

Rapid Communication

A first insight into the transatlantic population genetic structure of the beach flea, *Platorchestia platensis* (Krøyer, 1845)

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Abstract

Platorchestia platensis (Krøyer, 1845) is a cosmopolitan and cryptogenic semiterrestrial amphipod species inhabiting marine coasts all over the temperate and tropical regions of the world. Very little is known about its dispersal mechanisms, and there is little data on the genetic relatedness among local populations in various regions of the world. In this study, we provide first and preliminary molecular evidence that suggests conspecificity of *P. platensis* populations inhabiting European and North American marine coasts and potentially some genetic isolation of Mediterranean populations.

Key words: Talitridae, Amphipoda, COI, genetic uniformity, genetic isolation

Introduction

The Talitridae Rafinesque, 1815 are the only family of amphipods to contain semi- and euterrestrial representatives. They have an extremely broad ecological range, inhabiting a wide array of habitats, including forests, salt- or brackish- or freshwater marshes, marine, lagoon and lake coastlines or river banks (Bousfield 1982). Most studies point to very low intraspecific genetic variability in talitrids with very few examples of cryptic diversity (Cheng et al. 2011; Henzler and Ingólfsson 2008), especially in comparison to what has been shown in freshwater amphipods (i.e. Weiss et al. 2014; Mamos et al. 2014, 2016; Copilaş-Ciocianu and Petrussek 2015, 2017; Katouzian et al. 2016, Grabowski et al. 2017).

There are currently seventeen species of beach fleas belonging to the genus *Platorchestia* Bousfield, 1982 (Serejo and Lowry 2008; Cheng et al. 2011). *Platorchestia platensis* (Krøyer, 1845) is a cosmopolitan and cryptogenic, semiterrestrial species, inhabiting marine coasts all over the temperate and tropical regions of the world (Behbehani and Croker 1982): from North and South America (Bousfield

1973; Serejo 2004), through Bermuda (Kunkel 1910), Europe (Dahl 1946; Persson 2001; Spicer and Janas 2006), South Africa (Diemer et al. 2016), to Korea (Jo 1988) and Japan (Morino 1978); and even such isolated archipelagos as Hawaii (Stephensen 1935). The species has been described by Krøyer in 1845, based on individuals from the Río de la Plata estuary near Montevideo in Uruguay (Serejo and Lowry 2008). However, it is not known whether this locality represents the native or the non-native range. In Europe, *P. platensis* is considered as an alien invasive species, firstly introduced in Scandinavian waters, expanding its range and successfully outcompeting other species, such as *Orchestia gammarellus* (Pallas, 1766) (Jensen 2010). In Europe, Dahl (1946) was among the first to report rapid spread of this species in the Scandinavian Region and hypothesised that it may be a result of secondary dispersal i.e. rafting. However, despite the wide distribution, still very little is known about the genetic population structure of *P. platensis*, and particularly relatedness between populations on both sides of the Atlantic.

Due to the lack of a planktonic larval dispersal stage amphipods are generally considered to have

Table 1. Material of *Platorchestia platensis* used in our study.

Locality	N	Haplotype counts	Accession number	Reference
Canada: New Brunswick	3	H2 (2), H3(1)	FJ581856 (H2) FJ581857 (H2) FJ581858 (H3)	Radulovici et al. (2009)
USA: New York, Forest Hills, Meadow Lake	1	H2 (1)	KR941564 (H2)	NCBI BioProject: PRJNA159485
Bermuda: Bailey's Bay	3	H2 (1), H3 (2)	KX360499 (H3) KX360547 (H3) KX360596 (H2)	Wildish et al. (2016)
Bermuda: Lagoon Park	2	H1 (1), H3 (1)	KX360549 (H1) KX360561 (H3)	Wildish et al. (2016)
Bermuda: Tobacco Bay Park	1	H2 (1)	KX360583 (H2)	Wildish et al. (2016)
Bermuda: Tynes Bay	3	H2 (3)	KX360517 (H2) KX360576 (H2) KX360588 (H2)	Wildish et al. (2016)
Sweden: Vägeröd	3	H2 (1), H4 (2)	MF544022 (H4) MF544023 (H2) MF544024 (H4)	This study
Italy: Lago di Veneto, Fusina	2	H2 (2)	MF544031 (H2) MF544032 (H2)	This study
Sicily: Lago di Ganzirri, near Messina	6	H2 (4), H5 (2)	MF544025 (H2) MF544026 (H5) MF544027 (H5) MF544028 (H2) MF544029 (H2) MF544030 (H2)	This study

