



The introduction history of the non-native shrimp *Palaemon macrodactylus* in the Baltic Sea indicates repeated anthropogenic dispersal

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ABSTRACT

The shrimp species *Palaemon macrodactylus*, Rathbun 1902 is native to the Pacific coast of Japan, East China, and Korea. It has successfully spread to non-native habitats in North and South America, Australia, and the entire European coastline. Recently, this species was also found in the Baltic Sea near the Port of Gdańsk and the Kiel Canal. However, the latter population could not be considered established. To reconstruct the recent colonization of the Baltic Sea and determine the most probable pathways and vectors of this expansion, molecular analysis and ecological surveys were conducted. A total of 78 sequences of a fragment of the cytochrome oxidase subunit 1 (COI) from 10 different populations from the Baltic Sea and North Sea were generated and complemented with publicly available sequences. This resulted in the estimation of a haplotype network and the calculation of genetic differentiation and diversity. The results provide the first record of an established population of *P. macrodactylus* in the Kiel Canal area and reveal a complex expansion of this species with multiple introductions into the Gdansk Marina. Additionally, the distribution of this species in the Baltic Sea is mainly limited to port areas, indicating that shipping, particularly biofouling on boat hulls, is the primary dispersal vector.

1. Introduction

Non-native species are a major threat to global biodiversity (Molnar et al., 2008). They are expanding their ranges at an ever-increasing rate due to increasing shipping intensity and climate change (Rahel and Olden, 2008; Havel et al., 2015; Slišković et al., 2021). The Baltic Sea is one of the aquatic hotspots of such species introductions (Leppäkoski and Olenin, 2000; Casties et al., 2016; Geburzi et al., 2022). The introduction rate of non-native species has increased significantly in the Baltic Sea since the 1950s (Ojaveer et al., 2017; HELCOM, 2018): In the period between 2000 and 2024 alone, 206 introduction events were documented, resulting in the introduction of 116 species. This means that on average about five new aquatic species have appeared in the Baltic Sea each year within this time period (AquaNIS. Editorial Board, 2015). The exact pathways and vectors of introduction are often unknown, as well as their direct origin. Natural secondary dispersal into the Baltic Sea from the connected North Sea is likely as it is the colonization route for many native species (Geburzi et al., 2022), but given

the prevalence for non-native species to be dispersed anthropogenically, other pathways and vectors should be considered as well. Especially secondary dispersal with ships, either on hulls or in ballast tanks through man-made canals, is common (Minchin et al., 2009; Katsanevakis et al., 2013). In addition, a long-overlooked pathway for short to intermediate-distance dispersal are recreational vessels (Gollasch, 2002; Clarke Murray et al., 2011; Outinen et al., 2021).

A species that has recently expanded into the Baltic Sea is the Oriental Shrimp *Palaemon macrodactylus*, Rathbun 1902. This species is native to the Pacific coastal waters of Japan, eastern China and Korea. Its large non-native range includes North and South America, as well as Australia and Europe (González-Ortegón et al., 2007). In Europe, *P. macrodactylus* was first recorded in the Stour Estuary (England) in 1992 (Worsfold and Ashelby, 2008) (Fig. 1). Since 1997, further finds were described from the Guadalquivir estuary in Spain (Cuesta et al., 2004) and Westerschelde in the Netherlands (d'Udekem d'Acoz et al., 2005). Since 2004, *P. macrodactylus* has been recorded on the German North Sea coast, first in the Weser estuary (González-Ortegón et al.,

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2007) and since 2009 also at the breakwaters into the Jade Bay (Buschbaum et al., 2012).

The initial documentation of the species in the Baltic Sea was conducted by Janas and Tutak (2014) at the mouth of the Wisła Śmiała River near Gdańsk in 2014. However, Dürr (2010) had previously reported *P. macrodactylus* in his diploma thesis from the Kiel Canal in the western Baltic Sea as early as 2009 (AquaNIS. Editorial Board, 2015). Six years later *P. macrodactylus* was reported in the Ports of Flensburg, Kiel and Lübeck-Travemünde and in 2019 in the area between Rendsburg and Holtenau located in the eastern part of the Kiel Canal (Bock and Lieberum, 2017, 2019). In 2024, *P. macrodactylus* was recorded for the first time in east Germany, in the ports of Wismar and Stralsund (IFAÖ Institut für Angewandte Ökosystemforschung GmbH, 2024). In Poland, *P. macrodactylus* was found in 2018 in Gdańsk Port and in 2021 in Gdynia Port (AquaNIS. Editorial Board, 2015; Spich et al., 2024). While Janas and Tutak (2014) also observed females with eggs as well as young individuals in Polish waters, it is not clear from the current German records whether *P. macrodactylus* has established a population in the area of the Kiel Bay.

