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Research Article

Modelling habitat range and seasonality of a new, non-indigenous polychaete *Laonome* sp. (Sabellida, Sabellidae) in Pärnu Bay, the north-eastern Baltic Sea

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Abstract

An as-yet-undescribed, non-indigenous polychaete species was found at very high densities in the eastern part of the Baltic Sea in Estonia in 2012. The species belongs to the sabellid genus *Laonome* Malmgren, 1866, but it could not be assigned to any of the previously described species. To date, the species has established a stable population after surviving a notably cold winter (2012/2013). To study the local distribution and abundance of the species, a spatial grid with some stations repeated seasonally and interannually was sampled in a quantitative manner. Based of the survey data and available environmental data, the variables that contributed significantly to explaining variation in the abundance of the polychaete were determined using the Boosted Regression Trees modelling approach. Molecular barcodes to characterize the identity of the species were also established. The abundance of *Laonome* sp. exhibited strong seasonal variation, peaking between July and November. Besides seasonality, the quantity of decomposed microalgae in the sediment and wave exposure best explained the variation in abundance. *Laonome* sp. is now well-established in the Baltic Sea and locally reached high densities in low salinity areas. This non-indigenous polychaete may potentially modify sediment morphology and chemistry and disrupt the natural infaunal communities. *Laonome* sp. could displace or even completely eliminate some species currently present in the study area and beyond if it spreads; however, it could also facilitate currently-present species through the provision of alternative substrate and/or food. Given its persistence and high abundance in Pärnu Bay, colonization of other low-salinity areas of the Baltic Sea can be expected.

Key words: Benthic, brackish, COI barcoding, establishment, nonindigenous, shallow water, spatial modelling

Introduction

Ship-mediated marine invasions are a growing concern leading to the point that invading species constitute a major threat to native marine biodiversity world-wide. The Baltic Sea is already one of the highest trafficked seas in the world and maritime activity is expected to increase in coming years (HELCOM 2009). Owing to its low salinity and short geological history, the Baltic Sea is characterized by low species diversity (Segerstråle 1957) and is considered to be particularly sensitive to invasion by non-native species, which may negatively affect the structure and functioning of this ecosystem (Olenin et al. 2014).

Recently, the Baltic Sea, especially in its northern parts, has witnessed an unprecedented increase in the number of biological invasions (e.g. Kotta and Ojaveer 2012; Katajisto et al. 2013; Kotta et al. 2013; Galil et al. 2014). Although the reasons for this increase are poorly understood, the evidence suggests a major role of intensified or modified invasion vectors associated with ballast water and hull fouling (Ojaveer and Kotta 2015).

In 2012, we found an unidentified sabellid polychaete in the Pärnu Bay area of the Gulf of Riga, northeastern Baltic Sea (Figure 1). Based on morphology, this species belongs to the genus *Laonome* Malmgren, 1866; however, it could not be assigned to any of the currently described species. Although benthic invertebrates have been studied
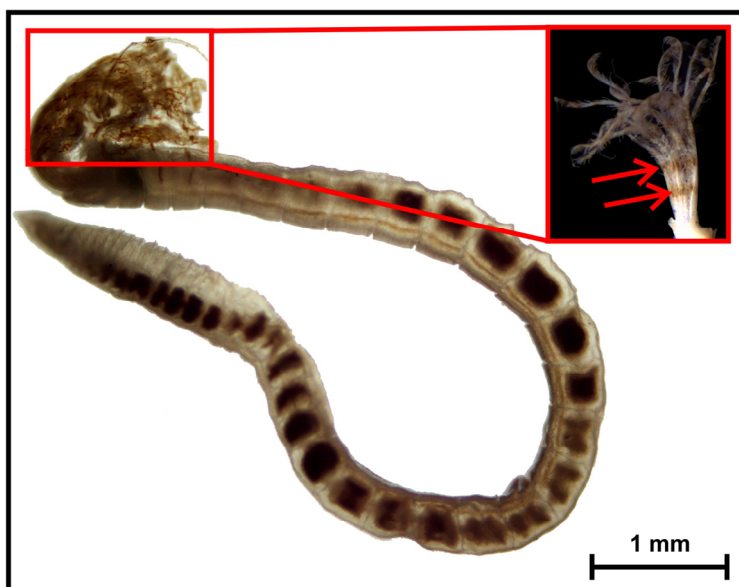
Figure 1. Photograph of *Laonome* sp. Anterior end with branchial crown is enlarged. Note the pigmentation on the branchial crown; the radioles and pinnules are crossed by a series of 6 to 8 brown bands (indicated by arrows). Photograph by J. Kotta and A. Bick.

on a monthly basis since the early 1970s (e.g. Kotta et al. 2004, 2009) no sabellid polychaetes have been previously found in Pärnu Bay. Thus, the observed polychaete represents a non-indigenous species in the ecosystem. The collected specimens were between 9 and 16 mm long, with about 45 to 50 chaetigers. The most obvious character that differentiates the new *Laonome* sp. from all other known *Laonome* species is the presence of spine-like capillary notochaetae on the first thoracic chaetigers. This non-indigenous species was present in densities as high as 752 individuals m^{-2}, and it was the numerically dominant species in the rivermouth area. To our knowledge, the species has not as yet been observed elsewhere in the Baltic Sea.