rather limited natural dispersal potential (Friend and Richardson 1986; Myers 1993). Ballast waters, ectozoochory and rafting have been proposed as potential transatlantic vectors, yet without any solid confirmation (Simpson 2011). Semi-terrestrial species associated with floating substrates (like wood or kelps), may occasionally be transported over very long distances via rafting (Thiel and Haye 2006). Wildish (1988) suggested three methods of passive movement for supralittoral talitrids: on wrack or driftwood, by ectozoochory with bird or mammal and human-mediated i.e. in ship cargoes. However, long distance dispersal has its limitations like the longevity of floating material, the sea currents, the distance of the dispersal and behaviour of the animals (Wildish 2012). On the other hand, long-distance migration of semi-terrestrial talitrids on driftwood was a successful way of colonising several oceanic islands (Wildish 2012; Wildish et al. 2012; Pavesi et al. 2015) and recently it has been demonstrated feasible by predictive modelling for transatlantic dispersal of *O. gammarellus*, *Platorchestia monodi* Stock, 1996 and *P. platensis* (Wildish and Chang 2017).

The aim of our study is to provide a first, preliminary comparison of the genetic composition of *P. platensis* populations from both sides of the Atlantic Ocean, based on a limited number of individuals sequenced for a portion of cytochrome oxidase

(COI) gene. This marker has sufficient variability to be used commonly in studies upon molecular population structure and cryptic diversity of various invertebrates, including amphipods (e.g. Henzler and Ingólfsson 2008; Weiss et al. 2014; Mamos et al. 2016; Grabowski et al. 2017). Data presented here are the first to investigate the hypothesis of the relative genetic uniformity of individuals across the Atlantic versus one that assumes presence of vicariant populations exhibiting some level of cryptic diversity and genetic divergence.

Material and methods

Platorchestia platensis from European coasts were collected at three sampling sites, from Vägeröd, Sweden (n = 3) (58.2424N; 11.4909E) in the Baltic Sea, and from the Mediterranean, in Lago di Veneto near Fusina (n = 2) (45.4217N; 12.2580E), Italy and Lago di Ganzirri, near Messina, Sicily, Italy (n = 6) (38.2616N; 15.6244E) (Table 1). The animals were caught with tweezers (without damaging the individuals) and immediately fixed in 96% ethanol. All the material used in this study has been stored in the permanent collection of the Department of Invertebrate Zoology and Hydrobiology, University of Lodz, Poland. The beach fleas from the North American Atlantic coasts were represented by a set of respective

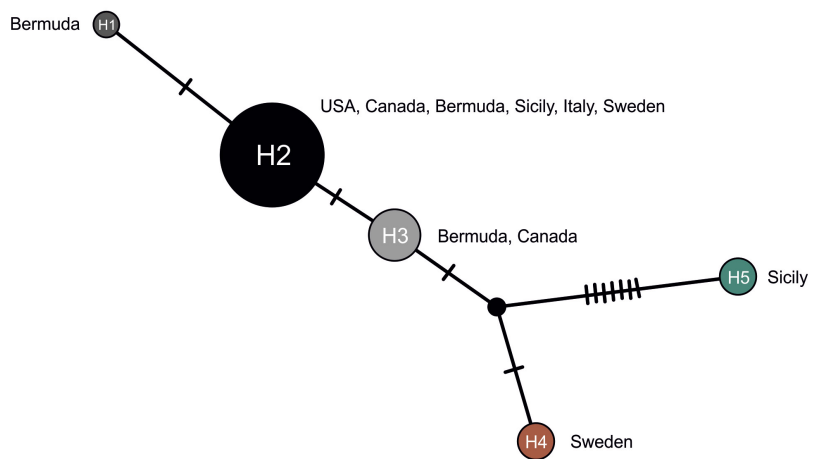


Figure 1. Median-joining network illustrating relationships between *Platorchestia platensis* haplotypes. Numbers in circles indicate haplotype names. Size of the circle reflects the number of individuals with particular haplotype with smallest circle representing one individual. Hash marks along the lines represent number of mutation steps separating haplotypes.

DNA sequences downloaded from NCBI GenBank (see below, Table 1).

