

Appendix A from J. M. Henshaw et al., “Local Gamete Competition Explains Sex Allocation and Fertilization Strategies in the Sea”

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Derivation of Fertilization Rates and Fitness

Here we derive average fertilization rates and fitness for populations using each of the six reproductive strategies. We also calculate these values for mutant individuals who invade these populations with a different egg size or reproductive strategy. This allows us to compare the fitness of mutants to the population average in order to determine whether the population strategy is evolutionarily stable or, alternatively, whether it can be invaded by another reproductive strategy.

Throughout this section, we mark any variable or parameter that relates to a mutant individual with a hat (i.e., \hat{X}). We mark with a tilde (i.e., \tilde{X}) any value relating to a typical individual in the population whose gamete densities change as a result of interacting with a mutant. Values relating to typical individuals whose gamete densities are unaffected by interactions with mutants are left unmarked.

Densities of gametes in a region are written in the form E_y^x (for eggs) and S_y^x (for sperm). The subscript y denotes the type of region (c = fertilization cavity; n = neighborhood; o = open water). The superscript x distinguishes between “local” gametes that have never left their parent’s neighborhood and “foreign” gametes that have arrived from elsewhere. By assumption, only local gametes are affected by LGC. We mark the densities of local gametes with a superscript i and those of foreign gametes with a superscript f , m , or h , according to whether the region is associated with a female, male, or hermaphrodite. In the open water, all gametes are treated as foreign, and so the superscript is omitted. Thus, the density of a female’s own eggs in her fertilization cavity is written as E_c^i . The density of allosperm in the neighborhood of a hermaphrodite is S_n^h .

Dioecious Broadcast Spawners

Gamete densities for a population of dioecious broadcast spawners are described by the following equations:

$$\begin{aligned}\frac{\partial E_n^i}{\partial t} &= I_c V_n^{-1} - F_{on} V_n^{-1} E_n^i - \mu_n^e E_n^i - \gamma E_n^i S_n^f, \\ \frac{\partial S_n^f}{\partial t} &= F_{on} V_n^{-1} (S_o - S_n^f) - \mu_n^s S_n^f - \gamma (E_n^i + E_n^f) S_n^f, \\ \frac{\partial E_n^f}{\partial t} &= F_{on} V_n^{-1} (E_o - E_n^f) - \mu_n^e E_n^f - \gamma E_n^f S_n^f, \\ \frac{\partial S_n^i}{\partial t} &= I_s V_n^{-1} - F_{on} V_n^{-1} S_n^i - \mu_n^s S_n^i - \gamma E_n^m S_n^i, \\ \frac{\partial E_n^m}{\partial t} &= F_{on} V_n^{-1} (E_o - E_n^m) - \mu_n^e E_n^m - \gamma E_n^m (S_n^i + S_n^m), \\ \frac{\partial S_n^m}{\partial t} &= F_{on} V_n^{-1} (S_o - S_n^m) - \mu_n^s S_n^m - \gamma E_n^m S_n^m, \\ \frac{\partial E_o}{\partial t} &= \rho F_{on} (E_n^i + E_n^f + E_n^m - 2E_o) - \mu_o^e E_o - \gamma E_o S_o, \\ \frac{\partial S_o}{\partial t} &= \rho F_{on} (S_n^i + S_n^f + S_n^m - 2S_o) - \mu_o^s S_o - \gamma E_o S_o.\end{aligned}$$

We find the steady state solution to these equations by setting each rate of change equal to zero and solving the resulting system of simultaneous equations numerically.

Once we have calculated gamete densities, the average rate of fertilization in the population is given by

$$f = \gamma[V_n(E_n^i S_n^f + E_n^f S_n^i + E_n^m S_n^i + E_n^m S_n^m) + \rho^{-1} E_o S_o].$$

Average fitness is then simply

$$w = \frac{1}{2} f s.$$

Female with Different Egg Size Invades

Suppose a mutant female with different egg size invades the population of dioecious broadcast spawners. Gamete densities in her neighborhood are given by

$$\begin{aligned} \frac{\partial \hat{E}_n^i}{\partial t} &= \hat{I}_c V_n^{-1} - F_{on} V_n^{-1} \hat{E}_n^i - \mu_n^e \hat{E}_n^i - \gamma \hat{E}_n^i \tilde{S}_n^f, \\ \frac{\partial \tilde{S}_n^f}{\partial t} &= F_{on} V_n^{-1} (S_o - \tilde{S}_n^f) - \mu_n^s \tilde{S}_n^f - \gamma \hat{E}_n^i \tilde{S}_n^f - \gamma \tilde{E}_n^f \tilde{S}_n^f, \\ \frac{\partial \tilde{E}_n^f}{\partial t} &= F_{on} V_n^{-1} (E_o - \tilde{E}_n^f) - \mu_n^e \tilde{E}_n^f - \gamma \tilde{E}_n^f \tilde{S}_n^f. \end{aligned}$$

