

REVIEW

Tadpole Shrimps – A General Review of the Little Known Crustaceans of Ephemeral Waterbodies

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ABSTRACT

In time of global climate changes, astatic inland water reservoirs that contribute to water retention and alleviation of adverse effects of periodic river floods, are getting more and more important. Small, periodically drying off water reservoirs are also rich hubs of biodiversity. Animals especially connected to such ecosystems are primitive but unique crustaceans called tadpole shrimps (order Notostraca). Those animals seem to have universal significance – both ecological and economic. Though their primitive morphology and small size, they can radically affect the nature of their habitats, sometimes even helping us fight with noxious pests. Unfortunately, due to progressing global warming, intensification in agriculture, and urbanisation, habitats of notostracans are disappearing rapidly. Simultaneously, because of their rare occurrences and taxonomic difficulties, tadpole shrimps have been insufficiently studied. However, protection of these crustaceans is inseparably connected with conservation of once numerous, periodically drying reservoirs as tadpole shrimps are referred as keystone species of such habitats. Thus, the aim of this review article is to sum up and disseminate current state of knowledge about Notostraca by a general overview of available international literature. This might help to engage more scientists into research and conservation of these little known, yet interesting crustaceans and their unique habitats.

1. Introduction

Notostraca is an order of crustaceans leading solely aquatic life, insufficiently studied and extremely old in evolutionary terms, with origins dating back to Carboniferous period, and sometimes even Devonian period (ca. 350 million years ago) ^[1,2]. In addition, fossilized remains of such animals from 200 million years ago (late Triassic) found in Central European lowland (present day Germany) are barely discernible from one of their today's equivalent – *Triops canfriformis* (Figure 1.) ^[1,2,3]. Thus tadpole

shrimps are sometimes dubbed "living fossils" ^[2]. Together with Anostraca and Diplostraca, Notostraca form a group of so-called large branchiopods. They are cosmopolitan crustaceans whose ecology is closely connected with periodically drying off (sometimes for years at a time) inland reservoirs of lentic water ^[4,5]. Those animals can thrive in an ephemeral environment not only due to absence of pressure from fish ^[5], but also due to unique capability of producing extremely resistant cysts that may survive heavy droughts for years in diapause condition ^[6]. Also, Tadpole shrimps play multiple important ecologic roles

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^[2,7,8] and thus they are more and more widely considered as keystone species in astatic water reservoirs ^[7]. Correctly managed, such crustaceans may become human allies, especially in the context of eliminating pests, such as mosquitoes or weeds ^[8,9,10], and due to their unique properties, appearance and interesting behaviours, Notostraca had already found recognition among breeders a long time ago ^[5,8]. Unfortunately, despite their cosmopolitan rangeland ^[4,11] tadpole shrimps (and other large Branchiopoda) become increasingly rare in many regions of the world ^[11]. This is caused mostly by irreversible disappearance of their habitats ^[12], which are particularly susceptible to climate changes ^[5,13], intensive farming ^[1,14] and human interference with natural shape of river valleys ^[1]. Nevertheless, ephemeral aquatic habitats are not only important biodiversity hubs ^[15] or migratory birds stopover sites ^[2]. Such reservoirs alleviate adverse effects of floods within river valleys ^[1] and therefore the importance of protecting such ecosystems is gaining more and more traction. The purpose of this review article is an overview of available literature and papers about Notostraca, the little known order of crustaceans. Thus, the work sums up taxonomy, biology, ecology and significance, as well as hazards to which notostracans are exposed and which make them increasingly rare group of organisms. We believe this paper might encourage more scientists into tadpole shrimps research in order to better understand their taxonomy, biology and ecology.