Given the patchy distribution of *P. macrodactylus* in the Baltic Sea, natural dispersal seems unlikely. The aim of this study is to reconstruct this most recent colonization of the Baltic Sea by *P. macrodactylus*. An update is provided on the distribution and establishment of this species in this region, and the most probable pathways and vectors of expansion into the Baltic Sea are reconstructed using a combination of molecular analysis and ecological surveys. It is hypothesized that there was a west to east expansion from the North Sea into the Baltic Sea, given the timing of introduction events (Fig. 1). It is also hypothesized that this expansion

was anthropogenic rather than natural, given the patchy occurrence of *P. macrodactylus* in the Baltic Sea and across Europe. Furthermore, it is hypothesized that there were cryptic introductions from other parts of the introduced range or from the native range, given the global distribution of this shrimp species and increases in global shipping.

Molecular data are well-suited to reconstruct such introduction histories (Geller et al., 2010; Cristescu, 2015): genetic diversity is expected to decline during the secondary spread of non-native species, and repeated introductions from the native range can be recognized by the presence of haplotypes not observed anywhere else in the non-native range, and specifically not in the neighboring populations. Ecological surveys, on the other hand, provide evidence for the establishment of a population and therefore its persistence over time.

2. Material and methods

2.1. Ecological surveys

Ecological surveys to find *P. macrodactylus* took place at several locations within the Baltic Sea between 2008 and 2022 (Fig. 2). It was only discovered in two locations: Lake Flehmude in Germany and the Vistula River Mouth in Poland. Lake Flehmude was surveyed in 2008, 2009 and 2022 for the presence of *P. macrodactylus*. In 2008 and 2009, the location was surveyed using hand nets, and in 2022 with baited Gee-minnow traps (Normant-Saremba et al., 2020). Lake Flehmude has a direct connection to the Kiel Canal (Fig. 2A). The Kiel Canal connects North and the Baltic Sea and is the globally most frequented waterway; it is an important passage for cargo ships as well as for recreational vessels