Since gametes in the open water are presumed not to interact locally, we can assume without loss of generality that once the mutant female's eggs reach the open water, they are spread evenly over a region of volume ρ^{-1} . Then we have

$$\begin{aligned} \frac{\partial \hat{E}_n^f}{\partial t} &= F_{on} V_n^{-1} (\hat{E}_o - \hat{E}_n^f) - \mu_n^e \hat{E}_n^f - \gamma \hat{E}_n^f S_n^f, \\ \frac{\partial \hat{E}_n^m}{\partial t} &= F_{on} V_n^{-1} (\hat{E}_o - \hat{E}_n^m) - \mu_n^e \hat{E}_n^m - \gamma \hat{E}_n^m (S_n^i + S_n^m), \\ \frac{\partial \hat{E}_o}{\partial t} &= \rho F_{on} (\hat{E}_n^i + \hat{E}_n^f + \hat{E}_n^m - 2\hat{E}_o) - \mu_o^e \hat{E}_o - \gamma \hat{E}_o S_o. \end{aligned}$$

The mutant's rate of fertilization is then

$$\hat{f} = \gamma[V_n(\hat{E}_n^i \tilde{S}_n^f + \hat{E}_n^f S_n^f + \hat{E}_n^m S_n^i + \hat{E}_n^m S_n^m) + \rho^{-1} \hat{E}_o S_o].$$

Her fitness is

$$\hat{w} = \frac{1}{2} \hat{f} \hat{s}.$$

Hermaphrodite Invades

Similarly, consider the invasion of a hermaphrodite with sex allocation \hat{r} . Gamete densities in the mutant's neighborhood are given by

$$\begin{aligned} \frac{\partial \hat{E}_n^i}{\partial t} &= (1-d)(1-\hat{r})I_c V_n^{-1} - F_{on} V_n^{-1} \hat{E}_n^i - \mu_n^e \hat{E}_n^i - \gamma \hat{E}_n^i \tilde{S}_n^h, \\ \frac{\partial \hat{S}_n^i}{\partial t} &= (1-d)\hat{r}I_s V_n^{-1} - F_{on} V_n^{-1} \hat{S}_n^i - \mu_n^s \hat{S}_n^i - \gamma \tilde{E}_n^h \hat{S}_n^i, \\ \frac{\partial \tilde{E}_n^h}{\partial t} &= F_{on} V_n^{-1} (E_o - \tilde{E}_n^h) - \mu_n^e \tilde{E}_n^h - \gamma \tilde{E}_n^h (\hat{S}_n^i + \tilde{S}_n^h), \\ \frac{\partial \tilde{S}_n^h}{\partial t} &= F_{on} V_n^{-1} (S_o - \tilde{S}_n^h) - \mu_n^s \tilde{S}_n^h - \gamma (\hat{E}_n^i + \tilde{E}_n^h) \tilde{S}_n^h. \end{aligned}$$

If we assume that once the mutant's gametes reach the open water, they are spread over a region of volume ρ^{-1} , then we have

$$\begin{aligned}\frac{\partial \hat{E}_n^f}{\partial t} &= F_{\text{on}} V_n^{-1} (\hat{E}_o - \hat{E}_n^f) - \mu_n^e \hat{E}_n^f - \gamma \hat{E}_n^f S_n^f, \\ \frac{\partial \hat{S}_n^f}{\partial t} &= F_{\text{on}} V_n^{-1} (\hat{S}_o - \hat{S}_n^f) - \mu_n^s \hat{S}_n^f - \gamma (E_n^i + E_n^f) \hat{S}_n^f, \\ \frac{\partial \hat{E}_n^m}{\partial t} &= F_{\text{on}} V_n^{-1} (\hat{E}_o - \hat{E}_n^m) - \mu_n^e \hat{E}_n^m - \gamma \hat{E}_n^m (S_n^i + S_n^m), \\ \frac{\partial \hat{S}_n^m}{\partial t} &= F_{\text{on}} V_n^{-1} (\hat{S}_o - \hat{S}_n^m) - \mu_n^s \hat{S}_n^m - \gamma E_n^m \hat{S}_n^m, \\ \frac{\partial \hat{E}_o}{\partial t} &= \rho F_{\text{on}} (\hat{E}_n^i + \hat{E}_n^f + \hat{E}_n^m - 2\hat{E}_o) - \mu_o^e \hat{E}_o - \gamma \hat{E}_o S_o, \\ \frac{\partial \hat{S}_o}{\partial t} &= \rho F_{\text{on}} (\hat{S}_n^i + \hat{S}_n^f + \hat{S}_n^m - 2\hat{S}_o) - \mu_o^s \hat{S}_o - \gamma E_o \hat{S}_o.\end{aligned}$$

