Predators as Control Agents of Mosquito Larvae in Micro-Reservoirs (Review)

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Received February 19, 2021; revised March 26, 2021; accepted April 22, 2021

Abstract—The article reviews predators that are able to control populations of mosquito larvae (Culicidae) in phytotelmata and their anthropogenic analogs. The spectrum of mosquito larva consumers in micro-reservoirs is listed. It includes flatworms, crustaceans, arachnids, insects, vertebrates, and carnivorous plants. The biology and practical use of the two most effective biological control agents, predatory mosquitoes Toxorhynchites and copepods, are considered in more detail. Prospects of invertebrate predators as controlling agents for the mosquito larvae in micro-reservoirs in temperate climate zones are briefly discussed.

Keywords: biological control, Toxorhynchites, copepods, Aedes, phytotelmata, micro-reservoirs, container habitat

DOI: 10.1134/S1995082922010138

INTRODUCTION

The ecology of the true mosquito larvae (Culicidae) inhabiting micro-aquatic environments is of particular interest mostly due to their ability to spread pathogens of human infectious and parasitic diseases. Aedes aegypti (L., 1762) and A. albopictus (Skuse, 1895) lead the list of the typical inhabitants of micro-reservoirs (Becker et al., 2010). Aedes albopictus is a vector for the Dengue, Zika, and West Nile fevers, Chikungunya, and La Crosse encephalitis (Dahmana and Mediannikov, 2020), Ae. aegypti is a vector for the Dengue and Zika fevers, yellow fever, Chikungunya, Sindbis, and Mayaro viruses, and other infections (Alto et al., 2005; Long et al., 2011; Dutra et al., 2016). Micro-water bodies are also inhabited by some representatives of genus Anopheles, known vectors of malaria, as well as filariasis, some arboviruses, and other infections (Kitching, 2000; Becker et al., 2010). Insecticides are widely used to control the larvae of dangerous mosquitoes, but this method has a number of well-known disadvantages and limitations. Insecticides have a negative effect on other arthropods, and target species often develop resistance to a toxic substance (Papchenkova and Makrushin, 2013; Su et al., 2019). In this context, biological methods of control seem to be promising. They include the use of natural predators to control mosquito larvae. Moreover, the study of the trophic ecology of mosquitoes also has theoretical significance. Mosquito larvae are often abundant in fresh waters, and after metamorphosis they leave water bodies. Thereby, they transfer biomass and nutrients to the land, strengthening the linkage between terrestrial and aquatic ecosystems (Baxter et al., 2005). In addition, micro-reservoirs inhabited by mosquitoes can themselves become interesting model objects of trophic ecology (Srivastava and Lawton, 1998; Srivastava et al., 2004).

This study considers predators that can control the abundance of mosquito larvae in phytotelmata and their anthropogenic analogs (Supplementary materials, Fig. 1S). Phytotelmata (singular phytotelma) are micro-water bodies formed in plant cavities, for example, in treeholes, leaf axils, bromeliad rosettes, cavities of bamboo stalks, pitchers of predatory plants, etc. The volume of such reservoirs varies from 3–10 mL (water bodies in the leaf axils) to ≥30 L (large treeholes), but most often they are less than 1 L. Small phytotelmata can be drained and filled, depending on the precipitation and evaporation, while large treeholes can retain water for years. The basis of food chains in phytotelmata is detritus, primarily leaf litter, as well as the decaying material of the plant which forms the reservoir (Williams, 1987; Kitching, 2000). Artificial analogs of phytotelmata are flower vases, drinkers and baths for animals, and accumulations of water in old tires and cans (Thorpe and Rogers, 2015). All these water bodies partly correspond to the term “container habitats” which, however, also includes larger water bodies, such as water-collecting tanks.
GENERAL OVERVIEW OF CONTAINER MOSQUITO PREDATORS

Flatworms (Platyhelminthes). Some Turbellaria representatives are able to feed on mosquito larvae (Medved and Legner, 1974; Dambach, 2020). Turbellaria are found in phytotelmata (Kitching, 2000), although their ability to influence the abundance of mosquitoes is not yet known. Some Turbellaria (Girardia aniceps (Kenk, 1930) (Tricladiida: Dugesiidae), Mesostoma ehrenbergii (Focke, 1836) and Bothromesostoma cf. elevinae Marcus, 1946 (Rhabdocoela: Typhloplanidae), not detected in phytotelmata, can successfully survive in artificial micro-water bodies and feed on the mosquitoes. They probably can be used to control mosquitoes (Tranchida et al., 2009).

Arachnids (Arachnida). Mosquito larvae can be eaten by aquatic and semi-aquatic spiders, such as the European Argyroneta (Cymbaeidae), the widespread Dolomedes (Pisauridae), Pirata, and Pardosa (Lycosidae) (Perevozkin et al., 2004). However, the presence of these predators is not typical for micro-aquatic habitats (Kitching, 2000). The only known example of a spider that preys on mosquito larvae in phytotelmata (bamboo stem cavities) is Paracyrba wanlessi Zakba et Kovac, 1996 (Salticidae) (Zakba and Kovac, 1996). Water mites of genus Arrhenurus (Arrhenuridae) can feed on first instar of mosquito larvae (Rajendran and Prasad, 1994) and are found in phytotelmata (Kitching, 2000). However, there are no studies on arachnids as biological control agents for mosquitoes.

Crustaceans (Crustacea). Copepods (Copepoda) are important control agents for container mosquito populations (Lazar et al., 2015). A separate section of this article is devoted to them. Among other crustaceans, mosquitoes are known to be eaten by tadpole shrimps (Notostraca) (Tietze and Mulla, 1991) and some decapods (Decapoda) (Collins, 1998). Although, these crustaceans are not found in phytotelmata (Fiers et al., 2013).

