nature sustainability

ARTICLES

https://doi.org/10.1038/s41893-019-0301-7

Modelled effects of prawn aquaculture on poverty alleviation and schistosomiasis control

Christopher M. Hoover[1], Susanne H. Sokolow[2,3,4,22], Jonas Kemp[5,21], James N. Sanchirico[6], Andrea J. Lund[7], Isabel J. Jones[2], Tyler Higginson[8], Gilles Riveau[9], Amit Savaya[10,11], Shawn Coyle[12], Chelsea L. Wood[13], Fiorenza Micheli[2,14], Renato Casagrandi[15], Lorenzo Mari[15], Marino Gatto[15], Andrea Rinaldo[16], Javier Perez-Saez[16], Jason R. Rohr[17,18,19,20], Amir Sagi[10,11], Justin V. Remais[1,22] and Giulio A. De Leo[2,3,4,22]*

Recent evidence suggests that snail predators may aid efforts to control the human parasitic disease schistosomiasis by eating aquatic snail species that serve as intermediate hosts of the parasite. Here, potential synergies between schistosomiasis control and aquaculture of giant prawns are evaluated using an integrated bioeconomic–epidemiological model. Combinations of stocking density and aquaculture cycle length that maximize cumulative, discounted profit are identified for two prawn species in sub-Saharan Africa: the endemic, non-domesticated *Macrobrachium vollenhovenii* and the non-native, domesticated *Macrobrachium rosenbergii*. At profit-maximizing densities, both *M. rosenbergii* and *M. vollenhovenii* may substantially reduce intermediate host snail populations and aid schistosomiasis control efforts. Control strategies drawing on both prawn aquaculture to reduce intermediate host snail populations and mass drug administration to treat infected individuals are found to be superior to either strategy alone. Integrated aquaculture-based interventions can be a win–win strategy in terms of health and sustainable development in schistosomiasis endemic regions of the world.

Schistosomiasis is a debilitating disease of poverty, affecting around 200 million people worldwide[1,2]. It is caused by trematode parasites of the genus *Schistosoma* that undergo a life cycle involving passage between definitive human hosts and freshwater snails that act as intermediate hosts. While safe and effective treatments, such as the anthelmintic drug praziquantel, are available to reduce the parasite burden (W_{parasite}) and associated symptoms from infected individuals, rapid reinfection in highly endemic areas leads to persistent hot spots of infection[3,4]. Successful long-term elimination efforts may require strategies that go beyond conventional mass drug administration (MDA) campaigns to explicitly target the environmental reservoir of the disease[5].

There is a rich history of environmental interventions for schistosomiasis that target the intermediate snail hosts[6]. Molluscicides are effective in reducing snail populations and have been used in integrated campaigns to control schistosomiasis in areas of South America, Northern Africa and Southeast Asia[6–8]. However, these approaches generally require repeated applications of chemicals that may negatively affect non-target species in addition to *Schistosoma*-bearing snails[9,10].

Another option for reducing transmission is cultivating snail predators, such as river prawns, via aquaculture. Such snail predators have been shown to reduce schistosomiasis transmission associated with *Schistosoma haematobium* infection by consuming *Bulinus* snails in the aquatic environment where people contact infested water[11,12].

In addition to being voracious predators of snails[13,14], river prawns are a valuable food commodity[15,16]. The giant freshwater prawn *Macrobrachium rosenbergii* has been domesticated and widely used in commercial hatchery-based aquaculture[17], providing a key source of protein and encouraging local economic development[18]. Furthermore, advances in the production of non-breeding *M. rosenbergii* monosex populations reduces the risk of prawn invasion in areas where this species is not native, suggesting safe use of this biological control agent globally[19,20].

In sub-Saharan Africa, where at least 90% of schistosomiasis cases occur[1,21], the native African river prawn *Macrobrachium*

---

[1]Division of Environmental Health Sciences, University of California Berkeley, School of Public Health, Berkeley, CA, USA. [2]Hopkins Marine Station, Stanford University, Pacific Grove, CA, USA. [3]Woods Institute for the Environment, Stanford University, Stanford, CA, USA. [4]Center for Innovation in Global Health, Stanford University, Stanford, CA, USA. [5]Program in Human Biology, Stanford University, Stanford, CA, USA. [6]Department of Environmental Science and Policy, University of California, Davis, Davis, CA, USA. [7]Emmett Interdisciplinary Program in Environment and Resources, School of Earth, Energy and Environmental Sciences, Stanford University, Stanford, CA, USA. [8]Middlebury Institute of International Studies at Monterey, Monterey, CA, USA. [9]EPLS Biomedical Research Center, Saint Louis, Senegal. [10]Department of Life Sciences, Ben Gurion University of the Negev, Beer Sheva, Israel. [11]National Institute for Biotechnology in the Negev, Ben Gurion University of the Negev, Beer Sheva, Israel. [12]Aquaculture Research Center, Aquaculture Division, Kentucky State University, Frankfort, KY, USA. [13]School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, USA. [14]Center for Ocean Solutions, Stanford University, Pacific Grove, CA, USA. [15]Dipartimento di Elettronica, Informazione e Bioingegneria, Politecnico di Milano, Milan, Italy. [16]Laboratory of Ecohydrology, School of Architecture, Civil and Environmental Engineering, Ecole Polytechnique Fédérale de Lausanne, Lausanne, Switzerland. [17]Department of Biological Sciences, University of Notre Dame, Notre Dame, IN, USA. [18]Eck Institute for Global Health, University of Notre Dame, Notre Dame, IN, USA. [19]Environmental Change Initiative, University of Notre Dame, Notre Dame, IN, USA. [20]Department of Integrative Biology, University of South Florida, Tampa, FL, USA. [21]Present address: Google Brain, Mountain View, CA, USA. [22]These authors jointly supervised this work: Susanne H. Sokolow, Justin V. Remais, Giulio A. De Leo. *e-mail: deleo@stanford.edu

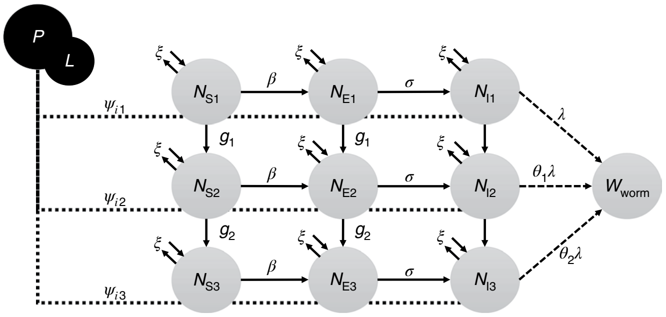

Fig. 1 | A model schematic representing the three components of the integrated aquaculture–epidemiological model. Prawn aquaculture is modelled by the state variables P_{prawn} and L. The epidemiological model consists of the size- and age-structured snail population state variables (N_{ij}) in grey circles and the mean W_{worm} in the human population. These two components are linked via size- and density-dependent prawn predation on snails, estimated as ψ_{ij}. Parameters governing transitions between snail classes and migration in and out of each class are shown: ξ is the rate of migration between the external snail population and the population at the modelled intervention site; β is the man-to-snail transmission parameter; σ is the inverse of the prepatent period of snails; g_1 and g_2 are the growth rates of snails in size class 1 and 2, respectively; λ is the snail-to-man transmission parameter; and θ_1 and θ_2 represent the increased contribution of larger snails to human infection.

vollenhovenii has been proposed as an alternative to *M. rosenbergii* for aquaculture[19]. Furthermore, extensive prawn aquaculture—consisting of large enclosures, low prawn densities (P_{prawn}), and no use of supplemental feed, substrate or additional oxygenation—is increasingly common in developing countries[15–17]. It can also be easily integrated into rice agriculture, which is increasingly an important part of food production and is already present in many schistosomiasis endemic areas[22,23].

Given that schistosomiasis is a disease of poverty, combining the nutritional and economic benefits of prawn aquaculture with disease control via prawn predation on snails may offer a sustainable approach to combat schistosomiasis and improve well-being and economic development in endemic areas. Here, an integrated model consisting of (1) a bioeconomic production model of *Macrobrachium* species aquaculture, (2) an epidemiological model of *S. haematobium* transmission dynamics and (3) a size- and density-dependent prawn predation model is developed and parameterized via the results of previous laboratory, modelling and field-based empirical studies (Fig. 1)[12,13]. The model is used to investigate whether extensive prawn aquaculture (using either endemic *M. vollenhovenii* or domesticated *M. rosenbergii*) can be managed at schistosome transmission sites such as rice paddies or enclosed points of water contact where people are exposed[12], to simultaneously maximize profit and control schistosomiasis. Estimates of the disability-adjusted life years (DALYs) lost due to *S. haematobium* infection derived from the integrated model are used to compare reductions in disease burden achieved via aquaculture-based prawn interventions with conventional MDA interventions, and to estimate the benefits of utilizing both MDA and prawn aquaculture for schistosomiasis control.