This apparent invasion may have substantial ecosystem-level impacts because the polychaetes previously present in Baltic Sea rarely disperse into waters that have salinity < 5, and their reproduction in such a diluted environment is hindered (e.g. Daunys et al. 2000). Among polychaetes known to occur in the study area are the non-indigenous *Marenzelleria neglecta* Sikorski and Bick, 2004 and the native *Hediste diversicolor* (O. F. Müller, 1776); however, their densities are low compared to the newly established sabellid polychaete species (Kotta et al. 2008). Prior to the current colonization event, the clay-silt sediment now colonized by the burrowing polychaete was devoid of any ecosystem engineers. The non-indigenous polychaete produces extensive mucus

tubes, which can modify sediment characteristics including sediment stability. Moreover, due to its high density, the polychaete may serve as a novel prey for other invertebrates and fish.

Owing to high density and potential ecological impacts of this non-indigenous polychaete, there is a need to evaluate the environmental tolerance and invasion capacity of the species. The aim of the current study was to provide the first data on the spatial distribution and seasonal dynamics of the invading species and identify environmental proxies that could be used to predict the future distribution patterns of the species in the area. We also provide molecular barcodes to help to characterize the identity of the species.

Material and methods

Field surveys

Bottom samples were collected from 20 stations in the Pärnu Bay area (Figure 2). Of these, the Estonian national coastal monitoring stations K5 and K21 were sampled monthly from April to November in 2009−2014 whereas other stations were visited once on 15 May 2013. Sample collection and analysis followed the guidelines developed for the HELCOM COMBINE program (HELCOM 1999). An Ekman-type bottom grab sampler (0.02 m^2) was used. Three replicate grab samples were taken in each station and sampling date. During sampling the geographic coordinates,

Figure 2. The sampling stations in Pärnu Bay, the Gulf of Riga, northern Baltic Sea, on 15 May 2013. Red dots indicate stations where *Laonome* sp. was found. K21 and K5 denote the Estonian national coastal monitoring sites, and these sites were sampled monthly during ice-free seasons, 2012−2014. The blue line shows the five metre isobath. Red square map denotes the location of Pärnu Bay.
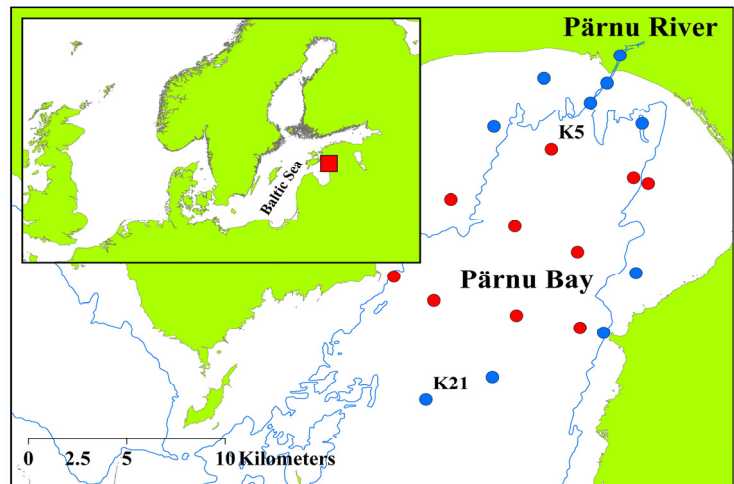
depth, and the proportion of different sediment types were recorded. Water temperature and salinity were also routinely monitored during sampling. Samples were sieved through a 0.25 mm mesh and the residuals were placed in plastic bags. Samples were preserved frozen at -20 °C. Specimens for taxonomic and genetic studies were fixed in a 4% solution of formaldehyde in seawater and 96% ethanol, respectively. In the laboratory, all benthic invertebrate species were counted in each sample including, of course, the non-indigenous polychaetes.

The grab sediment was sampled for chlorophyll *a*, phaeopigments and organic content (diameter of the core 9.6 mm, sampling depth 50 mm). Care was taken that all macrofauna was excluded from the samples before these analyses. The chlorophyll *a* samples were extracted in 96% ethanol overnight. Chlorophyll *a* was quantified fluorometrically and corrected for phaeopigments (Strickland and Parsons 1972). The measurement of sediment organic matter was quantified as a loss of ignition (3 h at 500 ºC).