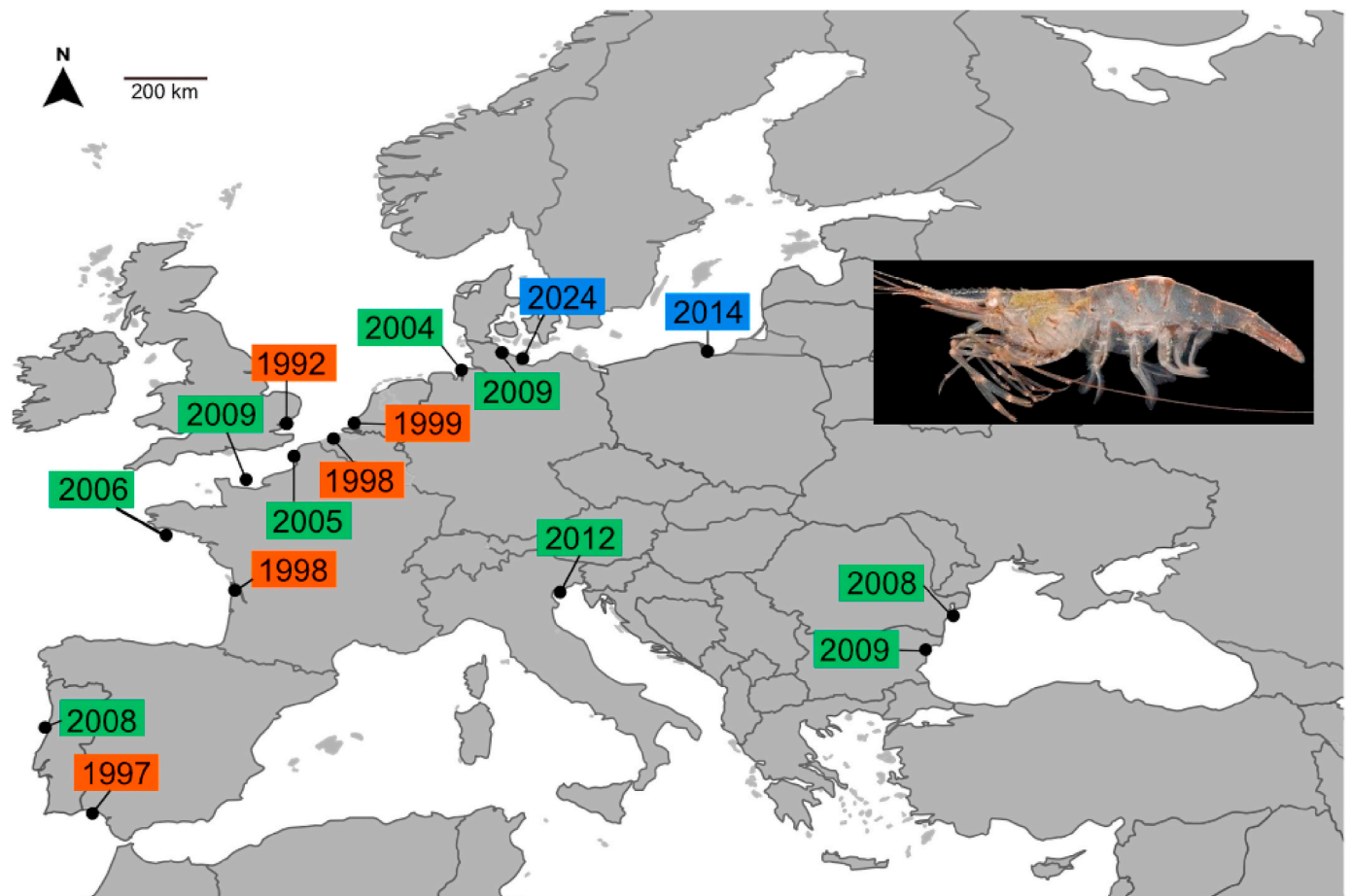


Fig. 1. Geographic spread of the oriental shrimp *Palaemon macrodactylus* in Europe based on the AquaNIS and OBIS databases. Colors correspond to early (before 2000 = red), intermediate (2000–2010 = green) and recent (after 2010 = blue) introductions. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