The mutant's rates of fertilization through each sex are then

$$\begin{aligned}\hat{f}_{\text{female}} &= \gamma [V_n (\hat{E}_n^i \tilde{S}_n^f + \hat{E}_n^f S_n^f + \hat{E}_n^m S_n^i + \hat{E}_n^m S_n^m) + \rho^{-1} \hat{E}_o S_o], \\ \hat{f}_{\text{male}} &= \gamma [V_n (\tilde{E}_n^i \hat{S}_n^f + E_n^i \hat{S}_n^f + E_n^f \hat{S}_n^f + E_n^m \hat{S}_n^m) + \rho^{-1} E_o \hat{S}_o].\end{aligned}$$

Its fitness is

$$\hat{w} = \frac{1}{2} (\hat{f}_{\text{female}} + \hat{f}_{\text{male}}) s.$$

Egg-Retaining Female Invades

Consider now a mutant female that retains her eggs instead of releasing them. Gamete densities in her fertilization cavity and neighborhood are given by

$$\begin{aligned}\frac{\partial \hat{E}_c^i}{\partial t} &= I_c V_c^{-1} - \mu_c^e \hat{E}_c^i - \gamma \hat{E}_c^i \tilde{S}_c^f, \\ \frac{\partial \tilde{S}_c^f}{\partial t} &= F_{\text{nc}} V_c^{-1} \tilde{S}_n^f - \mu_c^s \tilde{S}_c^f - \gamma (\hat{E}_c^i + \tilde{E}_c^f) \tilde{S}_c^f, \\ \frac{\partial \tilde{E}_c^f}{\partial t} &= F_{\text{nc}} V_c^{-1} \tilde{E}_n^f - \mu_c^e \tilde{E}_c^f - \gamma \tilde{E}_c^f \tilde{S}_c^f, \\ \frac{\partial \tilde{S}_n^f}{\partial t} &= -F_{\text{nc}} V_n^{-1} \tilde{S}_n^f + F_{\text{on}} V_n^{-1} (S_o - \tilde{S}_n^f) - \mu_n^s \tilde{S}_n^f - \gamma \tilde{E}_n^f \tilde{S}_n^f, \\ \frac{\partial \tilde{E}_n^f}{\partial t} &= -F_{\text{nc}} V_n^{-1} \tilde{E}_n^f + F_{\text{on}} V_n^{-1} (E_o - \tilde{E}_n^f) - \mu_n^e \tilde{E}_n^f - \gamma \tilde{E}_n^f \tilde{S}_n^f.\end{aligned}$$

Her rate of fertilization is then

$$\hat{f} = \gamma V_c \hat{E}_c^i \tilde{S}_c^f.$$

Her fitness is

$$\hat{w} = \frac{1}{2} \hat{f} s.$$

Sperm-Retaining Male Invades

Similarly, gamete densities near a mutant sperm-retaining male are given by

$$\begin{aligned}\frac{\partial \hat{S}_c^i}{\partial t} &= I_s V_s^{-1} - \mu_c^s \hat{S}_c^i - \gamma \tilde{E}_c^m \hat{S}_c^i, \\ \frac{\partial \tilde{E}_c^m}{\partial t} &= F_{nc} V_s^{-1} \tilde{E}_n^m - \mu_c^e \tilde{E}_c^m - \gamma \tilde{E}_c^m (\hat{S}_c^i + \tilde{S}_c^m), \\ \frac{\partial \tilde{S}_c^m}{\partial t} &= F_{nc} V_s^{-1} \tilde{S}_n^m - \mu_c^s \tilde{S}_c^m - \gamma \tilde{E}_c^m \tilde{S}_c^m, \\ \frac{\partial \tilde{E}_n^m}{\partial t} &= -F_{nc} V_n^{-1} \tilde{E}_n^m + F_{on} V_n^{-1} (E_o - \tilde{E}_n^m) - \mu_n^e \tilde{E}_n^m - \gamma \tilde{E}_n^m \tilde{S}_n^m, \\ \frac{\partial \tilde{S}_n^m}{\partial t} &= -F_{nc} V_n^{-1} \tilde{S}_n^m + F_{on} V_n^{-1} (S_o - \tilde{S}_n^m) - \mu_n^s \tilde{S}_n^m - \gamma \tilde{E}_n^m \tilde{S}_n^m.\end{aligned}$$

