

1 **Prawn aquaculture as a method for schistosomiasis control and poverty**
2 **alleviation: a win-win approach to address a critical infectious disease of**
3 **poverty**

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39

40 **Abstract**

41 Recent evidence suggests crustacean snail predators may aid schistosomiasis control
42 programs by targeting the environmental component of the parasite's life cycle through
43 predation of the snail species that serve as intermediate hosts of the parasite. We evaluate
44 costs, benefits, and potential synergies between schistosomiasis control and aquaculture of
45 giant prawns using an integrated bio-economic-epidemiologic model. We identified
46 combinations of stocking density and aquaculture cycle length that maximize profit and offer
47 disease control benefits for sustainable schistosomiasis control. We consider two prawn
48 species in sub-Saharan Africa: the endemic, non-domesticated *Macrobrachium vollenhovenii*,
49 and the non-native, domesticated *Macrobrachium rosenbergii*. We find that, at profit-optimal
50 densities, both *M. rosenbergii* and *M. vollenhovenii* can complement conventional control
51 approaches (mass drug treatment of people) and lead to sustainable schistosomiasis control.
52 We conclude that integrated aquaculture strategies can be a win-win strategy in terms of
53 health and sustainable development in schistosomiasis endemic regions of the world.

54 **Main**

55 Schistosomiasis is a debilitating disease of poverty, affecting around 200 million people
56 worldwide^{1,2}. It is caused by trematode parasites of the genus *Schistosoma* that undergo a life
57 cycle involving passage between definitive human hosts and freshwater snails that act as
58 intermediate hosts. While safe and effective treatments, such as the anthelmintic drug
59 Praziquantel, are available to reduce parasite burden and associated symptoms from infected
60 individuals, rapid reinfection in highly endemic areas leads to persistent hotspots of
61 infection^{3,4}. Successful long-term elimination efforts may require strategies that go beyond
62 conventional mass drug administration (MDA) campaigns to explicitly target the
63 environmental reservoir of the disease⁵.

64 One option for reducing transmission is cultivating snail predators, such as river prawns,
65 via aquaculture. River prawns have been shown to reduce schistosomiasis transmission by
66 consuming snails in the aquatic environment where people contact infested water^{14,15}. Given
67 that schistosomiasis is a disease of poverty, combining the nutritional and economic benefits
68 of prawn aquaculture with disease control via prawn predation on snails may offer a
69 sustainable approach to combat schistosomiasis and improve well-being and economic
70 development in endemic areas. Here, we develop an integrated bio-economic-epidemiologic
71 model to investigate whether extensive prawn aquaculture (using either endemic *M.*
72 *vollenhovenii* or nonbreeding monosex aquaculture of *M. rosenbergii*) can be managed at
73 schistosome transmission sites such as rice paddies or enclosed points of water contact
74 where people are exposed¹⁵ to simultaneously maximize profit and control schistosomiasis.

75 There is a rich history of environmental interventions for schistosomiasis that target the
76 intermediate snail hosts⁶. Molluscicides are effective in reducing snail populations and have
77 been used in integrated campaigns to control schistosomiasis in areas of South America,
78 Northern Africa, and Southeast Asia⁶⁻⁸. However, these approaches generally require

79 repeated applications of chemicals that may negatively affect non-target species in addition
80 to *Schistosoma*-bearing snails^{9,10}. A more sustainable approach for snail control involves the
81 introduction of snail predators, such as river prawns, which have been shown to actively seek
82 out and consume important intermediate hosts for human schistosomes in laboratory
83 settings, including *Biomphalaria* and *Bulinus* snails¹¹⁻¹³. Field trials in which crustacean
84 predators have been introduced to reduce schistosomiasis transmission have been successful
85 in reducing reinfection rates in humans following MDA^{14,15}.

86 In addition to being voracious predators of snails^{13,16}, river prawns are a valuable food
87 commodity^{17,18}. The giant freshwater prawn *Macrobrachium rosenbergii* has been
88 domesticated and widely used in commercial hatchery-based aquaculture¹⁹, providing both
89 a key source of protein and encouraging local economic development²⁰. Furthermore,
90 advances in the production of nonbreeding *M. rosenbergii* monosex populations reduces the
91 risk of prawn invasion in areas this species is not native, suggesting safe use of this biological
92 control agent globally^{21,22}. In sub-Saharan Africa, where at least 90% of schistosomiasis cases
93 occur^{1,23}, the native African river prawn *M. vollehovenii* has been proposed as an alternative
94 to *M. rosenbergii* for aquaculture²¹. Research into scalable *M. vollehovenii* aquaculture is
95 ongoing, as the use of this native species may be more attractive due to its historical presence
96 in the local river ecology in western Africa.

97 Extensive prawn aquaculture, increasingly common in developing countries¹⁷⁻¹⁹,
98 consists of large enclosures, low prawn densities, and no use of supplemental feed, substrate,
99 or additional oxygenation. As such, extensive aquaculture is more compatible with the water
100 resource management needs of rural communities in key areas of sub-Saharan Africa, and
101 can be easily integrated into rice agriculture that is increasingly an important part of food
102 production and is present in many schistosomiasis endemic areas^{24,25}.

103 Scaling the prawn aquaculture approach for schistosomiasis control requires that the
104 economic goals of prawn aquaculture are compatible with the public health goal of
105 schistosomiasis control. Thus, we seek to identify conditions under which schistosomiasis
106 reinfection in the human population may be curbed while maximizing the economic benefit
107 of prawn aquaculture. We first develop a bio-economic production model of *Macrobrachium*
108 spp. aquaculture to identify the stocking density and duration of the grow out phase that
109 maximizes profit for *M. rosenbergii* and *M. vollehovienii*. Then, we expand an epidemiologic
110 model of schistosomiasis transmission dynamics to include snail size structure and infection
111 dynamics. This model is coupled with the aquaculture model through size- and density-
112 dependent prawn predation, and parameterized via results of previous laboratory and field-
113 based empirical studies. We use estimates of the disability adjusted life years (DALYs) lost
114 due to schistosomiasis infection derived from the integrated model to compare aquaculture-
115 based prawn interventions with conventional MDA interventions, and to estimate the
116 benefits of utilizing both MDA and prawn aquaculture for schistosomiasis control. We
117 conclude with an extensive sensitivity analysis to evaluate the feasibility of such
118 interventions in a variety of settings.

119 **Methods**

120 The integrated model has three components: a) a bio-economic aquaculture component,
121 simulating yields and accounting for density-dependent mortality and somatic growth of
122 *Macrobrachium* spp. prawns over a range of initial stocking densities; b) an epidemiologic
123 component to simulate the dynamics of mean schistosome worm burden in humans and
124 population and infection dynamics of intermediate-host snails through a size structured, SEI
125 compartmental model; and c) a predation function describing the rate at which prawns
126 consume snails as a function of snail density and of snail and prawn body sizes, which links
127 the epidemiologic and aquaculture models.

128 **(a) Aquaculture model**

129 We assume that a necessary supply chain of hatcheries and nurseries supplies juvenile
130 prawns to stock at the desired transmission sites. The dynamics of a cohort of P_0 juvenile
131 prawns of initial mean length, L_0 [mm], stocked at time $t = 0$ days in an enclosure of
132 $1,000 \text{ m}^2$ —a size consistent with either a large water contact site or a typical rice field in
133 small-scale, subsistence agriculture settings—are simulated over time as a function of
134 density-dependent and size-dependent growth and mortality.

135 Adult *Macrobrachium rosenbergii* males can be grouped in three different categories that
136 grow at different rates depending upon their body size and developmental phase: small males
137 (SM) between 5-20g, orange-clawed males (OC) between 30-180g, and blue-clawed male
138 (BC) reaching up to 250 g, with growth of some smaller prawns being suppressed by the
139 largest BC males ²⁶. Though this same social structure has not been investigated for *M.*
140 *volenhovenii*, we assume here that it is the same. Growth of individual crustaceans is typically
141 stepwise and occurs through a sequence of molting events, but here the population-average
142 growth of prawns is modeled as somatic growth with the von Bertalanffy growth equation
143 (VBGE) ²⁷:

144
$$\frac{dL}{dt} = k^*(L_\infty - L) \quad (1)$$

145 VBGE produces a classic increasing-and-saturating growth curve with length L at time t (days
146 after stocking) eventually approaching the mean asymptotic length, L_∞ . Based on
147 experimental stocking trials showing reduced growth rates of *M. rosenbergii* at high stocking
148 densities ²⁶, a modified Brody growth coefficient, k^* , was estimated as a decreasing function
149 of total population biomass, Ω :

150
$$k^*(\Omega) = \frac{k_{max}}{1 + \gamma\Omega(t)} \quad (2)$$

151 where k_{max} is the maximum value of the Brody coefficient at low densities and γ a coefficient
152 parameterized to produce a density-dependent reduction in somatic growth qualitatively
153 resembling that observed in experimental trials ²⁶.

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

$$156 \quad \Omega(t) = B(t)P(t) \quad (3)$$

157 Body size $B(t)$ is derived as an allometric function of prawn length, $L(t)$, from *M. rosenbergii*
158 grow-out data ^{28,29}:

$$159 \quad B(t) = a_p L(t)^{b_p} \quad (4)$$

160 As prawns are generalist consumers with a wide range of invertebrate fauna and organic
161 detritus in their diet ³⁰, growth as described by eq. 1-4 is assumed independent from snails'
162 density and the corresponding predation rates.

163 After stocking, the total number of prawns in the enclosure decreases over time, with *per-*
164 *capita* mortality rate modeled as an additive function of two components: (i) an exponentially
165 decreasing function of body size, $B(t)$, as large prawns exhibit lower mortality than small
166 prawns ³¹; (ii) a linearly increasing function of total population biomass, $\Omega(t)$, which accounts
167 for density-dependent competition for resources and cannibalism at high population
168 densities ²⁶. Accordingly, the dynamics of a cohort of initial size P_0 was described as follows:

$$169 \quad \frac{dP}{dt} = -P(\mu_p B^{-d} + \omega \Omega) \quad (5)$$

170 with parameters μ_p and d derived from previous studies ^{31,32} and ω parameterized to
171 produce density-dependent mortality outcomes qualitatively similar to those observed in the
172 experimental trials by Ranjeet and Kurup ²⁶. Natural recruitment is excluded from the
173 aquaculture model, as new prawns enter the system only in discrete, exogenously controlled

174 events, when P_0 prawns of initial average body size L_0 are stocked from nurseries and grown
175 out to market size. We assume natural, size- and density-dependent mortality are the only
176 causes of prawn population decline and do not consider other sources such as predation by
177 e.g. seabirds, escape from enclosures or rice fields, disease outbreaks, or declines in water
178 quality that may affect prawn health.

179 Prawns weighing <30g are generally not of commercial interest, therefore only OC and
180 BC males are considered marketable. Experimental trials by Ranjeet and Kurup with *M.*
181 *rosenbergii*²⁶ showed the fraction of retrievable, market-size (>30g) prawns decreases
182 linearly with increasing prawn stocking density. Accordingly, commercial yield at the end of
183 a production cycle of length $t = T$ is only a fraction of the total biomass:

$$184 \quad Y(T, P_0) = \zeta(P_0) \cdot \Omega(T) \quad (6)$$

185 where ζ , the fraction of marketable size prawns in the population, is a decreasing function of
186 initial stocking density P_0 estimated from data in the Ranjeet and Kurup experiments²⁶.

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

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

192 where p is the price per unit weight (USD/kg), c the per capita cost of stocked juvenile
193 prawns, and δ the discount rate to account for the time lag between initial stocking costs and
194 delayed revenues of commercial size prawns. Following the comprehensive price analysis by
195 Dasgupta and Tidwell, we set $c = \$0.10/P$ for a juvenile prawn of $L_0 = 40mm$

196 (corresponding to $\sim 0.35g$ juvenile prawns) and $p = \$12/kg$ harvested³³. The discount rate
197 is set to 7%, which is likely on the low end for sub-Saharan African countries endemic with
198 schistosomiasis but higher than the 3-4% rate used for discounting long term government
199 projects in the United States³⁴. Other costs such as maintaining nurseries to produce juvenile
200 prawns are considered external to the aquaculture scenario considered here and are
201 therefore not included in the profit estimation. The influence of such costs are considered in
202 additional sensitivity analyses described below.