Dragonflies and Damselflies (Odonata). The larvae of many species of dragonflies and damselflies can feed on mosquito larvae (Saidzhabarova et al., 2006; Kumar et al., 2008; Shaalan and Canyon, 2009; Barry and Roberts, 2014; Jacob et al., 2017), but for the phytotelmata inhabitants this aspect of biology has been studied only in a few species of darners (Aeshnidae), skimmers (Libellulidae), and representatives of the family Pseudostigmatidae (Corethrella, 1996; Fincke et al., 1997). Long-lasting development makes Odonata larvae promising biocontrol agents, but in temporary water bodies the species must be resistant to drying out. For relatively large artificial reservoirs, such as cisterns, methods for biological control of mosquitoes involving Odonata representatives have been developed (Sebastian et al., 1990).

True Bugs (Heteroptera). Many aquatic and semi-aquatic bugs, primarily backswimmers (Notonectidae), giant water bugs (Belostomatidae), and water boatmen (Corixidae), feed on mosquito larvae (Nam et al., 2000; Shaalan and Canyon, 2009; Nurushev et al., 2015; Dalal et al., 2020). In phytotelmata, predatory bugs of three families have been recorded: water striders (Gerridae), riddle bugs (Velidae), and water measurers (Hydrometridae) (Kitching, 2000; Mogi, 2000). Representatives of all three families are known predators of mosquitoes (Mogi, 2007; Oganesyan, 2012). At present, true bugs are practically not used as agents of biological control of mosquitoes; in this regard, they have been little studied. However, some authors (Sivagnaname, 2009) suggest using Diplonchus indicus Venkatesan et Rao, 1980 (Belostomatidae) as they can survive and effectively control mosquitoes in tire water.

Beetles (Coleoptera). Predatory beetles able to prey on mosquito larvae at the larval and/or imago stage are found among predaceous diving beetles (Dytiscidae), water scavenger beetles (Hydrophilidae), and some other families (Mogi, 2007; Becker et al., 2010). Dytiscidae and Hydrophilidae have been described in phytotelmata (Greeney, 2001), although their food preferences remain unexplored. As far as we know, nowadays not a single species of beetle is used in practice as an agent for controlling dangerous mosquitoes in micro-aquatic bodies, although there are some experimental studies in this direction (Aditya et al., 2006).

Diptera. The larvae of some mosquitoes are obligate or facultative predators that attack other mosquito larvae (Mogi, 2007; Shaalan and Canyon, 2009), but they are poorly studied as a control for dangerous mosquito species. The exception is representatives of genus Toxorhynchites; a separate section of this study is devoted to them (see below). In some studies, representatives of genus Lutzia, which inhabit phytotelmata and other micro-aquatic habitats, are studied and are also considered promising agents for mosquito control (Singh et al., 2014; Moirangthem and Singh, 2018).

Among other Diptera, larvae of the family Chaoboridae can be important consumers of true mosquitoes in micro-aquatic habitats. They, in contrast to larger predators, eat all mosquito larvae instars, and not only the last one (Cuthbert et al., 2019a). Laboratory and field studies indicate that chaoborids can be effective biocontrol agents (Borkent, 1980). Recently, it has been proposed to use Chaoborus larvae in combination with copepods (Cuthbert et al., 2020), as well as with dark water dyes. It has been shown that colored water is more attractive to female mosquitoes to lay eggs than uncolored water, while Chaoborus is successful in catching larvae in both cases. This means that small artificial reservoirs with dark water, into which Chaoborus are introduced, can be used as a kind of “egg traps”: mosquitoes will actively lay eggs in such habitats where predators can consume young larvae (Cuthbert et al., 2019d).

Corethrella larvae (Corethrellidae) have also been studied as mosquito control agents (McLaughlin,
1990; Alto et al., 2005). They are known to consume mainly the young larvae of mosquitoes and are also capable of being so-called compulsive killers (Lounibos et al., 2008). This phenomenon is described in more detail for Toxorhynchites and is discussed below in the relevant section.

Predators consuming mosquito larvae in phytotelmata are also found in other families of Diptera (Chironomidae, Ceratopogonidae, Tipulidae, Pericestidae, Syrphidae, Muscidae, Calliphoridae, Sarcophagidae) (Mogi, 2007). However, they have not been studied as potential agents of biological control.

Fish (Pisces). Insectivorous fish are considered one of the main regulators of the mosquito population in large water bodies and are widely used in practice (Walton, 2007). However, fish, as a rule, are not found in phytotelmata and other micro-aquatic habitats (Kitching, 2000).

Amphibians (Amphibia). The larvae of anurans, including those living in phytotelmata, may include mosquito larvae and eggs in their diet (Bowatte et al., 2013; Salinas et al., 2018), but most often, tadpoles are found with mosquito larvae in complex competitive relationships (Mokany and Shine, 2003a, 2003b). It was also shown that females of Ae. aegypti more often lay eggs in containers with tadpoles than in containers without them (Bowatte et al., 2013). Together, this makes amphibians potentially useful biological control agents for mosquitoes, and in recent years, there were some attempts to develop methods for breeding and release of amphibians into water bodies (Raghavendra et al., 2008; Sarwar, 2015).

