et al. 2012; Sabia et al. 2015). The general description of the *Pseudodiaptomus* genus was given by Walter (1986), and specific descriptions of *P. marinus* were given by Jones (1966), Grindley and Grice (1969) and Brylinski et al. (2012). Photographs of the specimens were taken by means of a Leica M205 stereomicroscope, and a Leica DM1000 microscope, both at the LifeWatch observatory, Flanders Marine Institute (VLIZ).

Physicochemical sampling

Water temperature and salinity were measured in situ with a CTD probe Seabird sbe25plus (Sea-Bird Scientific) at each station. Samples for nutrient analysis (i.e., dissolved inorganic nitrogen concentration, which is calculated as the sum of the concentrations of NH_4, NO_2 and NO_3) and chlorophyll *a* (chl *a*) analysis (a proxy of phytoplankton biomass) were collected at each station using a 5L Niskin bottle at 3 m below the water surface. Temperature, salinity, nutrient and pigment concentration data collected at the sea stations were provided by the LifeWatch observatory as part of the Flemish contribution to the LifeWatch ESFRI by Flanders Marine Institute (Flanders Marine Institute 2017a; Flanders Marine Institute 2017b), and the mode of processing is described by Mortelmans et al. (unpublished data).

Statistical analysis

DistLM (Linear Based Modelling) analysis (Primer 6, PERMANOVA) was performed on the Euclidean

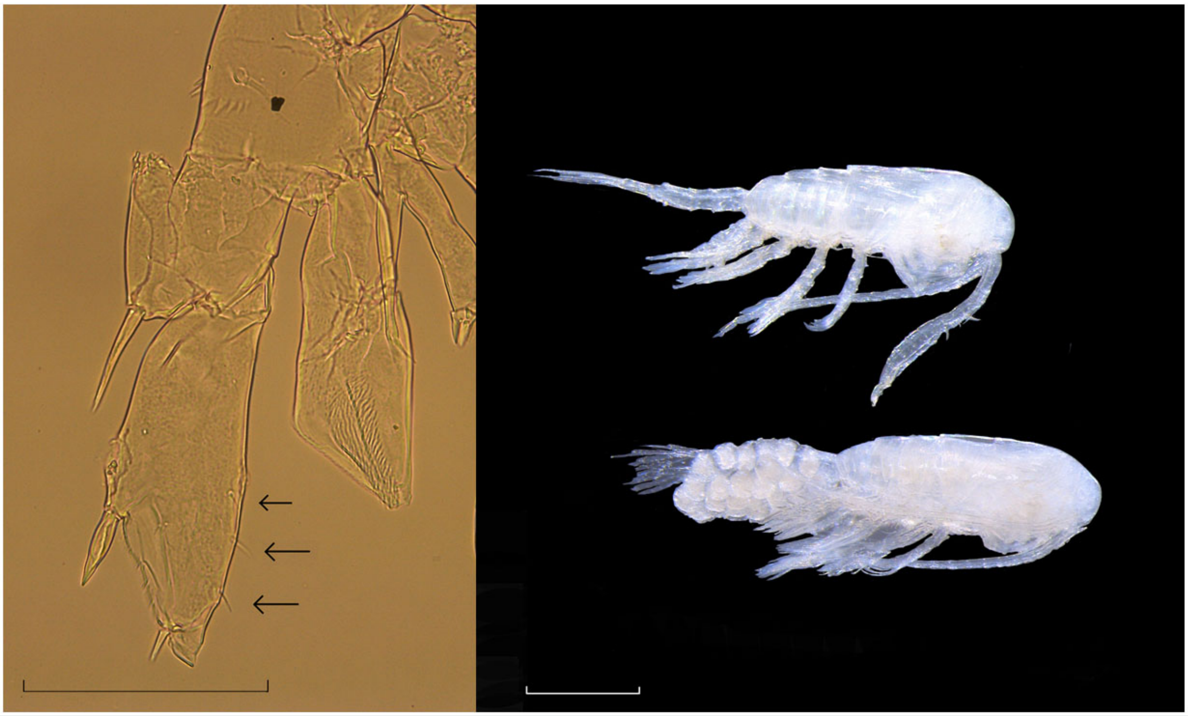

Figure 2. Left: *P. marinus* male: endopod of the right fifth leg, indicating the three minor setae characteristic for this subspecies (scale bar: 100 µm); upper right: male habitus, lateral view; lower right: gravid female habitus, lateral view (scale bar: 250 µm). Photographs by Jonas Mortelmans.