Model simulations

A time horizon of $T_{max} = 10$ years is used for comparability to similar analyses investigating different schistosomiasis intervention strategies[7,24]. The aquaculture component of the model is first used to simulate growth and mortality dynamics for each *Macrobrachium* species in a 1,000 m^2 enclosure. Because prawn body size increases and levels off with time, but prawn abundance decreases with time due to size- and density-dependent mortality, both stock biomass and cumulative profit, CP, are unimodal functions of time for any given initial stocking density, P_0. Additionally, harvesting before peak profit may afford the opportunity to increase the number of aquaculture cycles, n^{sp}, and therefore sacrifice short-term profits to maximize the long-term profit. The initial stocking density, P_0, and rotation time, T, that maximize CP for each species, CP^{sp}, are identified via numerical simulation. The surface of values (P_0, T, CP^{sp}) is related to the eumetric curve used in fishery science to identify the stocking density or fishing effort that maximizes profit[25]. As stocking costs increase linearly with P_0, while revenues increase less than linearly as a consequence of density-dependent growth and mortality, the surface is unimodal and its peak represents the maximum achievable CP, $\mathrm{CP}^{sp}_{opt} = \max(\mathrm{CP}^{sp})$. Therefore, it is possible to identify the initial stocking density, P^{sp}_{0opt}, and rotation time, T^{sp}_{opt}, that maximize cumulative profit, CP^{sp}_{opt}, here collectively defined as optimum management. The optimum management for each prawn species is identified using a grid search over P_0 ranging between 0.5 and 7.5 P m^{-2} and potential rotation times on each day between 1 and 730 d.

The epidemiological model of schistosomiasis transmission is an extension of the model presented by Sokolow et al.[12]. It describes the growth and infection dynamics of the intermediate host snail population as snails move from small to intermediate and then large size classes, and transition from susceptible (S) to exposed (E) and then infective (I; implying active shedding of larval cercariae, which infect humans) infection classes. It also tracks human infection via a state variable representing the mean worm burden (W_{worm}) in the human population. Finally, the epidemiological and aquaculture models are linked via a predation function parameterized via results from Sokolow et al.[13], representing the prawn population's size- and density-dependent rate of snail consumption, penalized for wild foraging conditions (see Methods). This linked model is subsequently referred to as the integrated model, and is used for additional simulations of potential prawn- and MDA-based interventions.

In the integrated model, prawn stocking and harvesting are simulated at regular intervals of T^{sp}_{opt} days as instantaneous events that reset the values of P_{prawn} and the mean prawn body size, L, to match the initial conditions at the beginning of each stocking cycle (that is, P^{sp}_{0opt} and L_0). This assumes that all prawns—regardless of marketability—are harvested and replaced with P^{sp}_{0opt} juveniles in a single day. MDA is implemented as an instantaneous 85% reduction in the mean W_{worm} of the epidemiological model, and is assumed to affect the same 75% of the human population, corresponding to assumptions of 85% drug efficacy and 25% systematic non-compliance to treatment[24,26].

The integrated aquaculture–epidemiological model is run under the following scenarios: (1) ten years of annual MDA with no prawn intervention; (2) and (3) ten years of prawn stocking and harvesting under optimal aquaculture management for *M. rosenbergii* and *M. volenhovenii*, respectively, as described above, with no MDA; and (4) and (5) ten years of integrated intervention with both annual MDA and prawn stocking, and harvesting under optimum management for each species, respectively. In all scenarios, the system is simulated for an additional ten years without intervention to explore rebound in the community mean W_{worm} in the case of the intervention programme ceasing.

To compare the effects of different interventions, disability associated with schistosomiasis is modelled using the DALY, as in previous analyses[7,27]. Disability weights measuring the disability associated with a condition for a single year of life—where 0 is perfect health and 1 is death—were distributed among individuals with heavy (>50 eggs per 10 ml urine, H_{high}) and light ($0 <$ eggs per 10 ml urine ≤ 50, H_{low}) *S. haematobium* burdens, as defined by World Health Organization guidelines. Total DALYs lost are then estimated cumulatively over each simulation period (see Methods).

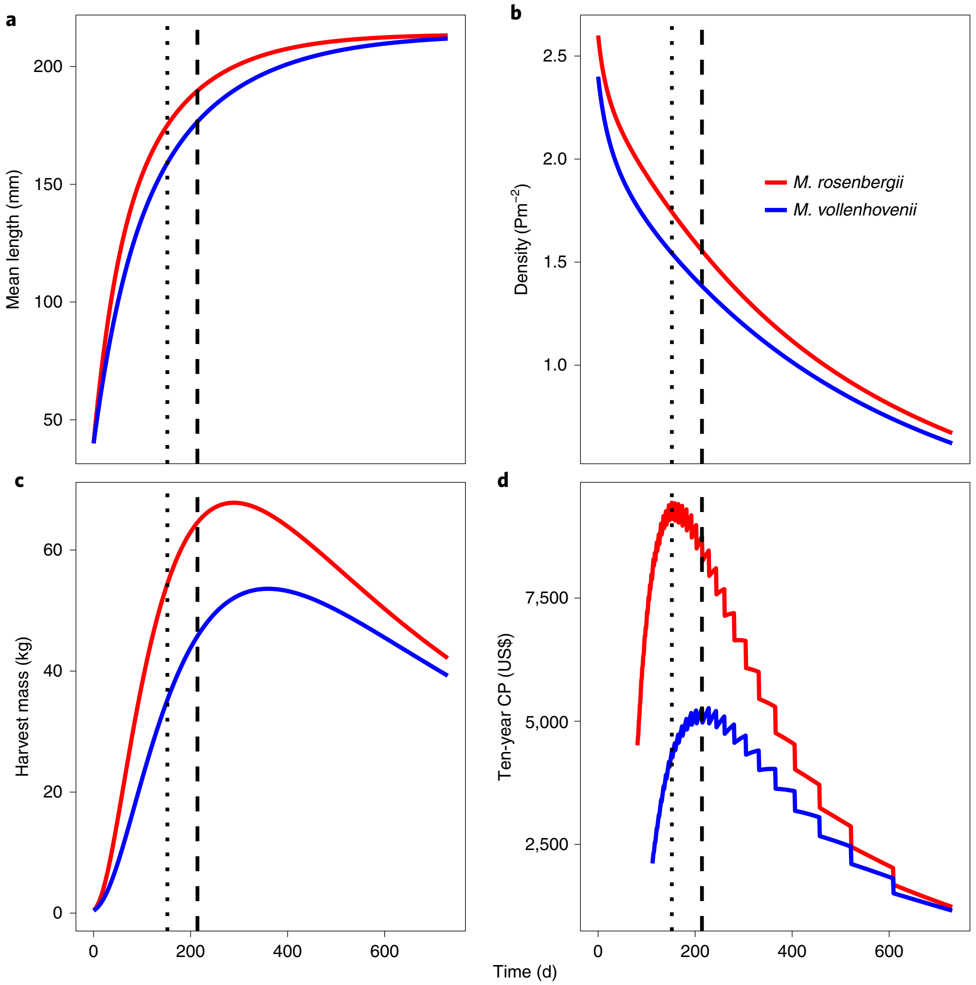

Fig. 2 | Prawn aquaculture model dynamics. a–d, Two-year aquaculture cycles for *M. rosenbergii* (red lines) and *M. vollenhovenii* (blue lines) under optimum management. Prawns grow in length over time (**a**), but decrease in density (**b**). This leads to a single peak in harvest mass (**c**), but harvesting actually occurs before the peak to maximize ten-year CPs (**d**) by sacrificing profit per cycle for completing more aquaculture cycles. Vertical lines indicate the times at which harvest would occur for each species (dotted, *M. rosenbergii*; dashed, *M. vollenhovenii*). Harvest of the slower-growing *M. vollenhovenii* occurs later as they take longer to grow in size and biomass. Here, following ref. [32], the cost, *c*, for a juvenile prawn is US\$0.10, with $L_0 = 40$ mm (~0.35 g per juvenile prawn) and the selling price is $\wp = \mathrm{US}\$12\ \mathrm{kg}^{-1}$. Other parameters were set as in Table 1.

All simulations are performed across 1,000 candidate parameter sets derived from Latin hypercube sampling of the parameters and ranges listed in Supplementary Tables 1–3, to determine variability in model outputs arising from parametric uncertainty. These same parameter sets are used in global sensitivity analyses, using partial rank correlation coefficients in addition to specific sensitivity analyses to explore the influence of increased prawn mortality and fixed costs associated with stocking or harvesting prawns.

