

# Interspecific competition between two self-fertile and one related sexual species of tadpole shrimp *Triops* (Branchiopoda, Notostraca) with reproductive interference, Allee effect and environmental fluctuation

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**ABSTRACT.** Invasive alien species of tadpole shrimp *Triops*, originated from America, were first introduced into rice fields of Japan in the 1910s and have spread around Japan. In the 1950s, a European species of *Triops* also seems to have entered Japan. Originally, Japanese paddy fields had Asian *Triops* species as a prehistoric naturalised animal. A new invasive *Triops* from Western Australia has been reported in the south part of Japan, occasionally forming mixed populations. The expansion of *Triops* has resulted in negative ecological and potential economic impact. Longhurst's revision did not contain any specimens of the richest collection in the world, i.e., Daday Collection in the Hungarian Natural History Museum. And therefore, Naganawa surveyed at least 20 times as many samples as those by Longhurst, and number the named *Triops granarius* s.l. species group from Africa-India to Siberia-Asia at eight species, organised in the same genus. As for the establishment or extinction patterns, based on Tilman's competition model, we built a simple mathematical competition model between two self-fertile and one related sexual species of Japan, incorporating reproductive interference. To make the mathematical model more natural, we also assumed environmental fluctuation and Allee effect, which reduces the population growth rate of sexual species with low density. Intense reproductive interference drove the competition to sexual exclusion of self-fertile species. However, even under intense reproductive interference, Allee effect allowed self-fertile species to survive when the competition started with the lower densities; contrary to the survival of sexual species when the competition started with the higher densities.

**Keywords:** inland water crustaceans, rice fields, The Hungarian Natural History Museum, Daday Collection, Tilman's competition model, Allee effect

## 1. Introduction

The generally-accepted notostracan classification of Longhurst (1955) does not include information on the Daday Collection in the Hungarian Natural History Museum (Budapest), which is the world richest collection. Furthermore, his "*Triops granarius*" (an "Asian" species in the broadest sense), which is ranging from Africa through Eurasia and even to Japan, has been regarded as a single cosmopolitan species with wide morphological variations. However, the molecular phylogenetic analysis conducted by Naganawa (2018) revealed that it was actually a hotchpotch of multiple species. If a regional endemic species has been misidentified as a broadly-distributed one (i.e., this is the most problematic matter of Longhurst's

systematics), any zoogeographical results based on this would be far from the real nature; and therefore, first of all, it was needed for us to verify its species definition.

## 2. Materials and methods

We used available specimens of tadpole shrimps from Ural, Irkutsk region, Buryatia, Mongolia, Inner Mongolia (P.R. China) and Japan for molecular and morphological analyses.

## 3. Results and discussion

Naganawa conducted specimen surveys in 2019 on more than 20 times as many type and reference

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specimens at several natural history museums in Europe as Longhurst did at that time of his research. Thus, “*Triops granarius*” sensu Longhurst is never to be a widely-ranging species of tadpole shrimp from Africa to Asia, being revised and redescribed as 8 independent species in the same genus.

In the wild, multiple closely-related species of tadpole shrimps cannot share the same niche, so there is usually only one constituent species in a single body of water. Naganawa, however, found such an interesting case in the south part of Japan as a rice field where three species of tadpole shrimps are coexisting. In order to estimate the pattern of establishment or extinction of alien tadpole shrimps, we developed a simple mathematical competition model based on Tilman’s (1982) that incorporates reproductive interference between two self-fertile species (invaded from the USA and Australia) and one related sexual species (i.e., an ancient Asian species of Japan).

Our results suggest that if the populations can be managed appropriately, a new method for the selective eradication of harmful invasive tadpole shrimps can be proposed by releasing the native species of tadpole

shrimp into the troublesome rice fields, i.e., by using the competition principle inherent in these animals, without use of any pesticides.

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