Zoology 118 (2015) 424–432

Contents lists available at ScienceDirect

Zoology

journal homepage: www.elsevier.com/locate/zool

Plasticity in fecundity highlights the females' importance in the spiny-cheek crayfish invasion mechanism

Lucian Pârvulescu[a,*], Mălina Pîrvu[a], Loredana-Giorgiana Moroşan[a], Claudia Zaharia[b]

[a] Department of Biology—Chemistry, Faculty of Chemistry, Biology, Geography, West University of Timisoara, 16A Pestalozzi St, 300115 Timisoara, Romania
[b] Department of Mathematics, Faculty of Mathematics and Computer Science, West University of Timisoara, V. Parvan Blvd., 300223 Timisoara, Romania

ARTICLE INFO

Article history:
Received 29 January 2015
Received in revised form 19 July 2015
Accepted 26 August 2015
Available online 8 September 2015

Keywords:
Colonisation
Invasive species
Oocytes
Orconectes limosus
Population dynamics

ABSTRACT

Invasion is one of the most consequential phenomena affecting the distribution of native species. Few in number of species, European crayfish are losing the competition with introduced North American crayfish. The spiny-cheek crayfish, *Orconectes limosus*, is an outstanding example, successfully competing against the native narrow-clawed crayfish, *Astacus leptodactylus*. For four years, we collected data regarding crayfish occurrences, their relative abundance, and the structure of populations in the ongoing colonisation process of *O. limosus* in the lower Danube. The mature females of both invasive and indigenous crayfish species were analysed with respect to biometry and production of oocytes in relation to the dynamics of invasion. The interspecific comparisons showed no significant differences regarding body size, with an average of approximately 102 mm total length and 31 g wet weight for both species. However, the fecundity of the indigenous species was found to be constant throughout the investigated area, whereas the number of eggs produced by the invasive females was significantly increased at the active front of the invasion. The maximum number of ovarian eggs found was 887 and 1156 in the indigenous species and the invasive species, respectively. We propose the scenario that the invasive species, which carries the deadly crayfish plague, creates an ecological advantage by reducing the populations of indigenous crayfish. Subsequently, the invasive females opportunistically use the available resources to enhance their fecundity, resulting in the acute growth of populations. However, the long-term competitiveness and colonisation success of *O. limosus* still remain in question.

1. Introduction

Human activities have caused the spread of species worldwide, and some of these species have become invasive and pose a threat to the native biota and ecosystems (Chucholl, 2013; Twardochleb and Olden, 2013; Germano et al., 2015). Active invasions are often accomplished by opportunistic species with a higher ability to utilise a wider variety of habitats and resources compared to local residents (Duyck et al., 2007). Moreover, some biological features of invasive species (e.g. higher growth rate and fecundity, resistance to pathogens) enable them to be successful colonisers (Yeh and Price, 2004; Moyle and Marchetti, 2006; MacDougall et al., 2013). Different strategies play distinct roles in ecological successions during biological invasions (Baldridge and Lodge, 2014; Jackson and Britton, 2014; Rewicz et al., 2014). Acute invasions are usually achieved by better colonists, while long-term residence characterises better competitors (Duyck et al., 2007). Compared to long-established populations, the expanding active populations often reveal more accurately the drivers behind successful invasions (Dawson et al., 2010; Bronnenhuber et al., 2011; Schulte et al., 2013).

One of the most successful invaders in Europe is the spiny-cheek crayfish *Orconectes limosus*, a North American species introduced in Barnówko, Poland in 1890 for commercial purposes (Filipová et al., 2011). The species expanded, and it presently inhabits most European river basins from the Garonne in the southwest to the Rhein, Elbe, and Oder in the north, and to the Danube in the east (Kouba et al., 2014). The colonisation of the Danube began in 1985 from two populations artificially established in Germany and Hungary (Nesemann, 1986; Puky and Schád, 2006). The presence of *O. limosus* in the lower Danube has been known since 2008 (Pârvulescu et al., 2009), and they successfully compete against the indigenous narrow-clawed crayfish *Astacus leptodactylus* (Pârvulescu et al., 2012). Like other crayfish species introduced from North America, *O. limosus* is a resistant carrier of the crayfish plague pathogen *Aphanomyces astaci*, which causes one of the worst diseases

* Corresponding author.
E-mail address: lucian.parvulescu@e-uvt.ro (L. Pârvulescu).

http://dx.doi.org/10.1016/j.zool.2015.08.003
0944-2006/

affecting European crayfish species (Holdich et al., 2009; Hatcher et al., 2012). In spite of sporadic evidence that the long-term coexistence of *A. astaci* and different indigenous crayfish species is possible (Harlioğlu, 2008; Svoboda et al., 2012; Caprioli et al., 2013; Kušar et al., 2013), this disease continues to damage wild indigenous crayfish populations by causing mass mortalities (Alderman, 1996; Strauss et al., 2012; Filipová et al., 2013).

The biology of *O. limosus* and *A. leptodactylus* differs in terms of life history. In short-lived species, fecundity strongly influences population size (Sæther and Bakke, 2000; Nagy and Holmes, 2005). *A. leptodactylus* displays a moderate life span of up to 5 years, reaching sexual maturity in the third or fourth year (Huner and Lindqvist, 1991; Lindqvist and Huner, 1999), with a fecundity reaching on average 300 pleopodal eggs (Harlioğlu et al., 2004). *O. limosus* is a typical *r*-strategist, exhibiting a short life cycle of around 4 years and reaching maturity in the second year (Henttonen and Huner, 1999; Kozák et al., 2007). The species has a relatively high fecundity, with average pleopodal fecundity ranging from 100 to 400 pleopodal eggs (for details see Kozák et al., 2006). Although unconfirmed in the field, the invasive species has been found to be capable of facultative parthenogenesis (Buřiè et al., 2011). All these features are plausible advantages responsible for the invasion success of *O. limosus* in Europe (Buřič et al., 2013).