Results

Aquaculture model. With the parameters reported in Supplementary Table 1, stocking *M. rosenbergii* at $P_0 = 2.6\,\mathrm{Pm}^{-2}$ and harvesting at $T^{\mathrm{ros}}_{\mathrm{opt}} = 165$ d maximizes the cumulative ten-year profit, while stocking at $P_0 = 2.4\,\mathrm{Pm}^{-2}$ and harvesting at $T^{\mathrm{vol}}_{\mathrm{opt}} = 260$ d maximizes the CP for *M. vollenhovenii*. These stocking densities and rotation times were used to simulate aquaculture cycles for each species. Figure 2 shows the dynamics of each species run continuously through two years, with vertical dashed lines indicating the optimum time of harvest, $T^{\mathrm{sp}}_{\mathrm{opt}}$. Prawns grow in length, L, and weight over time (Fig. 2a) while the population size (measured as P_{prawn}) decreases with time as a result of density-dependent death from crowding and natural, size-dependent mortality (Fig. 2b). These competing effects lead to a humped function of total harvestable biomass, Ω, over time, with the peak occurring well before prawns grow to their full size (Fig. 2c). Ten-year CPs also have a single peak, which is determined by both the profit per cycle and the number of cycles possible within the ten-year time frame (Fig. 2d). Cumulative profits are maximized by harvesting well before the peak in harvestable biomass occurs, indicating that more, smaller harvests maximize profit over time.

The surface of values (P_0, T, $\mathrm{CP}^{\mathrm{sp}}$) resulting from the grid search to identify optimum management for each species is shown in Fig. 3. As expected, profits associated with aquaculture of the faster-growing *M. rosenbergii* are higher. Considering parametric uncertainty, the peak estimate of median CP for *M. rosenbergii* occurs at $P_0 = 2.9\,\mathrm{Pm}^{-2}$ and $T^{\mathrm{ros}}_{\mathrm{opt}} = 173$ d (interquartile range (IQR): 146–192), producing $\mathrm{CP}^{\mathrm{ros}}_{\mathrm{opt}} = \mathrm{US}\$5,364\ (\$3,192–\$8,111)$ per $1,000\,\mathrm{m}^2$ enclosure. The same estimates for *M. vollenhovenii* are $P_0 = 2.5\,\mathrm{Pm}^{-2}$, $T^{\mathrm{vol}}_{\mathrm{opt}} = 260\ \mathrm{d}\,(228–331)$ and $\mathrm{CP}^{\mathrm{vol}}_{\mathrm{opt}} = \mathrm{US}\$1,738\ (\$704–\$3,394)$. Cumulative profits are still feasible at much higher stocking densities for each species, with $\mathrm{CP}^{\mathrm{ros}}_{\mathrm{opt}} > 0$ at P_0 as high as $6.5\,\mathrm{Pm}^{-2}$ and $\mathrm{CP}^{\mathrm{vol}}_{\mathrm{opt}} > 0$ at P_0 up to $5.95\,\mathrm{Pm}^{-2}$. Additional outputs from the

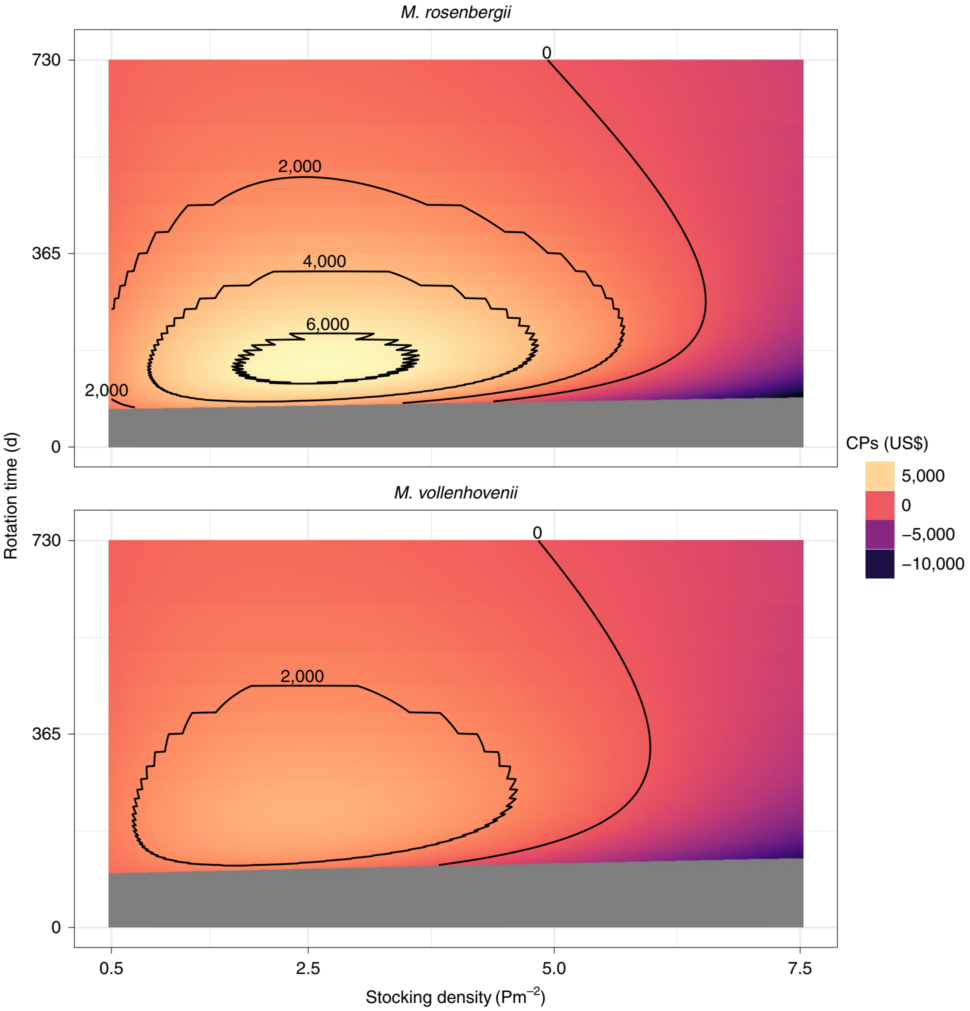

Fig. 3 | Grid search to identify optimum management decisions for each prawn species. CP^{sp} generated by the aquaculture model for each species across a range of potential stocking densities and rotation times. The grey regions indicate regions where harvesting is not feasible due to prawns not having reached a sufficient marketable size (30 g), due to insufficient time to grow and density-dependent growth rates. The contours indicate regions of CP^{sp} corresponding to the labelled value in 2018 US$.

aquaculture model that describe stock structure and aquaculture performance at optimum management are reported in Table 1.

Integrated aquaculture epidemiological model. Simulation of the integrated model reveals comparable performances of prawn intervention strategies and MDA strategies. As in previous analyses[7,12], annual MDA alone produces a pattern of gradually decreasing W_{worm} over time, characterized by a repeated rebound in infection following MDA (Fig. 4a, purple line). The prawn-only intervention causes the mean W_{worm} to gradually decline towards 0, eventually reducing the W_{worm} to comparable levels by year 10 (Fig. 4a, blue line). The combined MDA and prawn intervention leads to a rapid decline in the mean W_{worm} that nearly reaches 0 by year 10 (Fig. 4a, gold line).

These patterns can be explained by the underlying snail infection dynamics. Under MDA intervention, the snail population persists through repeated rounds of MDA, and even increases due to the reduced influence of infection on fecundity and mortality of the snail population (Fig. 4b). Most importantly, infected snails continue to shed infectious cercariae—albeit at lower levels—even as adult worms are removed from the treated human population through repeated MDA (Fig. 4b). Interventions in which prawns are introduced at profit-maximizing densities cause rapid declines in the snail population and near-elimination of infective snails (Fig. 4c). Extirpation of the entire snail population is prevented due to the assumption of a Holling's type III (S-shaped) functional response that produces decreased rates of predation at low snail density and immigration from an unaffected reservoir population (see Supplementary Fig 3 for snail infection dynamics without immigration and under a Holling's type II, logarithmic-shaped, functional response). Even though the entire snail population is not extirpated, transmission is effectively halted due to near-elimination of the infected snail population (Fig. 4c). Meanwhile, the mean W_{worm} decreases slowly due to natural worm mortality (Fig. 4a, blue line), or quickly in the presence of MDA (Fig. 4a, gold line). This heavy reduction in transmission coupled with the benefits of MDA translates to near-elimination of the parasite by year 10. Regardless of the intervention, ceasing efforts to control transmission after ten years results in rapid returns towards pre-intervention snail populations and community-level mean W_{worm} (Fig. 4a–c).

A comparison of total DALYs lost over ten-year simulation periods under each intervention shows comparable performances of the prawn-only intervention and MDA, and substantial additional DALYs are averted when combining MDA with prawn intervention. Without intervention, a median 324 (IQR: 119–502) DALYs are lost to *S. haematobium* infection. Annual MDA and profit-maximizing prawn stocking perform comparably, with 160 (IQR: 54–285) total

Table 1 | The optimum stocking and harvesting parameters for each prawn species

Parameter	Definition	*M. vollenhovenii*	*M. rosenbergii*
P^{sp}_{0opt}	Optimum stocking density (Pm^{-2})	2.4	2.6
L_0	Stocking size of juveniles (mm)	40	40
T^{sp}_{opt}	Optimum rotation time (d)	260 (228–331)	165 (146–192)
$L(T^{sp}_{opt})$	Mean length at harvest (mm)	167 (161–175)	167 (161–174)
$P(T^{sp}_{opt})$	Prawns harvested	1,056 (850–1,236)	1,559 (1,434–1,662)
$Y\,(T^{sp}_{opt}, P^{sp}_{0opt})$	Commercial yield per harvest (kg)	28 (21–36)	41 (34–49)
n^{sp}	Number of cycles in 10 years	14 (11–16)	22 (19–25)
CP^{sp}_{opt}	Cumulative profits over 10 years (US$)	1,891 (856–3,486)	5,403 (3,380–8,075)

Values are reported as medians (IQRs).

