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Regulation of laboratory populations of snails (*Biomphalaria* and *Bulinus* spp.) by river prawns, *Macrobrachium* spp. (Decapoda, Palaemonidae): Implications for control of schistosomiasis

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ABSTRACT

Human schistosomiasis is a common parasitic disease endemic in many tropical and subtropical countries. One barrier to achieving long-term control of this disease has been re-infection of treated patients when they swim, bathe, or wade in surface fresh water infested with snails that harbor and release larval parasites. Because some snail species are obligate intermediate hosts of schistosome parasites, removing snails may reduce parasitic larvae in the water, reducing re-infection risk. Here, we evaluate the potential for snail control by predatory freshwater prawns, *Macrobrachium rosenbergii* and *M. vollenhovenii*, native to Asia and Africa, respectively. Both prawn species are high value, protein-rich human food commodities, suggesting their cultivation may be beneficial in resource-poor settings where few other disease control options exist. In a series of predation trials in laboratory aquaria, we found both species to be voracious predators of schistosome-susceptible snails, hatchlings, and eggs, even in the presence of alternative food, with sustained average consumption rates of 12% of their body weight per day. Prawns showed a weak preference for *Bulinus truncatus* over *Biomphalaria glabrata* snails. Consumption rates were highly predictable based on the ratio of prawn: snail body mass, suggesting satiation-limited predation. Even the smallest prawns tested (0.5–2 g) caused snail recruitment failure, despite high snail fecundity. With the World Health Organization turning attention toward schistosomiasis elimination, native prawn cultivation may be a viable snail control strategy that offers a win–win for public health and economic development.

1. Introduction

Human schistosomiasis is a common parasitic disease of humans that is relatively easy to treat, but hard to control. Today, public health campaigns in endemic regions in the tropics and subtropics focus on mass drug administration using the oral drug, praziquantel. While praziquantel has a high cure rate, re-exposure to infected snails in the environment leads to rapid reinfection of treated patients in endemic areas (Fenwick et al., 2006; Fenwick and Webster, 2006; King et al., 2006; Tchuem Tchuente et al., 2013; Webster et al., 2013). In addition to drug treatment, a complementary approach is to control the populations of snails that serve as intermediate hosts. Snails are infected when parasite eggs, released in human urine or feces, are washed into the surface fresh water. A few weeks after infection, snails release larval schistosomes into the water where they can infect people, completing the lifecycle. Breaking this lifecycle through snail control was an approach used extensively for schistosomiasis control prior to the advent of the drug praziquantel. Snail control aims to reduce the number of parasitic larvae in the water, effectively reducing reinfection prevalence and intensity. Traditional approaches to snail control using molluscicide application and habitat modification can be expensive to implement and hard to maintain over the long-term. In some areas, researchers have documented a negative relationship between natural aquatic snail predators and the density of schistosome-susceptible snails, such as occurs in regions of Lake Malawi, where overfishing pressure may have caused snail populations to increase after predators were removed (Evers et al., 2006; Madsen and Stauffer, 2011). This suggests that in some ecological situations, control of snails through predator introductions could offer an effective snail control strategy that is affordable and sustainable and that may complement ongoing drug distribution campaigns. Here, we evaluate the potential for snail control by predatory freshwater prawns in the genus *Macrobrachium*.

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Macrobrachium vollenhovenii, is a freshwater prawn native to rivers and streams throughout West Africa. We hypothesized that *M. vollenhovenii* would be an effective snail predator because this species shares similar habitats with medically important snails, grows to a large size, and because the congener *Macrobrachium rosenbergii* (an Asian species) consumes snails as a preferred food (Lee et al., 1982; Roberts and Kuris, 1990). In Senegal, the construction of the Diama Dam to block tidal influence in the Lower Senegal River created a large freshwater irrigation system that offered abundant habitat to medically important snails, hosts of both *Schistosoma mansoni* and *Schistosoma haematobium*. This was associated with a severe and persistent outbreak of schistosomiasis involving both species, with increased snail abundance resulting from expanded low-flow, freshwater snail habitat after dam completion as well as probable immigration of infected agricultural workers to the region (Southgate, 1997; Sow et al., 2002). The Diama Dam also presumably blocked the migration of native *M. vollenhovenii* prawns to their estuarine breeding grounds. Although other impacts of the dam were not investigated, local fishermen reported that prawns were once common, but declined sharply after dam construction. Since prawns have been shown in laboratory studies to be voracious and effective predators of *Biomphalaria glabrata* (Lee et al., 1982; Roberts and Kuris, 1990), we speculate that a loss of prawns above Diama Dam may have contributed to the increase in snail intermediate hosts in the Lower Senagal River Basin, and therefore, an increase in schistosomiasis transmission. If so, restoration of *M. vollenhovenii* to the Senegal River might contribute to schistosomiasis control in that region or other similar regions of the world where schistosomiasis has increased after dam construction (Steinmann et al., 2006).