Plants (Plantae). It has been shown that the common bladderwort (Utricularia macrorhiza LeConte, Lentibulariaceae) and the waterwheel plant (Aldrovanda vesiculosa L., Droseraceae) effectively destroy mosquito larvae in small containers. Although these plants are not typical for micro-aquatic habitats, they can potentially be used as biological control agents for mosquitoes (Ogwal-Okeng et al., 2011; Couret et al., 2020).

Other Predators. Feeding on mosquito larvae was also noted for hydroids (Hydrozoa), leeches (Hirudinea), and larvae of caddisflies (Trichoptera) (Mogi, 2007; Becker et al., 2010); however, these organisms are not found or are extremely rare in phytotelmata (Kitching, 2000).

MOSQUITOES OF GENUS Toxorhynchites

Genus Toxorhynchites Theobald, 1901 includes 88 species of unusual mosquitoes, the largest representatives of the family Culicidae (adults reach 13 mm in length) (Coetzee, 2017). Their adults feed on flowers or fruits and are incapable of sucking blood, while the larvae (Supplementary materials, Fig. 2S) prey on other aquatic animals. The use of mosquitoes of genus Toxorhynchites to control the number of blood-sucking mosquitoes was first proposed at the beginning of the 20th century (Colledge, 1911, cited by (Collins and Blackwell, 2000)). Further research in this direction has been ongoing.

Most of the species of genus Toxorhynchites are distributed in forests of equatorial and tropical latitudes, although some species and subspecies (Toxorhynchites rutilus rutilus (Coquillet, 1896) and Toxorhynchites rutilus septentrionalis (Dyar et Knab, 1906)) are found in the temperate zone of the Northern Hemisphere (Trimble and Smith, 1978). The northern border of their distribution in North America passes through Lake Erie, although in Eurasia Toxorhynchites are not recorded to the north of 25° N, with the exception of the Korean Peninsula and Honshu Island (GBIF, 2021). Larvae inhabit almost all types of natural micro-water bodies, including phytotelmata, as well as artificial reservoirs, such as water accumulations in discarded cans and tires (Coetzee, 2017).

Features of the Biology and Ecology of Toxorhynchites

The biology of mosquitoes of genus Toxorhynchites has been described in detail (Steffan and Evenhuis, 1981; Collins and Blackwell, 2000; Focks, 2007). Here we consider only the most important aspects for controlling the populations of blood-sucking mosquitoes in micro-water bodies.

Larvae of Toxorhynchites spp. are active predators, feeding on the larvae of blood-sucking mosquitoes and other aquatic animals: larvae of other Diptera, small Odonata nymphs, tadpoles, crustaceans, and oligochaeta (Focks, 2007). At least two species, Toxorhynchites haemorrhoidalis (Fabricius, 1787) and T. rutilus, can capture land insects that have fallen into the water (Campos and Lounibos, 2000; Dézerald et al., 2015). Larvae of Toxorhynchites spp. are capable of cannibalism, especially in the absence of other prey of suitable size, which makes their breeding difficult (Coetzee, 2017; Schiller et al., 2019). In the absence of animal food, the larvae can switch to detritophagy (Steffan and Evenhuis, 1981).

Mosquito larvae are believed to be the main prey for Toxorhynchites spp. (Coetzee, 2017). Many studies confirm this, although this is not always observed. For example, analysis of the contents of the digestive tract of T. rutilus larvae inhabiting flooded treeholes and tires in Florida showed that they prefer ostracods and chironomid larvae, and only 5–6% of their victims are mosquito larvae (Campos and Lounibos, 2000). However, the reason for this fact may also be the small number of mosquitoes in the investigated reservoirs. Larvae of T. haemorrhoidalis in phytotelmata of bromeliads are more likely to choose ants that have fallen into the water than mosquito larvae, despite the fact that feeding on mosquitoes accelerates the development of this predator (Dézerald et al., 2015). On the contrary, Toxorhynchites splendens (Wiedemann,
In laboratory conditions, *Toxorhynchites* larvae actively consume many mosquito species, for example, *Ae. aegypti*, *Ae. albopictus*, *Culex quinquefasciatus* Say, 1823, *Armigeres subalbatus* (Ccqulleet, 1898), and *Anopheles stephensi* Liston, 1901 (Pramanik and Raut, 2003; Aditya et al., 2006, 2007; Albeny et al., 2011; Millado and Sumalde, 2018; Digma et al., 2019). With a high prey density, one late-instar *Toxorhynchites* larva kills 20–50 older *Aedes* larvae per day, although at a lower prey density this figure decreases greatly (Padgett and Focks, 1981; Arunkumar and Sangaran, 2013; Digma et al., 2019). The rate of consumption directly correlates with the density of prey and the size of the predator, and indirectly, with the volume of the container. The total number of prey consumed by one *Toxorhynchites* larva of the fourth instar, the most active feeder, can be up to 200 adults or 4500 young *Ae. aegypti* larvae (Padgett and Focks, 1980). *Toxorhynchites* larvae prefer prey of the corresponding size: the first instar predators prey on newly hatched mosquitoes, while the last (fourth) instar, on adult larvae and pupae (Lounibos, 1979; Padgett and Focks, 1981; Millado and Sumalde, 2018).

The abundance and availability of food strongly affects the duration of larval development, which can vary widely. It is also influenced by temperature. In some cases, development can take up to three months, although more often it is completed in three to four weeks (Trimble and Smith, 1978; Steffan and Evenhuis, 1981). This is significantly longer than the duration of the larval stage of most mosquitoes, which can be 7–10 days (Coetzee, 2017). In addition, larvae of at least one species of the temperate zone, *T. rutillus*, survive the winter in a state of diapause, which further lengthens the duration of larval development (Lounibos et al., 1998).