DALYs lost with annual MDA and 184 (IQR: 70–294) total DALYs lost with prawns, representing 51 and 43% of DALYs averted, respectively. Integrated interventions utilizing both MDA and prawn stocking reduce the median DALYs lost to 83 (IQR: 30–137), representing a 74% reduction in *S. haematobium*-related disability.

Discussion

Small-scale, extensive prawn aquaculture such as that considered here offers a profitable and sustainable method to improve food production, reduce schistosomiasis transmission and increase revenues for small-scale subsistence farmers, especially when paired with ongoing efforts such as rice cultivation[23]. In areas of high food insecurity, malnutrition and endemic schistosomiasis—conditions that reinforce each other and often result in 'poverty traps'[28,29]—the development of prawn aquaculture in transmission sites may be a solution for co-benefits of disease control and sustainable development.

To meet the goals for schistosomiasis reduction set out by the World Health Organization of morbidity control by 2020 and local elimination as a public health problem by 2025, additional control strategies are needed[1,30]. These results build on an increasing body of evidence indicating that consumption of snails by predator species such as *Macrobrachium* prawns can be an effective method for combating schistosomiasis transmission to people[11,12,31]. Specifically, by targeting the environmental reservoir of schistosome parasites, prawns can reduce reinfection rates that undermine the effects of MDA campaigns in high-transmission settings. By deploying prawn aquaculture with MDA, effective control—in which the schistosome parasite is suppressed in both human hosts and intermediate host snails—can be achieved. Furthermore, the use of prawns for snail control, as opposed to molluscicides that may have non-target effects on species other than schistosome-bearing snails, represents a more sustainable approach to schistosomiasis control.

Prawn interventions combined with established extensive aquaculture methods can also be profitable if carefully managed. Drawing on economic studies of existing aquaculture practices[17,32], we develop a dynamic model of prawn aquaculture to investigate optimum management practices. The model suitably simulates prawn stocking in a large enclosure or rice paddy, and the length of optimum cycles coincides with typical rice harvesting timelines[23]. This system produces short- and long-term profits, implying the potential for a sustainable, community-driven intervention, given the right capital investment and incentive programmes.

Under optimum management, extensive aquaculture of either *M. rosenbergii* or *M. vollenhovenii* leads to both profits and reductions of the snail population. The optimum stocking densities of each species are above the potential threshold of approximately 2 Pm^{-2} necessary for local snail extirpation, as identified in previous work[12], although our conservative inclusion of snail migration and a Holling's type III functional response restricts such an outcome in this analysis. Although this estimate of the threshold stocking density necessary for snail extirpation is based on a number of realistic assumptions regarding prawn mortality, snail population dynamics and behaviour, and prawn predation of snails, stocking densities at least three times higher than this are still economically viable. Alternative funding mechanisms (for example, that maximize the potential for snail control rather than for profit) may therefore be worth exploring.

Achieving these stocking densities may be challenging in sub-Saharan Africa where >90% of the global burden of schistosomiasis is found[21] and where strategies to complement ongoing MDA are most needed. Juvenile *M. rosenbergii* are readily available for purchase, and protocols for ideal rearing and management for aquaculture of this species have been established during 50 years of domestication[16,17]. Similar protocols for the African native *M. vollenhovenii* are still under development. Profits appear to be highly sensitive to parameters that regulate prawn growth, meaning continued research and development into *M. vollenhovenii* aquaculture—including nursery and hatchery protocols, better understanding of their growth and social structure, and selective breeding—may eventually provide comparable profits to *M. rosenbergii*, especially given the rapid expansion of aquaculture technologies and practices globally in recent years[33,34].

The stocking of *M. rosenbergii* in coastal regions where it is non-native should be approached with caution to avoid the establishment of an alien population with potentially unintended ecological consequences on local biodiversity. The establishment of aquaculture biotechnologies for either all-male[35–37] or all-female[38] populations that do not rely on genetically modified organisms suggests possible strategies to prevent invasions. Moreover, recent laboratory experiments have ruled out the possibility of cross-fertilization between mature female *M. vollenhovenii* and male *M. rosenbergii*, showing that male-only progeny of *M. rosenbergii* may be safely used for extensive aquaculture and schistosomiasis control in western Africa where *M. rosenbergii* is non-native[37,39].

Extensive sensitivity analyses reveal that key model outcomes, including profit generated by the aquaculture portion of the model and DALYs lost from the integrated model, are robust to uncertainty in key parameters governing profit estimation and the influence of prawn interventions on DALYs lost. Aquaculture performance—in terms of CPs—is most sensitive to parameters governing somatic growth, which have been estimated from the available literature, and supported by expert opinion[40,41]. This finding also suggests that if stock improvement or advances in husbandry practices can increase average prawn condition or size (that is, by supplementing feeds), further increases in profit may be possible. Selective harvesting methods that only remove market-size prawns, leaving the remaining stock to continue to grow, may also improve aquaculture performance. However, such selective harvesting may require additional investment (for example, in nets with different mesh sizes or pumps to drain waterbodies and further inspect prawns). The harvesting of all prawns in a single batch, as is assumed in these analyses, is therefore considered the easiest management strategy to implement.

Optimum aquaculture practices are also sensitive to the market price of adult prawns and the stocking cost of juvenile prawns,

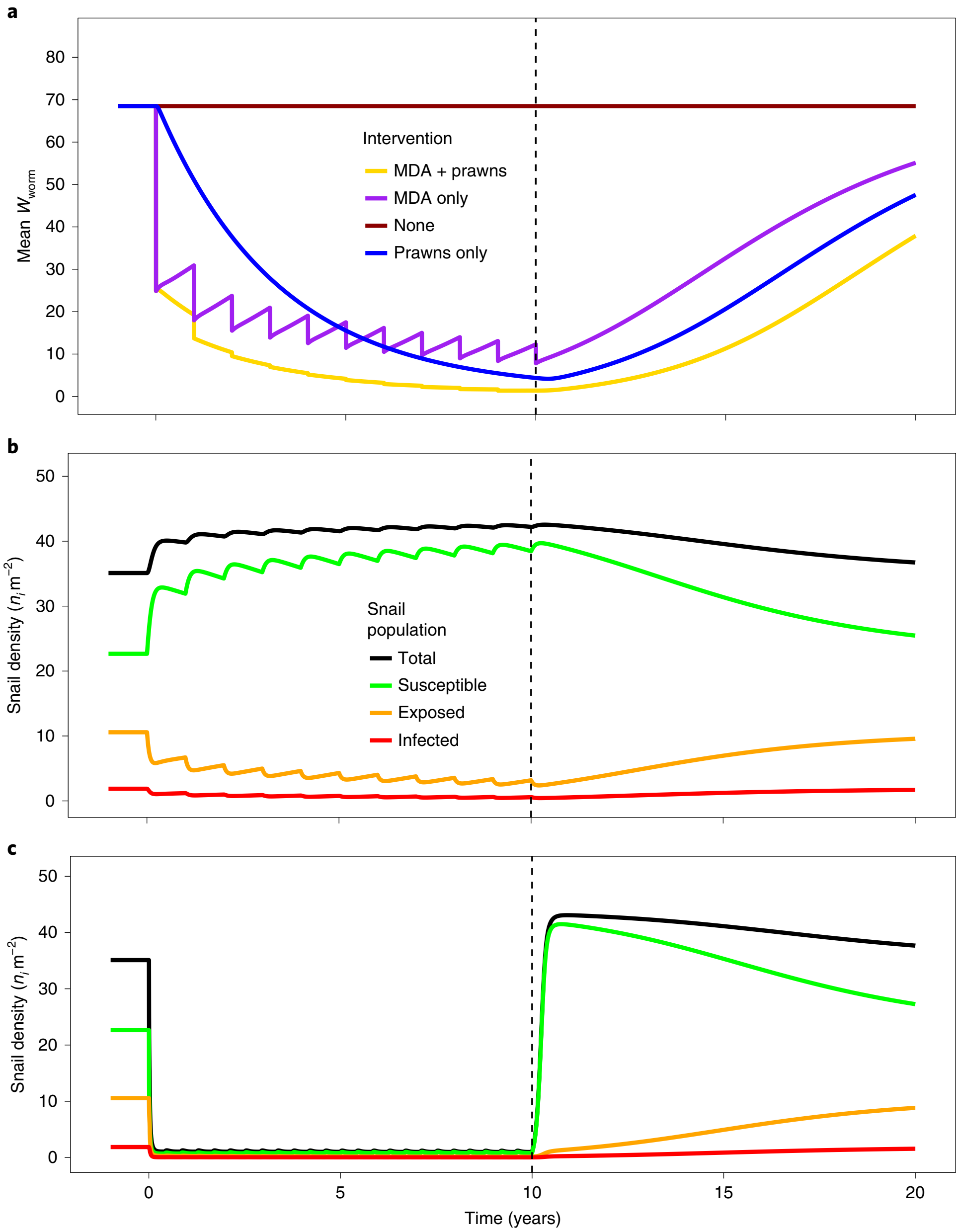

Fig. 4 | Outputs of the integrated model under different intervention scenarios implemented over ten years, followed by ten years of no intervention. **a**, Worm burden trajectories under no intervention (maroon), annual MDA only (purple), prawn stocking of *M. rosenbergii* under optimum management (blue), and both annual MDA and prawn stocking (gold). **b**,**c**, Snail infection dynamics under the MDA-only intervention (**b**) and prawn stocking intervention (**c**). Outputs from *M. volenhovenii* interventions are not shown as they approximately mirror those of *M. rosenbergii*, since the profit-maximizing stocking densities of both species result in maximum reductions in the snail population.