Roberts and Kuris (1990) published a series of laboratory trials that built on earlier work (Lee et al., 1982) demonstrating that *M. rosenbergii* – the most commonly aquacultured species of freshwater prawn worldwide – can consume *B. glabrata* snails. Roberts and Kuris concluded that prawn cultivation may offer a valuable complementary strategy for schistosomiasis control activities. Yet, to date, biological control using crustacean snail-predators has not been widely applied within schistosomiasis control programs. One of the major barriers to adoption is the lack of safe and effective *native* species for biological control. Introducing exotic species into habitats where they have never been previously naturalized can cause unwanted effects (Barbaresi and Gherardi, 2000; Fishar, 2006; Lodge et al., 2012). Nevertheless, there are a few examples where the introduction of exotic crustacean predators was successful in controlling schistosomiasis. For example, in Kenya, the introduction of a previously naturalized exotic crustacean, the Louisiana crayfish *Procambarus clarkii*, to village impoundments significantly reduced the prevalence and intensity of *S. haematobium* in schoolchildren for at least two years (Mkoji et al., 1999). Some additional evidence is emerging to suggest that invasions of this species throughout the Nile Delta may influence the rates of schistosomiasis transmission there (Khalil and Sleem, 2011). We argue that native predator augmentation would be similarly beneficial for schistosomiasis control programs while minimizing unwanted non-target effects associated with exotic introductions.

Here, we examine the long-term (days) consumption rates and characterize the functional response of two prawn species: *M. vollenhovenii* and *M. rosenbergii* feeding on two species of snails *B. glabrata* (a host of *S. mansoni*) and *Bulinus truncatus* (a host of *S. haematobium*). Our goals were: (1) to assess the capacity for prawns – especially the African native *M. vollenhovenii* for which there were no previous data – to control laboratory populations of *Biomphalaria* and *Bulinus* snails, hosts for human schistosomes in Africa and the Americas; (2) to compare the predation rates and preferences of small juvenile prawns versus large adult prawns and between Malaysian and African prawn species; and (3) to characterize the functional response of prawns when offered varying sizes and densities of snails, as would be found in natural populations. Finally, we aimed to synthesize this information to guide the development of a new strategy for sustainable schistosomiasis control and elimination through restoration or stocking of river prawns in schistosomiasis-endemic areas, especially throughout Africa where the highest schistosomiasis transmission rates are found today.

2. Methods

2.1. Animals

Uninfected, laboratory-reared *Biomphalaria glabrata*, strain NMRI, and *Bulinus truncatus*, subspp. *truncatus*, were supplied by the Schistosomiasis Resources Center (BEI Resources, Manassas, VA). Laboratory-reared *M. rosenbergii* juvenile prawns were supplied by the Aquaculture Department at Kentucky State University and delivered by airfreight to the University of California Santa Barbara. Captive populations of *M. vollenhovenii* prawns were not available, so wild-caught prawns were collected from the Lobe River, Cameroon (Gulf Aquatics-Cameroon, Duoung, Cameroon) and delivered by air freight in December 2011 to Kentucky State University's Aquaculture Department. At Kentucky State, the prawns were captively bred and the first generation juvenile prawns were delivered by airfreight to UC Santa Barbara in June 2012. Prawns and snails were housed in closed, recirculating freshwater tanks at UC Santa Barbara's Marine Biotechnology Laboratory. The tank system had both mechanical and biological filtration, continuous aeration, and 20% weekly water exchanges using conditioned tap water. Between experiments, prawns and snails were housed in holding tanks: a 400 L common holding tank for prawns, and four 25 L holding tanks for snails. Both during and between experiments, prawns were fed a commercial shrimp crumble diet with 40% protein content (Rangen Corporation, Buhl, ID) at a rate of 3–5% body weight per day, 5 days per week, and snails were fed organic romaine lettuce rinsed in DI water, *ad libitum*. In some trials, snails also fed on the shrimp diet (see below for details). Experiments were conducted in individual, clear polyethylene tanks with plastic lids, filled to 6 L with conditioned tap water, and connected by PVC and vinyl plumbing in a closed recirculating freshwater tank system. Tanks each had a single simulated prawn habitat refuge (a section of PVC pipe). Prawns were fasted, and all snails removed, for at least 24 h between trials to prevent cross-trial carryover effects.

2.2. Measuring consumption in terms of snail number versus snail biomass

In all experiments, consumption was measured and reported in terms of snail number, snail biomass, or both. For the most part, we focused on the number of snails eaten by prawns because of its relevance to biological control of parasite transmission: The number (not biomass) of infected snails determines transmission risk to humans throughout a transmission season. This is due to the several-month average lifespan of schistosome-susceptible snails, along with the long pre-patency and patency periods and the fact that small snails can be more susceptible to infection (Barbosa, 1963; Loreau and Baluku, 1987; Niemann and Lewis, 1990; Pfluger, 1980; Pfluger et al., 1984; Woolhouse and Chandiwana, 1990a, 1990b). Thus, we measured consumption mainly in terms of the number of snails consumed/time or, where appropriate, the number consumed/gram-prawn-biomass/time. A second benefit of focusing on the number of snails consumed was to allow comparison with other studies, since we used the classic