Supporting environmental variables and modelling

Estimates for 15 environmental variables were obtained for the study site (Table 1). Based on a bathymetry raster of 50 m pixel resolution (available at the Estonian Marine Institute, University of Tartu) the inclination of coastal slopes was calculated using the Spatial Analyst tool of ArcInfo software (ESRI 2011). High values of coastal slopes indicate the occurrence of topographic depressions or humps at the measured spatial scale. Low values refer to flat bottoms.

The Simplified Wave Model method (Isæus 2004) was used to calculate the wave exposure for mean wind conditions represented by the ten year period between 1 January 1997 and 31 December 2006. A nested-grids technique was used to take into account long distance effects on the local wave-exposure regime. The resulting grids had a resolution of 25 m. During the modelling, the shoreline was divided into suitable calculation areas, fetch and wave exposure grids were calculated, and subsequently the separate grids were integrated into a seamless description of wave exposure for the study area. This method results in a pattern where the fetch values are smoothed out to the sides in a similar way that refraction and diffraction make waves deflect around islands.

The values of water temperature and salinity were obtained from the results of hydrodynamical model calculations from the early January 2009 to the early August 2014. The calculations were based on the COHERENS model which is a primitive equation ocean circulation model. It was formulated with spherical coordinates on a $1'{\times}1'$ horizontal grid and 30 vertical sigma layers. The model was forced with hourly meteorological fields of 2 m for air temperature, wind speed, wind stress vector, cloud cover and relative humidity. The meteorological fields were obtained from an operational atmospheric model. The model was validated against water level, temperature and salinity measurements from the study area (Bendtsen et al. 2009).

Table 1. Environmental variables measured at sampling sites in Pärnu Bay. Arithmetic means, minima, and maxima are presented.

Variable	Unit	Mean	Minimum	Maximum
Temperature	deg C	10.9	2.3	20.2
Salinity	unitless	4.6	3.0	5.3
K_d	unitless	0.40	0.38	0.42
Chlorophyll *a* sediment	mg m^{-3}	8.3	0	48.9
Phaeopigments *a* sediment	mg m^{-3}	10.1	0	34.3
Organic content of sediment	%	1.8	0.3	8.6
Depth	m	6.4	2.9	12.0
Coastal slope	degrees	0.04	0	0.36
Share of silt sediment fraction	%	3	0	60
Share of clay sediment fraction	%	31	0	100
Share of sand sediment fraction	%	59	0	100
Share of gravel sediment fraction	%	2	0	35
Share of pebbles sediment fraction	%	1	0	20
Exposure to waves	m^2 s^{-1}	130864	0	183214
Proportion of ice cover in winter	unitless	0.23	0.19	0.25

Finnish Meteorological Institute provided ice cover and thickness over the study area for 2008–2014. Ice cover and thickness were produced on daily basis at a nominal resolution of 500 m and were based on the most recent available ice chart and synthetic aperture radar (SAR) image. The ice regions in the ice charts were updated according to a SAR segmentation and new ice parameter values were assigned to each SAR segment based on the SAR backscattering and the ice thickness range at that location.

As a proxy of eutrophication, we used the MODIS satellite derived water transparency (K_d) values. The satellite observations were generally carried out on weekly basis over the whole ice-free period; however, several observations were discarded due to cloudiness. The spatial resolution of satellite data was 1 km. False zeroes were removed from the data prior to the statistical analysis.

The contribution of different environmental variables to variation in the abundance of *Laonome* sp. was explored using the Boosted Regression Tree technique (BRT) as described by Kotta et al. (2013). The BRT technique combines the strength of data mining, machine learning, and statistical modelling. BRT has no need for prior data transformation or elimination of outliers and can fit complex nonlinear relationships. The BRT also avoid overfitting the data, thereby providing very robust estimates of reality. BRT models are capable of handling different types of predictor variables and their predictive performance is superior to most traditional modelling methods. The BRT iteratively develop a large ensemble of small regression trees constructed from random subsets of the data. Each successive tree predicts the residuals from the previous tree to gradually boost the predictive performance of the overall model. Although BRT models are complex, they can be summarized in ways that give powerful ecological insight (Elith et al. 2008).

When fitting a BRT, the learning rate and the tree complexity must be specified. The learning rate determines the contribution of each successive tree to the final model, as it proceeds through the iterations. The tree complexity fixes whether only the main effects (tree complexity = 1) or also interactions are included (tree complexity > 1). Ultimately, the learning rate and tree complexity combined determine the total number of trees in the final model. Multiple models were run varying in either the model learning rate (between 0.1 and 0.001), number of trees (between 1000 and 10,000), and number of splits (1 and 5). Then the optimum model was selected based on the model performance. In our study, the optimal learning rate and interaction depth were 0.01 and 5, respectively. Model performance was evaluated using the cross validation statistics calculated during model fitting (Hastie et al. 2001). All statistical analyses were done in the statistical software R version 2.0.1 using the gbm package (RDC Team 2013). We used the BRT script provided by Elith et al. (2008).