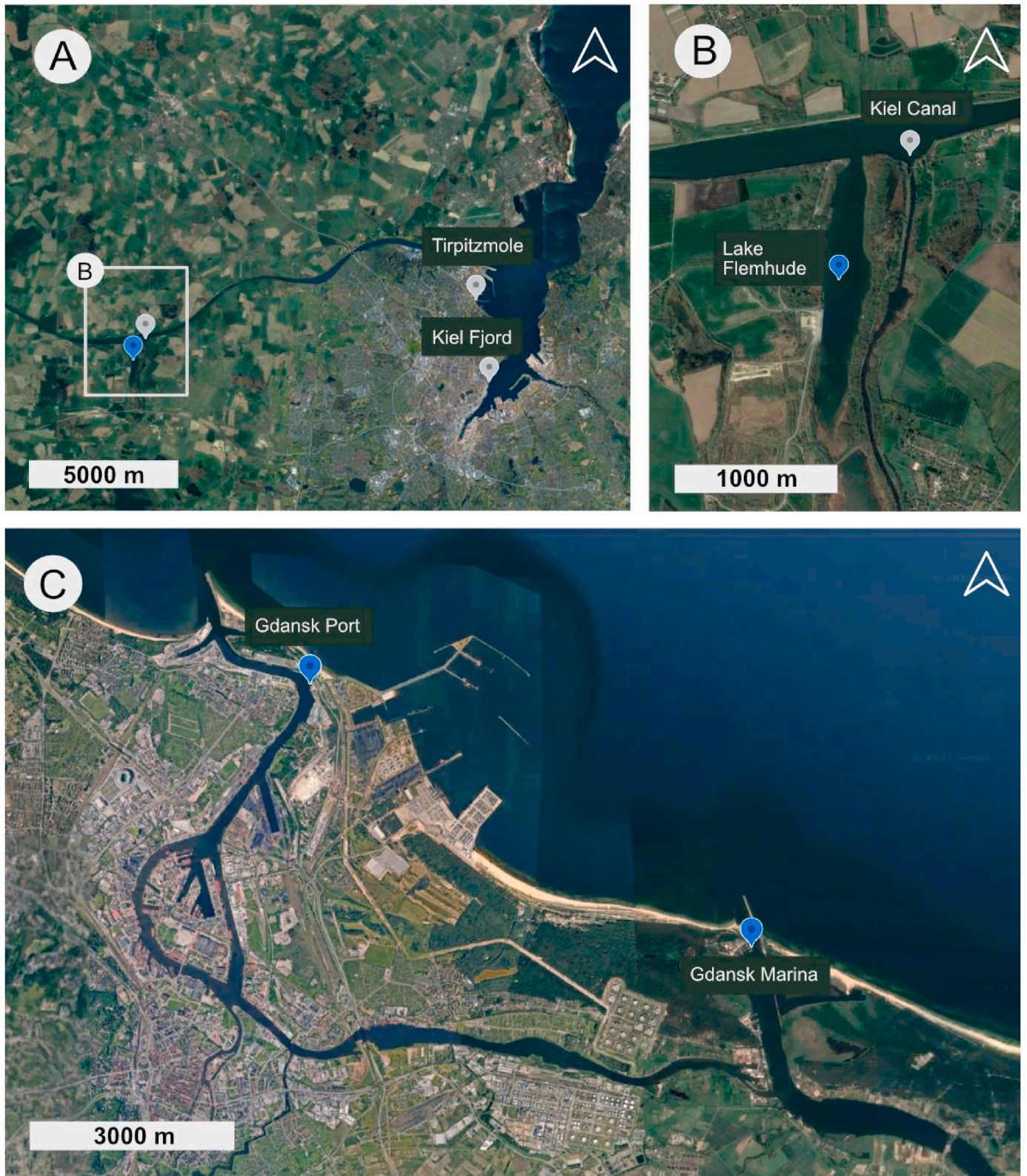


Fig. 2. Detailed maps of survey locations for *P. macrodactylus* in the Baltic Sea. Blue dots are locations where *P. macrodactylus* was found, grey dots represent locations where no *P. macrodactylus* were found. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(GDWS Generaldirektion Wasserstraßen und Schifffahrt). Lake Flemhude is located about 10 km from the Kiel Fjord (Fig. 2B) and the salinity rarely exceeds 14 psu. The shoreline is characterized by the presence of freshwater or brackish vegetation, most notably reeds. The substrate is predominantly composed of sand.

In the case of Vistula flowing to the Gulf of Gdańsk (Poland), two sites located at two tributary river branches have been surveyed in 2021–2022 for the presence of *P. macrodactylus*. The first site, called Gdańsk Marina, was located in the mouth of the Wisła Śmiała River, in a yacht port of the National Sailing Centre in Gdańsk, whereas the second one called Gdańsk Port was situated in Martwa Wisła River, which acts as a harbor channel for the inner Port of Gdańsk (Fig. 2C–Table 1). Both sites are missing a natural shoreline, with the presence of artificial canal walls. Furthermore, the substrate is characterized by a range of muddy to sandy soil types.

In the Gdańsk Marina, shrimps were collected in July 2021 and September 2022, and in Gdańsk Port in September 2021. At both sampling sites salinity was in the range 5.4–6.5 (Table 1). Shrimps were caught with baited Gee-minnow traps (Normant-Saremba et al., 2020) that were modified by being covered with an insect net of a mesh size 1 mm × 1 mm. After sampling, shrimps were preserved in 96 % ethanol. Taxonomic characters, like the number of spikes and rows of setae on the rostrum were confirmed based on d'Udekem d'Acoz et al. (2005) and González-Ortegón and Cuesta (2006).

2.2. Molecular analysis

2.2.1. DNA-Extraction, amplification and sequencing

A subset of 80 shrimps collected during the surveys was used for molecular analysis. DNA was extracted either from muscle tissue of the pleon using Chelex 100 Chelating Ion Exchange Resin (BIO RAD) following the protocol of Walsh et al. (1991) or the Roti®-Prep Genomic DNA MINI Kit for isolation of genomic DNA from tissues (ROTH) following the protocol provided by the manufacturer. Extraction methods were selected depending on how much tissue was available.

Table 1

Information on *P. macrodactylus* specimens collected during ecological surveys within the Baltic Sea between 2009 and 2022.

Date of collection	Location	Lat.	Long.	Salinity	N All	N ovigerous females
September 2009	Lake Flemhude (Kiel Canal)	54.3407	9.9645	no data	2	0
November 2009	Lake Flemhude (Kiel Canal)	54.3407	9.9645	no data	2	0
July 2021	Gdańsk Marina (Wisła Śmiała)	54.3675	18.7808	5.5	10	4
September 2021	Gdańsk Port (Martwa Wisła)	54.4018	18.682	5.4	42	8
May 2022	Lake Flemhude (Kiel Canal)	54.3407	9.9645	13	44	7
September 2022	Gdańsk Marina (Wisła Śmiała)	54.3675	18.7808	6.5	13	2
October 2022	Lake Flemhude (Kiel Canal)	54.3407	9.9645	14	5	1

Chelex requires less tissue, but PCR amplification can easily fail due to contamination. The Roti®-Prep Genomic DNA MINI Kit is a reliable method of DNA isolation that avoids contamination. However, the smaller shrimps used in this study had insufficient muscle tissue for reliable DNA isolation.