implying that optimum management may be influenced by fluctuations in market factors that may influence the price and cost of harvested and stocked prawns. Profit generated from selling harvested prawns is based on reasonable assumptions of prices in premium markets, although the actual selling price in subsistence economies might be lower and contingent on market access and local demand. However, the fixed cost sensitivity analysis shows that profitability is possible even with substantial additional costs associated with prawn stocking, and profitability persists across a wide range of stocking densities for each species. These results together assuage concerns that such market vagaries would impair the success of the proposed system, and suggest that prawn aquaculture can be economically viable even under non-optimum densities.

Surveys to identify potential prawn intervention sites, including rice paddies, ponds and water contact sites that can be enclosed with a net, would also be needed on a local scale. Such sites would require water quality compatible with prawn survival; therefore, activities such as laundry, car washing and the use of insecticides on nearby crops would have to be limited[42,43]. Still other sources of additional prawn mortality, such as disease outbreaks or predation by waterbirds, fish, amphibians or reptiles, are also possible, although extensive aquaculture would still be profitable with mortality rates as high as five times the natural mortality. Barring catastrophic events, this suggests that the proposed system should be resilient to such perturbations. Additional studies assessing prawn life expectancy, escapement rate, growth performance, changes in water quality and potential changes in human behaviour, which might affect aquaculture performance and/or snail abundance, transmission rates and epidemiological outcomes, should be pursued.

Prawn predation of the snail population as modelled here is also based on a number of assumptions, including the Holling's type III functional response and the prawn attack rate penalty. The type III functional response probably represents a conservative estimate of the relationship between prawn predation and snail density as it does not allow for the potential extirpation of the snail population. This necessitates combining the prawn intervention with MDA to be effective in reaching elimination targets. A wide range of attack rate penalties that regulate the number of snails consumed per prawn per day were also tested, as no previous estimates of prawn predation efficiency in non-laboratory settings were identified. Effective control is feasible even when penalizing the attack rate by an order of magnitude (implying a substantially reduced attacked rate).

Regarding schistosomiasis transmission dynamics, recent findings suggest that nonlinearities in the human-to-snail force of infection may decrease the efficacy of MDA and lead to faster post-MDA rebounds of schistosomiasis[44]. Although this may alter the effects of MDA in our simulations, we believe it strengthens the argument for strategies that explicitly target the intermediate host snail population, such as the prawn intervention proposed here. The model also makes simplifying assumptions that should be investigated in future research: that the production of infectious cercariae, and human contact with water containing infectious cercariae, both occur only in the site where prawns are stocked. Previous analyses have investigated the role of human movement and passive cercarial transport (for example, in river currents[45]), but these processes have not been incorporated here due to the existing complexity of the model and the lack of adequate data to quantify these phenomena in this setting. The effectiveness of the prawn intervention is expected to be reduced if people are frequently exposed to schistosome cercariae at or from other transmission sites.

Another recent finding suggests that snail control can actually lead to increased human risk of *Schistosoma* infection if the snail population is limited by resource competition before 'weak' control efforts[46]. In this scenario, remaining snails with higher per-capita resource availability may produce more cercariae. Given the large magnitude of snail reductions at the proposed prawn densities modelled here—even given the conservative Holling's III functional response—this effect is believed to be unlikely in our scenarios.

Finally, our model lacks seasonality, which may affect both schistosomiasis transmission and prawn growth as, for example, temperature and rainfall fluctuate through the year, especially in sub-tropical and near-temperate regions where schistosomiasis is still endemic, such as in northern Africa[47–49]. However, the assumption of a constant and large snail population carrying capacity represents a worst-case scenario, and introducing seasonal variation would probably not alter the results presented here. Furthermore, in regions where transmission predominately occurs in ephemeral ponds during the rainy season, prawn aquaculture is probably not a viable approach[48].

This bioeconomic analysis shows that an integrated intervention strategy that utilizes both MDA and a profitable prawn aquaculture system can successfully control schistosomiasis while generating profit. Since the intervention is driven by a profitable business model, it may be sustainable purely through market incentives, and thereby reduce the need for external support from donors or public health agencies. Subsidies are expected to be necessary only in the event that *M. rosenbergii* aquaculture is not suitable for the region, and obtaining large quantities of *M. vollenhovenii* juveniles is infeasible or expensive. Research and development for this system is indeed ongoing in Senegal, which will aid future analyses of the effectiveness and feasibility of this promising integrated strategy.

Methods

The integrated model has three components: (1) a bioeconomic aquaculture component, simulating yields and accounting for density-dependent mortality and somatic growth of *Macrobrachium* species prawns over a range of P_0; (2) an epidemiological component to simulate the dynamics of the mean *S. haematobium* worm burden in humans and the population and infection dynamics of intermediate host snails through a size-structured, susceptible–exposed–infected compartmental model; and (3) a predation function that links the epidemiological and aquaculture models and estimates the rate at which prawns consume snails as a function of snail density and of snail and prawn body sizes.

Aquaculture model. The dynamics of a cohort of P_0 juvenile prawns of initial mean length, L_0 (mm), stocked at time $t = 0$ d in an enclosure of 1,000 m^2—a size consistent with either a large water contact site or a typical rice field in small-scale, subsistence agriculture settings—are simulated over time as a function of density-dependent and size-dependent growth and mortality. Hatchery and nursery infrastructure is not explicitly considered in the model, but is assumed to supply juvenile prawns to stock at desired transmission sites.

Although prawns exhibit quite heterogeneous growth patterns depending on sex (with males growing larger than females) and social structure[50], an average growth rate through the population is simulated here. In addition, the growth of individual crustaceans is typically stepwise and occurs through a sequence of moulting events, but here the population-average growth of prawns is modelled as somatic growth with the von Bertalanffy growth equation[51]:

$$\frac{dL}{dt} = k^{*}(L_{\infty} - L) \tag{1}$$

The von Bertalanffy growth equation produces a classic increasing-and-saturating growth curve with length L at time t (days after stocking), eventually approaching the mean asymptotic length, L_{∞}. Based on experimental stocking trials showing reduced growth rates of *M. rosenbergii* at high stocking densities[50], a modified Brody growth coefficient, k^{*}, was estimated as a decreasing function of the total population biomass, Ω:

$$k^{*}(\Omega) = \frac{k_{\max}}{1 + \gamma\Omega(t)} \tag{2}$$

where $k_{\max}$ is the maximum value of the Brody coefficient at low densities, and γ is a coefficient parameterized to produce a density-dependent reduction in somatic growth qualitatively resembling that observed in experimental trials[50].

The total population biomass, $\Omega(t)$, is computed as the product of the mean prawn body size in grams, $B(t)$, and the number of individuals, $P(t)$, t days after stocking:

$$\Omega(t) = B(t)P(t) \tag{3}$$

Body size, $B(t)$, is derived as an allometric function of prawn length, $L(t)$, from *M. rosenbergii* grow-out data[40,52]:

$$B(t) = a_P L(t)^{b_P} \tag{4}$$

As prawns are generalist consumers with a wide range of invertebrate fauna and organic detritus in their diet[53], growth as described by equations (1)–(4) is assumed to be independent from snails' density and the corresponding predation rates.