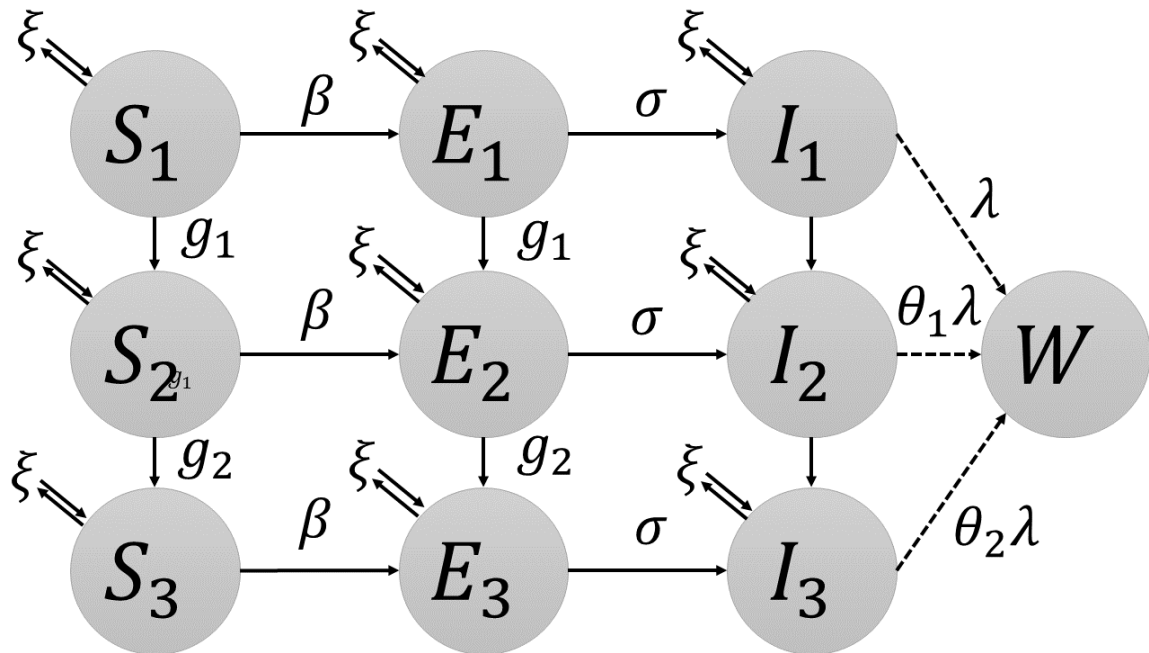
203 Cumulative discounted profits are maximized by jointly choosing the rotation length, T ,
204 and the initial stocking density, P_0 . Given the rotation length, the number of rotations in the
205 time period is determined, as T_{max} is given. Equation 7 has its basis in the optimal rotation
206 models in forestry (see, e.g.,³⁵) and commercial aquaculture operations (see, e.g.,^{36,37}) which
207 balance the marginal benefits of further growth against the opportunity costs of waiting to
208 harvest. The resulting optimal rotation length is therefore shorter than a simple rule of when
209 to harvest based solely on maximizing growth dynamics. In our setting, we expect the same
210 trade-off between benefits from waiting to harvest the prawns at a larger size against the
211 opportunity costs of delaying the economic returns from future harvests.

212 Parameters used in the prawn aquaculture model simulations are listed in Table S1.

213 **(b) Epidemiologic model**

214 Building on our previous modeling of *S. haematobium*^{15,38}, the infection dynamics of the
215 intermediate host snail population, N , are modeled as snails transition between $i \in \{S, E, I\}$
216 infection compartments corresponding to susceptible (S), exposed (E , pre-patent), and
217 infected (I , patent) states. Furthermore, the growth dynamics of snails are modeled as they
218 move through $j \in \{1, 2, 3\}$ size classes corresponding to $4mm$, $8mm$, and $12mm$ mean snail
219 diameter (Fig. 1). The model is further extended to include snail migration with a constant
220 migration rate, ξ , to and from an external population, N^E , that is not affected by prawn
221 interventions. For simplicity, the external population is conceptualized to originate from an
222 identical transmission site to the one in which interventions are modeled, though in reality,
223 multiple sites with heterogeneous transmission dynamics may contribute differentially to the
224 intervention site.

225



226

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228

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Figure 1: Epidemiologic model schematic with snail size and infection classes. Parameters governing transitions between classes and migration into and out of each class are shown.

230 New snails enter the population as susceptible juveniles, i.e. in infection class $i = S$ and
231 size class $j = 1$. Logistic snail population growth is modeled with *per-capita* recruitment, f ,
232 and carrying capacity, K . Neither small snails ($j = 1$) nor infectious snails ($i = I$) contribute
233 to recruitment due to sexual immaturity and parasitic castration, respectively³⁹. Pre-patent
234 snails' contribution to recruitment is reduced by a fraction $0 < z < 1$ ⁴⁰. Snails of each size
235 class are subject to both size-dependent natural mortality, μ_j , and predation mortality, ψ_j , a
236 function of both prawn and snail body size and density described in the next section. Small
237 and medium snails grow and transition to the next size class at the per capita rate g_1 (from
238 size class 1 to 2) and g_2 (from class 2 to 3), respectively.

239 New snail infections occur at the per capita rate, βM , where β is the transmission rate
240 and $M = 0.5\phi(W)WHm$ is an estimate of the overall number of *Schistosoma* miracidia (free
241 living infective stages) produced by mated adult female worms. This estimate is the product
242 of the size of definitive human host population, H , the mean parasite burden, W , (i.e., mean
243 number of adult worms per person), the rate at which mated adult female worms shed eggs
244 that hatch into infectious miracidia, m , and the function $\phi(W)$ representing the density-
245 dependent mating probability of adult worms⁴¹. The coefficient 0.5 accounts for the assumed
246 1:1 sex ratio of adult worms. For simplicity, we assume a constant human population and no
247 density dependent fecundity of female worms. Following infection, pre-patent snails, E ,
248 transition to the patent class, I , at rate σ , with σ^{-1} being the mean time necessary for
249 sporocyst development following snail infection with a miracidium.

250 The adult parasite population harbored by definitive human hosts is modeled as the mean
251 parasite burden in the human population, W , assuming a negative binomial distribution with
252 clumping parameter, ϕ ^{41,42}. Humans acquire adult worms as a result of contact with cercariae
253 shed from infected snails. Worm acquisition occurs at rate λ , an aggregate parameter
254 accounting for the *per capita* shedding rate of cercariae by infected snails, cercariae mortality,

255 contact rate, and probability of infection, as described in previous work ¹⁵. The cercarial
256 shedding rate of medium (N_{I2}) and large (N_{I3}) snails is assumed to exceed that of small (N_{I1})
257 snails by a factor θ_1 and θ_2 , respectively ⁴³.

258 The full system of differential equations describing the epidemiologic model can be found
259 in the supplementary information along with model parameters listed in Table S2.

260 (c) Prawn predation model

261 As in previous work ³⁸, the per-capita prawn predation rate on snails of each class, ψ_{ij} , is
262 modeled as a type III functional response, described by a generalization of Holling's disk
263 equation ⁴⁴. This produces a sigmoid-shaped function, which increases and saturates at high
264 prey densities and decreases to approach zero at low prey densities. Previous experiments
265 by Sokolow et al ¹³ show that prawn predation of snails changes predictably as a function of
266 the ratio of prawn biomass to snail body mass, r_j . Using these experimental data, the attack
267 rate, α , is estimated as a log-linear function of the biomass ratio: $\alpha = \alpha_m * \log(r_j(t))$. The
268 handling time, T_h , is estimated as a reciprocal function of the biomass ratio: $T_h =$
269 $(T_{h_m} r_j(t))^{-1}$ where α_m and T_{h_m} are coefficients estimated from ¹³ and r_j the ratio between
270 prawn body size and mean snail body size in each class. Laboratory experiments presented
271 in ¹³ show that small prawns are unable to feed on large snails ($j = 3$), accordingly, $\psi = 0$
272 when $r_j < 3$. In addition, the attack rate, α , derived by Sokolow et al. ¹³ in controlled
273 laboratory conditions in $1m^{-2}$ tanks is penalized by a factor $0 < \epsilon < 1$ to account for the
274 reduction in searching efficiency caused by the morphological complexity of foraging in wild
275 settings.

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

277
$$r_j(t) = \frac{B(t)}{a_N L_{N_j}^{b_N}} \quad (8)$$

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

$$282 \quad \psi_{ij} = \begin{cases} \frac{\alpha(r_j(t))\epsilon N_{ij}^n}{1 + \sum_{i=S}^L \sum_{j=1}^3 \alpha(r_j(t))\epsilon T_h(r_j(t))N_{ij}^n}, & r_j \geq 3 \\ 0, & r_j < 3 \end{cases} \quad (9)$$

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

288 Parameters of the snail predation component of the combined model are listed in Table S3.

289 **Model simulations**

290 We consider a time horizon of $T_{max} = 10$ years, for comparability to similar analyses
291 investigating different schistosomiasis intervention strategies^{7,45}. Because prawn body size
292 increases and levels off with time (eq. 1-3), but prawn abundance decreases in time (eq. 5),
293 both stock biomass and cumulative profit (eq. 7) are unimodal functions of time for any given
294 initial stocking density, P_0 . Additionally, harvesting prior to peak profit may afford the
295 opportunity to increase n^{sp} and therefore sacrifice short term profits to maximize long term
296 profit. It is thus possible to use equations 1-7 to simulate prawn aquaculture dynamics and
297 numerically find the stocking density, P_0 , and harvest time, T , that maximize cumulative
298 profit. The surface of values $(P_0, T, CP^{sp}(P_0, T, T_{max}))$ is related to the eumetric curve used in
299 fishery science to identify the stocking density that maximizes profit⁴⁶. As stocking costs
300 increase linearly with stocking size, P_0 , while revenues increase less than linearly as a

301 consequence of density-dependent growth and mortality, the surface is unimodal and its
302 peak represents the maximum achievable cumulative profit, $CP_{opt}^{sp} =$
303 $\max(CP^{sp}(P_0, T, T_{max}))$. Therefore, for each *Macrobrachium* species (*sp*) and a time period
304 of $T_{max} = 10$ years it is possible to identify the stocking density, P_{0opt}^{sp} , and harvest time, T_{opt}^{sp} ,
305 that maximize cumulative profit, CP_{opt}^{sp} , here collectively defined as *optimal management*. We
306 identify optimal management for each prawn species using a grid search over initial stocking
307 densities, P_0 , ranging between $0.5 - 7.5 Pm^{-2}$ and potential harvest times, T , on each day
308 between 1 – 730.

309 Given the optimal stocking density, P_{0opt}^{sp} , that maximizes cumulative profit and the
310 corresponding optimal harvest time in an individual cycle, T_{opt}^{sp} , the epidemiologic model is
311 run under the following scenarios: (1) 10 years of annual MDA with no prawn intervention;
312 (2) and (3); 10 years of prawn stocking and harvesting under optimal aquaculture
313 management for each species, as described above; and (4) and (5) 10 years of integrated
314 annual MDA and prawn intervention under optimal management. In all scenarios, we
315 simulate the system for an additional 10 years without intervention to explore the potential
316 for infection rebound in the case the intervention program is ceased.

317 Stocking and harvesting were simulated at regular intervals of T_{opt}^{sp} days, and were
318 implemented as instantaneous events that reset the values of P and L to match the initial
319 conditions at the beginning of each stocking cycle (i.e. P_{0opt}^{sp} and L_0). This assumes that all
320 prawns—regardless of marketability—are harvested and replaced with P_{0opt}^{sp} juveniles in a
321 single day. Mass drug administration is implemented as an instantaneous 85% reduction in
322 mean worm burden, W , in the same 75% of the human population, corresponding to
323 assumptions of 85% drug efficacy and 25% systematic non-compliance^{45,47}.

