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## Modelled effects of prawn aquaculture on poverty alleviation and schistosomiasis control

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### Abstract

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#### Contributions

GADL and SHS conceived the problem and designed the general modelling framework. CMH, SHS, JK, JVR, and GADL developed the analysis. CMH and JK wrote the simulations scripts. GR collected field data to parameterize the epidemiologic model. SHS provided experimental data to parameterize the predation component of the model. JNS provided guidance on profit estimation of the prawn aquaculture model. AS-A, SC, and AS provided guidance on dynamics of the aquaculture model. CMH, JK, JNS, JVR, and GADL drafted the manuscript and all authors contributed to its editing.

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Competing interests

The authors declare no competing interests

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. Potential synergies between schistosomiasis control and aquaculture of giant prawns are evaluated using an integrated bio-economic-epidemiologic 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.

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Schistosomiasis is a debilitating disease of poverty, affecting around 200 million people worldwide<sup>1,2</sup>. 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 parasite burden and associated symptoms from infected individuals, rapid reinfection in highly endemic areas leads to persistent hotspots of infection<sup>3,4</sup>. 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<sup>5</sup>.

There is a rich history of environmental interventions for schistosomiasis that target the intermediate snail hosts<sup>6</sup>. 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<sup>6-8</sup>. However, these approaches generally require repeated applications of chemicals that may negatively affect non-target species in addition to *Schistosoma*-bearing snails<sup>9,10</sup>.

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 *S. haematobium* infection by consuming *Bulinus* snails in the aquatic environment where people contact infested water<sup>11,12</sup>.

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

In sub-Saharan Africa, where at least 90% of schistosomiasis cases occur<sup>1,21</sup>, the native African river prawn *M. vollenhovenii* has been proposed as an alternative to *M. rosenbergii*

for aquaculture<sup>19</sup>. Furthermore, extensive prawn aquaculture—consisting of large enclosures, low prawn densities, and no use of supplemental feed, substrate, or additional oxygenation—is increasingly common in developing countries<sup>15–17</sup>. 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<sup>22,23</sup>.

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 bio-economic production model of *Macrobrachium* spp. aquaculture, 2) an epidemiologic model of *S. haematobium* transmission dynamics, and 3) a size- and density-dependent prawn predation model, is developed and parameterized via results of previous laboratory, modeling, and field-based empirical studies (Fig 1)<sup>12,13</sup>. The model is used to investigate whether extensive prawn aquaculture (using either endemic *M. vollehovenii* 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<sup>12</sup> 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<sup>7,24</sup>. The aquaculture component of the model is first used to simulate growth and mortality dynamics for each *Macrobrachium* species ( $sp$ ) in a  $1,000m^2$  enclosure. Because prawn body size increases and levels off with time, but prawn abundance decreases in time due to size- and density-dependent mortality, both stock biomass and cumulative profit are unimodal functions of time for any given initial stocking density,  $P_0$ . Additionally, harvesting prior to peak profit may afford the opportunity to increase the number of aquaculture cycles,  $n^p$ , and therefore sacrifice short term profits to maximize long term profit. The stocking density,  $P_0$ , and harvest time,  $T$ , that maximize cumulative profit for each species,  $CP^{sp}$ , are identified via numeric 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<sup>25</sup>. As stocking costs increase linearly with stocking density,  $P_0$ , 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 cumulative profit,  $CP_{opt}^{sp} = \max(CP^{sp})$ . Therefore, it is possible to identify the stocking density,  $P_{0opt}^{sp}$ , and harvest time,  $T_{opt}^{sp}$ , that maximize cumulative profit,  $CP_{opt}^{sp}$ , here collectively defined as *optimal management*. Optimal management for each prawn species is identified using a grid search over initial stocking densities,  $P_0$ , ranging between  $0.5 - 7.5 Pm^{-2}$  and potential harvest times,  $T$ , on each day between  $1 - 730$  days.

The epidemiologic model of schistosomiasis transmission is an extension of the model presented in Sokolow et al. 2015<sup>12</sup>. 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,  $W$ , in the human population. Finally, the epidemiologic and aquaculture models are linked via a predation function parameterized via results from Sokolow et al 2014<sup>13</sup>, 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* which 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  $T_{opt}^{sp}$  days as instantaneous events that reset the values of prawn density,  $P$ , and mean prawn body size,  $L$ , to match the initial conditions at the beginning of each stocking cycle (i.e.  $P_{0opt}^{sp}$  and  $L_0$ ). This assumes that all prawns—regardless of marketability—are harvested and replaced with  $P_{0opt}^{sp}$  juveniles in a single day. Mass drug administration is implemented as an instantaneous 85% reduction in the mean worm burden,  $W$ , of the epidemiologic 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<sup>24,26</sup>.

The integrated aquaculture-epidemiologic model is run under the following scenarios: (1) 10 years of annual MDA with no prawn intervention; (2) and (3) 10 years of prawn stocking and harvesting under optimal aquaculture management for *M. rosenbergii* and *M. volenhovenii*, as described above, with no MDA; and (4) and (5) 10 years of integrated intervention with both annual MDA and prawn stocking and harvesting under optimal management for each species. In all scenarios, the system is simulated for an additional 10 years without intervention to explore rebound in the community mean worm burden,  $W$ , in the case the intervention program is ceased.