Figure 1. *Triops cancriformis* – member of the order Notostraca [photo by Michał Rogacki]

2. Taxonomic Outline

Notostraca order belongs with Anostraca, Diplostraca and Cladocera to the phylum of primitive crustaceans - Branchiopoda ^[16]. Presently, all tadpole shrimps are included in a common family – Triopsidae ^[12] and one of

the two presently existing genera – *Triops* or *Lepidurus*, which have been in need of detailed taxonomic revision for a long time now ^[17]. The basic difference (also simple to determine) between them is the presence of appendage at the end of abdomen in *Lepidurus* genus, which is absent in species of *Triops* genus ^[2]. In addition, both genera never occur simultaneously, although they inhabit similar ecologic niches and habitats. This is due to individuals of both genera demonstrating different preferences with regard to ambient temperature - species in *Lepidurus* may be found in nature only in early spring, when the water is still cold enough. Species in *Triops* genus substitute them only at the turn of spring and summer, when water gets properly warm ^[11]. Most often a total of 11 ^[12] to 15 species have been isolated within both taxons ^[11]. Nevertheless, due to high morphologic plasticity of tadpole shrimps, identification of individuals in species is a serious challenge even for seasoned taxonomists ^[2,12]. Another problem, adding to difficulty, was that molecular studies of those crustaceans prove the existence of multiple cryptic species ^[14,20]. In 2019, Naganawa ^[16] based on morphological and molecular analyses of available specimens of tadpole shrimps from few different regions (Russia, Mongolia, China and Japan), isolated as many as 8 independent species within *Triops granarius*. Furthermore, two extinct genera – *Chenops* and *Jeholops* were identified in 2010 based on fossilized Notostraca discovered in China ^[2].

3. Occurance

Notostraca habitats may be found on all continents (except Antarctica) ^[6,8,11], even in remote and isolated oceanic islands ^[1,11,18], regardless of the moderate, desert or arctic climate conditions ^[6,19]. Tadpole shrimps inhabit periodically drying aquatic habitats, freshwater and salty (so-called astatic water reservoirs), such as field ponds, shallow lakes (natural and artificial), broads and flood plains, wetlands, and even small rainwater puddles, fish ponds and rice fields ^[1,5,16,21]. Depending on local climatic conditions and reservoir specifics, such ecosystems may be filled with water from once a year or multiple times a year, or even once every few years ^[5]. Although the rangeland of Notostraca is large, in many regions they are rare, with large populations occurring only locally ^[14,22]. As regards the rangeland, species *Lepidurus apus* stands out (its habitats may be found across continental Europe, Northern Africa and Asia) ^[2] and *Triops cancriformis* (occurrences in Europe, Northern and Southern Africa, Southern Asia and Japan) ^[1] stands out.

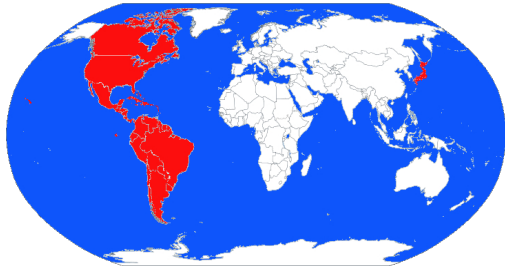


Figure 2. Range of *Triops longicaudatus*, including North America, South America, Carribean, Galapagos, Hawaii and Japan [graphics by Michał Rogacki].

4. Anatomy and Properties

Body of Notostraca individual may be divided into head, thorax and abdomen (Figure 3.). The main distinguishing feature of those animals is chitin carapace attached to the body only in the head section^[1,22]. A pair of compound eyes and one naupliar eye are located in the front section of the carapace^[1,14]. At the bottom of the head there are 2 pairs of short antennas, labrum, mandibles and ventral groove^[1]. Those organisms have from 35 to as many as 70 pairs of legs, located alongside the thorax. The first one is strongly elongated and tipped with endites projecting from under the carapace. It takes part in swimming and breathing.

Other legs are shorter and are used to move, to breathe, to dig and to manipulate food^[5,11]. egg pouches (Figure 4.), where eggs are stored for a time being (in females of *Triops cancriformis* one pouch can hold ca. 60 eggs)^[1,22]. The abdomen of those animals does not have legs and its last segment ends with furca^[1]. Some species may reach 10 cm in length (*T. cancriformis*)^[1,9], however the majority reach 3-5 cm^[22]. The larva – nauplius - measures ca. 0,4 mm at hatching, but with each moulting it looks more and more like adult^[24].