324 To compare the effects of different interventions, we model disability associated with
325 schistosomiasis using the disability adjusted life year (DALY) as in previous analyses ^{7,48}.
326 Disability weights measuring the disability associated with a condition for a single year of
327 life—where 0 is perfect health and 1 is death—were distributed among individuals with
328 heavy (> 50 eggs per 10mL urine, H_{hi}) and light ($0 < \text{eggs per 10mL urine} \leq 50$, H_{lo}) *S.*
329 *haematobium* burdens as defined by WHO guidelines. Total DALYs over the simulation period
330 are then estimated as:

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

331 Where DW_{hi} and DW_{lo} are the yearly disability weights associated with heavy and light *S.*
332 *haematobium* burdens, respectively, normalized to a daily estimate to match the dynamics of
333 the epidemiological component of the model. Details on estimating the number of individuals
334 in each burden class at each time step of the epidemiological model (H_{hi_t} and H_{lo_t}) are
335 provided in the supplementary information.

336 The model was coded in R version 3.5.0 and simulated using the solver lsoda from the
337 package deSolve ⁴⁹. To address concerns regarding reproducibility, all model code and data
338 are included as a supplementary file and are also made freely available online at
339 https://github.com/cmhoove14/Prawn_fisheries_Public_health.

340 **Sensitivity analyses**

341 To quantify the influence of uncertain parameter inputs on key model outcomes, latin
342 hypercube sampling is performed over parameter ranges in Table S1 to generate a set of
343 1,000 candidate sets. These parameter sets are used to derive estimates of uncertainty in the
344 simulations described above. Furthermore, global sensitivity analysis using latin hypercube
345 sampling and partial rank correlation coefficients (LHS-PRCC) ^{50,51} is performed with optimal

346 cumulative profit (CP_{opt}^{sp}) as the outcome in the prawn aquaculture model, equilibrium
347 infected snail density (N_I) and mean worm burden (W) absent prawn or MDA interventions
348 as the outcomes in the epidemiologic model, and total DALYs accumulated through simulated
349 10-year combined MDA and prawn interventions as the outcome in the integrated model.
350 Briefly, PRCC estimates the correlation between a model parameter and a model outcome by
351 first rank-transforming parameters drawn from an LHS scheme and the corresponding model
352 outputs, then removing the linear effects of all other model parameters on the parameter of
353 interest and the outcome, and finally measuring the linear relationship between the rank-
354 transformed parameter and outcome residuals⁵⁰. Monotonicity of the relationship between
355 model outputs and all parameters was assessed via scatterplots (Figs S1-S4) prior to
356 conducting LHS-PRCC sensitivity analyses.

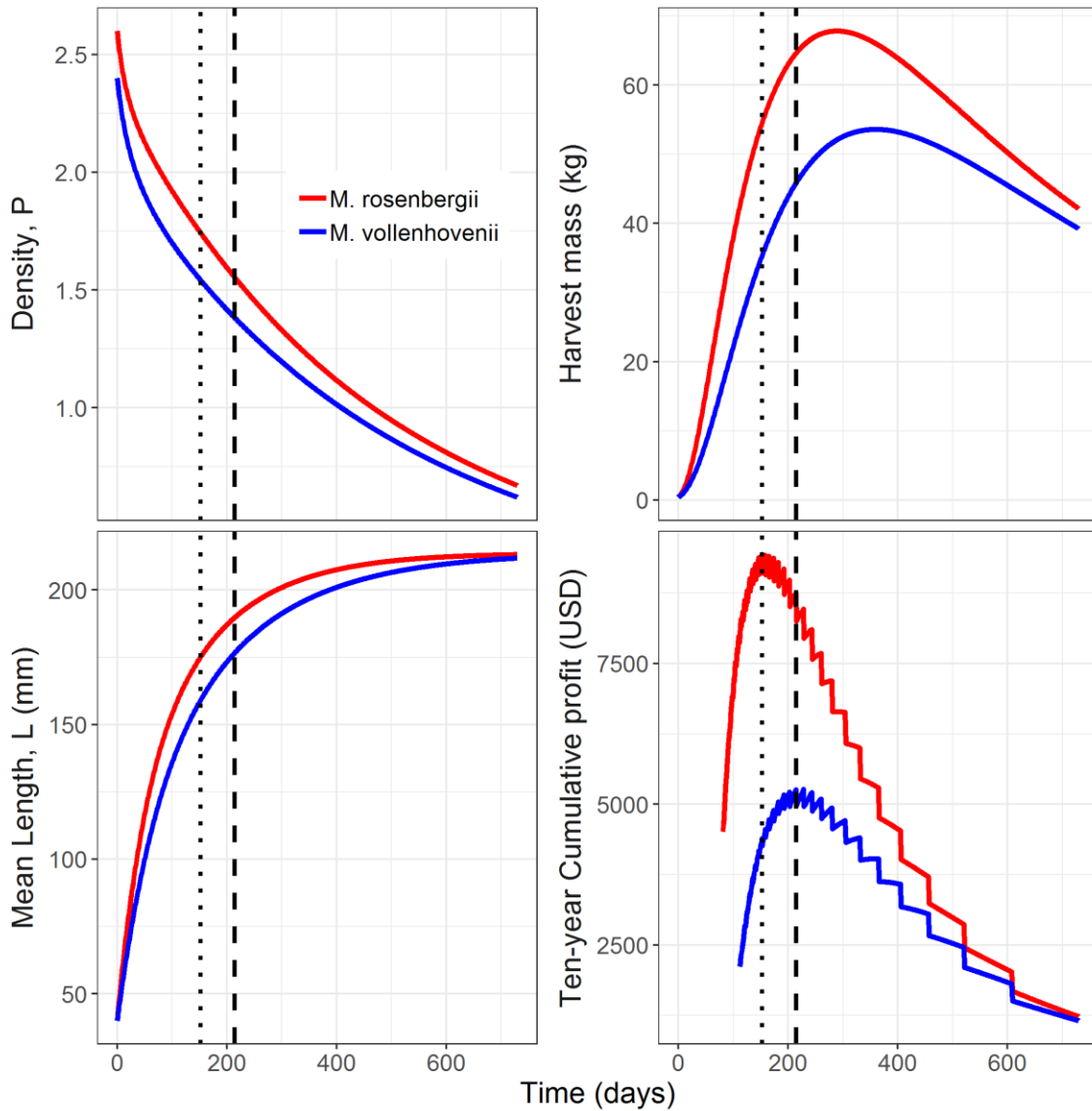
357 Two additional sensitivity analyses are performed to identify profitability thresholds for
358 the prawn aquaculture model. In the first, fixed costs, c_f , in the range \$0 – \$1,000 are added
359 to the per-cycle profit calculation (eqn 7; such that total cost for each cycle is $-(cP_0 + c_f)$) to
360 represent additional costs that may be incurred with each aquaculture cycle such as labor,
361 transport of prawns, and nursery costs leading up to stocking. In the second, the prawn
362 mortality rate, μ_p , is multiplied up to 10 times the estimated natural rate to account for
363 additional sources of prawn loss that may be incurred due to predation, escape, or other
364 sources of mortality, such as disease.

365 **Results**

366 **Aquaculture model**

367 With parameters fixed at the values shown in Table 1, stocking *M. rosenbergii* at $P_0 =$
368 $2.6 Pm^{-2}$ and harvesting at $T_{opt}^{ros} = 165 days$ maximizes cumulative ten-year profit while
369 stocking at $P_0 = 2.4 Pm^{-2}$ and harvesting at $T_{opt}^{ros} = 260 days$ maximizes cumulative profit

370 for *M. vollehovenii*. These stocking densities and harvesting times were used to simulate
371 aquaculture cycles for each species. Figure 2 shows the dynamics of each species run
372 continuously through two years with vertical dashed lines indicating the optimal time of
373 harvest, T_{opt}^{sp} . Prawns grow in length, L , and weight over time while population size
374 (measured as density, Pm^{-2}) decreases with time as a result of density dependent death from
375 crowding and natural, size-dependent mortality (Fig 2). These competing effects lead to a
376 humped function of total harvestable biomass, Ω , over time with the peak occurring well
377 before prawns grow to their full size. Ten-year cumulative profits also have a single peak,
378 which is determined both by the profit per cycle and the number of cycles possible within the
379 10 year time frame. Cumulative profits are maximized by harvesting well before the peak in
380 harvestable biomass occurs, indicating more, smaller harvests maximize profit over time.

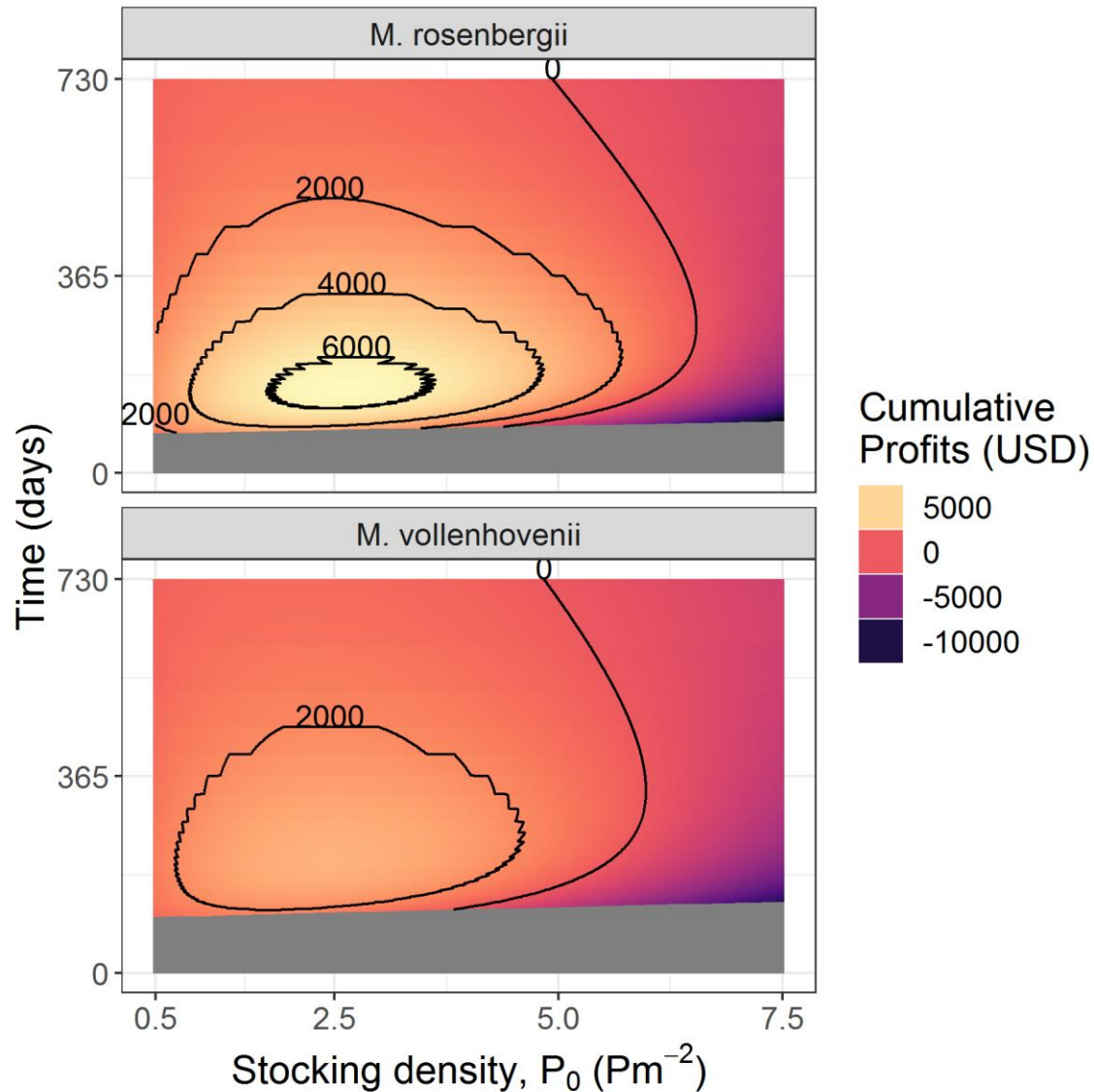


381

382 **Figure 2:** Prawn aquaculture model dynamics. Two-year aquaculture cycles for, *M. rosenbergii* (red
383 lines) and *M. vollenhovenii* (blue lines) under optimal management showing how prawns grow in
384 length over time (bottom-left), but decrease in density (top-left). This leads to a single peak in
385 harvest mass (top-right), but harvesting actually occurs prior to the peak in order to maximize ten-
386 year cumulative profits (bottom-right) by sacrificing profit-per-cycle for completing more
387 aquaculture cycles. Vertical dashed lines indicate time at which harvest would occur for each species
388 (small dashes - *M. rosenbergii*, large dashes - *M. vollenhovenii*). Here, following (19), we set the cost c
389 for a juvenile prawn to \$0.10 with $L_0 = 40\text{mm}$ ($\sim 0.35\text{g}$ per juvenile prawns) and selling price
390 $p = \$12/\text{kg}$. Other parameters set as in Table 1.