To compare the effects of different interventions, disability associated with schistosomiasis is modeled using the disability adjusted life year (DALY) as in previous analyses<sup>7,27</sup>. 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 10mL urine,  $H_{hi}$ ) and light ( $0 < \text{eggs per 10mL urine} \leq 50$ ,  $H_{lo}$ ) *S. haematobium* burdens as defined by WHO guidelines. Total DALYs lost are then estimated cumulatively over each simulation period (see methods).

All simulations are performed across 1,000 candidate parameter sets derived from latin hypercube sampling of the parameters and ranges listed in Tables S1–S3 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 parameters reported in Table S1, stocking *M. rosenbergii* at  $P_0 = 2.6 \text{ Pm}^{-2}$  and harvesting at  $T_{opt}^{ros} = 165 \text{ days}$  maximizes cumulative ten-year profit, while stocking at  $P_0 = 2.6 \text{ Pm}^{-2}$  and harvesting at  $T_{opt}^{vol} = 260 \text{ days}$  maximizes cumulative profit for *M. vollehovenii*. These stocking densities and harvesting 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 optimal time of harvest,  $T_{opt}^{sp}$ . Prawns grow in length,  $L$ , and weight over time (Fig 2a) while population size (measured as density,  $\text{Pm}^{-2}$ ) 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,  $\Omega$ , over time, with the peak occurring well before prawns grow to their full size (Fig 1c). Ten-year cumulative profits also have a single peak, which is determined by both the profit per cycle and the number of cycles possible within the 10-year time frame (Fig 1d). Cumulative profits are maximized by harvesting well before the peak in harvestable biomass occurs, indicating more, smaller harvests maximize profit over time.

The surface of values ( $P_0, T, CP^{sp}$ ) resulting from the grid search to identify optimal management for each species is shown in Figure 3. As expected, profits associated with aquaculture of the faster growing *M. rosenbergii* are higher. Considering parametric uncertainty, the peak estimate of median cumulative profit for *M. rosenbergii* occurs at  $P_0 = 2.9 \text{ Pm}^{-2}$  and  $T_{opt}^{ros} = 173 \text{ days}$  (IQR: 146 – 192), producing  $CP_{opt}^{ros} = \$5364$  (\$3192 – \$8111) per 1,000  $\text{m}^2$  enclosure. The same estimates for *M. vollehovenii* are  $P_0 = 2.5 \text{ Pm}^{-2}$ ,  $T_{opt}^{vol} = 260 \text{ days}$  (228 – 331), and  $CP_{opt}^{vol} = \$1738$  (\$704 – \$3394). Cumulative profits are still feasible at much higher stocking densities for each species with  $CP_{opt}^{ros} > 0$  at stocking densities as high as  $P_0 = 6.5 \text{ Pm}^{-2}$  and  $CP_{opt}^{vol} > 0$  at stocking densities up to  $P_0 = 5.95 \text{ Pm}^{-2}$ . Additional outputs from the aquaculture model that describe stock structure and aquaculture performance at optimal management are reported in Table 1.

### Integrated aquaculture epidemiologic model

Simulation of the integrated model reveals comparable performance of prawn intervention strategies to MDA strategies. As in previous analyses<sup>7,12</sup>, annual MDA alone produces a pattern of gradually decreasing worm burden over time characterized by repeated rebound in infection following MDA (Fig 4A, purple line). The prawn-only intervention causes mean worm burden to gradually decline towards 0, eventually reducing worm burden to comparable levels by year 10 (Fig 4A, blue line). The combined MDA and prawn intervention leads to a rapid decline in mean worm burden 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 Fig S3 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, mean worm burden 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 10 years results in rapid returns towards pre-intervention snail populations and community-level mean worm burdens (Fig 4A–C).

Comparison of total DALYs lost over 10-year simulation periods under each intervention shows comparable performance of the prawn-only intervention and MDA, and substantial additional DALYs 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 DALYs lost with annual MDA and 184 (IQR: 70 – 294) total DALYs lost with prawns; representing 51% and 43% DALYs averted, respectively. Integrated interventions utilizing both MDA and prawn stocking reduce 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<sup>23</sup>. In areas of high food insecurity, malnutrition, and endemic schistosomiasis—conditions which reinforce each other and often result in “poverty traps”<sup>28,29</sup>—the development of prawn aquaculture in transmission sites may be a solution for co-benefits of disease control and sustainable development.

To meet goals for schistosomiasis reduction set out by the World Health Organization (WHO) of morbidity control by 2020 and local elimination as a public health problem by 2025, additional control strategies are needed<sup>1,30</sup>. These results build on an increasing body of evidence indicating consumption of snails by predator species such as *Macrobrachium* prawns can be an effective method for combating schistosomiasis transmission to people<sup>11,12,31</sup>. 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<sup>17,32</sup>, we develop—to our knowledge—the first dynamic model of prawn aquaculture to investigate optimal management practices. The model suitably simulates prawn stocking in a large enclosure or rice paddy, and the length of optimal cycles coincides with typical rice harvesting timelines<sup>23</sup>. This system produces short- and long-term profits, implying the potential for a sustainable, community-driven intervention, given the right capital investment and incentive programs.