For amplification of a fragment of the mitochondrial cytochrome oxidase subunit 1 gene (COI), species-specific primers that amplify the Folmer fragment of COI (Folmer et al., 1994) were designed:

COI-Pal24F (forward): 5'-waa tca taa aga cat ygg ha-3'

COIPal725Rv2 (reverse): 5'-taa act tcw ggg tgm ccr aa-3'

The following components were used per reaction: 12.5 µl Roti®Pol TaqS Red Mix (2x) (ROTH), 4.5 µl purified Water, 2.5 µl each forward and reverse Primer (5 µM), 2 µl template DNA and 1 µl bovine serum albumin (BSA, 10 µM) to improve PCR success. Conditions for PCR reactions were 5 min at 95 °C, 35 cycles of 30 s at 95 °C, 1 min at 52 °C, 1 min at 72 °C, then 5 min at 72 °C. Sanger sequencing of PCR products was carried out by the Institute of Clinical Molecular Biology (IKMB) in Kiel using a 96-capillary sequencer (Applied Biosystems 3730xl DNA Analyzer).

Sequences were quality-checked, assembled, aligned and trimmed to the same length (560 bp) using Geneious Prime (Ver. 2020.0.3) (Kearse et al., 2012). The present study combined sequences obtained from the study's own research with sequences that were publicly available in the NCBI GenBank or the Barcoding of Life Database (BOLD) from several North Sea populations: Belgium (Bruges) (NCBI GenBank Acc. Nos. HG792278, HG792293 and HG792297), Germany (Wilhelmshaven) (NCBI GenBank Acc. Nos. KT208801, KT208984, KT208997, KT209340, KT209413, KT209554, KT209563 and KT209570), a single find from the sublittoral about 5 km offshore from the northern German coast near Amrum (NCBI GenBank Acc. No. NLGIM631-16) and three different locations in the Netherlands: Waddenzee (BOLD Acc. Nos. NLGIM707-16 and NLGIM708-16), Grevelingen (BOLD Acc. No. NLMAR224-20 and NLMAR311-20) and Oosterschelde (BOLD Acc. No. NLGIM709-16). All subsequent population genetic analyses were conducted in the R environment (Ver. 3.5.3) (R Core Team, 2020). A haplotype network was generated using the 'haplotype' package (Ver. 1.1) (Aktas, 2019). In addition, haplotype and nucleotide diversity for each population were calculated using the 'pegas' (Ver. 0.11) package (Paradis et al., 2019) and calculated the corresponding confidence intervals with custom R scripts. Population differentiation were estimated by calculating Jost's D and PhiST with the packages 'adegenet' (Ver. 2.1.2) (Jombart et al., 2020) and 'pegas' (Ver. 0.11) (Paradis et al., 2019), respectively. Both calculations were bootstrapped using 1000 replicates. Each haplotype was blasted against the NCBI nucleotide database (search option "megablast") to identify the sampling locations of previously sequenced individuals with the same haplotypes. These locations are possible sources for the Baltic and North Sea populations.

3. Results

3.1. Ecological surveys

In Lake Flemhude and both Gdańsk locations, males, females and ovigerous females of *P. macrodactylus* were collected (Table 1). At the Kiel Fjord, Tirpitzmole and Kiel canal proper locations, only the native species *Palaemon elegans* Rathke, 1836, *Palaemon adspersus* Rathke, 1836 and *Palaemon varians* Leach, 1814 were found during our surveys (Fig. 2).

4. Results

4.1. Molecular analysis

The final alignment of 78 sequences was 560 base pairs (bp) long (alignment in appendix). In this alignment, eight different haplotypes were identified (Fig. 3). The most common haplotypes were H2 and H1,

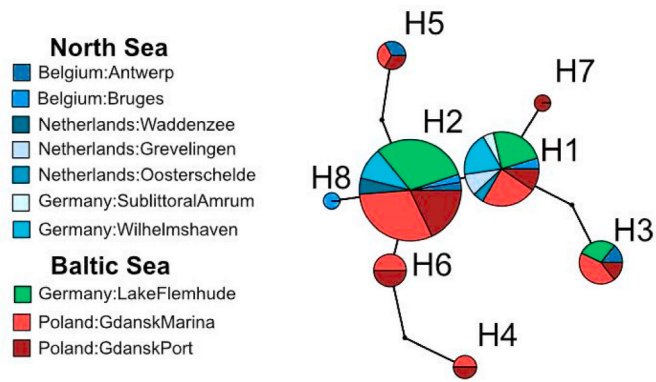


Fig. 3. Haplotype network for mitochondrial COI sequences of *P. macrodactylus* collected in the North and Baltic Sea. Each pie represents a haplotype, with colors corresponding to sampling locations. The size of the pies is proportional to the number of sequences that carried the haplotype. Each line is a mutational step, and small black dots are hypothetical haplotypes not recovered from our samples. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

present in both North and Baltic Sea. Within the study area, the two haplotypes H4 and H6 were detected exclusively in Baltic Sea populations (Fig. 4). Two of the eight haplotypes were represented by only one sequence: one of these singletons (H8) was the only one found exclusively in the North Sea, while the other (H7) was exclusively found in the Baltic Sea. North Sea haplotypes were separated by a maximum of two mutation steps.

