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Contrasting life history strategies in a phylogenetically diverse community of freshwater amphipods (Crustacea: Malacostraca)

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ABSTRACT

Differences in life histories are commonly exhibited within ecological communities, especially among species that display increased variations in body size and morphology and are phylogenetically distant. To examine the relationship between morphological dissimilarity and life history divergence, we investigated three morphologically distinct and distantly related species of freshwater amphipods that co-occur throughout the Danube lowlands – *Gammarus balcanicus dacicus*, *Niphargus valachicus* and *Synurella ambulans* – by collecting monthly samples during a one-year period. Results revealed that the studied species differ significantly with respect to fecundity, size at maturity, number of generations per year, duration and timing of the reproductive period and egg volume. Despite some overlap, each species possesses a unique combination of traits, supporting the hypothesis that life history variation within freshwater amphipod communities can reflect dissimilarities regarding body size, morphology and evolutionary relationships. However, it is not yet clear which of these factors has the most significant contribution to life history divergence.

1. Introduction

Life history differences are commonly exhibited among species within ecological communities and are thought to be a mechanism for fostering coexistence (Lusk and Smith, 1998; Bonsall et al., 2004; Cavender-Bares et al., 2004). Furthermore, body size and shape and phylogenetic relationships can have a significant influence on life history traits (Sainte-Marie, 1991; Miles and Dunham, 1992; Gittleman et al., 1996; Fišer et al., 2012b).

Gammaridean amphipod crustaceans are a morphologically highly diverse group making up more than 90% of the Amphipoda (Horton et al., 2013) and exhibiting great variability in life history traits in response to latitude, depth, phylogenetic and physiological constraints (Sainte-Marie, 1991). Species in marine/brackish amphipod communities exhibit such contrasting life history strategies as displaced breeding periods and differences in adult size and brood size (Kolding and Fenchel, 1979; Kolding, 1981; Beerman and Purz, 2013). In freshwater habitats, emphasis has been on the comparison of life history strategies in co-occurring invasive and native species, focussing on the detrimental effects of the invasive species on the native ones (e.g., Grabowski et al., 2007; Pöckl, 2007). Contrastingly, direct comparisons of life histories among species within native freshwater amphipod communities have been less frequent and focused on fewer taxa. Nevertheless, they revealed that such species can exhibit differences in size at maturity, egg size and number, and non-overlapping reproductive peaks (Wellborn, 1995; Fišer et al., 2007; da Silva Castiglioni and Bond-Buckup, 2007, 2008).

Three sympatric, native, gammaridean amphipod species, each belonging to a different family, are found throughout the lowlands of Romania and in some instances they can even co-occur (Fig. 1): *Gammarus balcanicus dacicus* Dobreanu and Manolache, 1942 (Gammaridae), *Niphargus valachicus* Dobreanu and Manolache, 1933 (Niphargidae) and *Synurella ambulans* Müller, 1846 (Crangonyctidae) (Motaş et al., 1962; Copilaş-Ciocianu et al., 2014). They are commonly encountered in various types of lowland habitats characterized by stagnant or slow-flowing waters with muddy substrate and rich vegetation such as ponds, marshes, canals and rivers (Copilaş-Ciocianu et al., 2014). The genera/families to which these species belong display distinct morphologies and are distantly related (Lowry and Myers, 2013). Species of *Gammarus* have stout, laterally compressed bodies, members of the genus *Niphargus* are usually subterranean, blind, depigmented and have long, slender bodies, whereas species of *Synurella* have short

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and stocky bodies (Karaman, 1974; Fišer et al., 2009; Lowry and Myers, 2013). This morphologically and phylogenetically diverse and widespread assemblage is therefore ideal for comparative studies of co-occurring local amphipod species.

The aim of the present study is to investigate and compare the life histories of these three co-occurring freshwater amphipod species. Considering that they exhibit distinct morphologies, different body sizes and distant phylogenetic relationships, we hypothesize that these species should exhibit divergent life history traits. To test this prediction, we collected monthly samples over a period of one year in order to thoroughly compare their life histories.

2. Materials and methods

2.1. Study species

While both *N. valachicus* and *S. ambulans* are regarded as valid taxa (Straškraba, 1972; Karaman, 1974), the subspecies *G. b. dacicus* is currently synonymized with the nominal species (Karaman and Pinkster, 1987). However, *G. balcanicus* represents a highly diverse species complex (Hou et al., 2011, 2014; Mamos et al., 2014) and *G. b. dacicus* is geographically and morphologically distinct from other lineages of the complex and can even co-occur with them (Copilaş-Ciocianu et al., 2014). Molecular data also supports this uniqueness (Copilaş-Ciocianu, unpublished data) and therefore we consider it a distinct entity.