Under optimal management, extensive aquaculture of either *M. rosenbergii* or *M. vollehovenii* leads to both profits and reductions of the snail population. The optimal 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<sup>12</sup>, though our conservative inclusion of snail migration and a Holling's type III functional response restricts such an outcome in this analysis. While 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 behavior, and prawn predation of snails, stocking densities at least three times higher than this are still economically viable. Alternative funding mechanisms (e.g. 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<sup>21</sup> 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<sup>16,17</sup>. Similar protocols for the African native *M. vollehovenii* are still under development. Profits appear to be highly sensitive to parameters that regulate prawn growth, meaning continued research and development into *M. vollehovenii* 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<sup>33,34</sup>.

Stocking *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. Establishment of aquaculture biotechnologies for either all-male<sup>35–37</sup> or all-female<sup>38</sup> populations that do not rely on genetically modified organisms (GMOs) suggest possible strategies to prevent invasions. Moreover, recent laboratory experiments have ruled out the possibility of cross-fertilization between mature female *M. vollehovenii* and male *M. rosenbergii*, demonstrating 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<sup>37,39</sup>.

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 cumulative profits—is most sensitive to parameters governing somatic growth, which have been estimated from available literature, and supported by expert opinion<sup>40,41</sup>. This finding also suggests that if stock improvement or advances in husbandry practices can increase average prawn condition or size, i.e. 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 e.g. in nets with different mesh sizes or pumps to drain waterbodies and further inspect prawns. Harvesting all prawns in a single batch, as is assumed in these analyses, is therefore considered the easiest management strategy to implement.

Optimal aquaculture practices are also sensitive to the market price of adult prawns and the stocking cost of juvenile prawns, implying that optimal management may be influenced by fluctuations in market factors that may influence price and cost of harvested and stocked prawns. Profit generated from selling harvested prawns is based on reasonable assumptions of prices in premium markets, though the actual selling price in subsistence economies might be lower and contingent on market access and local demand. However, the fixed cost sensitivity analysis demonstrates 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 success of the proposed system and suggest that prawn aquaculture can be economically viable even under non-optimal 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<sup>42,43</sup>. Still other sources of additional prawn mortality such as disease outbreaks or predation by waterbirds, fish, amphibians or reptiles are also possible, though extensive aquaculture would still be profitable with mortality rates as high as five times 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 behavior which might affect aquaculture performance and/or snail abundance, transmission rates, and epidemiologic outcomes should be pursued.

Prawn predation of the snail population as modeled 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 likely 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 prior 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 non-linearities in the human-to-snail force of infection may decrease the efficacy of MDA and lead to faster post-MDA rebounds of schistosomiasis<sup>44</sup>. While 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 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 e.g. in river currents<sup>45</sup>, 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 prior to “weak” control efforts<sup>46</sup>. 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 modeled here—even given the conservative Holling’s III functional response—this effect is believed unlikely in our scenarios.

Finally, our model lacks seasonality, which may affect both schistosomiasis transmission and prawn growth as e.g. 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<sup>47–49</sup>. However, the assumption of a constant and large snail population carrying capacity represents a worst case scenario, and introducing seasonal variation would likely not alter the results presented here. Furthermore, in regions where transmission predominately occurs in ephemeral ponds during the rainy season, prawn aquaculture is likely not a viable approach<sup>48</sup>.

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. vollehovienii* 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: a) a bio-economic aquaculture component, simulating yields and accounting for density-dependent mortality and somatic growth of *Macrobrachium* spp. prawns over a range of initial stocking densities; b) an epidemiologic component to simulate the dynamics of 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 c) a predation function that links the epidemiologic 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.

### (a) Aquaculture model

The dynamics of a cohort of  $P_0$  juvenile prawns of initial mean length,  $L_0$  [mm], stocked at time  $t = 0$  days in an enclosure of  $1,000 \text{ m}^2$ —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 upon sex (with males growing larger than females) and social structure<sup>50</sup>, an average growth rate through the population is simulated here. In addition, growth of individual crustaceans is typically stepwise and occurs through a sequence of molting events, but here the population-average growth of prawns is modeled as somatic growth with the von Bertalanffy growth equation (VBGE)<sup>51</sup>:

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

VBGE produces a classic increasing-and-saturating growth curve with length  $L$  at time  $t$  (days after stocking) eventually approaching the mean asymptotic length,  $L_\infty$ . Based on experimental stocking trials showing reduced growth rates of *M. rosenbergii* at high stocking densities<sup>50</sup>, a modified Brody growth coefficient,  $k^*$ , was estimated as a decreasing function of total population biomass,  $\Omega$ :

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

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

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

$$\Omega(t) = B(t)P(t) \quad (3)$$

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

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

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

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

$$\frac{dP}{dt} = -P(\mu_P B^{-d} + \omega \Omega) \quad (5)$$

with parameters  $\mu_P$  and  $d$  derived from previous studies<sup>41,54</sup> and  $\omega$  parameterized to produce density-dependent mortality outcomes qualitatively similar to those observed in the experimental trials by Ranjeet and Kurup<sup>50</sup>. 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. Natural, size- and density-dependent mortality are assumed to be the only causes of prawn population decline, though additional sources of mortality or loss such as predation by e.g. seabirds, escape from enclosures or rice fields, disease outbreaks, or declines in water quality are considered in 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 <30g are generally not of commercial interest. Experimental trials by Ranjeet and Kurup with *M. rosenbergii*<sup>50</sup> showed the fraction of retrievable, market-size (>30g) prawns decreases linearly with increasing prawn stocking density. Accordingly, commercial yield at time  $t = T$  is only a fraction of the total biomass:

$$Y(T, P_0) = \zeta(P_0) \cdot \Omega(T) \quad (6)$$

where  $\zeta$ , the fraction of marketable size prawns in the population, is a decreasing function of initial stocking density  $P_0$  estimated from data in the Ranjeet and Kurup experiments<sup>50</sup>.