*Toxorhynchites* spp. larvae can show compulsive killing or surplus killing behavior: they often kill their potential victims, but do not eat them (Russo, 1986). This happens more often before pupation. It is assumed that in this way the larva protects the future defenseless pupa from animals that could potentially harm it (Collins and Blackwell, 2000). Other authors note that this phenomenon was registered in laboratory conditions and in the cases of artificial introduction of adult larvae into water bodies, while its existence in nature is dubious (Focks, 2007). In *T. rutillus* *rutilus*, a similar behavior of older larvae was noted during winter diapause (Lounibos et al., 1998). If compulsive killing occurs naturally, it can increase the effectiveness of *Toxorhynchites* spp. as agents of control of blood-sucking mosquitoes.

Predators can also indirectly influence their potential victims without killing. This aspect of the biology of *Toxorhynchites* has been relatively poorly studied. In experiments, larvae of *Culex mollis* Dyar et Knab, 1906, co-living with the larvae of *Toxorhynchites theobaldi* (Dyar & Knab, 1906), have increased development time and overall mortality. This effect is observed even when the predator is kept in the net and cannot eat the experimental larvae, but can release some substances that are captured by potential prey (Andrade, 2015).

It is known that potential prey can change their behavior in response to some of the chemical signals emitted by the predator. Different mosquito larvae behave differently in the presence of *Toxorhynchites* larvae. Thus, the larvae of *Aedes* (Ochlerotatus) triseriatus (Say, 1823) move and feed less frequently under the action of signals from a predator (*Toxorhynchites rutillus*), while the behavior of *Aedes albopictus* does not change (Kesavaraju and Juliano, 2006). Another study showed that *Ae. albopictus* and *Anopheles sinensis* Wiedemann, 1828 in the presence of *Toxorhynchites splendens* demonstrate low activity, in contrast to the larvae of *Aedes aegypti*, which continue to feed as actively as in the absence of the predator. As a result, *Toxorhynchites splendens* feeds on *Aedes aegypti* more often than on the other two species. Apparently, this is due to the fact that the larvae of *Toxorhynchites splendens* prefer not to swim after prey and actively catch it, but to wait motionlessly until they accidentally meet each other (Zuharah et al., 2015). The influence of predators on the behavior of prey requires further study and may be of great importance in the development of methods for biological control of populations of dangerous species.

Another variant of the predator influence on the biology of the prey is the influence on the choice of the water body by the female during oviposition. It is believed that female mosquitoes choose the water body for oviposition based on the availability of food for the larvae and the potential danger from predators (Albeny-Simões et al., 2014). It has been shown that the presence of insectivorous fish and even images of goldfish (*Carassius auratus* (Linnaeus, 1758)) reduces the attractiveness of reservoirs for female blood-sucking mosquitoes; however, experiments with *Toxorhynchites splendens* did not show a similar result (Dieng et al., 2017). On the contrary, there is evidence that *Aedes aegypti* females are more likely to lay eggs in containers with *Toxorhynchites theobaldi* larvae than with no *T. theobaldi*. Apparently, this can be explained by the formation of various rotting wastes during predator feeding that results in a significant increase of the number of bacteria, which attract females (Albeny-Simões et al., 2014).

*Toxorhynchites* as the agents for the control of blood-sucking mosquitoes. The experience of controlling the number of blood-sucking mosquitoes using *Toxorhynchites* is described in detail in several reviews (Collins and Blackwell, 2000; Focks, 2007; Schreiber, 2007; Shaalan and Canyon, 2009). Here,
we consider in more detail the general patterns and studies of recent years.

Many biological features make *Toxorhynchites* promising agents for the control of blood-sucking mosquitoes. *Toxorhynchites* larvae colonize micro-aquatic habitats that are inaccessible to many other predators, for example, fish. Female mosquitoes spread their eggs in the target water bodies. *Toxorhynchites* more often consume older larvae and pupae, which increases the effectiveness of the control: the effect of the predominantly preying on young larvae can be mitigated by the overall high mortality at this stage, while eating older larvae and pupae is devoid of this drawback. Finally, the *Toxorhynchites* adults are not dangerous to humans and do not act as a disease vector.

Representatives of genus *Toxorhynchites* are effective agents for biological control of blood-sucking mosquitoes in the Pacific and Caribbean islands, as well as in Africa, the USA, and Australia. Most of the studies are dedicated to the vectors of dangerous diseases: *Aedes aegypti*, *Ae. albopictus*, *Ae. polynesiensis* Marks, 1951, *Ae. africanus* (Theobald, 1901), *Ae. notoscriptus* (Skuse, 1889), *Culex quinquefasciatus*, and *Aedes subalbatus* (Brown, 1996; Collins and Blackwell, 2000; Shaalan and Canyon, 2009).

Despite the successes, some features of *Toxorhynchites* complicate their use as biological control and require additional study: temperature limitation, long development of the predator, differences in the population dynamics of the predator and the prey, and discrepancy between the preferences of predators and prey in the choice of water bodies (Focks, 2007).

Most *Toxorhynchites* species, as was noted above, prefer warm climate and their use in the temperate zone is limited by their low activity from autumn to spring. Even northern species and subspecies, for example *T. rutilus septentrionalis*, are not very active at the temperatures when the larvae of some blood-sucking mosquitoes, such as *Aedes triseriatus*, develop. The long duration of the development of predators results in the decrease of daily consumption of the prey (Trimble and Smith, 1979). However, it is assumed, that in temperate climate, *Toxorhynchites* can be released in spring to suppress the reproduction of the target species in summer.

