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## Life history of invasive Ponto-Caspian mysids (Crustacea: Mysida): A comparative study

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## ABSTRACT

In recent decades the Ponto-Caspian mysids Limnomysis benedeni, Hemimysis anomala, and Katamysis warpachowskyi expanded their ranges throughout the North Atlantic region and proved to have profound ecological impacts in the invaded waters. The aim of this study was to (1) provide a comprehensive description about the life history of the previously least known K. warpachowskyi, (2) reveal the number of generations produced annually by the three invasive Ponto-Caspian mysids, and to (3) compare the life history traits of the three species directly for the first time based on a simultaneous sampling. To obtain a high-resolution picture about their body length-frequency distributions, a very intensive (approximately weekly) sampling was carried out in an artificial embayment of the Danube River (in Hungary), where the three species coexist. The relatively large L. benedeni had five generations per year and produced comparatively low numbers of young, while the similar sized H. anomala completed only four generations, but compensated for this with a higher fecundity. The smaller sized K. warpachowskyi was able to produce more than five (probably 6) generations per year owing to its short maturation time and long reproductive season, and attained brood sizes close to those of L. benedeni. The generation numbers revealed by the study can be regarded as extraordinarily high considering the body size of the animals and the temperate climatic conditions, which might contribute to their invasion success by increasing the chance of establishment, especially in the course of jump dispersal events at which Ponto-Caspian mysids have proved very successful.

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## Introduction

Ponto-Caspian mysids got into the focus of scientific interest on account of their range expansions throughout the North Atlantic region and their profound ecological impacts in the invaded waters. Intentional introductions played a significant role in their spread especially in the former Soviet Union (e.g., Grigorovich et al., 2002), but three species (Hemimysis anomala G.O. Sars, 1907; Katamysis warpachowskyi G.O. Sars, 1893; and Limnomysis benedeni Czerniavsky, 1882) invaded European and North American inland waters without deliberate human assistance. At present, H. anomala has the widest distribution; in the last two decades it colonized the Baltic Sea basin, almost every major waterway in Central and Western Europe, and recently it also appeared in the British Isles as well as in the North American Great Lakes (summarized by Audzijonytė et al., 2008). L. benedeni is widely distributed in continental Europe (summarized by Audzijonytė et al., 2009), and it is also considered as a likely future invader of the Great Lakes (Ricciardi and Rasmussen, 1998). K. warpachowskyi expanded its range first of all in the River Danube basin (Wittmann, 2002, 2008); however,

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recently it was also found in Lake Constance (Hanselmann, 2010), projecting its further spread in the River Rhine and other connected catchments. In Hungary, *L. benedeni* was first detected in the middle of the 20th century (Woynárovich, 1954), whilst the other two species appeared around the millennium (Borza et al., 2011; Wittmann, 2002, 2007).

The ecological impact of the species is mainly associated with their trophic linkages. They represent prime food source for fish (e.g., Borcherding et al., 2006; Lantry et al., 2012; Specziár et al., 1997), so their presence may be beneficial for certain fish species, which served as the reason for their deliberate introductions into reservoirs and lakes. However, their diet also includes zooplankton, which may have unanticipated ecosystem-level implications; i.e., lengthened food chains may entail increased bioaccumulation of contaminants, new pathways of parasite transmission to fishes, and altered nutrient cycling, as observed in *Mysis* spp. introductions (Borcherding et al., 2006; Fink et al., 2012; Ketelaars et al., 1999; Lasenby et al., 1986; Ricciardi et al., 2012). As the latest Ponto-Caspian invader, *H. anomala* is anticipated to have especially significant impacts on the nearshore food web of the North American Great Lakes (Marty et al., 2010; Ricciardi et al., 2012).

Reliable information on the life history of invasive species is of primary importance in various fundamental and applied research issues; e.g., in revealing and modeling their population







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Fig. 1. The location of the sampling site: (A) Hungary, (B) Budapest and (C) Freeport of Csepel.

dynamics, assessing their production and biomass, and quantifying their impacts. Our current knowledge on the life history of invasive Ponto-Caspian mysids cannot be regarded as satisfying; I identified three gaps, which I tried to address in the present study.