Haplotype diversity was significantly higher in Poland and Belgium than in the other populations, which did not differ significantly in haplotype diversity (Fig. 5A). The nucleotide diversity showed the same pattern (Fig. 5B). Overall, haplotype and especially nucleotide diversity tended to be lowest in the Netherlands and Germany, and highest in the most eastern and western locations investigated. Jost’s D and PhiST values show no significant genetic differentiation between the populations (Table in appendix).

The BLAST results revealed that haplotypes H4, H5 and H6 have not been found anywhere outside our study region, while the remaining 5 haplotypes were previously identified by Lejeusne et al. (2015) in the native and non-native range (Table 2).

5. Discussion

The following hypotheses were put forward: A west-to-east expansion from the North Sea into the Baltic Sea; an anthropogenic dispersal rather than natural expansion, and cryptic introductions from other parts of the introduced range or from the native range.

5.1. Colonization routes

The timeline of the recordings of *P. macrodactylus* within the Baltic Sea suggested a west to east expansion of this species. However, since the juveniles can be easily confused with other *Palaemon* species, primarily based on similarities in their shape of rostrum or the number of rostrum teeth (González-Ortegón and Cuesta, 2006), it is quite possible that *P. macrodactylus* has been present in the Baltic Sea longer than previously assumed. In addition, ovigerous females were not discovered in Lake Flemhude until 2022. This uncertainty raises questions regarding the establishment, dispersal routes, and long-term persistence of the species in this location. It is therefore argued that the Lake Flemhude population was, at least prior to 2022, maintained through repeated introductions rather than local reproduction. The reproductive population observed since 2022 may originate from a reduced subset of the previously introduced haplotypes, potentially leading to a bottleneck effect and lower genetic diversity compared to the population in Gdansk. Consequently, the chronology of the previous records should not be the deciding factor for the reconstruction of the expansion pathways of *P. macrodactylus* within the Baltic Sea.

Since genetic diversity of non-native species is expected to decrease during secondary spread (Ewers-Saucedo and Wares, 2020), the observed decreasing east to west genetic diversity suggests a westward rather than the expected eastward expansion of *P. macrodactylus* in the Baltic Sea. Alternatively, the large diversity of haplotypes of populations from both Polish locations, especially Gdańsk Port, may be the result of multiple introductions from different locations around the world. An analysis of ship traffic from 2018 indicates that Polish ports receive vessels from as many as 11 marine regions, while German Baltic Sea ports only from one marine region (Hegele-Drywa et al., 2024). Furthermore, several Polish haplotypes were rare or absent from the North Sea. H7 was only found in the native range of Japan, while H1, H2, H3 and H8 are more globally represented. This confirms the repeated introductions from other marine regions into the Baltic Sea and especially Gdańsk Port.

Haplotype diversity is higher in both North Sea and Baltic Sea populations when the respective population originates from a port or its

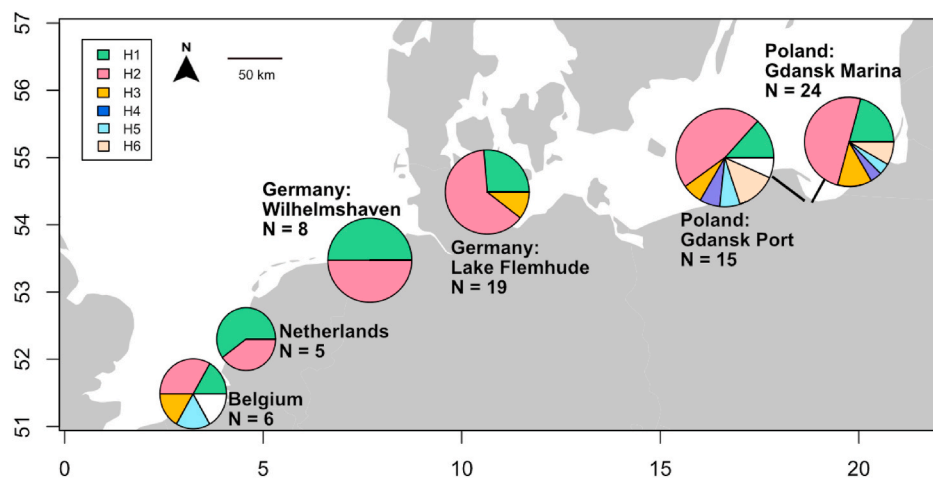


Fig. 4. Geographic distribution of haplotypes. The colors denote different haplotypes. White haplotypes are haplotypes identified only in a single individual (“singletons”). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