In addition, the larvae of *Toxorhynchites* develop at least three times longer than their prey; therefore, they are unable to respond quickly (by increasing their numbers) to the outbreaks of their prey. This does not affect long-term control, and short-term outbreaks in the number of target species can be suppressed by the release of additional batches of predators. Long development has other consequences as well. Thus, *Toxorhynchites* larvae are able to starve for a long time in anticipation of prey. Cannibalism among adult larvae is not very common, so starving predators can congregate in containers in relatively large numbers (Focks et al., 1980).

Females of genus *Toxorhynchites*, like the representatives of the other genera of Culicidae family, lay eggs in micro-water bodies, but in the anthropogenic landscape the preferences of predators and prey differ. *Toxorhynchites* often inhabit shaded water bodies, mainly treeholes or their artificial counterparts, also shaded, and usually associated with vegetation. Target blood-sucking species inhabit a wider range of habitats, including unshaded and plant-unrelated habitats, such as water accumulations in open dumps. Such preferences of water bodies are considered the main reason for the failure of introduced *Toxorhynchites* spp. to effectively control target species such as *Ae. albopictus* in Hawaii in the 1950s (Nakagawa, 1963) and *Ae. polynesiensis* in Fiji in the 1930s (Toohey et al., 1985). To solve this problem, it is proposed to manually introduce predator eggs into the specific water bodies, and this action has to be repeated regularly. However, this approach loses a number of advantages over other methods of control and increases the cost of procedures. Thus, after the first unsuccessful experiments, careful selection of habitats for the introduction of *Toxorhynchites* eggs made it possible to achieve effective control of *Aedes polynesiensis* in experimental locations on the Fiji Islands (Toohey et al., 1985). However, the mismatch in the choice of water bodies occurs only in anthropogenic landscapes, with abundant unshaded water bodies, but not in forests, where the absence of unshaded water bodies does not complicate the use of *Toxorhynchites*.

**Toxorhynchites** as a part of complex control methods. Since *Toxorhynchites* spp. belongs to the family Culicidae, they are also affected by many mosquito control methods, in particular, by many traditional insecticides and toxins of bacteria of genus *Bacillus*. This makes it difficult to use *Toxorhynchites* spp. as part of complex control methods. However, the use of insecticides with low toxicity for *Toxorhynchites* spp. (malathion, temefos, and dibroma) pay dividends (Collins and Blackwell, 2000). In New Orleans, the combination of *T. amboinensis* and malathion reduced the population density of *Aedes aegypti* by 96%, while using malathion alone, only by 29% (Focks et al., 1986).

Another direction in the development of complex measures that has appeared in recent years is the use of predatory mosquitoes in combination with entomopathogenic fungi. The larvae of *Toxorhynchites brevipalpis* Theobald, 1901 were shown to be resistant to relatively high concentrations of conidia and spores of fungus *Metarhizium brunneum* Petch (Ascomycota: Hypocreales). In laboratory experiments, the simultaneous use of *Toxorhynchites brevipalpis* and *Metarhizium brunneum* against *Aedes aegypti* showed a positive result, although less potent than the additive one (Alkhaibari et al., 2018). Some studies suggest combining *Toxorhynchites* with other predators. It has
been shown that adult larvae of *Toxorhynchites speciosus* (Skuse, 1889) and carnivorous copepods *Mesocyclops aspericomis* (Daday, 1906) can coexist in micro-aquatic habitats and reduce the number of larvae of *Aedes notoscriptus* and *Culex quinquefasciatus* (Brown, 1996).

**Artificial breeding of toxorhynchites and practical notes.** The use of mosquitoes of genus *Toxorhynchites* as biological control agents requires their breeding in captivity, which has some peculiarities. The rearing of predatory larvae is associated with the use of live food: other feeding options cannot provide normal development and reduce the size of adult mosquitoes (Focks, 2007). Larva cannibalism in co-rearing at the early stages is a serious problem. It is influenced by the abundance of forage insects, their size, and the range of sizes of the *Toxorhynchites* larvae themselves (Focks, 2007). Keeping larvae in separate containers helps to completely avoid cannibalism.

The most common breeding method for *T. rutillus* was proposed by Focks and Boston (1979). It involves the rearing of hundreds of larvae in large containers with an abundance of food (*Aedes aegypti* larvae of the appropriate age). The forage larvae, in turn, fed on dried liver powder and yeast and were bred in the same container in which the predatory larvae develop. Development of *Toxorhynchites rutillus* under such conditions takes approximately 2 weeks.

A new technique was proposed by Schiller et al. (2019). The authors note that the use of mosquito larvae as live food has a number of disadvantages. Synchronization of the life cycles of feeding and predatory mosquitoes causes difficulties, and individual larvae of *Aedes aegypti*, which happen to develop into adults, are dangerous, since they are a potential vector of human diseases. As an alternative, the authors propose to use less mosquito larvae but more other live food: nematodes, oligochaetes (Naididae), and larvae of nonbiting midges (Chironomidae). Another important difference is that *T. rutillus* larvae are housed singly in small containers, which negates cannibalism and helps to effectively remove uneaten food. The adults are kept in large numbers in net cages. This method of *T. rutillus* breeding is more effective than the previous one.

*Toxorhynchites* spp. breeding in the lab can be released at all stages of development. Eggs, larvae, and pupae need to be manually placed in target water bodies. This approach is time-consuming but allows treating all the habitats that need the presence of a predator. The release of adults is less laborious, but it also has its disadvantages: it should be carried out at a specific time of day (early morning or evening); females can lay eggs in non-target water bodies; raising adults in the laboratory requires a lot of space and labor.