391

392 The surface of values $(P_0, T, CP^{sp}(P_0, T, T_{max}))$ for each species is shown in Figure 3. As
393 expected, profits associated with aquaculture of the faster growing *M. rosenbergii* are higher.
394 Considering parametric uncertainty, the peak estimate of median cumulative profit for *M.*
395 *rosenbergii* occurs at $P_0 = 2.9 Pm^{-2}$ and $T_{opt}^{ros} = 173 \text{ days}$ (IQR: 146 – 192) , producing
396 $CP_{opt}^{ros} = \$5364$ ($\$3192 - \8111) per $1,000 m^2$ enclosure. The same estimates for
397 *M. vollehovenii* are $P_0 = 2.5 Pm^{-2}$, $T_{opt}^{vol} = 260 \text{ days}$ (228 – 331) , and $CP_{opt}^{vol} =$
398 $\$1738$ ($\$704 - \3394). Additional outputs from the aquaculture model that describe stock
399 structure and aquaculture performances at optimal management are reported in Table 1.
400



401

402 **Figure 3:** Grid search to identify optimal management decisions for each prawn species. Cumulative
403 profits (CP^{sp}) generated by the aquaculture model for each species across a range of potential
404 stocking densities (P_0) and harvest times (T) are shown. Grey regions indicate regions where
405 harvesting is not feasible due to prawns not having reached sufficient marketable size (30g).
406 Contours indicate regions of CP^{sp} corresponding to the labeled value in 2018 USD.

407

408 **Table 1:** Optimal stocking and harvesting parameters for each prawn species reported as median
 409 (interquartile range).

Parameter	Definition	<i>M. vollehovenii</i>	<i>M. rosenbergii</i>
P_{0opt}^{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	167mm (161 - 175)	167mm (161 - 174)
$P(T_{opt}^{sp})$	Prawns harvested	1056 (850 - 1236)	1559 (1434 - 1662)
$Y(T_{opt}^{sp}, P_{0opt}^{sp})$	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)

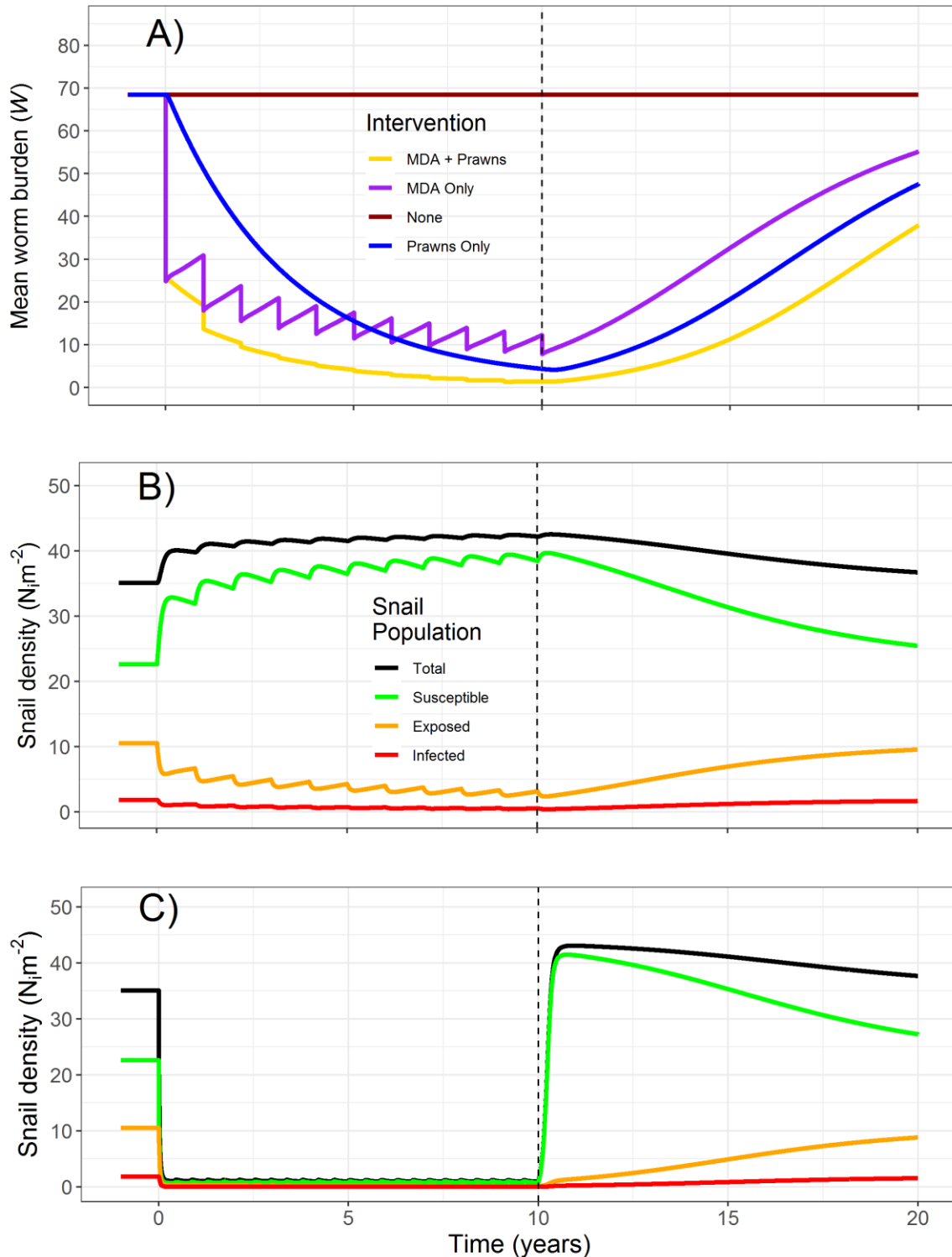
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412 **Integrated aquaculture epidemiologic model**

413 Simulation of the integrated model reveals comparable performance of prawn
414 intervention strategies to MDA strategies. As in previous analyses ^{7,15}, annual mass drug
415 administration alone produces a pattern of gradually decreasing worm burden over time
416 characterized by repeated rebound in infection following MDA (Fig 4A, purple line). The
417 prawn-only intervention causes mean worm burden to gradually decline towards 0,
418 eventually reducing worm burden to comparable levels by year 10 (Fig 4A, blue line). Finally,
419 the combined MDA and prawn intervention leads to a rapid decline in mean worm burden
420 that nearly reaches 0 by year 10 (Fig 4A, gold line).

421 These patterns can mostly be explained by the underlying snail infection dynamics. Under
422 MDA intervention, the snail population persists through repeated rounds of MDA and even
423 increases due to the reduced influence of infection (Fig 4B). Most importantly, a population
424 of infected snails is able to sustain transmission—albeit at lower levels—even as adult worms
425 are removed from the treated human population by MDA (Fig 4B). Interventions in which
426 prawns are introduced at profit-optimal densities produce rapid declines in the snail
427 population that heavily reduce this environmental reservoir of transmission (Fig 4C).
428 Extirpation of the entire snail population is prevented due to the assumption of a Holling's
429 type III functional response and immigration from an unaffected reservoir population (see
430 Fig S3 for snail infection dynamics without immigration and under a Holling's type II
431 functional response), but transmission is effectively halted due to near elimination of the
432 infected snail population (Fig 4C). This heavy reduction in transmission coupled with the
433 benefits of MDA translates to near elimination of the parasite by year 10. Regardless of the
434 intervention, ceasing efforts to control transmission after 10 years results in rapid returns to
435 pre-intervention snail populations and community-level mean worm burdens (Fig 4A-C).



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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*.

443 Comparison of total DALYs lost over ten year simulation periods under each intervention
444 shows comparable performance of the prawn only intervention to MDA and substantial
445 additional DALYs averted when combining MDA with prawn intervention. Without
446 intervention a median 324 (IQR: 119 – 502) DALYs are lost to *S. haematobium* infection.
447 Annual MDA and profit-optimal stocking of prawns perform comparably with 160 (IQR: 54 –
448 285) total DALYs lost with annual MDA and 184 (IQR: 70 – 294) total DALYs lost with profit-
449 optimal prawn stocking; representing 51% and 43% DALYs averted, respectively. Integrated
450 interventions utilizing both MDA and prawn stocking reduce median DALYs lost to 83 (IQR:
451 30 – 137), representing a 74% reduction in *S. haematobium* related disability.

452 **Sensitivity Analyses**

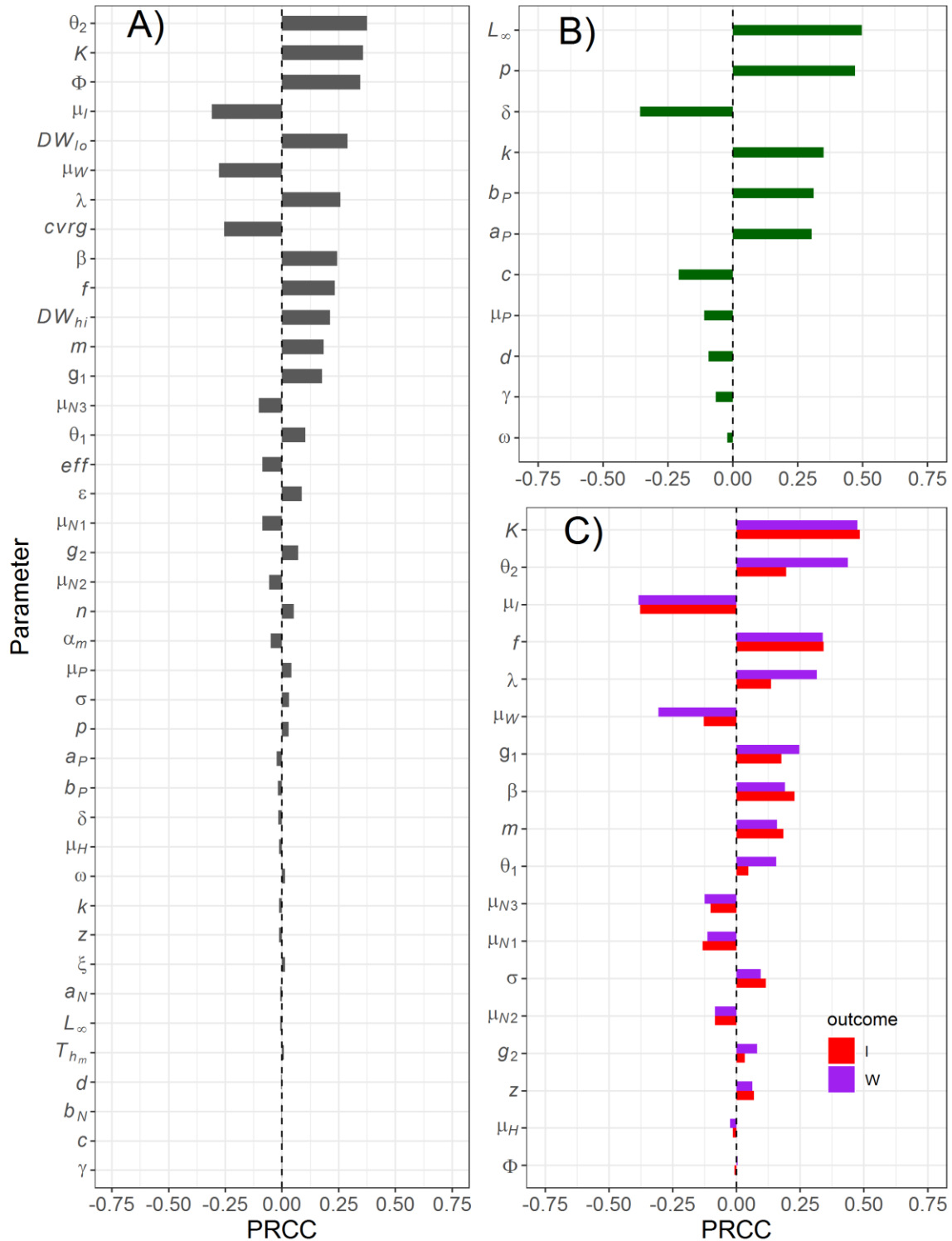
453 Substantial sensitivity analyses reveal that profitability of the prawn aquaculture system
454 and reductions in schistosomiasis burden associated with prawn introductions are robust to
455 model assumptions and parameters (Figs S1 and S2). The addition of fixed costs associated
456 with each aquaculture cycle and additional sources of mortality reveal aquaculture of *M.*
457 *rosenbergii* remains profitable with fixed costs of up to \$550 per cycle (Fig S1) and mortality
458 rates up to 5.2 times higher than the baseline estimate (Fig S2). Aquaculture of *M.*
459 *vollenhovenii* remains profitable with fixed costs of up to \$400 per cycle (Fig S1) and
460 mortality rates up to 3.6 times higher than the baseline estimate (Fig S2). Global sensitivity
461 analysis using LHS-PRCC shows that the parameters of the VBGE that govern prawn growth
462 dynamics (L_{∞}, κ) and parameters governing estimates of discounted profits (δ, p) are most
463 correlated with 10-year cumulative profits (Fig 5B)

464 Exploration of snail infection dynamics under prawn interventions also reveals that the
465 Holling's type III functional response and the inclusion of snail migration represent
466 conservative structural model assumptions. Figure S3 shows that snail extirpation is only
467 possible when both of these assumptions are relaxed. Parameters governing snail predation

468 by prawns (ϵ, n) are also shown to have moderate influence on estimates of 10-year
469 cumulative DALYs lost (Fig 5A).