From each of the eleven newly collected individuals, about 3 mm³ of muscle tissue was extracted from the mesosome and the pleopods with a sharp-edged forceps and incubated overnight at 55 °C in a 1.5-ml tube containing 200 µl of Queen's lysis buffer with 5 µl of proteinase K (20 mg mL⁻¹). DNA was extracted using standard phenol/chloroform method (Hillis and Davis 1986). Air-dried DNA pellets were resuspended in 100 µl of TE buffer, pH 8.00, stored at 4 °C until amplification and finally long-term stored at -20 °C. The individuals were barcoded for COI gene fragment using LCO1490-JJ and HCO2198-JJ primers (Astrin and Stüben 2008). Polymerase chain reaction was performed in a total volume of 10 µl containing 5 µl of DreamTaq Master Mix (2x) Polymerase (Fermentas), 0.8 µl of each primer (concentration 5 µM), 2.4 µl of ultrapure water and 1 µl of DNA template. PCR settings for amplifying COI sequences consisted of initial denaturing of 60 s at 94 °C, five cycles of 30 s at 94 °C, 90 s at 45 °C, 60 s at 72 °C, then 35 cycles of 30 s at 94 °C, 90 s at 51 °C, 60 s at 72 °C, and final 5 min extension at 72 °C (Hou et al. 2007). PCR products were cleaned up by exonuclease I (20 U mL⁻¹, Fermentas) and alkaline phosphatase FastAP (1 U mL⁻¹, Fermentas) treatment, according to the manufacturer's guidelines, and sequenced directly using the same primers as at the amplification stage. Sequencing of the PCR products was performed using BigDye terminator technology by MacroGen Inc.

Resulting sequences were assembled, aligned and trimmed to the same length (597 bp) in Geneious software (Kearse et al. 2012). The alignment was performed using MAFFT plugin (Kato et al. 2002).

The DNAsp software (Librado and Rozas 2009) was used to define the haplotypes and to calculate the haplotype and nucleotide diversity. The K2P pairwise genetic distances were calculated in MEGA7 software (Kumar et al. 2016). Thirteen COI sequences of *P. platensis* from North American Atlantic coast available in NCBI GenBank were used for the comparison between the members of the populations from various sites (Table 1). The relationships between haplotypes were illustrated with the median-joining network (Bandelt et al. 1999) in PopArt (Leigh and Bryant 2015). Relevant voucher information, GPS coordinates and trace files are accessible through the public data set "*Platorchestia platensis* of Europe" (data set PPLA, available publicly in BOLD) in the Barcode of Life Data Systems (BOLD; www.boldsystems.org; Ratnasingham and Hebert 2007), where also Barcode Index Number (BIN) discordance has been done (Ratnasingham and Hebert 2013). In addition, all the sequences were deposited in GenBank (MF544022 to MF544032).

Results

The overall mean distance between all individuals of *P. platensis* did not exceed 1.7% K2P and all of them were ascribed to a single BIN (BOLD: AAA2949). This likely indicates that all the studied populations are uniform enough to be conspecific (Costa et al. 2007). We identified five haplotypes in the dataset composed of the twenty four 597-bp COI sequences including material from the Baltic Sea, Mediterranean, Atlantic coast of North America and Bermuda Islands (Figure 1). Most individuals of *P. platensis* on both sides of the Atlantic shared the same most common haplotype (Figure 2). The overall