The decision to use a particular strategy should be made in accordance with the working conditions in each particular case (Focks, 2007; Schiller et al., 2019).

**COPEPODA**

Predatory Copepoda are widespread crustaceans in fresh waters. They are considered the most effective agents for controlling the number of mosquitoes among invertebrate predators, including micro-aquatic habitats (Marten and Reid, 2007).

**Copepoda biology and ecology.** The biology of freshwater copepods is described in detail (Thorp and Rogers, 2015). In the context of biological control of mosquito populations, cyclops (Cyclopoida: Cyclopidae) with ~800 species in fresh waters, many of them predatory (Marten and Reid, 2007; Thorp and Rogers, 2015) have been studied most among the copepods. In recent years, attention has also been paid to the predatory calanoids (*Calanoida*: Diaptomidae) (Cuthbert et al., 2018b).

Predatory copepods inhabit large permanent and temporal water bodies and micro-water bodies, including phytotelmata (Fiers et al., 2013; Schneider, 2013). Their small size and wide food specialization allow them to reach high abundance in a variety of miniature habitats associated with human activities (Schreiber et al., 1996; Kay et al., 2002). Up to 500 individuals of *Mesocyclops longisetus* (Thiebaud, 1912) can inhabit one tire with water (Marten et al., 1994).

Different species of copepods tolerate desiccation differently. Calanoids form dormant eggs that are resistant to desiccation (Dambach, 2020). Many cyclopoids can enter diapause at the stages of late copepodites and adults (Thorp and Rogers, 2015). *Acanthocyclops* and *Diacyclops* even master complete drying of water bodies in this state (Wyngaaard et al., 1991). Some species of *Mesocyclops*, which effectively consume mosquitoes, are able to survive in moist soil without free water, but they cannot withstand drying of the soil below a certain threshold (Zhen et al., 1994). This can complicate the use of copepods as biological control agents in small periodically drying water bodies.

Copepods are relatively small animals. Only large species, over 1 mm in size, are capable of feeding on mosquito larvae (Marten and Reid, 2007). Most of them prey on the larvae of the first, less often, the second instar. Only some species (for example, *Loewenula raynerae* Suárez-Morales, Wasserman, et Dalu, 2015 (Diaptomidae) prey on large larvae (Cuthbert et al., 2018b). Copepods do not specialize in preying mosquitoes. They feed on a variety of aquatic organisms of a suitable size, including cladocerans, fish larvae, rotifers, ciliates and other protozoa, and even planktonic algae (Kumar and Rao, 2003; Frimpong and Lochmann, 2005; Thorp and Rogers, 2015; Cuthbert et al., 2019b). An alternative prey can reduce the efficiency of preying on mosquito larvae, which, for example, has been shown in laboratory experiments for two *Mesocyclops* species, which consumed culicides and cladocerans, as well as for *Macrocyclops albidus* (Jurine, 1820) and *Megacyclops viridis* (Jurine, 1820),
which consumed larvae of mosquitoes and ciliates (Kumar and Rao, 2003; Kumar et al., 2008; Cuthbert et al., 2019b). On the other hand, wide food spectrum allows copepods to exist for a long time in reservoirs not inhabited by mosquitoes, and after the appearance of larvae, they switch to feeding on them.

Even young mosquito larvae are comparable in size to or are larger than copepods. So, crustaceans have to use specific techniques to capture such large prey. Copepods, at least the studied species, most often attack larvae from the side or from behind, damaging the abdomen or siphon (Schaper and Hernández-Chavarria, 2006). It has been shown that trauma to the siphon is the most dangerous for Aedes aegypti, apparently, due to disruption of the respiratory system (Awasthi et al., 2012). Copepods usually hold the victim until it dies and then eat it. Large crustaceans can eat young Aedes larvae almost entirely (Awasthi et al., 2012). However, when there is an excess of prey, the copepods attack them one after another, eating only part of each larva, and, accordingly, kill more mosquitoes than they can eat (Marten and Reid, 2007).

The most efficient cyclopoids (for example, some Mesocyclops species) in small habitats are capable of killing up to 50 Aedes larvae per day (Marten et al., 1994), although for Anopheles and especially Culex larvae these figures are lower (Mittal et al., 1997; Kumar and Rao, 2003). In larger containers, crustaceans kill mosquitoes less actively (Marten et al., 1994; Dieng et al., 2002). The calanoids Lovenula kill up to five Culex larvae per hour (Cuthbert et al., 2018b).

Copepods also indirectly affect their prey. In the presence of epibenthic copepods Megacyclops formosanus (Harada, 1931), Aedes aegypti larvae spend less time filtering and collecting food, and also leave the bottom water layer, where copepods are found, moving closer to the surface (Awasthi et al., 2015). It was also noted that in the presence of crustaceans, the larvae begin to move and bend more actively, which can prevent predators from catching them (Awasthi et al., 2012). The impact on prey behavior can influence the effectiveness of biological control, but this issue remains poorly understood in relation to copepods.

The use of copepods to control populations of blood-sucking mosquitoes. By the publication of the review by Marten and Reid (2007), 48 copepod species from 15 genera have been tested as biocontrol agents. The work on the study of other species is ongoing. In recent years, the effectiveness of cyclopoids Megacylops formosanus, Megacylops gigas (Claus, 1857), Cyclops diversgens (Lindberg, 1936), Cyclops heberti Einsle, 1996, and Acanthocyclops einslei Manchorlullayev et Defaye, 2004 (Kalimuthu et al., 2014; Früh et al., 2019), as well as calanids Lovenula raynerae Suárez-Morales, Wasserman, et Dalu, 2015 and Paradiaptonus lamellatus Sars, 1895 have been proven (Cuthbert et al., 2018b, 2019c; Balakrishnan et al., 2019). Many promising species still remain unexplored. Among them are numerous representatives of genera Megacyclops, Mesocyclops, and Mesocyclops.