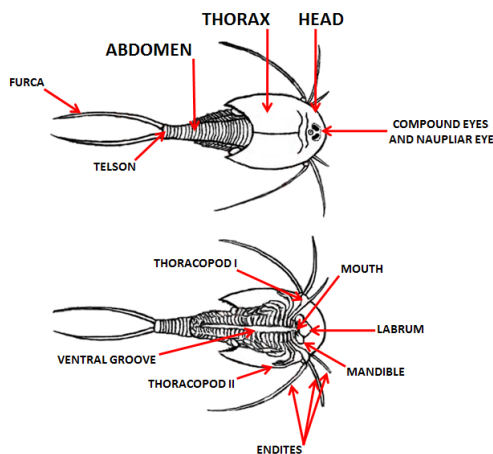


Figure 3. Basic anatomy of tadpole shrimp [graphics by Michał Rogacki]

Those crustaceans are characterised, among others, by high immunity to extreme oxygen deprivation, common in shallow water reservoirs, which they owe to production of haemoglobin^[14,24]. It is, however, very fast metabolism and high fertility of those crustaceans that deserve particular attention. Tadpole shrimps can enclose their full lifecycle within 2 weeks (sometimes long before e.g. puddle they live in dries out) when they start laying large quantities of eggs^[14,22]. In her lifetime, a female may produce over 1000 eggs^[25]. Such intense metabolism comes however with very short lifespan of tadpole shrimps. For example, *Triops longicaudatus* may reach a maximum body length within 8-10 days^[24], but at 15°C it barely lives a month (or as little as 11-12 days at 30°C)^[26].

The animals are further characterized with wealth of reproductive strategies. We may list here gamogenesis, parthenogenesis, hermaphroditism (hermaphroditic individuals being able to mate with males and asexually), as well as androdioecy - extremely rare in animal kingdom (sole occurrence within one population of male and hermaphroditic individuals)^[6,22,27].

The most important feature defining Notostraca is exceptional longevity of their eggs (cysts). When laid and dug in the ground, cysts go into diapause (resting phase)^[28]. In this form, tadpole shrimps are immune to multi-year droughts, high temperatures (up till boiling point), freezing, mechanical damage, extreme oxygen deprivation, ultraviolet radiation, as well as digestive enzymes of predatory animals (fish, amphibians and birds)^[5,6,28,29]. Although documented cases mention coming Notostraca cysts from 27-year long diapause^[30], it is estimated that the creatures may survive in this latent phase as long as decades and centuries^[6,12].

Furthermore, cysts are the great tool of passive dispersion. Due to small dimensions, large adhesion and resistance, cysts of tadpole shrimps may be transferred not only by floodwater and wind, but also by animals (in particular migratory wading birds), humans, and even mechanical equipment^[6,14,29,31,14], sometimes covering very long distances^[2]. Under beneficial circumstances, e.g. low osmotic pressure (characteristic to rain water), optimum pH, temperature and long enough photo period^[1,14], ca. 24 hours following covering with water the larvae, nauplius, start hatching from cysts^[24]. After each watering only part of cysts begin to hatch, which is a protecting mechanism in case water in the reservoir does not stay long enough to enable the animals reaching sexual maturity^[29]. However, the incredible longevity of cysts combined with rapid development and ability of Notostraca to reproduce asexually means that one individual is sufficient to colonize a completely new territory successfully^[29].



Figure 4. *Triops australiensis* with its egg pouch visible [photo by Natalia Dobrowolska]

5. Significance in Nature

Notostraca are so highly specialized with regard to ephemeral aquatic habitats that they occupy a series of significant niches. In the original phase of life (larvae) the animals feed by filtering organic suspension (bacteria, algae, fungi, diatoms and protozoa) [24]. Adult tadpole shrimps are in turn apex predators (and omnivores), effectively modifying the number of organisms on lower trophic levels [7,8,29]. Tadpole shrimps diet includes, i.a. insect larvae, other Branchiopoda, Oligochaeta, and even tadpoles of some amphibian species. In addition, when digging the bottom in search for food they feed on aquatic plants or detritus, thus acting as reducers decomposing dead organic matter [1,5,7]. Those crustaceans are no strangers even to cannibalism [24]. Sometimes tadpole shrimps fall prey to larger animals. Since a large part of their habitats overlap migratory routes – tadpole shrimps make a valuable source of proteins and energy to many species of migratory birds which often rest and feed near astatic reservoirs [2]. In addition, specie *Lepidurus arcticus* living in Iceland and in Nordic countries, is a vital dietary component of not only birds, but also economically significant Salmonidae fish, e.g. sea trout (*Salmo trutta*) or arctic char (*Salvelinus alpinus*) [19,31]. It is also probably the only tadpole shrimp species found even in periodically dry rivers [31].