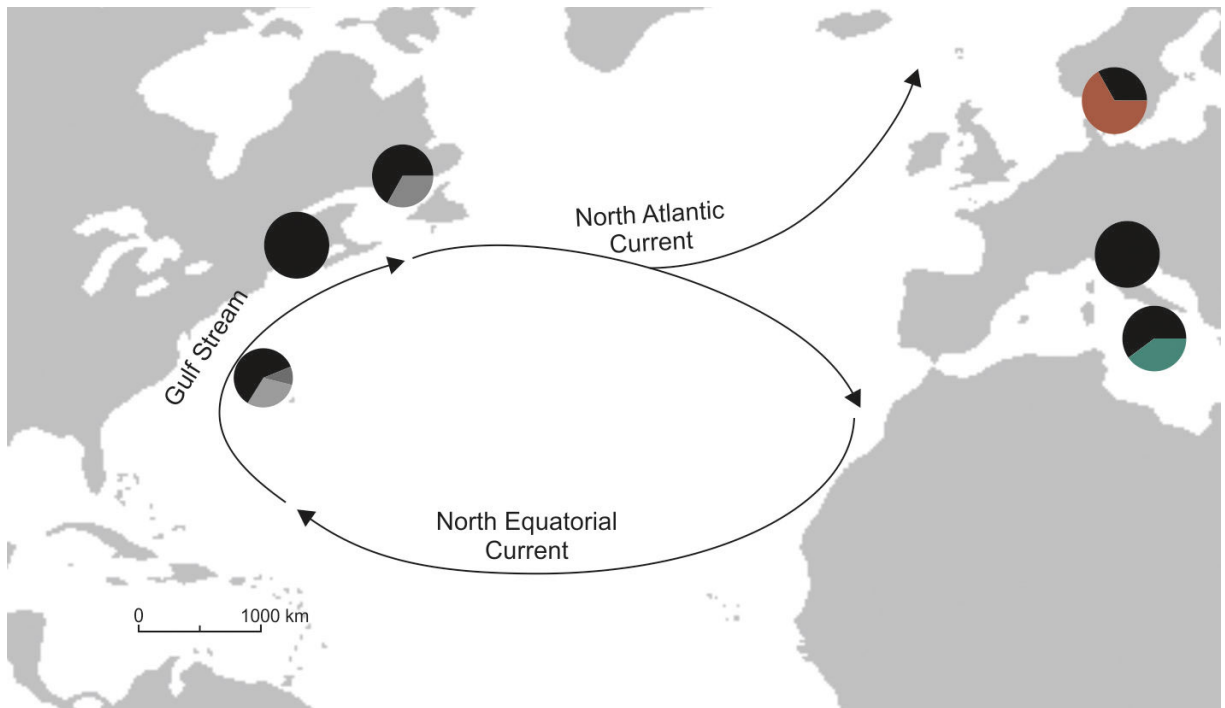


Figure 2. Map of the Atlantic Ocean showing the proportion of haplotypes in each studied population. The directions of the main Atlantic currents are indicated with arrows. Colour codes as in Figure 1.

haplotype diversity was high ($Hd = 0.573 \pm 0.104$), whereas nucleotide diversity ($Pi = 0.00342 \pm 0.00127$) was low. Generally, the haplotype divergence was very low, except for one divergent haplotype from Sicily (Figure 1). The populations from the Atlantic coast of North America and from Lago Di Veneto in Italy were composed only of the most common haplotype, which was absent from only one population from Lagoon Park in Bermuda. Three haplotypes were identified in the Bermuda population, whereas in Sicily and Sweden two haplotypes were found, including one unique for each locality (Figures 1 and 2).

Discussion and conclusions

We found that genetic divergence among studied populations of *P. platensis* from both sides of the Atlantic was consistent with them being conspecific. Interestingly, De Mattheis et al. (2000), based on the allozyme polymorphism, indicated very weak population structure of this species on a smaller, Mediterranean, scale. The question arises what is the reason behind such pattern. A plausible explanation would be the population connectivity via past or recent transoceanic dispersal, either frequent or occasional. A recent study by Wildish and Chang (2017) demonstrated the plausibility of passive dispersal by

this species on driftwood. However, they suggested that given the speed and direction of ocean currents and durability of the driftwood rafts, it would be only possible in the direction from west to east. Henzler and Ingólfsson (2008) evidenced recent, transoceanic dispersal for another widespread talitrid, *O. gammarellus*. On the other hand, one cannot exclude other means like ectozoochory or human aided introductions with ballast waters or ship cargo (Simpson 2011). Thus, the origin of the species remains unknown and needs further examination, however it is most likely a non-indigenous species in European waters (Jensen 2010). On the other side, the presence of unique haplotypes in some populations (Bermuda, Sweden) cannot be neglected. This may result from the already ongoing local diversifications, founder effect or genetic drift but, most likely, it is a result of our very limited sample sizes. Especially interesting is the haplotype from Sicily, most divergent from all the others, yet still grouped under the same BIN. This finding may also indicate more than one source of the populations of *P. platensis* in Mediterranean. This result is hard to interpret with such limited data. However, it is worth mentioning that past morphological studies have put in doubt taxonomical identity of *P. platensis* from different regions of the world (Miyamoto and Morino 2004;

Serejo and Lowry 2008) while the molecular data provided in our study favours the idea of uniformity of this species.

In conclusion, we provide the first molecular evidence for close genetic relatedness of *P. platensis* populations across the Atlantic. Certainly, it is necessary to gather molecular data from a wider range of sites, especially from its locus typicus area in Uruguay, to draw any firm conclusions including the taxonomic position of NE Atlantic and Mediterranean populations. Yet, our findings provide a starting point towards understanding the distribution of genetic variation in this species globally. More detailed study are required to resolve the evolutionary history and phylogeography of this cosmopolitan species.

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