470 Key outcomes from the epidemiologic model including equilibrium estimates of infected
471 snail density (I) and mean worm burden (W) and of DALYs lost over 10-year intervention
472 periods is mostly influenced by epidemiologic parameters, rather than parameters governing
473 prawn population or predation dynamics (Fig 5A & 5C). We also compared parameter sets in
474 which the MDA only intervention was superior to the prawn only intervention in terms of
475 DALYs averted. We find that the MDA only intervention leads to more DALYs averted when
476 the coverage and efficacy are high, while the prawn-only intervention performs better when
477 the snail population carrying capacity (K) is higher (Fig S4).

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Figure 5: Sensitivity of key model outcomes to model parameters assessed with LHS-PRCC. Sensitivity to all parameters of DALYs lost following 10 years of combined MDA and prawn intervention (A), cumulative 10-year profit sensitivity to prawn aquaculture parameters (B), and sensitivity of mean worm burden and equilibrium infected snail density to epidemiologic parameters (C). Parameter definitions and baseline values can be found in supplementary tables 1-3.

486 **Discussion**

487 Small-scale, extensive prawn aquaculture such as that considered here offers a profitable
488 and sustainable method to improve food production, reduce schistosomiasis burdens, and
489 increase revenues for small-scale subsistence farmers, especially when paired with ongoing
490 efforts such as rice cultivation ²⁵. In areas of high food insecurity, malnutrition, and endemic
491 schistosomiasis—conditions which reinforce each other and often result in “poverty traps”
492 ^{52,53}—an integrated system of prawn aquaculture may be a solution for co-benefits of disease
493 control and sustainable development.

494 Our results are consistent with an increasing body of evidence that consumption of snails
495 by predator species such as *Macrobrachium* prawns can be an effective method for combating
496 schistosomiasis transmission to people ^{14,15,54}. Specifically, by targeting the environmental
497 reservoir of schistosome parasites, prawns can reduce reinfection rates that plague MDA
498 campaigns in high transmission settings. By deploying prawn aquaculture with MDA,
499 effective control—in which the schistosome parasite is suppressed in both human hosts and
500 intermediate host snails—can be achieved.

501 We also show that such prawn interventions combined with established extensive
502 aquaculture methods can be profitable if carefully managed. Drawing on economic studies of
503 existing aquaculture practices ^{19,33}, we develop—to our knowledge—the first dynamic model
504 of prawn aquaculture to investigate optimal management practices. The model suitably
505 simulates prawn stocking in a large water contact site or rice paddy, and the length of optimal
506 cycles coincides with typical rice harvesting timelines ²⁵. We find that this system produces
507 short- and long-term profits, implying the potential for a sustainable, community-driven
508 intervention, given the right capital investment and incentive programs.

509 Under optimal management, extensive aquaculture of either *M. rosenbergii* or *M.*
510 *vollenhovenii* leads to both profits and reductions of the snail population. The optimal

511 stocking densities of each species are above the potential threshold of approximately $2 Pm^{-2}$
512 necessary for local snail extirpation as identified in previous work ¹⁵, though our conservative
513 inclusion of snail migration and a Holling's type III functional response restricts such an
514 outcome in this analysis.

515 Achieving these stocking densities may be challenging in sub-Saharan Africa where >90%
516 of the global burden of schistosomiasis is found ²³ and where the proposed intervention is
517 likely to provide the most benefit. More than 50 years of domestication of *M. rosenbergii* has
518 established protocols for ideal rearing and management of aquaculture efforts with this
519 species ^{18,19}, whereas similar protocols for the African native *M. vollenhovenii* are still under
520 development. Profits appear to be highly sensitive to parameters that regulate prawn growth,
521 meaning continued research and development into *M. vollenhovenii* aquaculture may
522 eventually provide comparable profits to *M. rosenbergii*. However, in the short term, all male
523 stocking of *M. rosenbergii* may be a superior strategy.

524 This strategy of stocking the non-native *M. rosenbergii* in coastal regions where it is non-
525 native should be approached with caution to avoid the establishment of an alien population
526 with potentially unintended ecological consequences on local biodiversity. Establishment of
527 non-GMO aquaculture biotechnologies for either all-male ⁵⁵⁻⁵⁷ or all-female ⁵⁸ populations
528 suggest possible strategies to prevent invasions. Moreover, recent laboratory experiments
529 (Savaya-Alkalay et al. submitted) have ruled out the possibility of cross-fertilization between
530 mature female *M. vollenhovenii* and male *M. rosenbergii*, demonstrating that male-only
531 progeny of *M. rosenbergii* may be safely used for extensive aquaculture and schistosomiasis
532 control in western Africa where *M. rosenbergii* is non-native.

533 Extensive sensitivity analyses reveal that key model outcomes including profit generated
534 by the aquaculture portion of the model and DALYs lost from the integrated model are robust
535 to key parameters that govern profit estimation and the influence of prawn interventions on

536 DALYs lost. The prawn aquaculture model is most sensitive to parameters governing somatic
537 growth, which have been estimated from available literature, and supported by expert
538 opinion ^{28,32}. This finding also suggests that if stock improvement or improvements in
539 husbandry practices can increase average prawn condition or size, i.e. by supplementing
540 feeds, further increases in profit may be possible. Selective harvesting methods that only
541 remove market-size prawns, leaving the remaining stock to continue to grow, may also
542 improve aquaculture performance.

543 Optimal aquaculture practices are also sensitive to the market price of adult prawns and
544 the stocking cost of juvenile prawns, implying that optimal management may be influenced
545 by fluctuations in market factors that may influence price and cost of harvested and stocked
546 prawns. Profit generated from selling harvested prawns is based on reasonable assumptions
547 of prices in premium markets, though the actual selling price in subsistence economies might
548 be lower and contingent on market access and local demand. However, the fixed cost
549 sensitivity analysis demonstrates profitability is possible even with substantial additional
550 costs associated with prawn stocking, and profitability persists across a wide range of
551 stocking densities for each species. These results together assuage concerns that such
552 vagaries of the market would impair the success of the proposed system and suggest that
553 prawn aquaculture should be economically viable even under non-optimal management
554 densities.

555 Additional sources of mortality could result from declines in water quality caused by
556 prawn stocking, disease outbreaks, or predation by waterbirds, fish, amphibians or reptiles.
557 We demonstrate that extensive aquaculture is still profitable with mortality rates as high as
558 five times greater than natural mortality. Barring catastrophic events, this demonstrates that
559 the proposed system should be resilient to such perturbations. Therefore, further field work
560 is required to assess prawn life expectancy, escapement rate, growth performances, changes

561 in water quality, and potential changes in human behavior which might affect either
562 aquaculture performances and/or snail abundance, transmission rates, and epidemiologic
563 outcomes.

564 Prawn predation of the snail population as modeled here is also based on a number of
565 assumptions including the Holling's type III functional response and the prawn attack rate
566 penalty. We consider the type III functional response a conservative estimate of the
567 relationship between prawn predation and snail density as it does not allow for the potential
568 extirpation of the snail population. We also test a wide range of attack rate penalties as we
569 identified no prior estimates of prawn predation efficiency in non-laboratory settings, and
570 find that effective control is feasible even when increasing this parameter by an order of
571 magnitude (implying a substantially reduced attacked rate).

572 Regarding schistosomiasis transmission dynamics, recent findings suggest non-
573 linearities in the human-to-snail force of infection may decrease the efficacy of MDA and lead
574 to faster post-MDA rebounds of schistosomiasis ⁵⁹. While this may alter the effects of MDA in
575 our simulations, we believe it strengthens the argument for strategies that explicitly target
576 the intermediate host snail population, such as the prawn intervention proposed here.
577 Another recent finding suggests that snail control can actually lead to increased human risk
578 of *Schistosoma* infection if the snail population is limited by resource competition prior to
579 "weak" control efforts ⁶⁰. In this scenario, remaining snails with higher per-capita resource
580 availability may produce more cercariae. Given the large magnitude of snail reductions at the
581 proposed prawn densities modeled here—even given the conservative Holling's III functional
582 response—we believe this effect is unlikely in our scenarios. Finally, our model lacks
583 seasonality, which would likely affect both schistosomiasis transmission and prawn growth
584 as e.g. temperature and rainfall fluctuate through the year, especially in sub-tropical and near
585 temperate regions where schistosomiasis is still endemic, such as in northern Africa ^{61,62}.

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

595 **Data Availability**

596 All data and code used to conduct this analysis are provided as a supplementary file and are
597 freely available at https://github.com/cmhoove14/Prawn_fisheries_Public_health

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615 **Author information**

616 **Contributions**

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

624 **Competing interests**

625 The authors declare no competing interests

626

627 *Supplementary Information*

628 **Table S1:** Parameters of the prawn aquaculture model and ranges used in the global sensitivity
629 analysis

Parameter	Value & Units	Description	Source	Range
L_{∞}	214 mm	Maximum length used in von Bertalanffy growth equation	32	[184, 234]
κ	$0.0034 \frac{mm}{day}$	Growth rate of <i>Macrobrachium vollenhovenii</i>	32,63	[0.0078, 0.012]
	$0.0104 \frac{mm}{day}$	Growth rate of <i>Macrobrachium rosenbergii</i>	29	
γ	$3.5 \times 10^{-6} g^{-1}$	Density dependent growth reduction	26	$[3.5 \times 10^{-6}, 6.5 \times 10^{-6}]$
a_p	0.00244	Allometric parameter for <i>Macrobrachium</i> length-weight conversion	28	[0.066, 0.081]
b_p	3.55	Allometric parameter for <i>Macrobrachium</i> length-weight conversion		[3.46, 3.64]
μ_p^{\dagger}	$0.0061 \frac{P}{day}$	Daily prawn mortality rate	32,63	[0.0054, 0.012]
d	-0.382	Size-dependent mortality scaling coefficient	31	[-0.461, -0.289]
ω	$5.5 \times 10^{-9} g^{-1}$	Density dependent mortality factor	26	$[7.5 \times 10^{-9}, 3.5 \times 10^{-9}]$
p	$\frac{\$12}{kg}$	Price per kg of harvested market-size prawns	33,64,65	[11, 22]
δ	$\frac{1.99 \times 10^{-4}}{day}$	Discount rate	(7% annual)	[3%, 20%]
c^{\dagger}	$\frac{\$0.10}{P}$	Cost of a stocked juvenile prawn	33	[0.045, 0.12]