Tadpole shrimps also affect biocenoses of astatic water reservoirs by way of non-trophic relationships. By way of bioturbation (digging through and disturbing the structure of bottom deposits due to feeding), those crustaceans can dramatically alter the nature of their habitat [7]. Although the precise effect of Notostraca relationships is barely studied it is known that it brings a series of diverse consequences. On one hand, tadpole shrimps comb the bottom reducing macrophytes' access to light, which they additionally uncover and uproot (depriving multiple

small organisms of their habitats). On the other hand, bioturbation modifies the topography of reservoir bottom and sometimes even stimulates microbial activity in bottom deposits by improving their oxygenation. Foraging tadpole shrimps also uncover and release to the environment multiple cysts of other animals and plants (potentially increasing biodiversity), substituting pioneer macrophytes with species featuring more enduring root systems, and even protect weaker organisms from predators that rely on their eye sight (by silting up of water). In addition, the species *Daphnia atkinsoni* reaps direct benefits from the presence of tadpole shrimps, as the crustaceans eliminate other species competing for food (*D. atkinsoni* developed effective defence mechanisms against tadpole shrimps, such as hispid appendices) [7,33].

Complex effect of tadpole shrimps to their habitats makes them being considered more and more as keystone and flagship species in astatic inland water reservoirs [7,14]. Furthermore, specific demands of those animals towards the environment (e.g. *L. arcticus* requires clean, alkaline freshwaters to hatch, and cysts of *T. cancriformis* will not hatch in water with pH exceeding 9) [19,30] and their susceptibility to pesticides [16] makes them potential bioindicative species.

6. Significance to Humans

From the economic perspective, an interesting feature of tadpole shrimps is that those crustaceans often prey on larvae of mosquitoes [7,32]. Although there are only a few studies on the effectiveness of tadpole shrimps in control of those insects, some of them suggest that the American species of Notostraca, namely *Triops longicaudatus*, significantly controlled the number of larvae of mosquito species *Culex tarsalis* under laboratory conditions [9]. Similar results, this time under field conditions, were obtained with other Notostraca species – *Triops newberryi*, which effectively reduced the population of mosquito species *Psorophora columbiae* [9]. In yet another experiment it was demonstrated that in sporadically flooded gardens of date palms in California, the number of mosquitoes in the presence of tadpole shrimps was reduced by 73 to 99% [8]. In addition, these crustaceans effectively prevent adult mosquito females from laying eggs in water [32]. Despite being susceptible to pesticides [16], tadpole shrimps seem to be resistant to some of them – so called biopesticides, e.g. larvicide *Bacillus thuringiensis israelensis* (Bti). It was demonstrated that tadpole shrimps withstand concentration of the preparation hundreds times higher than lethal concentration for mosquitoes in *Culex* genus. Furthermore, ongoing searching of the bottom by tadpole shrimps is related to prolonged presence of larvicides in water,

which would otherwise sink and accumulate in bottom deposits losing their biocidal properties^[9]. The favourable effect of Notostraca in control of mosquito population is further enhanced by their ease of transport - in the form of small cysts. Effectiveness of the crustaceans shall always depend on successful colonization and the nature of a given water reservoir (rather periodically drying reservoir)^[32].

Properties of tadpole shrimps are also useful in paddy fields, where the animals feed on a broad range of undesired weeds^[12,34]. As rice fields are flooded even a few times a year, they perfectly emulate natural habitats of tadpole shrimps, creating beneficial development conditions^[24,34]. However, in some cases tadpole shrimps may themselves become a noxious pest in paddy fields, since they feed on, uproot or reduce access to light to young cuttings, causing their death and sometimes huge loss of harvest^[5,8,24]. Furthermore, their cysts may be brought to new, previously not infected crops^[24]. Adverse effect of tadpole shrimps to crops may be avoided by replanting already grown cuttings to paddy fields instead of growing ones from the seed (which is quite a common practice e.g. in Japan). This is due to the fact that overgrown plants are no longer susceptible to foraging tadpole shrimps^[24,34].