Firstly, the information available on their life history is different among the species. In relation to its wide non-native range, *H. anomala* is the most thoroughly investigated of them (Borcherding et al., 2006; Dumont and Muller, 2010; loffe et al., 1968; Ketelaars et al., 1999; Marty et al., 2010; Nunn and Cowx, 2012; Taraborelli et al., 2012). The life history of *L. benedeni* is also relatively wellstudied (Gergs et al., 2008; Hanselmann, 2008; Szalontai, 2008); however, in the case of the most recent invader, *K. warpachowskyi*, no focused investigations have been conducted; only some general descriptions and ad hoc observations on some characters have been published (Cărăuşu et al., 1955; Daneliya, 2001; Hanselmann, 2010; Wittmann, 2002).

Secondly, the information available on different life history traits is also variable. Some characteristics, such as body length and fecundity are relatively easy to determine even from single samples. In contrast, assessing the number of generations produced per year – or generation time – of these seasonally breeding multivoltine iteroparous species is an inherently difficult task (Mauchline, 1980). Due to the natural scatter in the timing of reproduction among individuals and the production of more than one broods per female, generation structure becomes more and more obscure during the breeding season. Accordingly, information on this parameter of the invasive Ponto-Caspian mysids is scarce; most of the recent studies on the autecology of species did not deal with it, or were admittedly not suitable to assess it (Borcherding et al., 2006; Hanselmann, 2008; Taraborelli et al., 2012).

Thirdly, almost all the information published derives from single-species studies. Since the traits vary with environmental conditions, these studies do not allow the direct comparison of the results, which could lead to a characterization of the species in relative terms.

Accordingly, my goals in the present study were to (1) provide a comprehensive description about the life history of K. warpachowskyi, (2) reveal the number of generations produced annually by the three invasive Ponto-Caspian mysids, and to (3) compare their life history traits directly for the first time based on a simultaneous sampling. The Hungarian section of the River Danube offered fortunate circumstances for an investigation aimed at achieving these goals; in artificial inlets of the river the three species coexist in high abundance. Another key element of the study design was the sampling frequency. Most life history studies on mysids are based on monthly or biweekly sampling, which may be suitable for species living under colder climatic conditions, but apparently does not allow the identification of generations in species with more rapid life cycles. To overcome this, a very intensive (weekly) sampling was planned, revealing a high-resolution picture about the length-frequency distributions of the species.

### Materials and methods

### Study site

The samples were taken in an artificial inlet of the River Danube in Budapest (Hungary), the Freeport of Csepel ( $47^{\circ}26'31.18''$ N,  $19^{\circ}3'21.46''$ E). The sampling site was located in the ~300 m long, ~60 m wide entrance canal of the Y-shaped embayment (Fig. 1). The bank of this section is reinforced with homogeneous rip-rap embankments (composed of stones measuring ~20–80 cm in diameter). It serves busy ship traffic and it is dredged from time to time to impede sedimentation. Since the embayment is connected directly to the main channel of the river, its water level fluctuates accordingly; however, currents are negligible.

#### Sampling

The samples were taken with an approximately weekly frequency between 02.03.2009 and 20.05.2010, except for the winter months (altogether 50 samples). The sampling was carried out after sunset (by the onset of complete darkness) to make the effective collection of the nocturnally active *H. anomala* possible. Depending on the abundance of the species, 1 to 12 uniform hauls were made above the stones by hand net (aperture 40 cm  $\times$  30 cm, mesh size 450  $\mu$ m, handle length 3.9 m). Unfortunately, the complex, uneven surface formed by the stones presumably did not allow the collection of all the animals in the sampled area; therefore, the method cannot be regarded as quantitative. The proportion of the species owing to their different affinities to the surface; therefore, their contribution in the samples is not directly informative of their relative abundance.

As the species were collected simultaneously, it would have been ideal, if they had occurred in approximately equal density. If one of the species was rarer than the others by more than an order of magnitude, it was not possible to collect a sufficient amount of it. This was the case in late spring/early summer, when *K. warpachowskyi* did not seem to follow the high water levels, and in the autumn/spring, when the bulk of *H. anomala* probably migrated to the deeper parts of the water. *L. benedeni* could be collected efficiently in most of the cases (Appendix 1).

## Sample processing

The samples were preserved in 70% ethanol in the field. Mysids were sorted out and identified in the laboratory using stereomicroscope. Direct measurement of body length in mysids is impractical due to the usually bent posture of preserved specimens. To avoid this problem, other parameters showing strong correlation with body length can be measured (Mauchline, 1980). In this study the lateral carapax length (CL) of the animals was measured from dorsal view using ocular micrometer by  $20 \times$  magnification (allowing

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