Both *N. valachicus* and *S. ambulans* have overlapping distribution patterns and are often found co-occurring throughout the Danube lowlands, thriving in poorly oxygenated habitats with high temperatures such as oxbow lakes, ponds, temporary water bodies and rivers/streams with a slow current and muddy substrate (Nesemann et al., 1995; Copilaş-Ciocianu et al., 2014). Occasionally, they can also be found in groundwater habitats and springs (Motaş et al., 1962; Karaman, 1974; Meijering et al., 1995). *N. valachicus* is a typical eyeless niphargid apparently restricted to areas of dense vegetation where little light can penetrate (Fišer et al., 2014; Copilaş-Ciocianu, personal observation), while *S. ambulans* is a euryoecious species (Meijering et al., 1995; Copilaş-Ciocianu et al., 2014). Contrastingly, *G. b. dacicus* exhibits more altitudinal variability and can be encountered throughout the mountainous, submountainous and lowland regions of the Carpathian Arc. Its ecological requirements are typical of freshwater *Gammarus*, i.e. it inhabits relatively well oxygenated habitats with moderate to slow current and stony/muddy substrate (Copilaş-Ciocianu et al., 2014). In lowland regions its distribution seems to be limited by the availability of habitats with suitable oxygen levels such as springs, streams and rivers, and it has never been recorded in stagnant waters (Motaş et al., 1962; Copilaş-Ciocianu et al., 2014).

2.2. Study sites and sampling

The present study was conducted at two locations in close proximity (30 km apart) in western Romania: Timişoara, on the Bega River (45°45′18″N, 21°16′35″E), altitude 89 m, depth ~2 m, width 15 m, and Satchinez, on the Ier River (45°57′33″N, 21°03′02″E), altitude 91 m, depth ~1.5 m, and width 5 m (Fig. 1). Both are lowland flowing rivers characterized by slow-running water, muddy/sandy/rocky substrate and rich riparian vegetation. Although all three of the studied species occur at both localities, the sampling sites were chosen according to the species' density. Therefore, Timişoara was specifically used for the collection of *N. valachicus* and *S. ambulans*, while Satchinez was chosen for *G. b. dacicus*. These density differences likely reflect the species' substrate preferences (see Section 2.1): at Timişoara the substrate is predominantly muddy/sandy, while at Satchinez it is mostly rocky.

Material was collected and the environmental conditions were recorded on a monthly basis between October 2012 and September 2013. The amphipods were captured by sweeping through the dense riparian vegetation and bottom of the rivers using a 250 μm mesh hand net (25 cm diameter). Temperature, pH, dissolved oxygen and conductivity were measured (see Table S1 in the supplementary online Appendix) using a portable HQ40d multiparameter meter (Hach-Lange, Düsseldorf, Germany).

2.3. Sample processing and life history data analysis

Specimens were preserved in 70% ethanol in the field. Individuals were identified using the key of Copilaş-Ciocianu et al. (2014) and measured under a stereomicroscope from the ante-

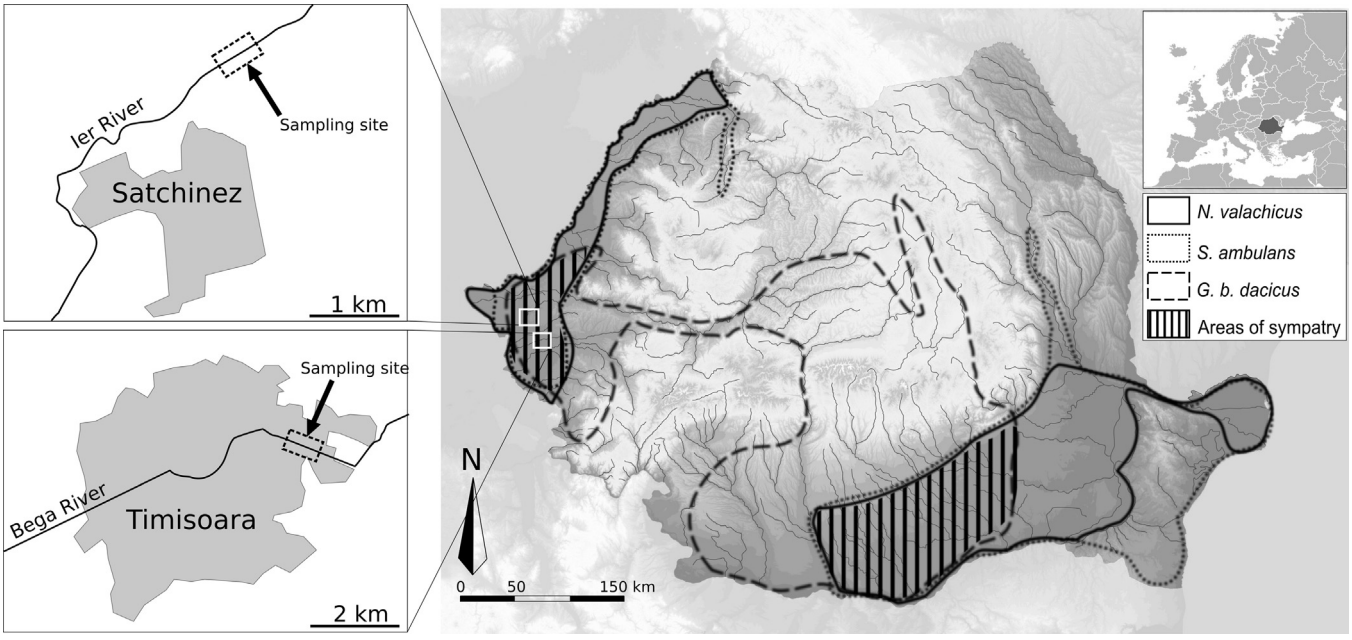

Fig. 1. Distribution patterns of *N. valachicus*, *S. ambulans* and *G. b. dacicus* in Romania (after Copilaş-Ciocianu et al., 2014) and location of sampling sites.