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 (sp) is

$n^{SP} = \text{round}(\frac{T_{max}}{T})$ . Cumulative discounted profit for each species,  $CP^{SP}$ , is then estimated as the sum of net discounted revenue for every cycle completed by  $T_{max}$ :

$$CP^{SP}(P_0, T, T_{max}) = \sum_{n=1}^{n^{SP}} (-cP_0 + pY(T, P_0))e^{-\delta nT} \quad (7)$$

where  $p$  is the price per unit weight (USD/kg),  $c$  the per capita cost of stocked juvenile prawns, and  $\delta$  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<sup>32</sup>,  $c = \$0.10/P$   $c$  for a juvenile prawn of  $L_0 = 40mm$  (corresponding to  $\sim 0.35g$  juvenile prawns) and  $p = \$12/kg$  harvested<sup>32</sup>. 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 likely 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<sup>55</sup>. Other costs such as maintaining nurseries to produce juvenile prawns are considered external to the aquaculture scenario considered 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 the rotation length,  $T$ , and the initial stocking density,  $P_0$ . Given the rotation length, the number of rotations in the time period is determined, as  $T_{max}$  is given. Equation (7) has its basis in the optimal rotation models in forestry (see, e.g.,<sup>56</sup>) and commercial aquaculture operations (see, e.g.,<sup>57,58</sup>), which balance the marginal benefits of further growth against the opportunity costs of waiting to harvest. The resulting optimal 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 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.

Parameters used in the prawn aquaculture model simulations are listed in Table S1. All results are expressed in USD to match the cost and price information identified in the literature and because of the common use of USD as an international reference currency.

## (b) Epidemiologic model

Building on our previous modeling of *S. haematobium*<sup>12,59</sup>, the infection dynamics of the intermediate host *Bulinus* snail population,  $N$ , are modeled as snails transition between  $i \in \{S, E, I\}$  infection compartments corresponding to susceptible ( $S$ ), exposed ( $E$ , pre-patent), and infected ( $I$ , patent) states. Furthermore, the growth dynamics of snails are modeled as they move through  $j \in \{1, 2, 3\}$  size classes corresponding to 4mm, 8mm, and 12mm mean snail diameter (Figure 4). The model is further extended to include snail migration with a constant migration rate,  $\xi$ , to and from an external population,  $N^E$ , 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 modeled, though in

reality, multiple sites with heterogeneous transmission dynamics may contribute differentially to the intervention site<sup>45</sup>.

New snails enter the population as susceptible juveniles, i.e. in infection class  $i = S$  and size class  $j = 1$ . Logistic snail population growth is modeled 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<sup>60</sup>. Pre-patent snails' contribution to recruitment is reduced by a fraction  $0 < z < 1$ <sup>61</sup>. Snails of each size class are subject to both size-dependent natural mortality,  $\mu_j$ , and predation mortality,  $\psi_j$ , a function of both prawn and snail body size and density 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  $\beta M$ , where  $\beta$  is the per-capita transmission rate and  $M = 0.5\phi(W)WHm$  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 definitive human host population,  $H$ , the mean parasite burden,  $W$ , (i.e., 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  $\phi(W)$  representing the density-dependent mating probability of adult worms<sup>62</sup>. 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, pre-patent snails,  $E$ , transition to the patent class,  $I$ , at rate  $\sigma$ , with  $\sigma^{-1}$  being the mean time necessary for sporocyst development following snail infection with a miracidium.

The adult parasite population harbored by definitive human hosts is modeled as the mean parasite burden in the human population,  $W$ , assuming a negative binomial distribution with clumping parameter,  $\phi$ <sup>62,63</sup>. 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  $\lambda$ , 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<sup>12</sup>. The cercarial shedding rate of medium ( $N_D$ ) and large ( $N_B$ ) snails is assumed to exceed that of small ( $N_L$ ) snails by a factor  $\theta_1$  and  $\theta_2$ , respectively<sup>64</sup>.

Total DALYs lost over a given simulation period of  $T_{max}$  days is 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 ( $H_{hi_t}$  and  $H_{lo_t}$ ):

$$\sum_{t=1}^{T_{max}} \frac{DW_{hi}}{365} H_{hi_t} + \frac{DW_{lo}}{365} H_{lo_t} \quad (10)$$

Additional information regarding the epidemiologic model including the full system of differential equations, epidemiologic model parameters (Table S2), and the process for estimating the number of individuals with heavy and light infection from the model can be found in the supplementary information.