distance matrix calculated from the *P. marinus* density data to estimate the contribution of the environmental variables in explaining the *P. marinus* population structure. For the DistLM analysis, best model construction was used in combination with the AICc selection criterion, which is a modification of the AIC selection criterion (Akaike 1973) suitable to handle situations where the number of samples is small relative to the number of predictor variables (Anderson et al. 2008). The variance inflation factor (VIF) was calculated in order to check for collinearity between the environmental variables, where variables with a VIF > 3 would have to be removed from the analysis (Zuur et al. 2009; Zuur et al. 2010). The environmental variables included in the models were water temperature, salinity, chlorophyll *a* concentration and the dissolved inorganic nitrogen concentration (DIN). *P. marinus* densities, chlorophyll *a* concentration, DIN and salinity were log (X+1) transformed prior to analysis. All values are reported as mean ± standard deviation. A two- way PERMANOVA (Primer 6) analysis with temperature as covariate was performed in order to check for spatial and temporal effects after accounting for temperature.

Results

Morphological characteristics of P. marinus *found in BPNS*

The male specimens found in the BPNS had three minor setae on the endopod of the right fifth leg (Figure 2), corresponding to the original description of the species from Northern Japan (Sato 1913) and the description of the specimens found along the coast of France (Brylinski et al. 2012).

Distribution of P. marinus *in the BPNS*

Pseudodiaptomus marinus represented 3% of the overall total pelagic copepod abundance. The most abundant copepods in the BPNS and the Belgian harbors were *Temora longicornis* (Müller, 1785) (40%), *Euterpina acutifrons* (Dana, 1847) (22%), *Acartia (Acartiura) clausi* (Giesbrecht, 1889) (20%), *Paracalanus parvus* (Claus, 1863) (9%), *Centropages hamatus* (Lilljeborg, 1853) and *Pseudocalanus elongatus* (Boeck, 1865) (3%). In Zeebrugge *P. marinus* was more abundant, as it was the third most abundant species constituting 8% of the total copepod abundance. The most abundant copepods at this station were *E. acutifrons* (62%) and *A. clausi* (19%).