After stocking, the total number of prawns in the enclosure decreases over time, with the per-capita mortality rate modelled as an additive function of two components: (1) an exponentially decreasing function of body size, $B(t)$, as large prawns exhibit lower mortality than small prawns[54]; and (2) a linearly increasing function of total population biomass, $\Omega(t)$, which accounts for density-dependent competition for resources and cannibalism at high population densities[50]. Accordingly, the dynamics of a cohort of initial size P_0 are described as follows:

$$\frac{\mathrm{d}P}{\mathrm{d}t} = -P\left(\mu_P B^{-d} + \omega\Omega\right) \tag{5}$$

with the parameters μ_P and d derived from previous studies[41,54] and ω parameterized to produce density-dependent mortality outcomes qualitatively similar to those observed in the experimental trials by Ranjeet and Kurup[50]. Natural recruitment is excluded from the aquaculture model, as new prawns enter the system only in discrete, exogenously controlled events, when P_0 prawns of initial average body size L_0 are stocked from nurseries and grown out to market size. Mortality (natural, or size and density dependent) is assumed to be the only cause of prawn population decline, although additional sources of mortality or loss (for example, predation by seabirds, escape from enclosures or rice fields, disease outbreaks or declines in water quality) are considered in the sensitivity analyses described below.

It is assumed that all prawns are harvested at the end of a production cycle of length $t = T$; however, prawns weighing <30 g are generally not of commercial interest. Experimental trials by Ranjeet and Kurup with *M. rosenbergii*[50] showed that the fraction of retrievable, market-size (>30 g) prawns decreases linearly with increasing prawn stocking density. Accordingly, commercial yield at time $t=T$ is only a fraction of the total biomass:

$$Y(T, P_0) = \zeta(P_0)\Omega(T) \tag{6}$$

where ζ, the fraction of marketable-size prawns in the population, is a decreasing function of P_0, as estimated from data in the Ranjeet and Kurup experiments[50].

Cumulative profits over a finite time horizon are determined by the profit produced per cycle and the number of cycles completed within the given time period. In a time period of $T_{\max}$ days, the number of aquaculture cycles completed for each *Macrobrachium* species is $n^{\text{sp}} = \text{round}\left(\frac{T_{\max}}{T}\right)$. The cumulative discounted profit for each species, CP^{sp}, is then estimated as the sum of the net discounted revenue for every cycle completed by $T_{\max}$:

$$\text{CP}^{\text{sp}}(P_0,\ T,\ T_{\max}) = \sum_{n=1}^{n^{\text{sp}}} (-cP_0 + \wp Y(T,\ P_0))e^{-\delta nT} \tag{7}$$

where $\wp$ is the price per unit weight (US$ kg^{-1}), c is the per-capita cost of stocked juvenile prawns, and δ is the discount rate to account for the time lag between initial stocking costs and delayed revenues of commercial-size prawns. Following the price analysis by Dasgupta and Tidwell[32], $c=$ US\$0.10/P for a juvenile prawn of $L_0=40$ mm (corresponding to ~0.35 g juvenile prawns) and $\wp=$ US\$12 kg^{-1} harvested[32]. For simplicity, it is assumed that prawns of various sizes are all sold at the same weight-based rate, whereas larger prawns are likely to fetch a higher price in real markets. The discount rate is set to 7%, which is probably on the low end for sub-Saharan African countries endemic with schistosomiasis but higher than the 3–4% rate used for discounting long-term government projects in the United States[55]. Other costs, such as maintaining nurseries to produce juvenile prawns, are considered external to the aquaculture scenario discussed here and are therefore not included in the profit estimation. The influence of such costs, as well as uncertainty in the cost of juveniles and the market price of harvested adults, are considered in additional sensitivity analyses described below.

Cumulative discounted profits are maximized by jointly choosing T and P_0. Given the rotation time, the number of rotations in the time period is determined, as $T_{\max}$ is given. Equation (7) has its basis in the optimum rotation models in forestry (see, for example, ref. [56]) and commercial aquaculture operations (see, for example, refs. [57,58]), which balance the marginal benefits of further growth against the opportunity costs of waiting to harvest. The resulting optimum rotation length is therefore shorter than a simple rule of when to harvest based solely on maximizing growth dynamics. Here, the same trade-off between the benefits from waiting to harvest the prawns at a larger size and the opportunity costs of delaying the economic returns from future harvests is expected.

The parameters used in the prawn aquaculture model simulations are listed in Supplementary Table 1. All of the results are expressed in US\$ to match the cost and price information identified in the literature, and because of the common use of US\$ as an international reference currency.

Epidemiological model. Building on our previous modelling of *S. haematobium*[12,43], the infection dynamics of the intermediate host *Bulinus* snail population, $\boldsymbol{N}$, are modelled as snails transition between $i \in \{\text{S, E, I}\}$ infection compartments corresponding to susceptible (S), exposed (E; pre-patent) and infected (I; patent) states. Furthermore, the growth dynamics of snails are modelled as they move through $j \in \{1, 2, 3\}$ size classes corresponding to mean snail diameters of 4, 8 and 12 mm (Fig. 1). The model is further extended to include snail migration with a constant migration rate, ξ, to and from an external population, $\boldsymbol{N}^{\text{E}}$, that is not affected by prawn interventions. For simplicity, the external population is conceptualized to originate from an identical transmission site to the one in which interventions are modelled, although in reality, multiple sites with heterogeneous transmission dynamics may contribute differentially to the intervention site[45].

New snails enter the population as susceptible juveniles (that is, in infection class $i=\text{S}$ and size class $j=1$). Logistic snail population growth is modelled with per-capita recruitment, f, and carrying capacity, K. Neither small snails ($j=1$) nor infectious snails ($i=I$) contribute to recruitment due to sexual immaturity and parasitic castration, respectively[59]. Prepatent snails' contribution to recruitment is reduced by a fraction $0<z<1$ (ref. [60]). Snails of each size class are subject to both size-dependent natural mortality, μ_j, and predation mortality, ψ_j—a function of both prawn and snail body size and density, as described in the next section. Small and medium snails grow and transition to the next size class at the per-capita rate g_1 (from size class 1 to 2) and g_2 (from class 2 to 3), respectively.

New snail infections occur at the rate βM, where β is the per-capita transmission rate and $M=0.5\varphi(W)WHm$ is an estimate of the overall number of *S. haematobium* miracidia (free-living larvae that infect snails) produced by mated adult *S. haematobium* female worms and shed in the urine of infected individuals. This estimate is the product of the size of the definitive human host population, H, the mean parasite burden, W_{parasite}, (that is, the mean number of adult worms per person), the rate at which mated adult female worms shed eggs that hatch into infectious miracidia, m, and the function $\varphi(W_{\text{worm}})$ representing the density-dependent mating probability of adult worms[61]. The coefficient 0.5 accounts for the assumed 1:1 sex ratio of adult worms. For simplicity, a constant human population and no density-dependent fecundity of female worms are assumed. Following infection, prepatent snails, E, transition to the patent class, I, at rate σ, with σ^{-1} being the mean time necessary for sporocyst development following snail infection with a miracidium.

The adult parasite population harboured by definitive human hosts is modelled as the mean W_{parasite} in the human population, assuming a negative binomial distribution with clumping parameter ϕ[61,62]. Humans acquire adult worms as a result of contact with cercariae (free-living larvae that infect humans) shed from patent snails. Worm acquisition occurs at rate λ—an aggregate parameter accounting for the per-capita shedding rate of cercariae by infected snails, cercariae mortality, contact rate and probability of infection—as described in previous work[12]. The cercarial shedding rate of medium (N_{12}) and large (N_{13}) snails is assumed to exceed that of small (N_{11}) snails by a factor θ_1 and θ_2, respectively[63].

Total DALYs lost over a given simulation period of $T_{\max}$ days are estimated as a function of: (1) disability weights associated with heavy and light infection (DW_{hi} and DW_{lo}, respectively) normalized to a daily estimate to match the dynamics of the model; and (2) the number of individuals in each burden class at each time step of the epidemiological model (H_{high_t} and H_{low_t}):

$$\sum_{t=1}^{T_{\max}} \frac{\text{DW}_{\text{high}}}{365} H_{\text{high}_t} + \frac{\text{DW}_{\text{low}}}{365} H_{\text{low}_t} \tag{8}$$

Additional information regarding the epidemiological model, including the full system of differential equations, epidemiological model parameters (Supplementary Table 2) and the process for estimating the number of individuals with heavy and light infection from the model, can be found in the Supplementary Information.

Prawn predation model. As in previous work[43], the per-capita prawn predation rate on *Bulinus* snails of each class, ψ_{ij}, is modelled as a type III functional response, described by a generalization of Holling's disk equation[64]. This produces a sigmoid-shaped function, which increases and saturates at high prey densities and decreases to approach zero at low prey densities. Previous experiments by Sokolow et al.[13] show that prawn predation of snails changes predictably as a function of the ratio of prawn biomass to snail body mass, r_j. Using these experimental data, the attack rate, α, is estimated as a log-linear function of the biomass ratio: $\alpha = \alpha_{\text{m}} \log[r_j(t)]$. The handling time, T_{h}, is estimated as a reciprocal function of the biomass ratio: $T_{\text{h}} = (T_{\text{hm}} r_j(t))^{-1}$, where α_{m} and T_{hm} are coefficients estimated from Sokolow et al.[13], and r_j is the ratio between prawn body size and mean snail body size in each class. Laboratory experiments presented in Sokolow et al.[13] show that small prawns are unable to feed on large snails ($j=3$); accordingly, $\psi=0$ when $r_j<3$. In addition, the attack rate, α, derived by Sokolow et al.[13] in controlled laboratory conditions in 1 m^{-2} tanks, is penalized by a factor $0<\epsilon<1$ to account for the reduction in searching efficiency caused by the morphological complexity of foraging in wild settings.