### (c) Prawn predation model

As in previous work<sup>59</sup>, the per-capita prawn predation rate on *Bulinus* snails of each class,  $\psi_{ij}$ , is modeled as a type III functional response, described by a generalization of Holling's disk equation<sup>65</sup>. 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<sup>13</sup> 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,  $\alpha$ , is estimated as a log-linear function of the biomass ratio:  $\alpha = \alpha_m * \log(r_j(t))$ . The handling time,  $T_h$ , is estimated as a reciprocal function of the biomass ratio:  $T_h = (T_{hm} r_j(t))^{-1}$ , where  $\alpha_m$  and  $T_{hm}$  are coefficients estimated from Sokolow et al<sup>13</sup>, 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<sup>13</sup> 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,  $\alpha$ , derived by Sokolow et al.<sup>13</sup> in controlled laboratory conditions in  $1m^{-2}$  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:

$$r_j(t) = \frac{B(t)}{a_N L_{N_j}^{b_N}} \quad (8)$$

where  $B(t)$  is prawn body size derived with eq. (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:

$$\psi_{ij} = \begin{cases} \frac{\alpha(r_j(t)) \epsilon N_{ij}^n}{1 + \sum_{i=S}^I \sum_{j=1}^3 \alpha(r_j(t)) \epsilon T_h(r_j(t)) N_{ij}^n} & , r_j \geq 3 \\ 0 & , r_j < 3 \end{cases} \quad (9)$$

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, though 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 Table S3.

The model was coded in R version 3.5.0 and simulated using the deSolve package<sup>66</sup>. To address concerns regarding reproducibility, all model code and data are provided as a supplementary folder to the manuscript and are freely available online at [https://github.com/cmhoove14/Prawn\\_fisheries\\_Public\\_health](https://github.com/cmhoove14/Prawn_fisheries_Public_health).

## Data Availability

All data and code used to conduct this analysis are freely available at [https://github.com/cmhoove14/Prawn\\_fisheries\\_Public\\_health](https://github.com/cmhoove14/Prawn_fisheries_Public_health), are provided as a supplementary folder, and are available from the corresponding author upon request

## Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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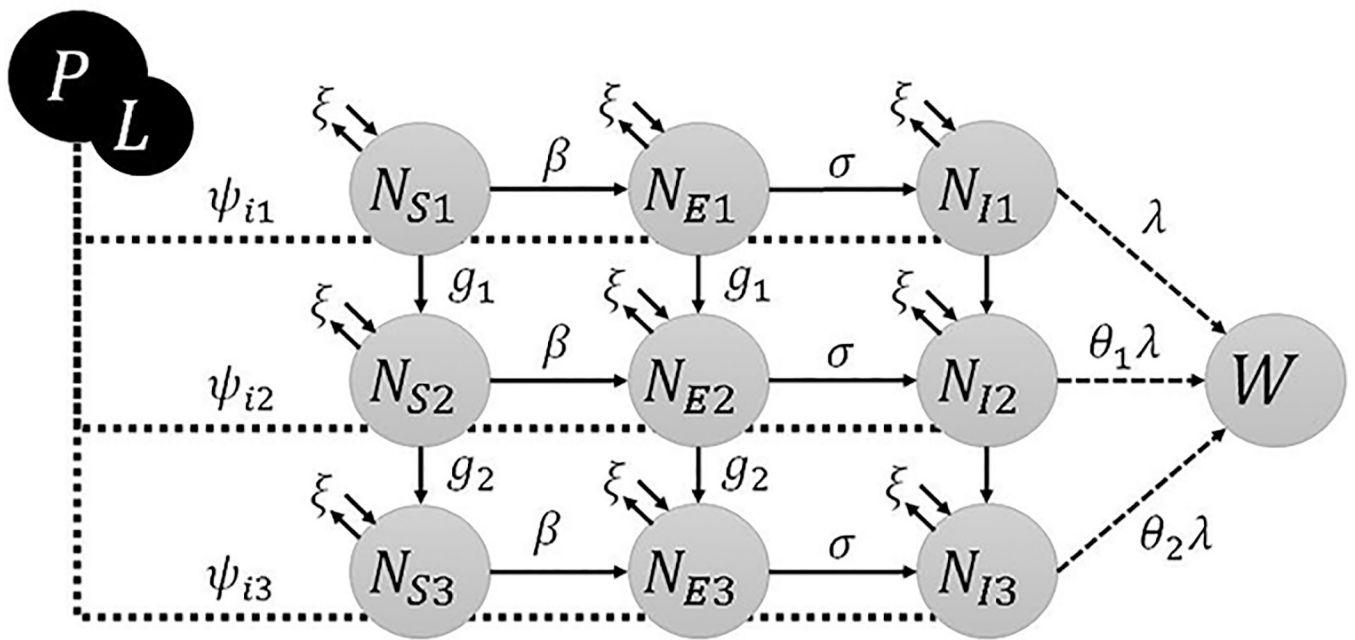
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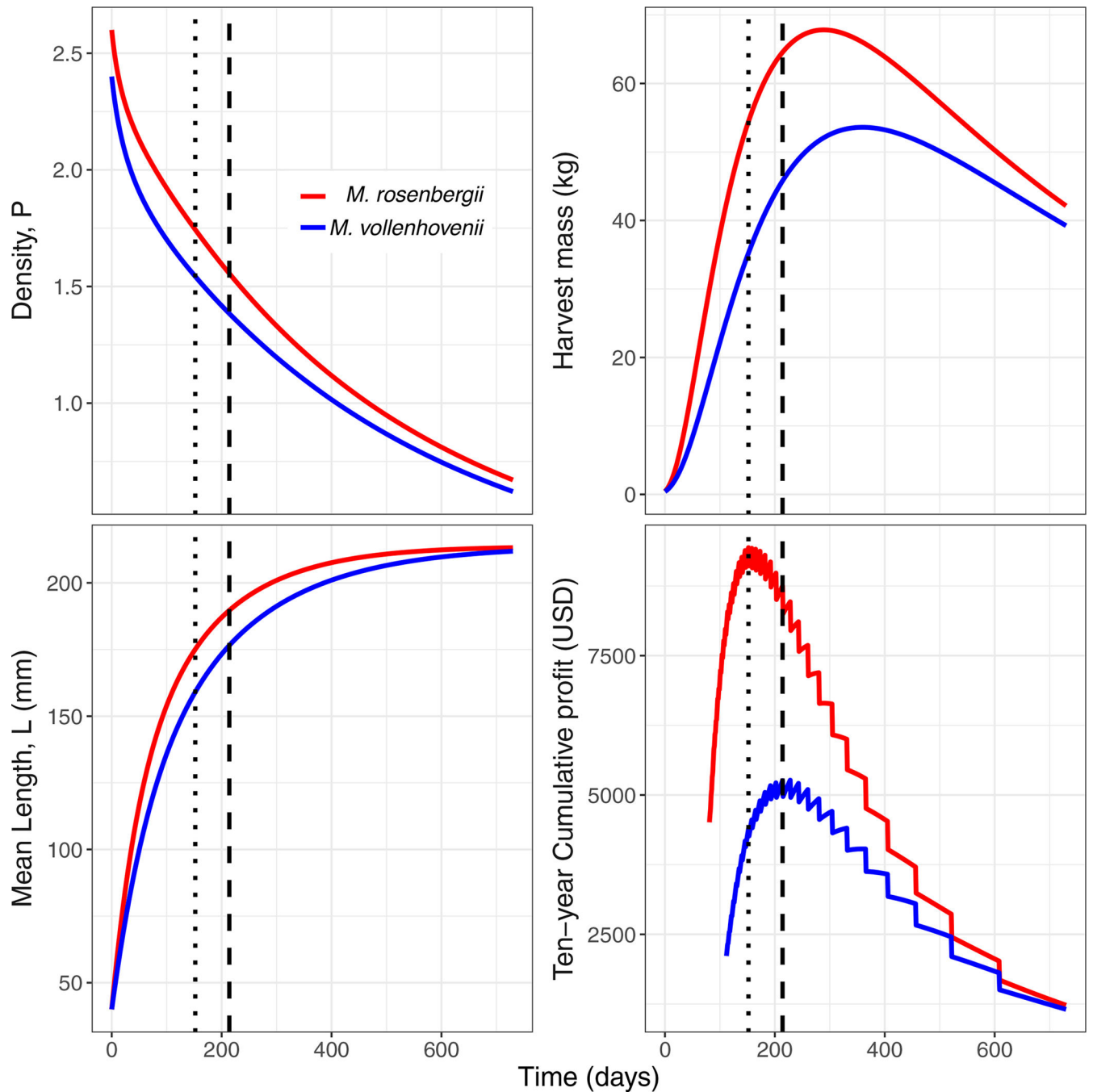
**Figure 1:** Model schematic representing the three components of the integrated aquaculture-epidemiologic model. Prawn aquaculture is modeled via state variables  $P$  and  $L$ . The epidemiologic model consists of the size- and age-structured snail population state variables ( $N_{ij}$ ) in grey circles and the mean worm burden in the human population,  $W$ . These two components are linked via size- and density-dependent prawn predation on snails estimated as  $\psi_{ij}$ . Parameters governing transitions between snail classes and migration into and out of each class are shown:  $\xi$  is the rate of migration between the external snail population and the population at the modeled intervention site,  $\beta$  is the man-to-snail transmission parameter,  $\sigma$  is the inverse of the pre-patent period of snails,  $g_1$  and  $g_2$  are the growth rates of snails in size class 1 and 2 respectively,  $\lambda$  is the snail-to-man transmission parameter, and  $\theta_1$  and  $\theta_2$  represent increased contribution of larger snails to human infection.