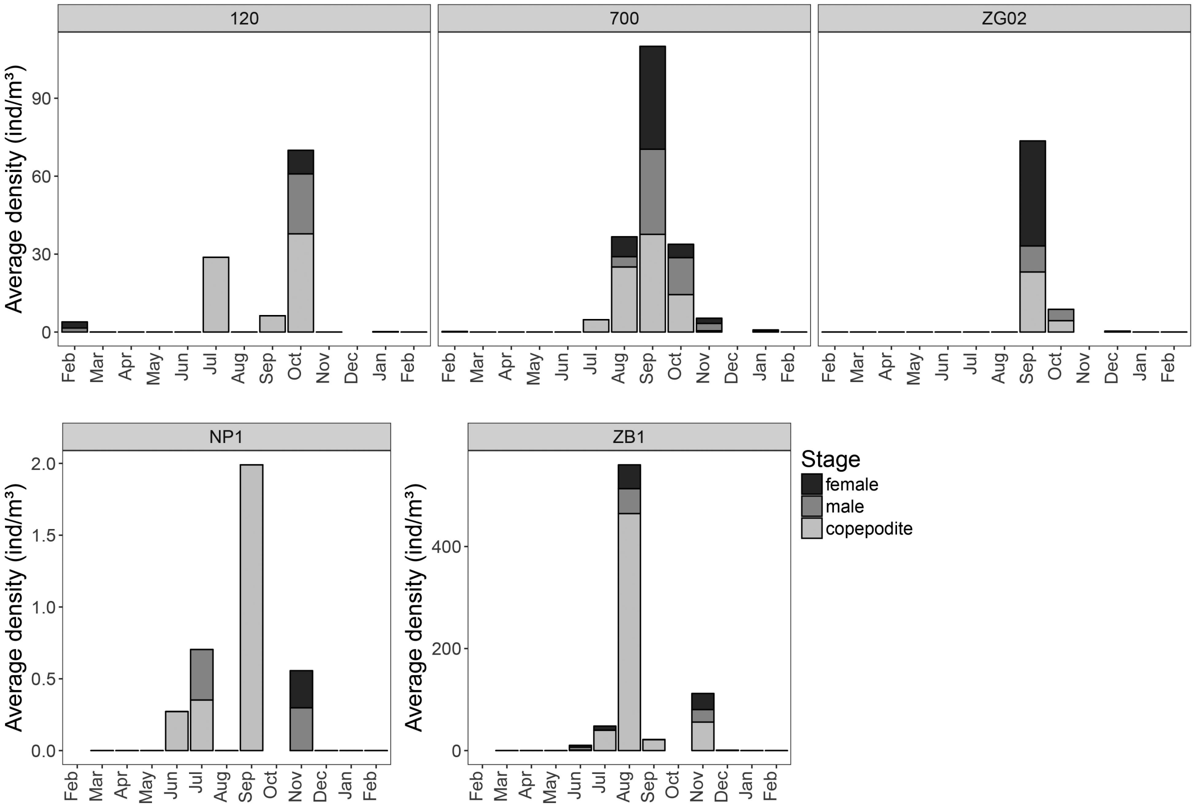

Figure 3. Monthly (February 2015–February 2016) mean abundance (n = 3) of *P. marinus* adult females, adult males and copepodites (stage IV and V) in five stations (harbors: Nieuwpoort (NP1) and Zeebrugge (ZB1); nearshore zone: station 120 and station 700; midshore zone: station ZG02).

Even though *P. marinus* was found at all stations sampled, considerable spatial and temporal differences were found in terms of the total abundance (adults plus copepodites). The highest *P. marinus* densities were found in Zeebrugge harbor (ZB1) with a peak density (560 ± 163 ind.m^{-3}, August 2015) that was five times higher than the second highest peak density found in the sea station close to Zeebrugge harbor (station 700: 110 ± 41 ind.m^{-3}, September 2015). Peak densities in the other stations ranged from 27 ± 6 ind.m^{-3} (Nieuwpoort harbor, September 2015) and 70 ± 11 ind.m^{-3} (nearshore station 120, October 2015) to 74 ± 15 ind.m^{-3} (ZG02, September 2015) (Figure 3).

For the series of samples, two patterns of abundance of the species were found in the BPNS (Figure 3). The first pattern was characterized by only one density peak during autumn (September 2015) at stations ZG02 (74 ± 15 ind.m^{-3}), 700 (110 ± 41 ind.m^{-3}) and Nieuwpoort harbor (NP1) (27 ± 6 ind.m^{-3}). The second pattern consisted of two density peaks, one strong and one mild peak, at stations 120 and ZB1. In station 120, a mild peak occurred during summer (July 2015, 29 ± 17 ind.m^{-3}) and a strong peak during autumn (October 2015, 70 ± 11 ind.m^{-3}). In station ZB1, the strong peak was reached during summer (August 2015, 560 ± 163 ind.m^{-3}), while the mild peak was observed in autumn (November 2015, 112 ± 50 ind.m^{-3}).

Population structure of P. marinus *in the BPNS*

One third (33%) of the *P. marinus* specimens found in the BPNS were adults, 42% were copepodites stage V and 25% were copepodites stage IV. Slightly more adult females (591 individuals) were found than adult males (515 individuals) across all samples and stations, leading to a female/male sex ratio of 1.15:1. During August and October, a deviant female/male sex ratio of 0.8:1 was found across all sites. Even though low densities were registered from December 2015 to January 2016 in stations 120 and 700, it should be noted that only females were found. No clear spatial or temporal trend in the demographic features of the population was found (Figure 3, Table S2).