Considering rapid development, easy reproduction and economic potential, notostracans are still being studied for their role in aquaculture^[8,10]. Also, because of their modest demands, interesting appearance and behaviour, tadpole shrimps are popular among breeders (Figure 5)^[5,8]. Moreover, cysts of Anostraca, closely related to Notostraca, exposed to outer space vacuum, were still able to hatch and develop into young crustaceans^[4], which makes Branchiopoda a viable test subject in astrobiological experiments. Due to ease of storage (in the form of cysts) and modest needs they are a rewarding object of observation and laboratory studies, especially that they cover a multiple cryptic species^[16,20], whose identification requires in-depth morphologic and genetic analyses.



Figure 5. Domestic culture of *Triops australiensis* with the albino individual in the foreground [photo by Natalia Dobrowolska]

7. Threats and Protections

Although large branchiopods have large rangeland, many of them (including some tadpole shrimps) are today particularly rare or endangered in many regions of the world^[11,35]. For example, *T. cancriformis* became endangered species^[1,14] in the United Kingdom, where, despite the extensive research, its occurrences were confirmed only in a few standings^[6,14]. Such disturbing state of endangerment of Notostraca (and other large branchiopoda) is mostly due to the loss of their fragile habitats. As estimated, since the time of war England alone lost over 40% of ponds (ca. 1% annually)^[12]. In State of California, from 50 to over 90% of small springtime astatic reservoirs were lost^[12]. Among the threats to ephemeral astatic water habitats are, among others, intensification of agriculture, progressing urbanization^[1,14], superficial flows of pollutants (mostly biogens and not biobased pesticides), as well as land improvement and regulation of rivers^[1]. Global warming seems also to be a threat^[5,13]. Local climate changes in some regions, e.g. higher temperatures and lower air humidity may intensify water evaporation while poor rainfall may result in insufficient amounts of accumulated water in many puddles and ponds for tadpole shrimps to reach sexual maturity^[5]. Selling cysts of various species for breeding in aquariums is another potential threat to tadpole shrimps. Penetration of such forms into natural habitat may lead to possible interspecies competition (unfortunately, information on the subject is still insufficient)^[14]. Ensuring the continued existence of astatic water reservoirs is critical to survival of populations of large branchiopods^[1,5,14]. Methods effective in protection of such habitats include preventing drying off of land, reducing the use of chemicals (mostly pesticides, some fertilizers), maintaining the natural form of rivers, establishing buffer zones around small water reservoirs (e.g. in the form of vegetation) as well as raising the social awareness of significance that small ponds have (e.g. accumulation of floodwater, alleviating the effects of drought, resting or mating place for valuable species of plants and animals)^[1,5,15]. Extensive agriculture and traditional pasturing of farm animals also seem to promote the maintenance of ephemeral ponds. Grazing farm animals prevent the overgrowth of such habitats^[14].

8. Summary

Notostraca is the extremely old order of aquatic crustaceans, which since its origins had survived at least three mass extinctions. Those organisms inhabit periodically drying water reservoirs in which they play a variety of

roles, and therefore are being increasingly considered as so-called keystone species. Tadpole shrimps also have economic value. High vitality and dispersity of those animals, through remarkably resistant cysts, enables them to safely wait through multi-year droughts and colonize successfully even the most remote territories. Despite that, nowadays tadpole shrimps are getting increasingly rare in many places around the world, due to loss of their habitats. Due to significant taxonomic issues and rare occurrences, those crustaceans are of niche interest and the latest studies only prove how little we know about them. Thus, this review is to summarize the current state of available information about Notostraca in order to get more people interested in those unique crustaceans. We also hope this might motivate some scientists to conduct valuable research on tadpole shrimps as many aspects of their ecology, taxonomy or conservation remain unknown to date.

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