The statistical programme 'PRIMER' version 6.1.5 was used to analyse if and how the taxonomic composition and dominance structure of benthic invertebrate communities differed between pre- and post-invasion periods (Clarke and Gorley

Table 2. Primers used for amplification and sequencing of four molecular marker genes.

Gene/Primer	Sequence	Direction	Reference
18S rRNA			
18Sfw	5'-CCTA(CT)CTGGTTGATCCTGCCAGT-3'	Forward	Englisch and Koenemann 2001
18L	5'-GAATTACCGCGGCTGCTGGCACC -3'	Reverse	Halanych et al. 1995
18F997	5'-TTCGAAGACGATCAGATACCG-3'	Forward	Struck et al. 2002
18Srev	5'-TAATGATCCTTCCGCAGGTT-3'	Reverse	Englisch and Koenemann 2001
18F509[1]	5'-CCCCGTAATTGGAATGAGTACA-3'	Forward	Struck et al. 2002
18R1256[1]	5'-AGCTCTCAATCTGTCAATCCT-3'	Reverse	Struck et al. 2002
28S rRNA			
1274	5'-GACCCGTCTTGAAACACGGA-3'	Forward	Møller et al. 2008
1276	5'-CTAGTTGCTTCGGCAGGTGAG-3'	Reverse	Møller et al. 2008
16S rRNA			
16Sar	5'-CGCCTGTTTATCAAAAACAT-3'	Forward	Kessing et al. 1989
16Sbr	5'-CCGGTCTGAACTCAGATCACGT-3'	Reverse	Kessing et al. 1989
COI			
LCO1490	5'-GGTCAACAAATCATAAAGATATTGG-3'	Forward	Folmer et al. 1994
HCO2198	5'-TAAACTTCAGGGTGACCAAAAAATCA-3'	Reverse	Folmer et al. 1994

[1]Internal primers used for sequencing only

2006). Based on untransformed abundances of benthic invertebrate taxa, similarities between each pair of samples were calculated using a zero-adjusted Bray–Curtis coefficient. Statistical differences in benthic invertebrate communities among the studied periods (pre- and post-invasion data) were assessed by the ANOSIM permutation test. The contribution of each benthic invertebrate taxon to dissimilarities was investigated using the similarities percentages procedure (SIMPER). Nonmetric multidimensional scaling (nMDS) was used to present visual images of the differences in composition and dominance structure of benthic invertebrate communities between pre- and post-invasion periods.

Molecular characterization

An attempt to further characterize the taxonomic identity of the apparently undescribed polychaete species was made by sequencing fragments of four commonly employed marker genes: the mitochondrial 16S rRNA and COI (cytochrome c oxidase subunit I) genes, and the nuclear 18S rRNA and 28S rRNA genes. Up to eight specimens per gene were sequenced from the Pärnu Bay station K5. Total DNA was extracted from ethanol-preserved tissue by a spin column kit procedure, and the appropriate primers (Table 2) were used for amplification of the gene fragments using standard PCR protocols and for sequencing them with the BigDye Terminator v. 1.1 kit (Applied Biosystems) on ABI capillary sequencing platforms. The resulting sequences were compared against

global sequence archives in the public GenBank and BOLD (COI barcoding; Ratnashingham and Hebert 2007) databases.

Results

Habitat range and seasonality

The survey carried out in the Pärnu Bay area in May 2013 showed that *Laonome* sp. occupied a large part of the bay with highest densities occurring in deeper areas. Overall, the species was observed at 10 sampling locations out of the 20 visited (Figure 2). *Laonome* sp. displayed large variability in their abundance between sampling sites. The abundance was highest (752 ind m^{-2}) at station K5 adjacent to Pärnu rivermouth. Elsewhere, the species occurred sporadically and at much lower abundances of around 50−100 ind m^{-2}.

In the seasonal sampling at site K5, the abundance was relatively low (< 100 ind m^{-2}) from April to June, increased to a peak in July (up to 752 ind m^{-2}) and then gradually levelled off towards the end of the productive season (Figure 3). The observed seasonality patterns at site K5 did not differ markedly between the three studied years. *Laonome* sp. was not detected at the other site (K21) sampled seasonally.