The biomass ratio for each snail size class is estimated as:

$$r_j(t) = \frac{B(t)}{a_N L_{N_j}^{b_N}} \tag{9}$$

where $B(t)$ is the prawn body size derived using equation (4), and the denominator represents snail mass in each class j, derived as a simple allometric function of snail shell diameter in each size class. The per-capita attack rate of prawns on snails of size j and infection class i is then estimated as:

$$\psi_{ij} = \begin{cases} \dfrac{\alpha(r_j(t))\epsilon N_{ij}^n}{1+\sum_{i=S}^{I}\sum_{j=1}^{3}\alpha(r_j(t))\epsilon T_{\text{h}}(r_j(t))N_{ij}^n} & ,\quad r_j \geq 3 \\ 0 & ,\quad r_j < 3 \end{cases} \tag{10}$$

Prawn stocking at the considered densities is assumed to have no negative effects on water quality that may affect prawn survival, growth, predation of snails or snail population dynamics, although ongoing field experiments in the lower Senegal River basin show that water quality may be negatively affected by nets installed to contain prawns introduced at transmission sites.

Parameters of the snail predation component of the combined model are listed in Supplementary Table 3.

The model was coded in R version 3.5.0 and simulated using the deSolve package[65]. To address concerns regarding reproducibility, all model code and data are provided in the Supplementary Code and Data folder and are freely available online at https://github.com/cmhoove14/Prawn_fisheries_Public_health.

Data availability

All data used to conduct this analysis are freely available at https://github.com/cmhoove14/Prawn_fisheries_Public_health, provided in the Supplementary Code and Data folder and available from the corresponding author on request.

Code availability

All code used to conduct this analysis is freely available at https://github.com/cmhoove14/Prawn_fisheries_Public_health, provided in the Supplementary Code and Data folder and available from the corresponding author on request.

Received: 9 November 2018; Accepted: 26 April 2019;

References

1. *Schistosomiasis: Progress Report 2001–2011, Strategic Plan 2012–2020* (WHO, 2013).
2. Lai, Y.-S. et al. Spatial distribution of schistosomiasis and treatment needs in sub-Saharan Africa: a systematic review and geostatistical analysis. *Lancet Infect. Dis.* **15**, 927–940 (2015).
3. Steinmann, P., Keiser, J., Bos, R., Tanner, M. & Utzinger, J. Schistosomiasis and water resources development: systematic review, meta-analysis, and estimates of people at risk. *Lancet Infect. Dis.* **6**, 411–425 (2006).
4. Colley, D. G. et al. Defining persistent hotspots: areas that fail to decrease meaningfully in prevalence after multiple years of mass drug administration with praziquantel for control of schistosomiasis. *Am. J. Trop. Med. Hyg.* **97**, 1810–1817 (2017).
5. Stothard, J. R. et al. Towards interruption of schistosomiasis transmission in sub-Saharan Africa: developing an appropriate environmental surveillance framework to guide and to support 'end game' interventions. *Infect. Dis. Poverty* **6**, 10 (2017).
6. Sokolow, S. H. et al. Global assessment of schistosomiasis control over the past century shows targeting the snail intermediate host works best. *PLoS Negl. Trop. Dis.* **10**, e0004794 (2016).
7. Lo, N. C. et al. Impact and cost-effectiveness of snail control to achieve disease control targets for schistosomiasis. *Proc. Natl Acad. Sci. USA* **115**, E584–E591 (2018).
8. King, C. H., Sutherland, L. J. & Bertsch, D. Systematic review and meta-analysis of the impact of chemical-based mollusciciding for control of *Schistosoma mansoni* and *S. haematobium* transmission. *PLoS Negl. Trop. Dis.* **9**, e0004290 (2015).
9. Andrews, P., Thyssen, J. & Lorke, D. The biology and toxicology of molluscicides, Bayluscide. *Pharmacol. Ther.* **19**, 245–295 (1982).
10. Dawson, V. K. Environmental fate and effects of the lampricide Bayluscide: a review. *J. Great Lakes Res.* **29**, 475–492 (2003).
11. Mkoji, G. M. et al. Impact of the crayfish *Procambarus clarkii* on *Schistosoma haematobium* transmission in Kenya. *Am. J. Trop. Med. Hyg.* **61**, 751–759 (1999).
12. Sokolow, S. H. et al. Reduced transmission of human schistosomiasis after restoration of a native river prawn that preys on the snail intermediate host. *Proc. Natl Acad. Sci. USA* **112**, 9650–9655 (2015).
13. Sokolow, S. H., Lafferty, K. D. & Kuris, A. M. Regulation of laboratory populations of snails (*Biomphalaria* and *Bulinus* spp.) by river prawns, *Macrobrachium* spp. (Decapoda, Palaemonidae): implications for control of schistosomiasis. *Acta Trop.* **132**, 64–74 (2014).
14. Roberts, J. K. & Kuris, A. M. Predation and control of laboratory populations of the snail *Biomphalaria glabrata* by the freshwater prawn *Macrobrachium rosenbergii*. *Ann. Trop. Med. Parasitol.* **84**, 401–412 (1990).
15. Islam, M. S. & Wahab, M. A. A review on the present status and management of mangrove wetland habitat resources in Bangladesh with emphasis on mangrove fisheries and aquaculture. *Hydrobiologia* **542**, 165–190 (2005).
16. *Report of the FAO Expert Workshop on the Use of Wild Fish and/or Other Aquatic Species as Feed in Aquaculture and its Implications to Food Security and Poverty Alleviation* (Food and Agriculture Organization of the United Nations, 2008).
17. New, M. B., Valenti, W. C., Tidwell, J. H., D'Abramo, L. R. & Kutty, M. N. *Freshwater Prawns: Biology and Farming* (Blackwell, 2010).
18. New, M. B. & Valenti, W. C. *Freshwater Prawn Culture: the Farming of Macrobrachium Rosenbergii* (Blackwell Science, 2000).
19. Savaya Alkalay, A. et al. The prawn *Macrobrachium vollenhovenii* in the Senegal River basin: towards sustainable restocking of all-male populations for biological control of schistosomiasis. *PLoS Negl. Trop. Dis.* **8**, e3060 (2014).
20. Levy, T. et al. All-female monosex culture in the freshwater prawn *Macrobrachium rosenbergii*—a comparative large-scale field study. *Aquaculture* **479**, 857–862 (2017).
21. Hotez, P. J. et al. The Global Burden of Disease Study 2010: interpretation and implications for the neglected tropical diseases. *PLoS Negl. Trop. Dis.* **8**, e2865 (2014).
22. Balasubramanian, V., Sie, M., Hijmans, R. J. & Otsuka, K. Increasing rice production in sub-Saharan Africa: challenges and opportunities. *Adv. Agron.* **94**, 55–133 (2007).
23. Ahmed, N. & Garnett, S. T. Sustainability of freshwater prawn farming in rice fields in southwest Bangladesh. *J. Sustain. Agric.* **34**, 659–679 (2010).
24. Lo, N. C. et al. Assessment of global guidelines for preventive chemotherapy against schistosomiasis and soil-transmitted helminthiasis: a cost-effectiveness modelling study. *Lancet Infect. Dis.* **16**, 1065–1075 (2016).
25. Beverton, R. J. H. & Holt, S. J. *On the Dynamics of Exploited Fish Populations* (Springer Netherlands, 1993).
26. Zwang, J. & Olliaro, P. L. Clinical efficacy and tolerability of praziquantel for intestinal and urinary schistosomiasis—a meta-analysis of comparative and non-comparative clinical trials. *PLoS Negl. Trop. Dis.* **8**, e3286 (2014).
27. Lo, N. C. et al. Comparison of community-wide, integrated mass drug administration strategies for schistosomiasis and soil-transmitted helminthiasis: a cost-effectiveness modelling study. *Lancet Glob. Health* **3**, e629–e638 (2015).
28. Ngonghala, C. N. et al. Poverty, disease, and the ecology of complex systems. *PLoS Biol.* **12**, e1001827 (2014).
29. King, C. H. Parasites and poverty: the case of schistosomiasis. *Acta Trop.* **113**, 95–104 (2010).
30. Toor, J. et al. Are we on our way to achieving the 2020 goals for schistosomiasis morbidity control using current World Health Organization guidelines? *Clin. Infect. Dis.* **66**, S245–S252 (2018).
31. Younes, A., El-Sherief, H., Gawish, F. & Mahmoud, M. Biological control of snail hosts transmitting schistosomiasis by the water bug, *Sphaerodema urinator*. *Parasitol. Res.* **116**, 1257–1264 (2017).
32. Dasgupta, S. & Tidwell, J. H. A breakeven price analysis of four hypothetical freshwater prawn, *Macrobrachium rosenbergii*, farms using data from Kentucky. *J. Appl. Aquac.* **14**, 1–22 (2003).
33. Asche, F. Farming the sea. *Mar. Resour. Econ.* **23**, 527–547 (2008).
34. Kumar, G. & Engle, C. R. Technological advances that led to growth of shrimp, salmon, and tilapia farming. *Rev. Fish. Sci. Aquac.* **24**, 136–152 (2016).
35. Karplus, I. & Sagi, A. in *Freshwater Prawns: Biology and Farming* 316–345 (Wiley-Blackwell, 2009).
36. Ventura, T. & Sagi, A. The insulin-like androgenic gland hormone in crustaceans: from a single gene silencing to a wide array of sexual manipulation-based biotechnologies. *Biotechnol. Adv.* **30**, 1543–1550 (2012).
37. Aflalo, E. D. et al. A novel two-step procedure for mass production of all-male populations of the giant freshwater prawn *Macrobrachium rosenbergii*. *Aquaculture* **256**, 468–478 (2006).
38. Levy, T. et al. A single injection of hypertrophied androgenic gland cells produces all-female aquaculture. *Mar. Biotechnol.* **18**, 554–563 (2016).
39. Savaya-Alkalay, A. et al. Exploitation of reproductive barriers between *Macrobrachium* species for responsible aquaculture and biocontrol of schistosomiasis in West. *Afr. Aquac. Environ. Interact.* **10**, 487–499 (2018).
40. Lalrinsanga, P. L. et al. Length weight relationship and condition factor of giant freshwater prawn *Macrobrachium rosenbergii* (De Man, 1879) based on developmental stages, culture stages and sex. *Turk. J. Fish. Aquat. Sci.* **12**, 917–924 (2012).
41. Nwosu, F. & Wolfi, M. Population dynamics of the Giant African River prawn *Macrobrachium vollenhovenii* Herklots 1857 (Crustacea, Palaemonidae) in the Cross River Estuary, Nigeria. *West African J. Appl. Ecol.* **9**, 1–14 (2009).
42. Halstead, N. T., Civitello, D. J. & Rohr, J. R. Comparative toxicities of organophosphate and pyrethroid insecticides to aquatic macroarthropods. *Chemosphere* **135**, 265–271 (2015).
43. Halstead, N. T. et al. Agrochemicals increase risk of human schistosomiasis by supporting higher densities of intermediate hosts. *Nat. Commun.* **9**, 837 (2018).
44. Gurarie, D., Lo, N. C., Ndeffo-Mbah, M. L., Durham, D. P. & King, C. H. The human–snail transmission environment shapes long term schistosomiasis control outcomes: implications for improving the accuracy of predictive modeling. *PLoS Negl. Trop. Dis.* **12**, e0006514 (2018).
45. Ciddio, M. et al. The spatial spread of schistosomiasis: a multidimensional network model applied to Saint-Louis region, Senegal. *Adv. Water Resour.* **108**, 406–415 (2016).
46. Civitello, D. J., Fatima, H., Johnson, L. R., Nisbet, R. M. & Rohr, J. R. Bioenergetic theory predicts infection dynamics of human schistosomes in intermediate host snails across ecological gradients. *Ecol. Lett.* **21**, 692–701 (2018).
47. Perez-Saez, J. et al. A theoretical analysis of the geography of schistosomiasis in Burkina Faso highlights the roles of human mobility and water resources development in disease transmission. *PLoS Negl. Trop. Dis.* **9**, e0004127 (2015).
48. Perez-Saez, J. et al. Hydrology and density feedbacks control the ecology of intermediate hosts of schistosomiasis across habitats in seasonal climates. *Proc. Natl Acad. Sci. USA* **113**, 6427–6432 (2016).
49. Sturrock, R. F. et al. Seasonality in the transmission of schistosomiasis and in populations of its snail intermediate hosts in and around a sugar irrigation scheme at Richard Toll, Senegal. *Parasitology* **123**, 77–89 (2001).
50. Ranjeet, K. & Kurup, B. M. Heterogeneous individual growth of *Macrobrachium rosenbergii* male morphotypes. *Naga* **25**, 13–18 (2002).
51. Von Bertalanffy, L. A quantitative theory of organic growth (inquiries on growth laws II). *Hum. Biol.* **10**, 181–213 (1938).