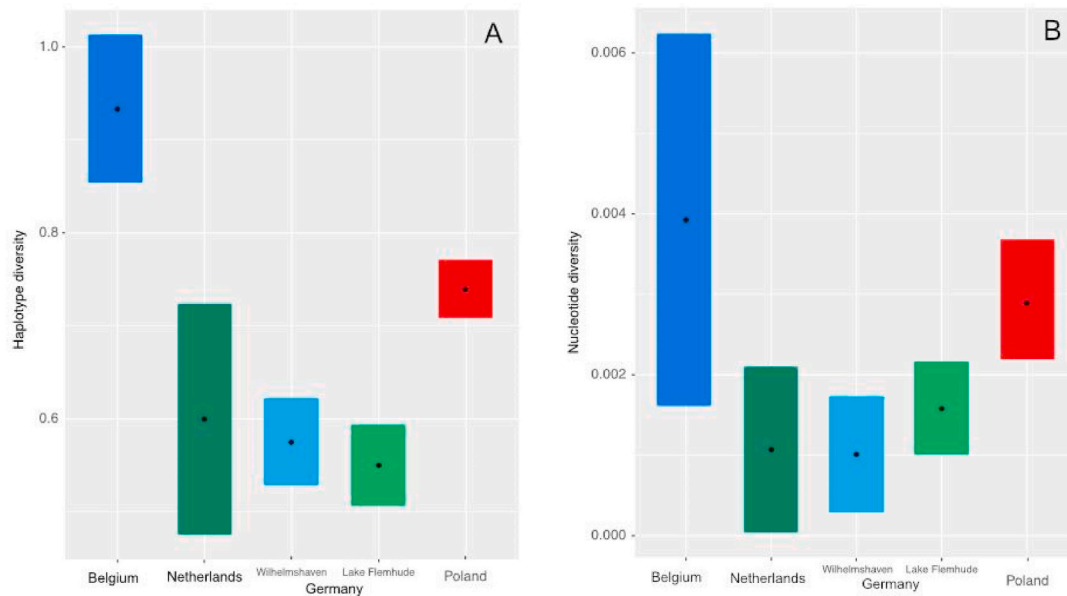


Fig. 5. Genetic diversity of *P. macrodactylus* in the North and Baltic Sea. A: haplotype diversity. B: nucleotide diversity. Bars indicate confidence intervals, dots point estimates. Colors match Fig. 3. Localities are ordered from east to west. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 2

Occurrences of haplotypes identified in this study that have previously been recognized in *P. macrodactylus*.

Haplotype	BLAST matches	Native locations	Non-native locations	Corresponding haplotype (Lejeune et al., 2015)
H1	HG792278.1	Japan	USA, England, France, Spain	Pm3
H2	HG792293.1 OQ322843.1	Japan, Korea	USA, Argentina, England, France, Spain	Pm18
H3	HG792304.1	Japan	Spain, France	Pm29
H4	No matches	No matches	No matches	No matches
H5	No matches	No matches	No matches	No matches
H6	No matches	No matches	No matches	No matches
H7	HG792276.1	Japan	No matches	Pm1
H8	HG792297.1	Japan	Spain	Pm22

vicinity, like Belgium or Gdańsk cases. This indicates that dispersal in both basins emanates from port areas.

The haplotype diversity of the population in Lake Flehmude is considerably lower than that of the Polish populations. Lake Flehmude is connected to Kiel Canal but is not in the vicinity of a port. It is likely that *P. macrodactylus* was accidentally introduced to Lake Flehmude via shipping and leisure boats. Without repeated introductions from other sources, haplotype diversity remains low.

5.2. Establishment of *P. macrodactylus* in the Baltic Sea

P. macrodactylus is in general found within the Baltic Sea in partially enclosed habitats with low tidal currents, such as marinas or lakes with a connection to the sea. These habitats are relatively low in salinity, ranging from 5.4 to 14 psu, but this is not an unusual habitat for a strong osmoregulator such as *P. macrodactylus* (Ashelby et al., 2013). Thus, *P. macrodactylus* shows similar habitat preferences within the Baltic Sea as in the North Sea or North Atlantic populations.