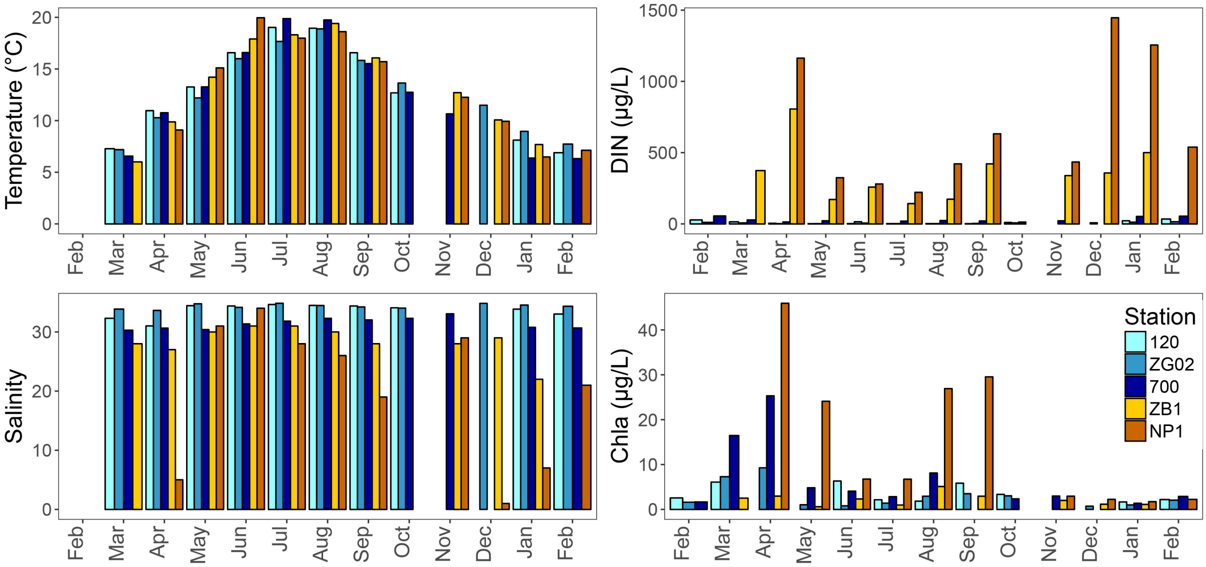

Figure 4. Environmental variables measured at five different stations from February 2015 to February 2016. Top left: Water temperature (°C), top right: Dissolved Inorganic Nitrogen (DIN) (µg/L), bottom left: Salinity, bottom right: chl *a*: station codes: harbors: Nieuwpoort (NP1) and Zeebrugge (ZB1); nearshore zone: station 120 and station 700; midshore zone: station ZG02.

Environmental conditions in the BPNS

The seasonal cycle of water temperature was comparable across all stations, with mean temperatures ranging from 6.8 ± 0.6 °C (March 2015) to 19.1 ± 0.4 °C (August 2015) (Figure 4, Table S3). Dissolved inorganic nitrogen (DIN) concentration showed a decrease in spring and summer for all stations but was consistently higher in the harbour stations (yearly mean of 513 ± 367 µg.L^{-1}) than in the sea stations (yearly average of 15.0 ± 15.1 µg.L^{-1}). Higher DIN concentrations were consistently found in Nieuwpoort compared to Zeebrugge. Salinity was reasonably stable over the year at the sea stations, with higher salinities in the south-western sea stations 120 and ZG02 (yearly mean of 33.7 ± 1.2 and 34.3 ± 0.4, respectively) than in the south-eastern station 700 (yearly mean of 31.4 ± 0.8), which receives more fresh water inflow from the Scheldt river. Salinities in the harbours fluctuated more than in the sea stations due to riverine inputs, especially during the winter months (salinities in Nieuwpoort ranging from 1 ppt in December to 34 ppt in June). In general, chl *a* showed two peaks: a large peak in summer followed by a smaller peak in autumn. Highest chl *a* values were found in Nieuwpoort (up to 45.9 µg.L^{-1} in April), followed by the south-eastern nearshore station 700 (up to 25.3 µg.L^{-1} in April) and the south-western midshore station ZG02 (up to 9.3 µg.L^{-1}) (Figure 4, Table S3). *P. marinus* individuals were found at temperatures ranging from 6.4 °C to 20.0 °C, DIN concentrations ranging from 1.0 µg.L^{-1} to 632.3 µg.L^{-1}, salinities ranging from 19.0 to 34.8 ppt and chlorophyll *a* concentrations ranging from 0.7 µg.L^{-1} to 29.5 µg.L^{-1}.