When analysed against the environmental background data (Table 1), the BRT models explained 62% of the overall variation of the abundance of *Laonome* sp. Seasonality was the main component of variation with monthly differences explaining more than 50% of variability in the
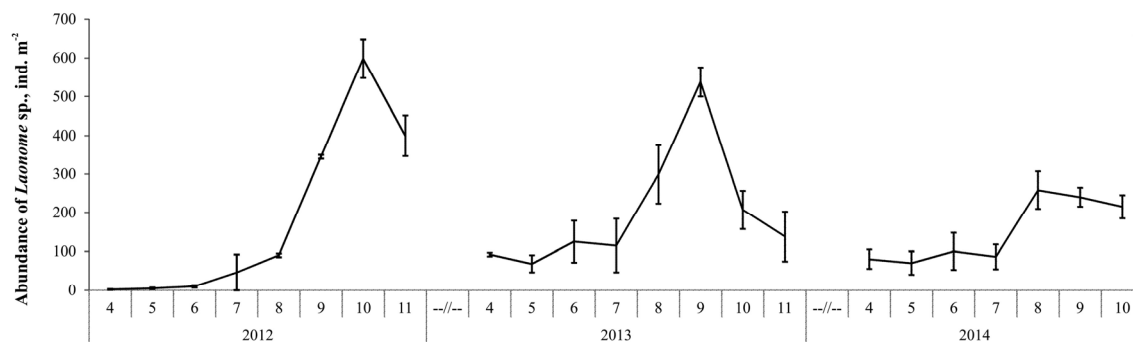
Figure 3. Mean (± SE, n = 3 replicates) monthly abundance of *Laonome* sp. at station K5 in 2012−2014.
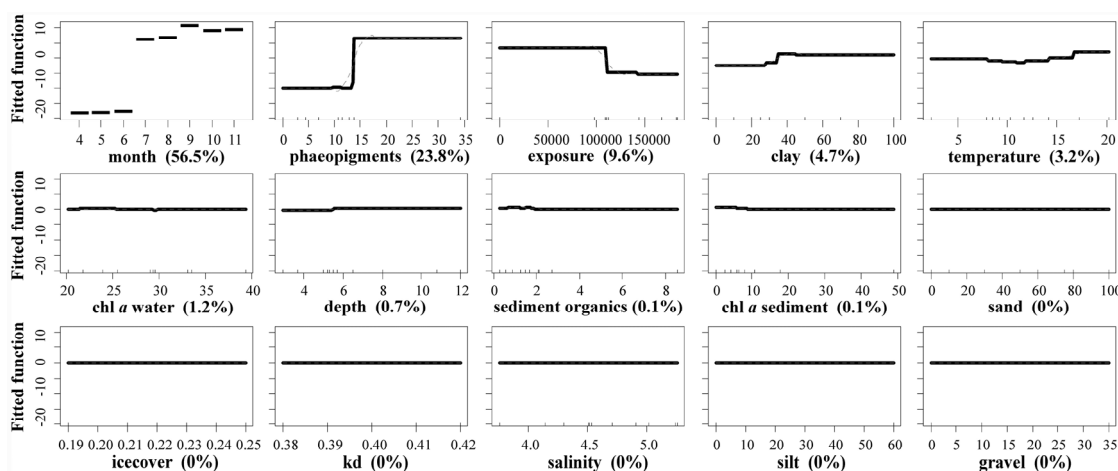
Figure 4. Standardized functional-form relationships showing the effect of environmental variables on the abundance of *Laonome* sp. within the distribution range of the polychaete, whilst all other variables are held at their means. The variables are ordered by their relative contribution in the BRT model (shown in brackets). Upward tickmarks on x-axis show the frequency of distribution of data along this axis.

Table 3. The results of SIMPER test showing mean (ind m^{-2} ± SE) abundances of benthic invertebrate taxa in the Pärnu Bay study area and contributions of these taxa (%) to overall differences in taxonomic composition and dominance of benthic invertebrate community among pre- and post-invasion periods.