630 † See additional sensitivity analyses below

631

632 **Epidemiologic model equations**

$$633 \quad \frac{dN_{S1}}{dt} = \xi N_{S1}^E + f \left(1 - \frac{N}{K} \right) (N_{S2} + N_{S3} + z(N_{E2} + N_{E3})) - (\mu_1 + g_1 + \psi_{S1}P + \xi + \beta M)N_{S1} \quad (S1)$$

$$634 \quad \frac{dN_{S2}}{dt} = \xi N_{S2}^E + g_1 N_{S1} - \psi_{S2}P - (\mu_2 + g_2 + \xi + \beta M)N_{S2} \quad (S2)$$

$$635 \quad \frac{dN_{S3}}{dt} = \xi N_{S3}^E + g_2 N_{S2} - \psi_{S3}P - (\mu_3 + \xi + \beta M)N_{S3} \quad (S3)$$

$$636 \quad \frac{dN_{E1}}{dt} = \xi N_{E1}^E + \beta M H N_{S1} - \psi_{E1}P - (\mu_1 + g_1 + \xi + \sigma)N_{E1} \quad (S4)$$

$$637 \quad \frac{dN_{E2}}{dt} = \xi N_{E2}^E + \beta M H N_{S2} - \psi_{E2}P - (\mu_2 + g_2 + \xi + \sigma)N_{E2} \quad (S5)$$

$$638 \quad \frac{dN_{E3}}{dt} = \xi N_{E3}^E + \beta M H N_{S3} - \psi_{E3}P - (\mu_3 + \xi + \sigma)N_{E3} \quad (S6)$$

$$639 \quad \frac{dN_{I1}}{dt} = \xi N_{I1}^E + \sigma N_{E1} - \psi_{I1}P - (g_1 + \mu_1 + \mu_I + \xi)N_{I1} \quad (S7)$$

$$640 \quad \frac{dN_{I2}}{dt} = \xi N_{I2}^E + \sigma N_{E2} + g_1 N_{I1} - \psi_{I2}P - (g_2 + \mu_2 + \mu_I + \xi)N_{I2} \quad (S8)$$

$$641 \quad \frac{dN_{I3}}{dt} = \xi N_{I3}^E + \sigma N_{E3} + g_2 N_{I2} - \psi_{I3}P - (\mu_3 + \mu_I + \xi)N_{I3} \quad (S9)$$

$$642 \quad \frac{dW_t}{dt} = \lambda(N_{I1} + \theta_1 N_{I2} + \theta_2 N_{I3}) - (\mu_W + \mu_H)W_t \quad (S10)$$

$$643 \quad \frac{dW_u}{dt} = \lambda(N_{I1} + \theta_1 N_{I2} + \theta_2 N_{I3}) - (\mu_W + \mu_H)W_u \quad (S11)$$

644

645 **MDA Implementation and DALYs estimation**

646 The model tracks treated and untreated segments of the population by dividing the
647 worm burden based on MDA coverage, such that total worm burden is a weighted average
648 of each population: $W = cvrgW_t + (1 - cvrg)W_u$. When MDA is implemented, mean worm
649 burden in the treated compartment is reduced by $W_t(1 - eff)$. We assume the dispersion
650 parameter of the negative binomial distribution in each population is constant over the
651 simulation period. To estimate the total number of individuals with heavy and light egg
652 burdens, H_{hi} and H_{lo} , respectively, we first sample $n = H * cvrg$ draws from a negative

653 binomial distribution with mean W_t and dispersion, φ , to represent the distribution of adult
654 worms in the treated segment of the human population. Similarly, we sample $n = H * (1 -$
655 *cvrg*) draws from a negative binomial distribution with mean W_u and dispersion, φ , to
656 represent the distribution of adult worms in the untreated segment of the human
657 population. We then convert these individual level adult worm counts, denoted W_h , to
658 estimates of egg burden, denoted B_h , as: $B_h = 0.5W_h\phi(W_h)\mathcal{E}$ where $0.5W_h\phi(W_h)$ provides
659 an estimate of the number of mated female (i.e. egg producing) worms and \mathcal{E} is an estimate
660 of *S. haematobium* eggs per 10mL urine per mated adult female worm from [CITE]. With the
661 full distribution of B_h , we can then estimate the number of individuals with heavy (> 50
662 eggs per 10mL urine, H_{hi}) and light ($0 < \text{eggs per 10mL urine} \leq 50$, H_{lo}) *S. haematobium*
663 burdens as defined by WHO guidelines and subsequently estimate DALYs as in equation 10.

664 **Table S2:** Parameters of the schistosomiasis epidemiologic model

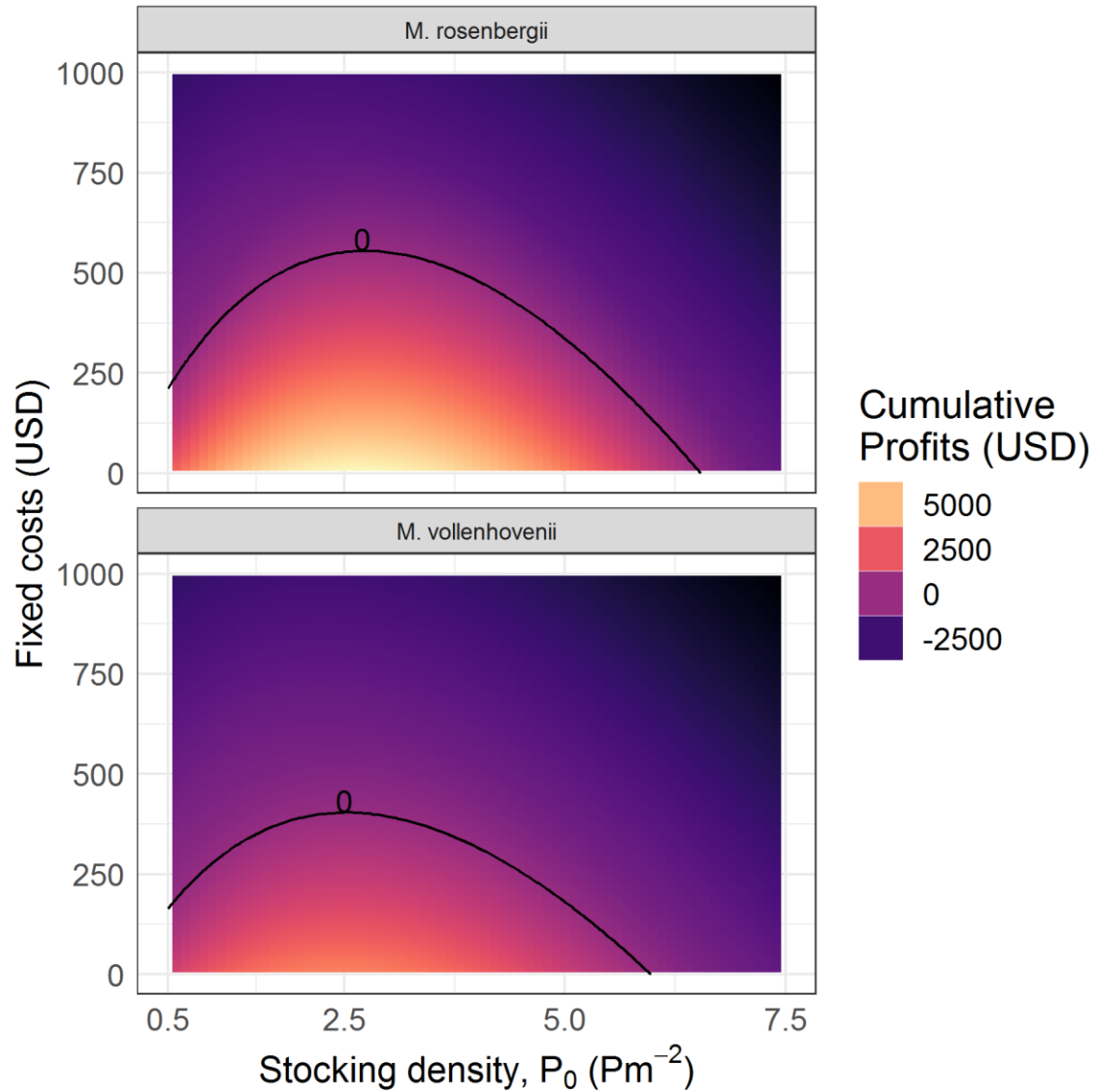
Parameter	Value & Units	Description	Source	Range
f	$0.26 N_{s1} day^{-1}$	Per-capita recruitment rate of reproductive snails	15	[0.06, 0.36]
K	$50 \frac{N}{m^2}$	Snail population carrying capacity	66	[25, 75]
z	0.5	Proportion of pre-patent snails that reproduce	40	[0.25, 1]
μ_1	$\frac{1}{50} day^{-1}$	Mortality rate of snails in size class 1		[25, 100]
μ_2	$\frac{1}{75} day^{-1}$	Mortality rate of snails in size class 2	67,68	[50, 125]
μ_3	$\frac{1}{100} day^{-1}$	Mortality rate of snails in size class 3		[75, 150]
μ_I	$\frac{1}{10} day^{-1}$	Mortality rate of snails in infection class I	40	[7, 20]
ξ	$\frac{1}{5} year^{-1}$	Migration rate of snails	69	[0, 1]
g_1	$\frac{1}{37} day^{-1}$	Growth rate of snails in size class 1	70	[20, 60]
g_2	$\frac{1}{62} day^{-1}$	Growth rate of snails in size class 2		[40, 100]
σ	$\frac{1}{50} day^{-1}$	Pre-patent period; transition rate of snails in infection class E to infection class I	71	[30, 70]
m^\dagger	0.8	Infectious miracidia produced per mated adult female worm		[0.5, 1.5]
β^\dagger	4×10^{-7}	Pre-patent snails produced per infectious miracidia	15	$[2.0 \times 10^{-7}, 8 \times 10^{-7}]$
λ^\dagger	7.5×10^{-6}	Adult worms produced per infectious cercaria shed by infected snails		$[5.0 \times 10^{-6}, 1.0 \times 10^{-5}]$
θ_1	1.31	Increased relative production of infectious cercariae by snails in class N_{I2}	43	[1, 5]
θ_2	7.88	Increased relative production of infectious cercariae by snails in class N_{I3}		[2, 10]
φ	0.08	Clumping parameter of the negative binomial distribution	38	[0.01, 0.3]
μ_w	$\frac{1}{3.3} year^{-1}$	Mortality rate of adult worms	15	[2, 4]
μ_H	$\frac{1}{60} year^{-1}$	Mortality rate of humans harboring adult worms		[50, 70]
DW_{hi}	0.05	Disability weight associated with heavy <i>S. haematobium</i> egg burden	7,72	[0.03, 0.15]
DW_{lo}	0.014	Disability weight associated with heavy <i>S. haematobium</i> egg burden	7,72	[0.003, 0.03]
eff	0.85	MDA efficacy		[0.75, 0.95]
$cvrg$	0.75	MDA coverage		[0.5, 0.95]
\mathcal{E}^\dagger	3.6	Eggs produced per 10mL urine per mated adult female worm	73	[2, 5]

665 † Units provided in description

666 **Table S3:** Parameters regulating snail predation of snails, linking the aquaculture model to the
 667 epidemiologic model