Field experiments also confirm the effectiveness of copepods as biocontrol agents. In micro-water bodies, representatives of genus Aedes most often become objects of control. Various wells, jugs, flower vases, cisterns, barrels, tires, and other container habitats, as well as treeholes, and burrows of land crabs are usually used as experimental water bodies. Some crustacean species reduce the number of Aedes larvae in experimental reservoirs by 90–100% (Riviere et al., 1987; Marten, 1990; Kay et al., 2002; Rey et al., 2004). However, the combination of several species of copepods in one water body can redue the efficiency of mosquito consumption, apparently due to the fact that some crustaceans begin to prey on others (Dieng et al., 2002).

In South Townsville Australia) Mesocyclops have been used to reduce the number of larvae of mosquitoes Ochlerotatus spp. and Aedes spp. in the rainwater drainage system. It turned out that it was enough to populate only 50 individuals of crustaceans in one sewer hatch for the copepods to spread over most of the city’s sewer system in two rainy years. Predators significantly decreased the number of larvae (in some cases up to complete disappearance). It has also been shown that copepods Mesocyclops and Metacyclops are able to survive dry periods in sewers (Kay et al., 2002).

Unfortunately, small-scale studies, even when successful in decreasing the larva number in experimental reservoirs, have failed to achieve a noticeable decrease in the number of adults. Such results require larger-scale experiments that can affect the local mosquito population. Such studies are conducted in some regions, but their effectiveness is often limited by organizational capabilities (Marten and Reid, 2007; Lazaro et al., 2015).

In Vietnam, a unique in scale study has been carried out to reduce the number of Aedes aegypti. The main method was the introduction of copepods of genus Mesocyclops in natural and artificial water bodies, as well as cleaning the surroundings of the villages from waste that collects water. In the 1990s, a pilot project was carried out on the scale of one village (Nam et al., 1998), then a similar model was implemented in a region with a population of ~400000 people (Nam et al., 2000, 2005, 2012; Kay et al., 2002; Kay and Nam, 2005). It resulted in a significant decrease or even in complete elimination not only of Aedes aegypti larvae, but also of the adults. This success was driven by the wide involvement of the local population that, in turn, affected a wide range of water bodies in large territories. As far as we know, this is the most extensive use of copepods as biological control agents.

Effective biocontrol does not necessary depend on colonization of all water bodies with copepods. Lakes with predators turn into “egg traps” for mosquitoes, which waste energy for reproduction. It was shown that
female mosquitoes prefer to lay eggs in water bodies inhabited by copepods (Vonesh and Blaustein, 2010), although this issue requires further study. Almost complete destruction of the local population of mosquitoes can be achieved when copepods colonize 90% of mosquitoes' breeding sites (Nam et al., 1998).

However, in some cases, copepods, which have shown good results as mosquito controlling agents in the laboratory, were unable to significantly affect the number of mosquitoes in the field. It is believed that the effectiveness of control depends primarily on the duration of the presence of the crustacean population in a water body and on its density. Decrease of these indicators, and consequently, the effectiveness of control, can result from the drying of the reservoirs, regular withdrawal of water decrease of the size of individuals, starvation, inadaptability to local climatic conditions, and accumulation of toxins in the water (Marten et al., 1994; Marten and Reid, 2007). Below we consider the mentioned factors in more detail.

Many copepods do not tolerate complete drying; therefore, their introduction to the temporal water bodies requires re-introduction after the next filling with water. This problem can be solved by careful selection of the reservoir and the species of crustaceans, as well as by artificially maintaining the water content in the reservoirs during the dry season. Sometimes, released copepods are able to settle in new habitats and repopulate treeholes that were previously dried up and later re-filled with water (Riviére et al., 1987).

Some copepod species rapidly multiply in a new habitat, deplete food resources and, as a result, become smaller. By the time mosquito larvae enter the pond, the copepods are too small to prey on them. The most effective crustacean species seem to lack such a disadvantage due to their tendency to cannibalism (Marten, 1990). Copepods can disappear from tanks not only because of complete drying of the water, but also due to the insufficient reproduction rates of crustaceans to compensate for their losses due to regular withdrawal of water. In such cases, most effective species are those who prefer to swim near the bottom and walls of containers, as these parts are less subjected to water withdrawal than the central part (Marten and Reid, 2007).

Copepods die due to lack of food in some types of reservoirs with clean water and more often this problem is observed not in micro-reservoirs, but in larger catchment tanks (Jennings et al., 1994).

Copepods are resistant to some insecticides, for example to the toxin of Bacillus thuringiensis israelensis Barjac, 1978 (Bti), permethrin, and pyriproxyfen. Therefore these substances can be used in combination with copepods to control mosquitoes (Riviére et al., 1987; Marten et al., 1993; Wang et al., 2005). Piperine and eugenol affect copepods negatively, but the lethal doses for copepods are higher than for mosquito larvae; therefore, these two substances can also be used in combination with crustaceans (Dhanker et al., 2013). The available data on the effects of insecticides on freshwater carnivorous copepods are provided in the review (Lorenzo et al., 2014).