52. Sampaio, C. M. & Valenti, W. C. Growth curves for *Macrobrachium rosenbergii* in semi-intensive culture in Brazil. *J. World Aquac. Soc.* **27**, 353–358 (1996).
53. Lima, J.d.F., Garcia, J.d.S. & da Silva, T.C. Natural diet and feeding habits of a freshwater prawn (*Macrobrachium carcinus*: Crustacea, Decapoda) in the estuary of the Amazon River. *Acta Amaz.* **44**, 235–244 (2014).
54. Lorenzen, K. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. *J. Fish Biol.* **49**, 627–647 (1996).
55. *Discount Rates for Cost-Effectiveness Analysis of Federal Programs* (Office of Management and Budget, 2018).
56. Reed, W. J. Optimal harvesting models in forest management—a survey. *Nat. Resour. Model.* **1**, 55–79 (1986).
57. Karp, L., Sadeh, A. & Griffin, W. L. Cycles in agricultural production: the case of aquaculture. *Am. J. Agric. Econ.* **68**, 553–561 (1986).
58. Guttormsen, A. G. Faustmann in the sea: optimal rotation in aquaculture. *Mar. Resour. Econ.* **23**, 401–410 (2008).
59. Lafferty, K. D. & Kuris, A. M. Parasitic castration: the evolution and ecology of body snatchers. *Trends Parasitol.* **25**, 564–572 (2009).
60. Mangal, T. D., Paterson, S. & Fenton, A. Effects of snail density on growth, reproduction and survival of *Biomphalaria alexandrina* exposed to *Schistosoma mansoni*. *J. Parasitol. Res.* **2010**, 186792 (2010).
61. Anderson, R. M. & May, R. M. *Infectious Diseases of Humans: Dynamics and Control* (Oxford Univ. Press, 1991).
62. May, R. M. Togetherness among schistosomes: its effects on the dynamics of the infection. *Math. Biosci.* **35**, 301–343 (1977).
63. Chu, K. Y. & Dawood, I. K. Cercarial production from *Biomphalaria alexandrina* infected with *Schistosoma mansoni*. *Bull. World Health Organ.* **42**, 569–574 (1970).
64. Holling, C. S. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can. Entomol.* **91**, 293–320 (1959).
65. Soetaert, K., Petzoldt, T. & Setzer, R. W. Solving differential equations in R: package deSolve. *J. Stat. Softw.* **33**, 1–25 (2010).

Acknowledgements

C.M.H., J.V.R., G.A.D.L., I.J.J., A.J.L., S.H.S., G.R. and J.R.R. were supported by National Institutes of Health grant R01TW010286 (to J.R.R. and J.V.R.). C.M.H. and J.V.R. were additionally supported in part by National Science Foundation 'Water Sustainability and Climate' grants (1360330 and 1646708 to J.V.R.), National Institutes of Health grant R01AI125842 (to J.V.R.) and the University of California Multicampus Research Programs and Initiatives award MRP-17-446315 (to J.V.R.). G.A.D.L., I.J.J., A.J.L. and S.H.S. were additionally funded by a grant from the Bill and Melinda Gates Foundation (OPP1114050) and a GDP SEED grant from the Freeman Spogli Institute at Stanford University. G.A.D.L., I.J.J., A.J.L., S.H.S. and J.N.S. were also supported by National Science Foundation 'Dynamics of Coupled Natural and Human Systems' grant 1414102. G.A.D.L., S.H.S., C.M.H., J.V.R., J.N.S., R.C., L.M. and M.G. were also supported by NIMBioS through the working group on the Optimal Control of Environmentally Transmitted Disease. J.P.-S. and A.R. acknowledge funds provided by the Swiss National Science Foundation via the project 'Optimal control of intervention strategies for waterborne disease epidemics' (200021-172578/1). C.L.W. was supported by the Michigan Society of Fellows at the University of Michigan and by a Sloan Research Fellowship from the Alfred P. Sloan Foundation. R.C. and L.M. were also supported by Politecnico di Milano through the Polisocial Award programme (project MASTR-SLS).

Author contributions

G.A.D.L. and S.H.S. conceived the problem and designed the general modelling framework. C.M.H., S.H.S., J.K., J.V.R. and G.A.D.L. developed the analysis. C.M.H. and J.K. wrote the simulation scripts. G.R. collected field data to parameterize the epidemiological model. S.H.S. provided experimental data to parameterize the predation component of the model. J.N.S. provided guidance on profit estimation of the prawn aquaculture model. A.Savaya, S.C. and A.Sagi. provided guidance on the dynamics of the aquaculture model. C.M.H., J.K., J.N.S., J.V.R. and G.A.D.L. drafted the manuscript. All authors contributed to editing the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41893-019-0301-7.

Reprints and permissions information is available at www.nature.com/reprints.

Correspondence and requests for materials should be addressed to G.A.D.