Factors predicting P. marinus *density*

Total *P. marinus* densities were best explained by a model including only temperature as an explanatory variable, explaining ~ 17.46% of the variation in *P. marinus* log densities (P-value temp = 0.0027). None of the other explanatory variables were statistically significant over and above this (P-value log(DIN) = 0.8673, log(chl *a*) = 0.6665, log(sal) = 0.6141), although together they explained ~ 19.19% of the variation (Table 1). A two-way PERMANOVA analysis including temperature as a covariate showed that both month and station are significant, even after accounting for temperature and that temperature does not interact with either of them (P-value month = 0.0083, station = 0.0064, temperature × month = 0.1822, temperature × station = 0.0654).

Discussion

Extensive sampling campaigns on a monthly basis allowed us to examine the distribution of *P. marinus* in the Belgian part of the North Sea (BPNS) from February 2015 to February 2016. The abundances found were unexpectedly high, taking into account that previous sampling campaigns in the BPNS in

2009 and 2010 did not record this species at all (Van Ginderdeuren et al. 2012, 2014). *Pseudodiaptomus marinus* was recorded for the first time in the Southern Bight of the North Sea in 2010 in Calais harbour and in the coastal waters off Gravelines (Brylinski et al. 2012). At that point, very low numbers of *P. marinus* were found (0.2 to 4.0 ind m^{-3}), with only a few ovigerous females and very low numbers of copepodites (Brylinski et al. 2012). In 2011, abundances up to 3 ind m^{-3} were recorded in the North Sea between The Netherlands and the British coasts (Jha et al. 2013). Fewer historic data is available on the zooplankton in the harbors, but from the few data sources we have (Kerckhof et al. 2007), *P. marinus* appears to be a relatively recent arrival within the Belgian harbors as well. The first record of *P. marinus* in the BPNS dates from 2010 in Zeebrugge from locations at Ostend, the Westerscheldt and Vlakte van de Raan (Van Ginderdeuren 2013). Unfortunately these records do not contain information on collection date, exact location, *P. marinus* sex, or *P. marinus* abundances. The collected material could not be recovered, and metadata associated with these records is assumed lost (pers. comm. K. Van Ginderdeuren; N. Breine). Subsequent observations are known from 2011 and 2013 from the Dutch Scheldt Estuary in several locations: Bath, Hansweert, Terneuzen, and Zandvliet (Rijkswaterstaat 2017). Finally, material of *P. marinus* from the Scheldt near Antwerp, collected in 2011, is stored in the collection of the Smithsonian Institution (T. Chad Walter). The origin of this record is doubtful, and it is not clear whether these records are part of the above collections from Rijkswaterstaat or belong to another campaign (pers comm. T. Chad Walter, M. Tackx). The high abundances of the species in our study, especially in the harbor of Zeebrugge, together with the high relative abundances of copepodites indicate that the species is able to reproduce within the BPNS and the Belgian harbors and that it might be able to establish a permanent population.

Coastal zones, estuaries and harbors are often most impacted by non-indigenous species as they are subject to intense human pressure, eutrophication and pollution (Reise et al. 1999; Sabia et al. 2015). In addition, *Pseudodiaptomus* is typically abundant in transitional areas where high salinities meet low salinities (Sabia et al. 2015; Lučić et al. 2015), leading us to expect higher abundances in the coastal stations and the harbors of the BPNS. In our study this hypothesis was confirmed, as peak abundances were highest in Zeebrugge harbor and in the nearshore station close to Zeebrugge harbor (station 700). The higher densities found in these stations, compared to Nieuwpoort harbor and the two south-westerly sea stations 120 and ZG02, suggest more suitable conditions for *P. marinus*.