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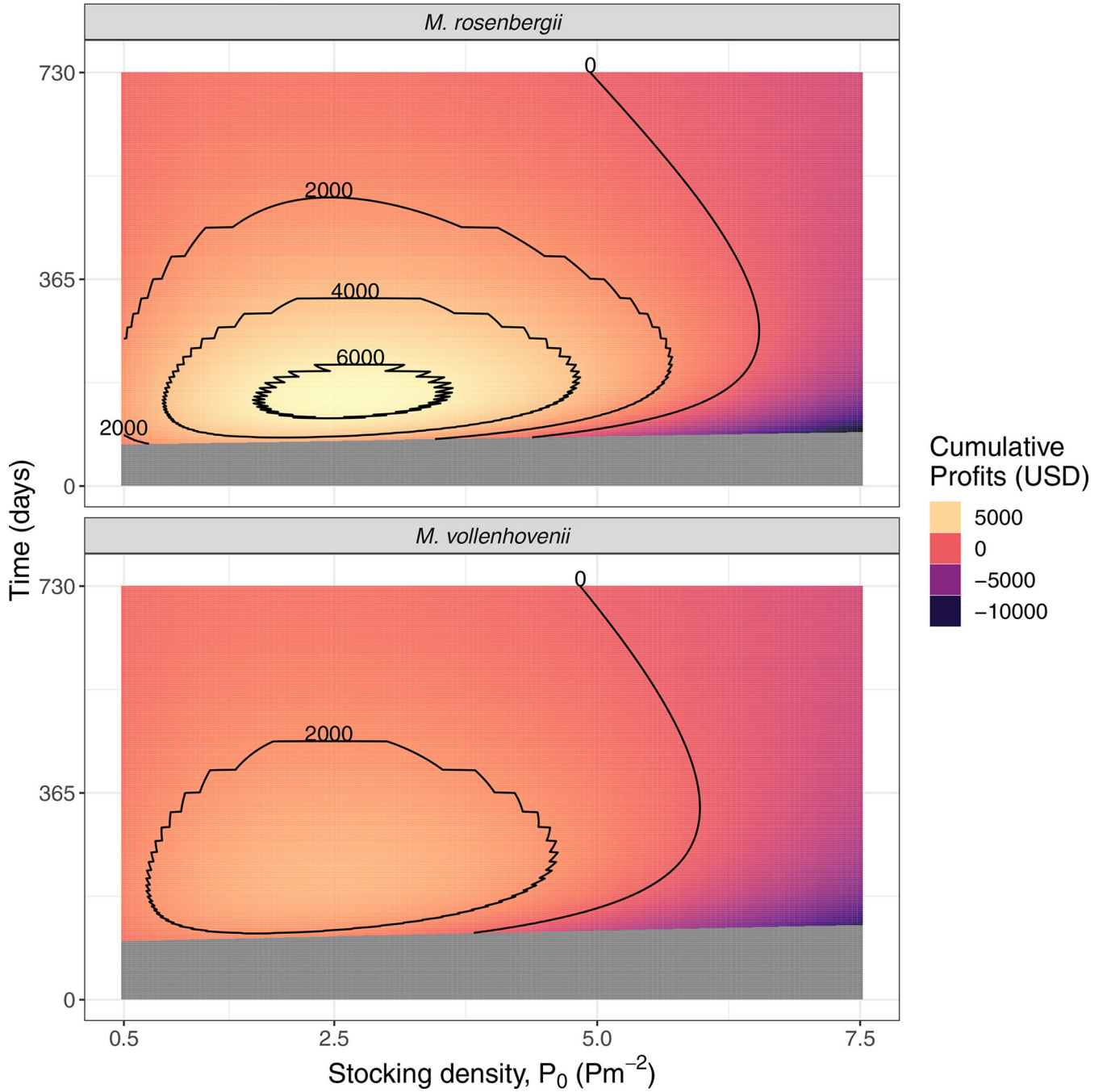
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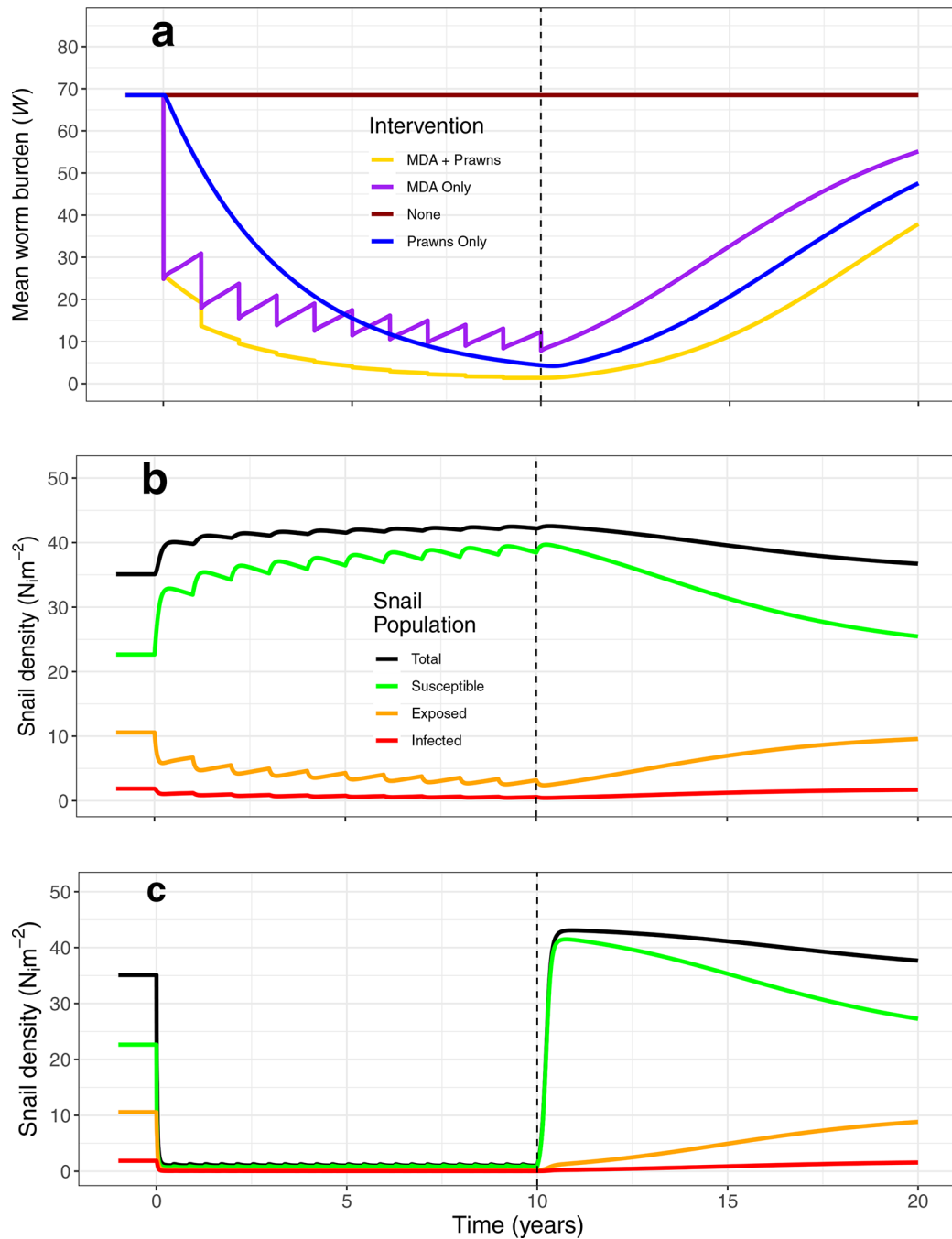
**Figure 2:**