Taxa	Preinvasion	Postinvasion	Contribution
Macoma balthica (Linnaeus, 1758)	508.4 ± 72.7	416.8 ± 50.5	39.3
Corophium volutator (Pallas, 1766)	107.5 ± 36.6	44.2 ± 24.9	11.9
Laonome sp.	0 ± 0	127.1 ± 30	11.7
Oligochaeta	40.8 ± 11.5	91.3 ± 18.8	10.6
Marenzelleria neglecta Sikorski & Bick, 2004	51.1 ± 13.5	72.1 ± 10.4	8.6
Dreissena polymorpha (Pallas, 1771)	36.1 ± 28.4	63.1 ± 33	7.4
Hediste diversicolor (O.F. Müller, 1776)	45.1 ± 12.4	8 ± 2.6	3.9
Amphibalanus improvisus (Darwin, 1854)	19.7 ± 9.5	12.7 ± 7.2	3
Cerastoderma glaucum (Bruguière, 1789)	8.6 ± 2.6	5.3 ± 2.6	1.4
Mya arenaria Linnaeus, 1758	6.4 ± 2.2	0.8 ± 0.6	0.8
Bathyporeia pilosa Lindström, 1855	8.3 ± 8.3	0 ± 0	0.4
Saduria entomon (Linnaeus, 1758)	2.8 ± 1.9	1.3 ± 0.8	0.3
Neomysis integer (Leach, 1814)	1.4 ± 1.4	2 ± 2	0.3
Chironomidae	1.5 ± 0.8	0 ± 0	0.1
Jaera albifrons Leach, 1814	0 ± 0	0.5 ± 0.5	0.1
Cyanophthalma obscura (Schultze, 1851)	0.6 ± 0.6	0 ± 0	0.1
Peringia ulvae (Pennant, 1777)	0.6 ± 0.6	0 ± 0	0.1
Halicryptus spinulosus von Siebold, 1849	0.6 ± 0.4	0 ± 0	0.1
Gammarus tigrinus Sexton, 1939	0.8 ± 0.8	0 ± 0	0.1
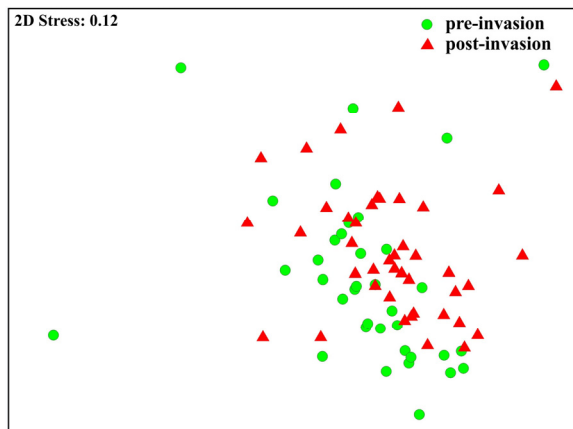
Figure 5. Non-metric multidimensional scaling (nMDS) plots comparing similarities of benthic communities among pre- and post-invasion periods. Closer distance between symbols depicts more similar communities.

Table 4. Sequence data of the Pärnu Bay *Laonome* sp. and their GenBank accession numbers. N – number of individuals sequenced, nh – number of different haplotypes observed.

Gene fragment	Length (bp)	N	nh	GenBank accession numbers
18S rDNA	1813	2	1	KP793139
28S rDNA	624	2	1	KP793140
16S rDNA	450	6	1	KP793138
COI	613	8	2	KP793136, KP793137

abundance of *Laonome* sp. (Figure 4). The content of phaeopigment in sediment was the second most important explanatory variable. The model identified two distinct states for *Laonome* sp. density: low abundances at low phaeopigment content (sites away from the Pärnu rivermouth) and high abundances at high phaeopigment content (site close to the Pärnu rivermouth). The third important variable was exposure to waves with *Laonome* sp. having elevated abundances at reduced exposure (Figure 4). Currently, the Pärnu Bay *Laonome* sp. inhabits a salinity range of 3.0 and 5.3 and within this range salinity had no effect in the BRT model.

In total, 19 taxa of benthic invertebrates were found at station K5 (Table 3). There were significant differences in taxonomic composition and dominance structure of benthic invertebrate communities between pre- and post-invasion period (ANOSIM, p = 0.001); however, the differences were not large (ANOSIM, R = 0.203). Similarly, nMDS showed no clear separation of pre- and post-invasion community data (Figure 5). The observed differences (> 5% contribution) were

mostly due to: a reduction in abundance of the dominant deposit-feeders *Macoma balthica* (Linnaeus, 1758) and *Corophium volutator* (Pallas, 1766); the appearance of the non-indigenous *Laonome* sp.; and increased abundances of the invasive polychaete *Marenzelleria neglecta* Sikorski and Bick, 2004, oligochaetes, and the invasive zebra mussel *Dreissena polymorpha* (Pallas, 1771).

Molecular characteristics

A total of 1063 base pairs of the mitochondrial DNA [16S (N=6) + COI (N=8)] and a total of 2437 bp of the nuclear 18S rDNA (N=2) and 28S rDNA (N=2) of *Laonome* sp. were sequenced (Table 4). There were no differences between individuals in any of the three ribosomal rRNA genes. Two haplotypes were recorded for COI, differing at a single nucleotide site (recorded in 5 and 3 individuals, respectively).

All sequences were unique to the new sabellid species. In comparing the 18S sequence with data in the global GenBank sequence database, the sequence appeared closest to other species in the Sabellidae, but showed no definite affinity to any particular species (no *Laonome* species were available for reference, though). Nucleotide blastn searches in GenBank for the three other genes, translated sequence searches (tblastx) for the protein-coding COI in the same database, or COI searches in the BOLD (Barcoding of Life) database in turn could not identify any closely related sequences informative of the phylogenetic position of *Laonome*.