Pseudodiaptomus marinus is a euryhaline and eurythermal species (Liang and Uye 1997; Sabia et al. 2015) known to thrive in environmental conditions similar to those observed at the stations where *P. marinus* was found. Based on the tolerance of this species to environmental fluctuations and anthropogenic influences (Sabia et al. 2014), it appears that there are no environmental restrictions for its potential successful introduction into the southern North Sea. Within its indigenous region, the densities of this species are mainly temperature dependent, with an optimal range of 20–25 °C (Uye et al. 1983). In our study, temperature was the most important variable explaining density variation in *P. marinus* within the BPNS and the Belgian harbours (Table 1). Lower salinity, higher DIN and high chl *a* concentrations (mainly in NP1) were found in the harbours (see Environmental conditions). This can indicate a large input of nutrient and detritus-rich waters from the rivers and it coincides with high *P. marinus* abundances in summer (August–September) and spring (April). As *P. marinus* is herbivorous and detritivorous (Uye et al. 1983), large concentrations of phytoplankton and detritus are expected to provide good feeding conditions favoring reproduction and growth. Nutrients and chlorophyll *a* were found to be of less importance, possibly due to the complex interactions between environmental variables, which are not taken into account in the DistLM model. Overall, the model was only able to explain 36.65% of the total variation in *P. marinus* densities. As temperature is naturally the driving factor when examining yearly fluctuations of a species, decadal data should be collected in order to evaluate the intra-seasonal trends in *P. marinus* abundances and how they are related to specific abiotic factors. Moreover, the importance of environmental drivers might differ spatially or may be masked by other factors not considered in this study (e.g., the introduction of new individuals through ballast water discharge). Nieuwpoort harbor exhibited large fluctuations in salinity between months, indicating frequent events of freshwater discharge through the sluice complex "De Ganzepoot" connecting Nieuwpoort harbor to the Ijzer river and several smaller drainage channels coming from the polders. Possibly, when *P. marinus* individuals are introduced to Nieuwpoort harbor, they are flushed to nearshore waters frequently, diminishing their chance of establishing dense populations.

Based on our samples, the distribution and abundance of *P. marinus* in the BPNS followed two different patterns characterized by the presence of one or two density peaks. Studies in this species' native region found a high density peak of this species during summer (June–August), followed by a mild peak in autumn (October) (Uye et al. 1982; Liang and Uye 1997). The population structure found in Zeebrugge and the sea station close to Nieuwpoort (120) are comparable to the population structures in its native environment. Furthermore, the sex ratio found here coincides with previous studies, as the abundances of females and males were similar during warm months but a higher abundance of females was recorded during winter months (Liang et al. 1982; Lučić et al. 2015).

Depending on the station, abundances in the winter and/or early spring were very low or even non-recordable with our sampling method. Inadequate sampling of low densities of *P. marinus* with our sampling method is possible due to the demersal nature of this species. As no resting stages have been recorded for *P. marinus* (Grindley 1984), more intensive sampling campaigns could help to elucidate whether *P. marinus* has established a permanent population that is able to survive winter conditions in the BPNS or whether the first individuals found in late spring are transported from a stock population in warmer waters (Otto et al. 1990; Jha et al. 2013; Brylinski et al. 2012; Sabia et al. 2015). At this point we cannot be sure of the exact process of introduction of *P. marinus* in the BPNS, but as this species is known to be a frequent inhabitant of ballast waters (Sabia et al. 2015) it is highly likely that ballast water discharge during intra-coastal traffic between the main French, Belgian, Dutch and German ports plays an important role here. Further research on ballast water contents is needed to estimate the importance of this route of dispersion (Brylinski et al. 2012; Otto et al. 1990; Jha et al. 2013). In addition, passive dispersion through the intense along-coast currents could have contributed to the apparent fast spread of *P. marinus* along the European coast (Otto et al. 1990; Jha et al. 2013). As the development time from egg to adult is on average 13 days, this species is capable of rapidly increasing abundance under favorable conditions (Huang et al. 2006), explaining the sudden increase in abundance in late spring. A regime shift from a cold dynamic regime towards a warm dynamic regime in the North Sea (Beaugrand 2004; Harris et al. 2014) might have facilitated the establishment of sustainable populations in the BPNS.

Pseudodiaptomus marinus shows strong adaptability to diverse environments, possessing several biological and ecological traits that enable it to have a high invasive potential (Sabia et al. 2015). Further studies concerning the distribution of this species for a longer period in order to determine the continuity of this species in the BPNS and the consequences of its establishment on local planktonic populations are crucial. Future research would especially benefit from multiple years of continuous data on this species, paying particular attention to younger copepodite stages.

Acknowledgements

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Supplementary material

The following supplementary material is available for this article:

Table S1. Geographic position of the sampling stations.

Table S2. Geo-referenced species record information.

Table S3. Geo-referenced data on dissolved inorganic nitrogen concentration (DIN), chlorophyll *a* concentration (chl *a*), water temperature (temp) and salinity (sal).

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