It is striking that there have been no findings of *P. macrodactylus* along the Baltic Sea coast between Kiel and Gdańsk until 2024. Nonetheless, the considerable geographic gap in distribution between Germany and Poland could be explained by the lack of intensive sampling dedicated to this particular species. During our surveys, hand nets and especially baited traps were effective in collecting *P. macrodactylus*. Such sampling methods were not included in standard methods applied during HELCOM monitoring. Port surveys are an exception to this, but they usually take place no more than every few years, so the likelihood of catching less common species is therefore low (Normant-Saremba et al., 2020). On the other hand, until 2024 *P. macrodactylus* has never been found even after yearly regular surveys on the East German Baltic coast (Michael Zettler pers. comm.). Moreover, many German ports are regularly surveyed for non-native species. Although the sampling methods are not optimal for catching *P. macrodactylus*, it is noteworthy that, except for Wismar and Stralsund, there have been no coincidental finds so far.

Even though surveys were conducted between 2008 and 2022, *P. macrodactylus* was not found in Kiel Canal or Kiel Fjord. It is therefore very likely that there is no established population of *P. macrodactylus* within the Kiel Fjord. The sole established population of *P. macrodactylus* in the Baltic Sea outside a port area is the one in Lake Flehmude. Accidental introduction by ships is highly likely as it opens into the Kiel Canal, a highly frequented link between the North Sea and the Baltic Sea.

It is unclear whether *P. macrodactylus* was established prior or after 2009 in Lake Flehmude, as different collection methods were used in different periods. Additionally, only small males were collected in 2009. It is therefore not possible to determine whether reproduction was already taking place in Lake Flehmude at that time, or whether these were isolated coincidental visitors. The low number of specimens collected before 2022 could also be a result of different sampling methods, whereby traps proved to be more effective. An explanation for the patchy distribution of *P. macrodactylus* could be larval retention as in several other brackish decapod species like *Rhithropanopeus harrisi* (Goold, 1841; Forward, 2009). The larval development of *P. macrodactylus* was first described by Little (1969), who identified five to seven zoea stages and a post-larva. Furthermore, it has been demonstrated that complete larval development is possible across a

salinity range of 12–34 psu, and larval retention under these conditions is considered likely (Vázquez et al., 2015).

Other explanations for the patchy distribution could be competition with other palaemonid shrimps like *P. elegans*, which is known for out-competing other species like *P. varians* or *P. adspersus* (Grabowski, 2006; Ovenbeck et al., 2023).

5.3. Probable dispersal vectors

Our data suggests that ship traffic is the most important vector for the dispersal of *P. macrodactylus*, since it was found almost exclusively in the immediate vicinity of ports. This supports the hypothesis of Lavesque et al. (2010) and O'Brian et al. (2017), who also noted ships as the most likely source of dispersal. Especially recreational vessels have more recently been identified as carriers of non-native species (Gollasch, 2002, Clarke Murray et al., 2011; Normant-Saremba et al. in prep.). In this context, biofouling appears to be a significant and possibly the most relevant factor in the dispersal of *P. macrodactylus*, as it provides a suitable habitat for this species. In addition, *P. macrodactylus* was found repeatedly in large numbers and also sporadically in samples scraped from the piers and hulls of leisure boats in Gdańsk Marina, respectively (M. Normant-Saremba, pers. obs.).

The patchy distribution of *P. macrodactylus* indicates that, so far, secondary natural dispersal within the Baltic Sea has likely played only a limited role, although it cannot be entirely ruled out. According to the literature review of Ahelby et al. (2013), *P. macrodactylus* often occurs in low abundances for several years after initial introduction and only increases in numbers when conditions are favorable. The population studied in Lake Flehmude between 2009 and 2022 may have followed a similar course. However, due to inconsistent sampling methods, this cannot be confirmed with certainty. It is possible that *P. macrodactylus* will spread in the Kiel Fjord in the coming years, similar to the case in Gdańsk. The extent and timing of this spread will likely depend on the species' ability to compete with other palaemonid shrimp species in this habitat.

CRedit authorship contribution statement

Kira Ovenbeck: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Investigation, Formal analysis, Data curation. **Dirk Brandis:** Supervision, Project administration, Conceptualization. **Monika Normant-Saremba:** Writing – review & editing, Resources, Investigation. **Jonas Schoelnyck:** Resources, Investigation. **Christine Ewers:** Writing – review & editing, Supervision, Project administration, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2025.107214>.

Data availability

Data will be made available on request.

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