Discussion

Benthic communities of the Pärnu Bay area have been regularly sampled since the 1970s and we have no earlier indication of *Laonome* sp. in the bay (e.g. Kotta et al. 2004, 2009). In the current study, a comparison of benthic communities before and after this invasion also shows a lack of benthic polychaetes in Pärnu Bay except for the invasive *Marenzelleria neglecta*. Following the establishment of *Laonome* sp., no substantial alteration in the benthic community was observed. Nevertheless, a decline of abundances of prevailing deposit-feeders and a disappearance of some invertebrate species suggest that competition for food is being intensified. Such competitive interactions among native and newcoming species are not uncommon as shown recently for *M. neglecta* and *Gammarus tigrinus* Sexton, 1939 to name but a few (e.g. Ojaveer and Kotta 2015).

At present, nine species are recognized within the genus *Laonome*. They are known from marine, brackish and freshwater habitats. Only *Laonome kroyeri*, the type species of the genus, originally described from Spitsbergen by Malmgren (1866), has previously been reported from the brackish Baltic Sea. Several *Laonome* species have already been described as invaders transported to new areas by human activities, most likely by ballast water. Very recently another feather-duster worm of the genus *Laonome* was found in fresh and brackish waters in the Netherlands (Capa et al. 2014). This species was determined as *L. calida* Capa, 2007, which has originally been described from estuaries and open water of tropical and subtropical Australia. Morphological differences between specimens from the two localities have been found but were considered insufficient to warrant species distinction (Capa et al. 2014). The specimens of *Laonome* from Pärnu Bay and from Australia also differ in some diagnostic characters. Further examples of introduced species are *L. elegans* from the Red Sea to the Mediterranean Sea (Zenetos et al. 2005), and *L. triangularis* from Australia to the Mediterranean Sea (Cinar 2009). The formal description of the Baltic *Laonome* sp. is currently under preparation and will be provided by us elsewhere.

We also characterized the new *Laonome* species using several DNA sequence markers. This provides a reference that should now allow the identification of any individuals (including larvae, or tissues) in, for example, molecular barcoding approaches. So far, however, there are no genetic data available on other *Laonome* species to assist in assessing the phylogenetic position of the new species within the genus. Of the four genes, only the 18S marker retained a signal of the affinity of the new species even with other Sabellidae (rather than other families in Sabellida), which are well represented in the databases. There was also remarkably little variation among the several individuals sequenced from Pärnu Bay, i.e. only two very closely related COI haplotypes. Such low variability could plausibly result from a population bottleneck in the colonization phase. Nevertheless this cannot be verified before discovery of the source population.

Laonome sp. in Pärnu Bay survived a very cold winter of 2012/2013 when ice cover lasted more than 4 months and seawater temperature remained permanently below 2°C (databases of the Estonian Weather Service). Since then *Laonome* sp. has been revealing a relatively uniform seasonal dynamics suggesting that the sabellid

population has formed a stable population. To date, the abundance of *Laonome* sp. was high only at site K5 adjacent to Pärnu rivermouth, whereas the species occurred sporadically but at much lower abundances elsewhere in the Pärnu Bay area. The BRT model described relatively high percentage of the overall variability in the abundance, which may be unexpected considering that the species has just recently arrived to the study area and probably is still expanding its distribution range. Specifically, it is plausible that when the invasion is still at an early stage the non-indigenous species has not yet fully exploited all potential habitats in the recipient environment. At this stage, the invasion is more likely constrained by propagule availability than by habitat requirements. Therefore, interactions between environment and the biota are expected to be weaker as compared to those for the established species inhabiting the area (Kotta et al. 2009). Although the current BRT model described much of the spatio-temporal variation in abundance of *Laonome* sp., making predictions on species-spread with the model should be done with caution. The abundance of the polychaete may still abruptly increase in the study area facilitating an establishment of the species to local habitats not as yet colonized (Rouget and Richardson 2003). Thus, considering the recent arrival and presumably strong invasive potential of the species, *Laonome* sp. may occupy a wider range of habitats in future than observed in this study. It seems that the abundance of *Laonome* sp. may immediately have reached up to the carrying capacity of its most preferred habitat, as the yearly abundance cycle did not change in the second and third years of observation at site K5. At other stations, however, lower or higher abundance could be expected.