In the present study, we aimed to enhance the knowledge of invasion mechanisms by investigating the process of colonisation of *O. limosus* in the lower Danube. We focused on the dynamics of the competing indigenous and invasive crayfish populations in light of what we hypothesised to be the main source of the population growth: their fecundity.

2. Materials and methods

We analysed the crayfish populations' structure and dynamics in relation to fecundity, expressed by the number of ovarian eggs (oocytes). We chose to quantify ovarian eggs because the number of pleopodal eggs is less reliable. This is primarily due to the stress of capture leading to a partial or even complete loss of clutches (Rhodes and Holdich, 1982), and secondly because when females are carrying pleopodal eggs or juveniles they are less active, thus lowering capture success (Moore et al., 2013).

2.1. Study design

According to Holdich et al. (2006), the emission of eggs in crayfish usually occurs in winter or early spring. Our previous field research in the lower Danube (2009–2011) indicated that females of both species generally carried pleopodal eggs starting at the end of February (unpublished data). We collected crayfish for four years (2011–2014) between December and February. The sampling sites were selected along the lower Danube starting at its entrance into Romanian territory and were chosen to reflect the various stages of invasion (Fig. 1). Each sampling site was visited once per month. In order to avoid differences in the size and number of oocytes in relation to oogenesis (Nakata and Goshima, 2004), we counted only females whose oocytes were well individualised with cortical crypts formed (Yano, 1988), since we considered this stage, just before extrusion, to be the most stable one.

According to invasion stage, sampling sites were categorised into three sectors: residential (R), encompassing all sites where the invasive species' presence had been documented for at least two years; marginal (M), comprising sites with less than two years of the invasive species' presence; and invasion front (F), denoting for each year the most downstream sites where a relevant number (>10) of the invasive species was collected. Control sites (C) were sampled downstream of the invasion front. Although

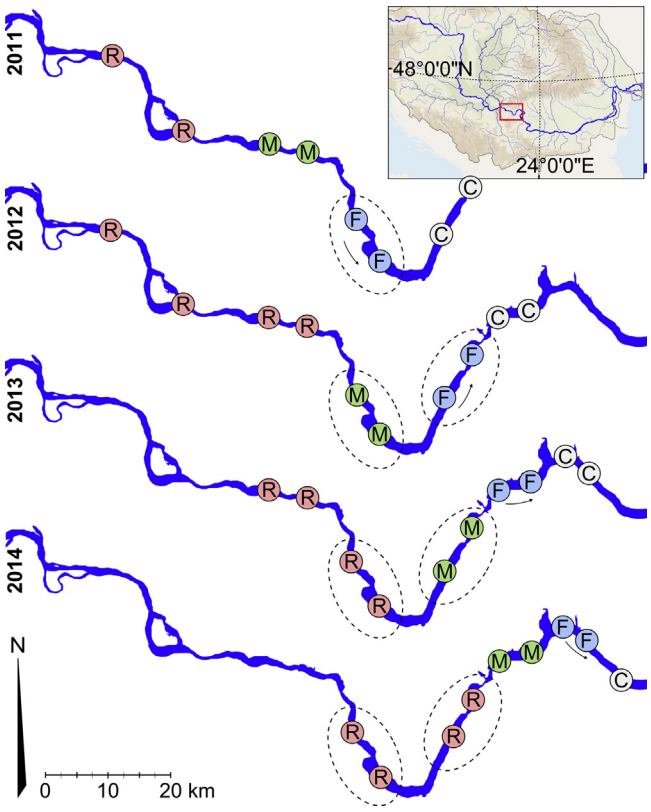

Fig. 1. Map displaying the sites of crayfish collection according to the dynamics of invasion in the lower Danube during 2011–2014. Upstream to downstream sites are marked as residential (R, red), marginal (M, green), invasion front (F, blue), and control (C, grey). Circles with dotted lines around them indicate groups of sites passing through all three stages of invasion (left — two sites grouped around the village Şvinița; right — two sites grouped around the village Dubova). The global geographical position of the lower Danube is presented in the corner map. Arrows indicate the direction of the invasion.

invasive crayfish were found at control sites, their number was too low to constitute a relevant dataset. During the investigations, the stage of the sampling sites was updated along with the progression of the invasion, which advanced at a rate of ~15 km/year (Puky and Schád, 2006; Pârvulescu et al., 2012). Each of the sampling sites which attained residential status during the course of the investigation was analysed as such for two consecutive years.

2.2. Data collection

Crayfish were captured by using bottom fishing nets of 1.5 m height, 25 m width, and a mesh size of ~30 mm, baited with fish and emptied daily. The estimation of crayfish density in a large river such as the lower Danube involves a huge collecting effort (Pilotto et al., 2008). For comparison between the sites, we used the semi-quantitative estimation of capture per unit effort (CPUE), expressed as the total number of crayfish collected in five days per 25 m of fishing net per site. The female proportion was calculated as the percent of females among the captured crayfish of each species.

The collected specimens were preserved in 4% formaldehyde for later analysis. In the laboratory, individuals were sexed and measured for total length (TL), maximum cephalothorax width (MCW), maximum abdominal width (MAW), and wet weight (WW). These data were recorded using a digital calliper (Stanley Black and Decker, New Britain, CT, USA) of 0.01 mm accuracy and a precision balance (Kern & Sohn GmbH, Balingen, Germany) of 0.01 g accuracy. We weighed the specimens after detaching their chelae appendages due to the fact that we found some individuals