Prawn aquaculture model dynamics. Two-year aquaculture cycles for *M. rosenbergii* (red lines) and *M. vollehovenii* (blue lines) under optimal management showing how prawns grow in length over time (bottom-left), but decrease in density (top-left). This leads to a single peak in harvest mass (top-right), but harvesting actually occurs prior to the peak in order to maximize ten-year cumulative profits (bottom-right) by sacrificing profit-per-cycle for completing more aquaculture cycles. Vertical dashed lines indicate time at which harvest would occur for each species (small dashes – *M. rosenbergii*, large dashes – *M.*

*vollenhovenii*). Harvest of the slower-growing *M. vollehovenii* occurs later as they take longer to grow in size and biomass. Here, following<sup>32</sup>, the cost  $c$  for a juvenile prawn is \$0.10 with  $L_0 = 40\text{mm}$  (~0.35g per juvenile prawns) and the selling price is  $p = \$12/\text{kg}$ . Other parameters set as in Table 1.



**Figure 3:** Grid search to identify optimal management decisions for each prawn species. Cumulative profits ( $CP^P$ ) generated by the aquaculture model for each species across a range of potential stocking densities ( $P_0$ ) and harvest times ( $T$ ) are shown. Grey regions indicate regions where harvesting is not feasible due to prawns not having reached sufficient marketable size (30g) due to insufficient time to grow and density-dependent growth rates. Contours indicate regions of  $CP^P$  corresponding to the labeled value in 2018 USD.

**Figure 4:**

Outputs of the integrated model under different intervention scenarios implemented over ten years followed by ten years of no intervention. Worm burden trajectories under no intervention (red), annual MDA only (purple), prawn stocking of *M. rosenbergii* under optimal management (blue), and both annual MDA and prawn stocking (gold) (A); snail infection dynamics under MDA-only intervention (B); and snail infection dynamics under prawn stocking interventions (C). Outputs from *M. volenhovenii* interventions not shown as



they approximately mirror those of *M. rosenbergii* since the profit-maximizing stocking densities of both species result in maximal reductions in the snail population.

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**Table 1:**

Optimal stocking and harvesting parameters for each prawn species reported as median (interquartile range).

Parameter	Definition	<i>M. vollehovonii</i>	<i>M. rosenbergii</i>
$P_{0_{opt}}^{SP}$	Optimal stocking density	2.4 $Pm^{-2}$	2.6 $Pm^{-2}$
$L_0$	Stocking size of juveniles	40mm	40mm
$T_{opt}^{SP}$	Optimal harvest time	260 days (228 – 331)	165 days (146 – 192)
$L(T_{opt}^{SP})$	Mean length at harvest	167 mm (161 – 175)	167 mm (161 – 174)
$P(T_{opt}^{SP})$	Prawns harvested	1056 (850 – 1236)	1559 (1434 – 1662)
$Y(T_{opt}^{SP}, P_{0_{opt}}^{SP})$	Commercial yield per harvest	28 kg (21 – 36)	41 kg (34 – 49)
$n^{SP}$	Number of cycles in 10 years	14 (11 – 16)	22 (19 – 25)
$CP_{opt}^{SP}$	Cumulative profits over 10 years	\$1891 (\$856 – \$3486)	\$5403 (\$3380 – \$8075)

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