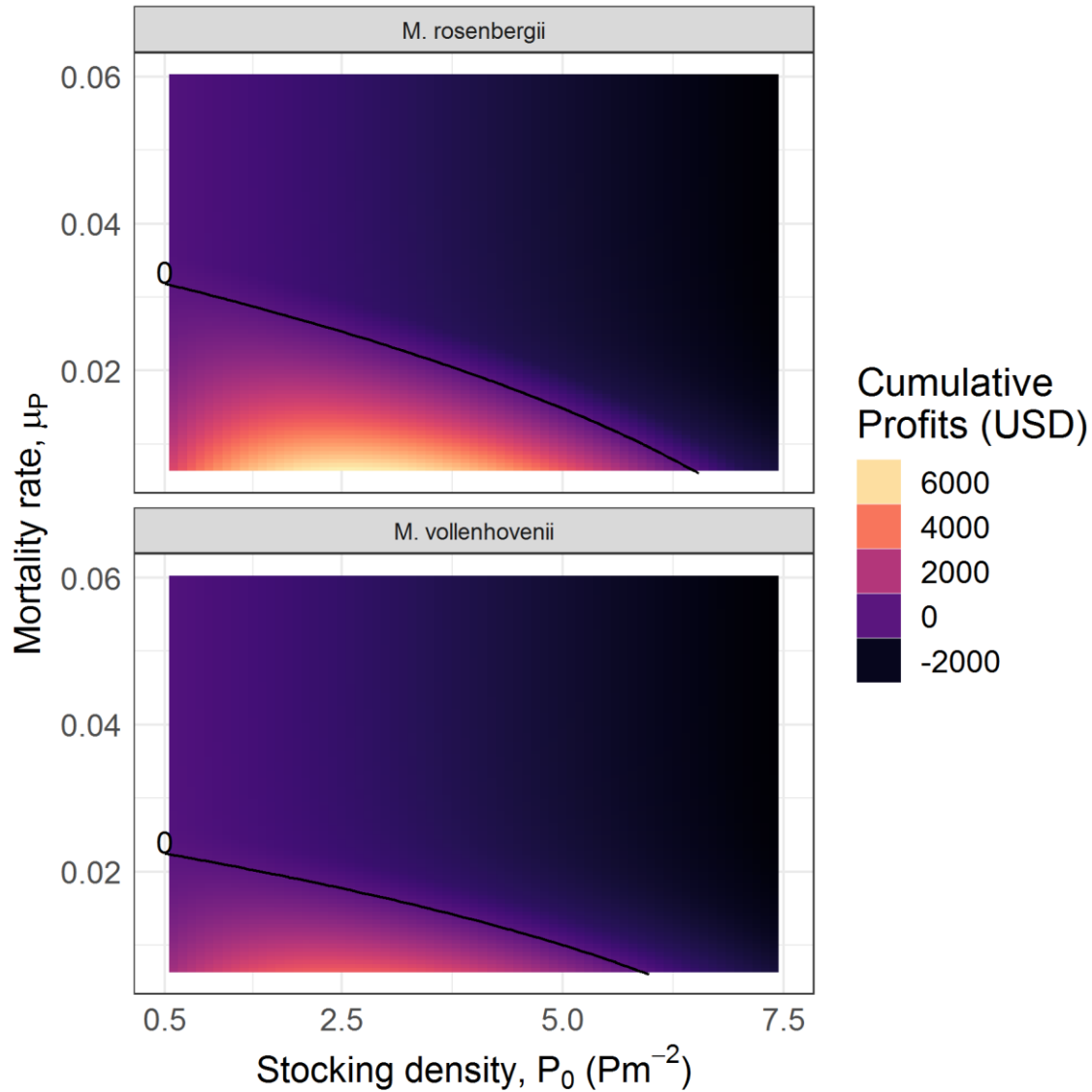
Parameter	Value & Units	Description	Source	Range
a_N	0.19	Allometric parameter for snail shell width-weight conversion		[0.1, 0.3]
b_N	2.54	Allometric parameter for snail shell width-weight conversion		[2, 3]
α_m	0.91	Parameter to estimate prawn attack rate from prawn-snail biomass ratio	13	[0.5, 1.5]
T_{hm}	0.39	Parameter to estimate prawn handling time from prawn-snail biomass ratio		[0.2, 0.5]
n	2	Exponent of Holling's type III functional response	38	[1.1, 4]
ϵ	10%	Prawn predation attack rate penalty associated with searching for prey in wildlife rather than laboratory conditions	Estimated as 10% of laboratory-determined rates with wide range investigated in sensitivity analysis	[1, 100]

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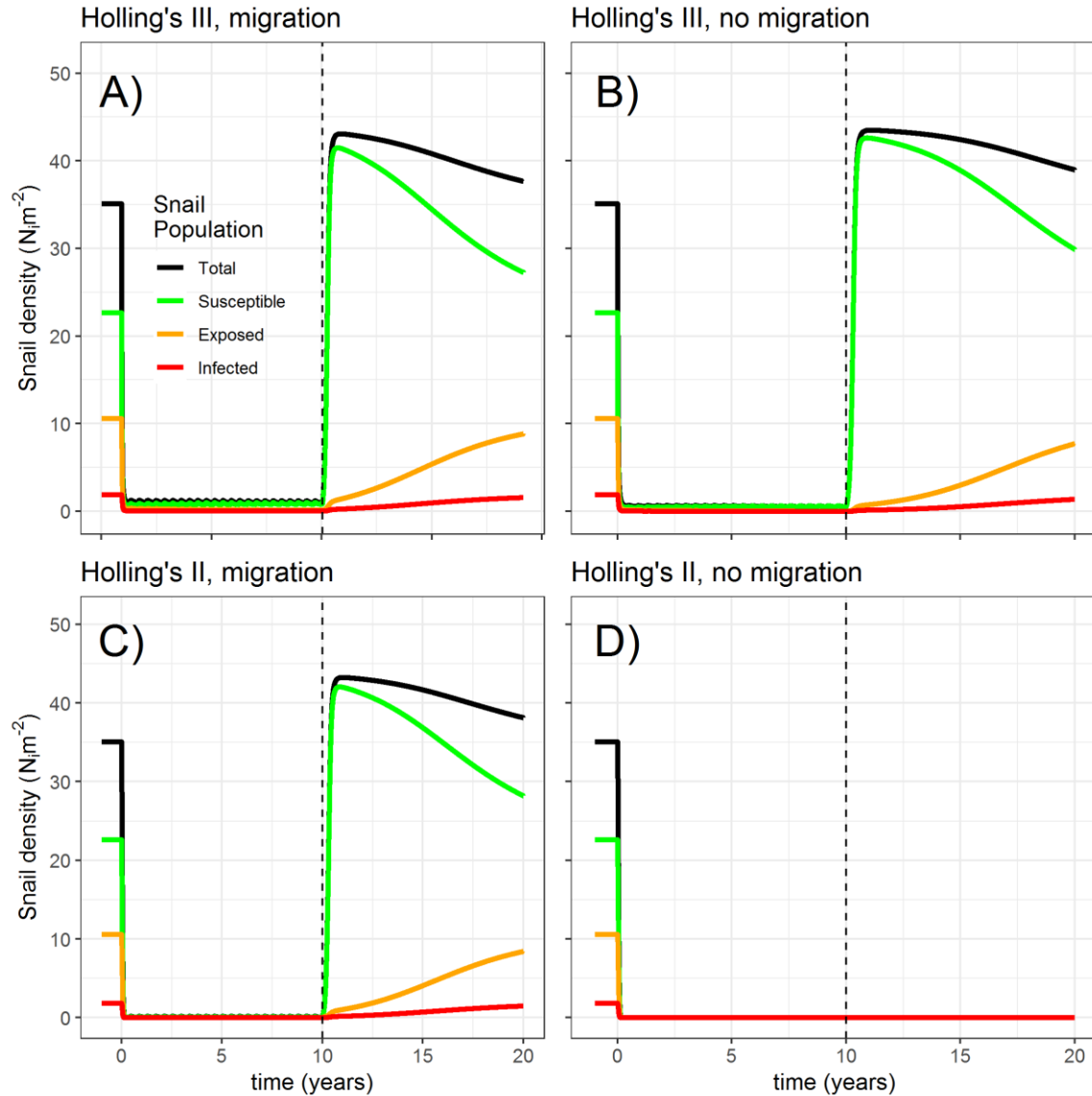
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Figure S1: Sensitivity analysis investigating the influence of fixed costs incurred each aquaculture cycle on profits generated by the prawn aquaculture model. Color indicates the 10-year cumulative profits generated by optimal management with stocking at the density indicated on the x-axis. The black line delineates the maximum boundary of profitability.



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Figure S2: Sensitivity analysis investigating the influence of increased mortality rates (baseline $\mu_P = 0.006$) on profits generated by the prawn aquaculture model. Color indicates the 10-year cumulative profits generated by optimal management with stocking at the density indicated on the x-axis. The black line delineates the maximum boundary of profitability.



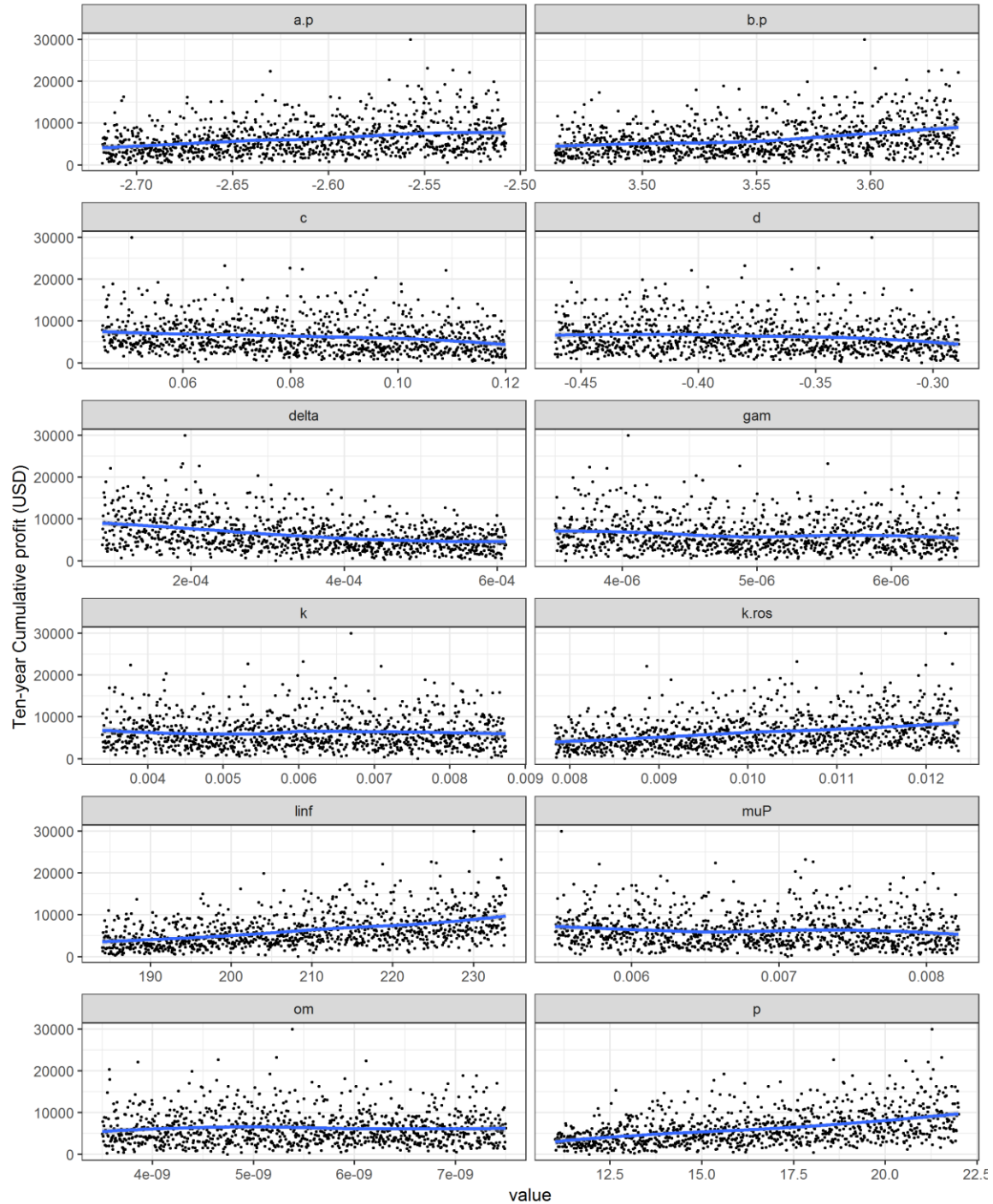
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Figure S3: Sensitivity analysis investigating the influence of the predation functional response and migration on snail infection dynamics. The model is simulated assuming a type III functional response and migration from an external source (A), a type III functional response with no migration (B), a type II functional response with migration (C), and a type II functional response with no migration (D). Simulations indicate that as long as migration is present or predation dynamics follow a type III response (indicating decreased predation rates at low densities due to e.g. prey switching or the presence of prey refugia) the snail population rapidly reestablishes after prawn interventions are discontinued.