Good results are obtained by using copepods in combination with extracts of various plants (Murugan et al., 2011; Kalimuthu et al., 2013, 2014) and even metal nanoparticles, which are toxic to mosquito larvae, but less toxic to copepods (Naresh Kumar et al., 2013; Murugan et al., 2015). Another developing direction is the combination of predators, including copepods, with dyes for water (the principle of this method is described above) (Cuthbert et al., 2018a). All these studies were carried out in laboratory conditions, and have not yet been tested in large-scale field experiments.

**Artificial breeding of copepods and practical notes.** The method of breeding and introduction of copepods is well developed and described (Nam et al., 2000; Balakrishnan et al., 2019). The main idea is that native copepod species, typical of the area in which mosquito control activities are planned, are bred in the laboratory and released into new habitats. For copepod breeding, containers with a volume from 3–5 to 150 L are used. The initial crustaceans for further breeding and culturing are caught in natural reservoirs by plankton nets. Microalgae or ciliates are used as food for copepods; they are cultivated in the same containers with copepods. 50 Mesocyclops individuals, introduced to a 150-L container, in 21 days, breed into 4500 individuals (Nam et al., 2000). In Vietnam, for convenient transportation and storage of copepods, Nam et al. (2000) used small pieces of expanded polystyrene that
absorbs water but maintains moisture sufficient for crustacean survival.

It should be noted, that some copepods are intermediate hosts of the dangerous parasite *Dracunculus medinensis* (Linnaeus, 1758) (guinea-worm disease). In areas where dracunculiasis is widespread, it is necessary to choose species that do not act as the guinea-worm disease vector. There is evidence that copepods can also participate in the transmission of the cholera pathogen (Marten and Reid, 2007). In any case, both of these problems can be solved by filtering the drinking water from the crustaceans.

**CONCLUSIONS**

**Possible directions for future research.** Expanding knowledge on the biology of potential predators seems to be an important area of studies. Many species of carnivorous copepods remain unstudied, including representatives of the promising genera *Macrocylops*, *Megacyclops*, and *Mesocyclops*, as well as dozens of species of predatory mosquitoes of tropical genus *Toxorhynchites*. Little is known about indirect effects of predators on the mosquitoes: on their behavior, food preferences, and the choice of a water body by females for oviposition. Development of the control methods involving predators, even well-studied ones, is only on the initial stages of elaboration.

Interactions of predators of different species and groups in micro-reservoirs deserve special consideration. Some studies show the potential efficiency of the combined use of *Toxorhynchites* and copepods (Marten, 1990; Brown, 1996). However, three different species of copepods in the same container were found to be much less effective control agents than the same crustaceans separately (Dieng et al., 2002). A theoretical basis has been developed to describe the system of interaction of several predators (Sih et al., 1998), although it is rarely applied to micro-aquatic communities.

The use of predators to control the mosquito population in Russia and neighboring countries. Currently, in Russia and other countries of the Commonwealth of Independent States, predator-based methods for controlling the number of mosquitoes barely exist. However, in the future they may be useful. Thus, in Turkmenistan, some dangerous species of mosquitoes develop in treeholes. They include, for example, *Aedes caspius* (Pallas, 1771), which is a vector of tularemia, filariasis, and some arboviruses (Mamedniyazov, 1995). We assumed that it would be effective to use predators against this and other dangerous phytotelmata species. In the temperate latitudes, for most species of mosquitoes, treeholes and similar micro-aquatic habitats are considered to be not the main and even insignificant breeding sites, in contrast to larger water bodies, temporary or permanent (Malkova et al., 2013). Methods for controlling mosquitoes in lakes and swamps are well developed, but they do not consider the possibility of using predatory invertebrates, although such predators that effectively consume mosquito larvae have been described in many regions (Dubitskii, 1970; Kukharehuk, 1981; Akhmetbekova et al., 1982; Nazarova et al., 2019).

In recent years, the appearance of dangerous *Ae. aegypti* and *Ae. albopictus* has been recorded in the southern regions of Russia (in Krasnodar krai and Crimea) (Ryabova et al., 2005; Ganushkina et al., 2012; Fedorova et al., 2018; Kovalenko et al., 2020). Their distribution is limited by the January isotherms of 0°C for the first and from –1°C to –3°C for the second species. Thus both species are believed to inhabit the Black Sea coast, but not further north. The range of mosquitoes is expected to expand with climate warming, although the possibility of epidemic outbreaks of *Aedes*-related fevers is very low (Akiner et al., 2016; Yasyukevich et al., 2017). The confinement of these mosquito species to artificial micro-water bodies allows assuming the possibility of the use of predators to control the abundance of *Ae. aegypti* and *Ae. albopictus* populations. The use of copepods, which have shown good results as agents of biological control of the *Ae. aegypti* and *Ae. albopictus* in different parts of the world, looks promising. It is also important to note that in Russia there are large carnivorous copepods, for example, of the genera *Cyclops* and *Mesocyclops*, adapted to local climatic conditions (Alekseev and Barabanshchikov, 2006; Lazareva and Zhdanova, 2020).

**FUNDING**

The study was carried out within a State Assignment of the Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences on the topics Problems of Environmental Safety (AAAA-A18-118042490053-3) and Tropical Ecology and Tropical Medicine (AAAA-A18-118090390074-0).

**COMPLIANCE WITH ETHICAL STANDARDS**

**Conflict of interest.** The authors declare that they have no conflicts of interest.

**Statement on the welfare of animals.** This article does not contain any studies involving animals or human participants performed by any of the authors.

**SUPPLEMENTARY INFORMATION**

Additional materials (Figs. 1S, 2S) are published only in electronic form at https://link.springer.com and are accessible for authorized users at https://doi.org/10.1134/S1995082922010138.

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*Translated by T. Kuznetsova*