It seems that *Laonome* sp. prefers eutrophicated, soft, silt-clay bottoms rich in organic debris and decomposing microalgae. However, the range of substrates occupied may be much wider. To date, the substrates where *Laonome* sp. has been observed range between true hard bottoms (our unpublished observation made at artificial reef units placed all around the bay at 0.5−2 m depth in September 2012) and mixed sediments to fine soft clay habitats (this study). Based on the BRT models, neither salinity nor temperature limited the distribution of the polychaete in the study area. However, it is important to note that spatial variability in salinity and temperature is not large in the study area. Furthermore, it can be speculated that the species has not yet

established in many suitable habitats in part because the population is still in the early growth phase.

The larvae of the Baltic *Laonome* sp. were observed in April-May (M. Simm, Estonian Marine Institute, Pärnu Bay area, personal observation) but it is possible that the free-living larvae occur in other seasons as well. The success of larval production and settlement are expected to control the further spread of the polychaete. In the tropical waters, *Laonome albicingillum* Hsieh, 1995 is known to have a long, more than half year reproductive season, spawning is asynchronous among individuals and settlement takes place within 1−2 days from fertilization (Hsieh 1997). We are not aware of similar data from temperate waters; however, judging from the observed seasonality of the Pärnu Bay *Laonome* sp., the reproductive season is much shorter in the Baltic Sea. Potentially, the duration of winter may set limit to the northernmost range of *Laonome* sp. Although we lack winter data from December to March, it seems most likely that the abundance of *Laonome* sp. declines abruptly with the onset of ice cover. If ice-free season is too short then, with an expected life span of one year or two, *Laonome* sp. has no time to build up its population abundance in order to resist the next winter. Seemingly, temperature *per se* was not behind the seasonality of *Laonome* sp. as an exclusion of the variable "month" did not increase the contribution of temperature in the BRT model. It is plausible that food availability controls the seasonal dynamics of the non-indigenous polychaete in the Pärnu Bay area.

The BRT model showed that, apart from seasonality (i.e. life cycle), the quantity of decomposed microalgae in the sediment was a key variable explaining the observed abundance of *Laonome* sp. This suggests that the abundance of the species is controlled by pelagic and/or benthic microalgal production and therefore the risk for successful colonization at additional sites increases with the degree of local nutrient enrichment. Considering that nutrient loads to the Baltic Sea are still very high, and eutrophication is the key environmental concern (Schiewer et al. 2008; Conley et al. 2011), further deterioration of water quality may facilitate the colonization of the whole Baltic Sea by this non-indigenous polychaetes.

Particulate organic matter in the water column, and uni-cellular algae, constitute the main food of other *Laonome* polychaetes (Hsieh et al. 2002).

Potentially, the Baltic *Laonome* sp. may also feed on benthic microalgae including diatoms. For example, in our study area, the diet of the invasive suspension-feeder bivalve *Dreissena polymorpha* is not coupled with the water column phytoplankton but instead consists of benthic microalgae (Lauringson et al. 2014). Seemingly, resuspended sediments in the water column may comprise the main energy source in this shallow water ecosystem for benthic suspension feeders, including the newcomer *Laonome* sp.

Another important aspect of this invasion is that *Laonome* sp. is both an allogenic and auto-genic ecosystem engineer (*sensu* Jones et al. 1994); i.e., they modify the environment mechanically and by themselves. The current study area lacks an abundant, native suspension feeder on the soft-bottom habitat (Table 4). Thus, a dense population of *Laonome* sp. may filter out significant part of phytoplankton and thereby alter turbidity and light penetration, and control the depth at which photosynthesis can occur. Currently, the invasive *Dreissena polymorpha* (Pallas, 1771) performs a similar function on hard-bottom habitats of the Pärnu Bay area (Lauringson et al. 2007) but, owing to limited amount of such habitats, their impact does not extend beyond nearcoastal areas. On the other hand, *Laonome* sp. builds tubes out of sediment grains embedded in mucus. The density of such tubes may reach tens or even hundreds of thousand per m^2. A provision of such ephemeral habitat may disrupt natural infaunal communities by establishing new ecological relationships, displacing or completely disassembling native communities but likely facilitating some native species owing to improved availability of alternative substrate and/or food (Zühlke 2001). Given their high abundance and shallow-water distribution, it is likely that *Laonome* sp. are used as a source of food by invertebrate predators, fish, shore birds and/or bottom-feeding ducks. Such mixed ecosystem-level effects have been recently recorded for the invasive tubeworm *Ficopomatus enigmaticus* (Fauvel, 1923) in a Californian estuary (Heiman and Micheli 2010).

Conclusions

The newly discovered polychaete *Laonome* sp. has formed a local stable population in the Pärnu Bay area of the north-eastern Baltic Sea. Currently, the species is limited to highly enriched soft-bottom habitats characterised by low wave exposure. However, as *Laonome* sp. has a pelagic larval phase, the species may quickly spread to

adjacent locations and other habitat-types in the near future. Owing to its high densities and multiple potential ecological impacts, the species may considerably modify the invaded ecosystems.

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