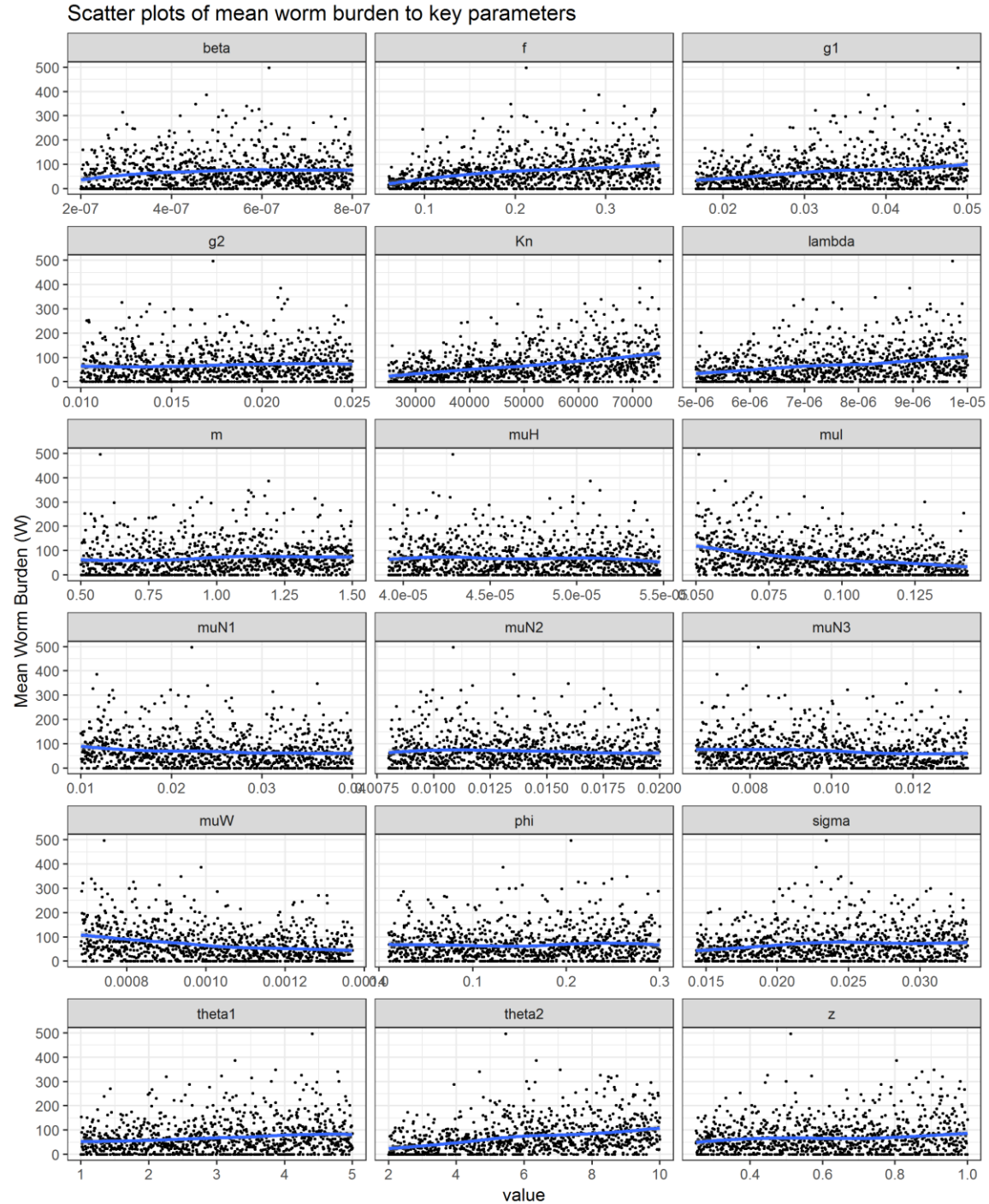
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Figure S4: Centered distributions of model parameters stratified by whether more DALYs were averted in MDA-only or in Prawn-only intervention simulations compared to no intervention simulations. Comparisons show that the MDA intervention tends to perform superior when MDA coverage (*cvrg*) and efficacy (*eff*) are higher and when infected snail and prawn mortality are higher (μ_I and μ_P , respectively). The prawn intervention performs notably better when the snail population carrying capacity (*K*) is higher.



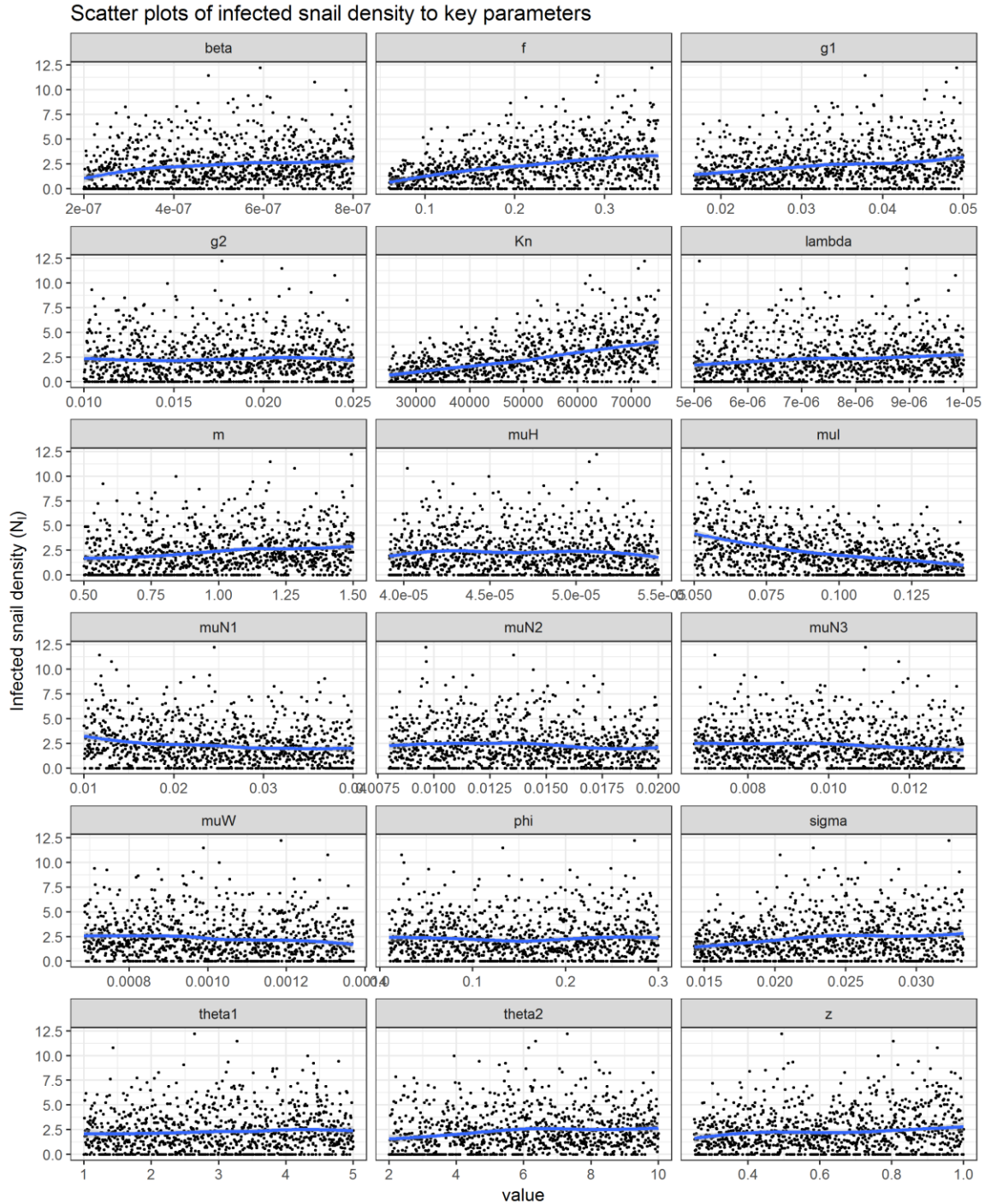
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Figure S5: Scatterplots used to verify monotonicity between parameters of the prawn aquaculture model and estimates of ten year cumulative profits. Blue lines represent loess smoothing.



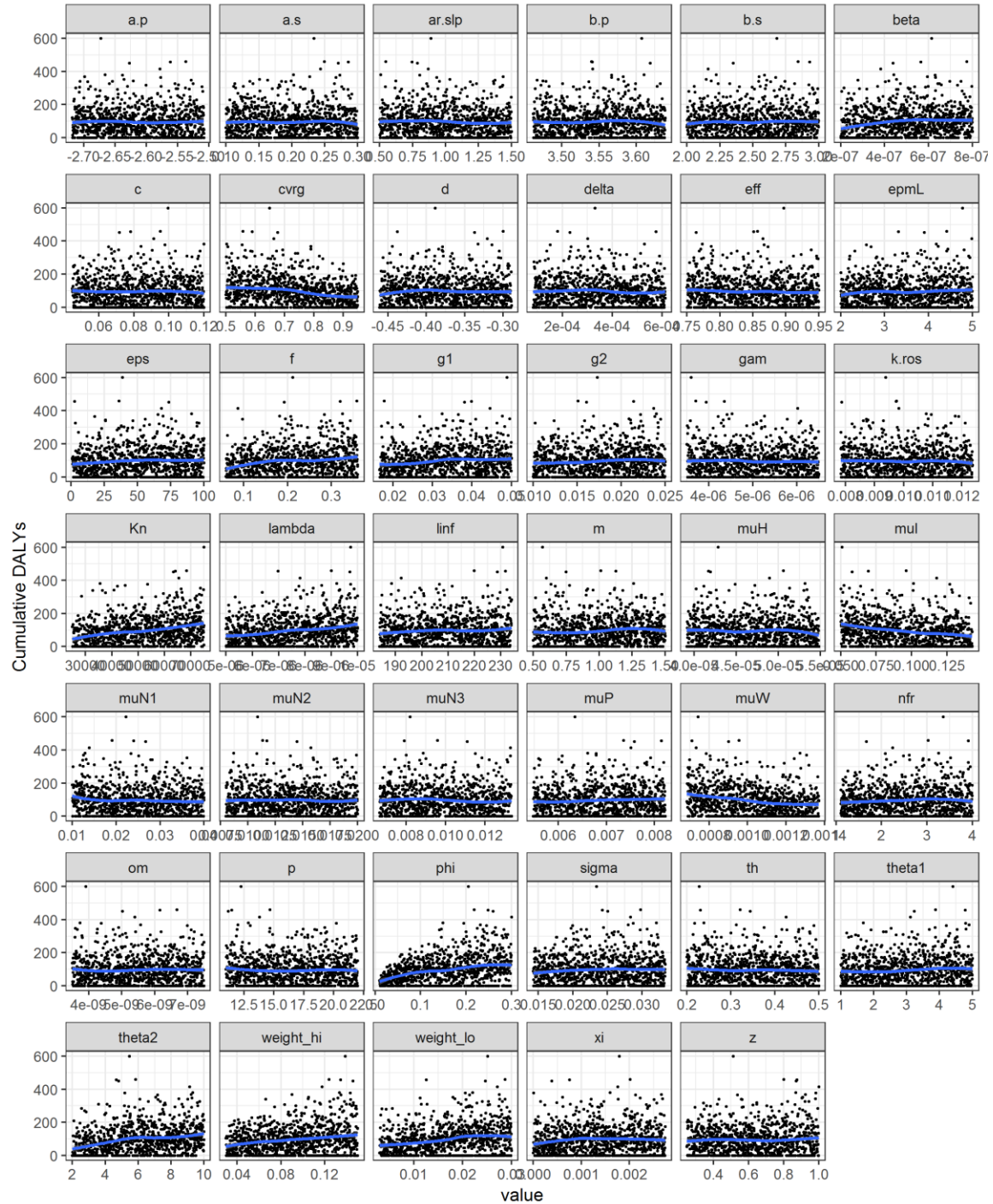
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Figure S6: Scatterplots used to verify monotonicity between parameters of the epidemiologic model and estimates of equilibrium mean worm burden. Blue lines represent loess smoothing.



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Figure S7: Scatterplots used to verify monotonicity between parameters of the epidemiologic model and estimates of equilibrium infected snail density. Blue lines represent loess smoothing.



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Figure S8: Scatterplots used to verify monotonicity between parameters of the combined model and estimates of DALYs lost during ten years of integrated MDA and prawn intervention. Blue lines represent loess smoothing.

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