His rate of fertilization is

$$\hat{f} = \gamma V_s \tilde{E}_c^m \hat{S}_c^i.$$

His fitness is

$$\hat{w} = \frac{1}{2} \hat{f} s.$$

Hermaphroditic Broadcast Spawners

We present equations for the remaining five reproductive strategies similarly: first the gamete densities, fertilization rates, and fitness for a population of individuals all doing the same thing; then the results for mutants invading such a population. For a population of hermaphroditic broadcast spawners, gamete densities are given by

$$\begin{aligned}\frac{\partial E_n^i}{\partial t} &= (1-d)(1-r)I_e V_n^{-1} - F_{on} V_n^{-1} E_n^i - \mu_n^e E_n^i - \gamma E_n^i S_n^h, \\ \frac{\partial S_n^i}{\partial t} &= (1-d)rI_s V_n^{-1} - F_{on} V_n^{-1} S_n^i - \mu_n^s S_n^i - \gamma E_n^h S_n^i, \\ \frac{\partial E_n^h}{\partial t} &= F_{on} V_n^{-1} (E_o - E_n^h) - \mu_n^e E_n^h - \gamma E_n^h (S_n^i + S_n^h), \\ \frac{\partial S_n^h}{\partial t} &= F_{on} V_n^{-1} (S_o - S_n^h) - \mu_n^s S_n^h - \gamma (E_n^i + E_n^h) S_n^h, \\ \frac{\partial E_o}{\partial t} &= 2\rho F_{on} (E_n^i + E_n^h - E_o) - \mu_o^e E_o - \gamma E_o S_o, \\ \frac{\partial S_o}{\partial t} &= 2\rho F_{on} (S_n^i + S_n^h - S_o) - \mu_o^s S_o - \gamma E_o S_o.\end{aligned}$$

The average rate of fertilization in the population is then

$$f = \gamma [2V_n (E_n^i S_n^h + E_n^h S_n^i + E_n^h S_n^h) + \rho^{-1} E_o S_o].$$

Average fitness is

$$w = \frac{1}{2} f s.$$

Mutant with Different Egg Size Invades

Gamete densities near a mutant hermaphrodite with different egg size are given by

$$\begin{aligned}\frac{\partial \hat{E}_n^i}{\partial t} &= (1-d)(1-\hat{r})\hat{I}_e V_n^{-1} - F_{on} V_n^{-1} \hat{E}_n^i - \mu_n^e \hat{E}_n^i - \hat{\gamma} \hat{E}_n^i \tilde{S}_n^h, \\ \frac{\partial \hat{S}_n^i}{\partial t} &= (1-d)\hat{H}_s V_n^{-1} - F_{on} V_n^{-1} \hat{S}_n^i - \mu_n^s \hat{S}_n^i - \gamma \tilde{E}_n^i \hat{S}_n^i, \\ \frac{\partial \tilde{E}_n^h}{\partial t} &= F_{on} V_n^{-1} (E_o - \tilde{E}_n^h) - \mu_n^e \tilde{E}_n^h - \gamma \tilde{E}_n^h (\hat{S}_n^i + \tilde{S}_n^h), \\ \frac{\partial \tilde{S}_n^h}{\partial t} &= F_{on} V_n^{-1} (S_o - \tilde{S}_n^h) - \mu_n^s \tilde{S}_n^h - \hat{\gamma} \hat{E}_n^i \tilde{S}_n^h - \gamma \tilde{E}_n^h \tilde{S}_n^h.\end{aligned}$$

If we assume that once the mutant's gametes reach the open water, they are spread over a region of volume $(2\rho)^{-1}$, then we have

$$\begin{aligned}\frac{\partial \hat{E}_n^h}{\partial t} &= F_{on} V_n^{-1} (\hat{E}_o - \hat{E}_n^h) - \mu_n^e \hat{E}_n^h - \hat{\gamma} \hat{E}_n^h (S_n^i + S_n^h), \\ \frac{\partial \hat{S}_n^h}{\partial t} &= F_{on} V_n^{-1} (\hat{S}_o - \hat{S}_n^h) - \mu_n^s \hat{S}_n^h - \gamma (E_n^i + E_n^h) \hat{S}_n^h, \\ \frac{\partial \hat{E}_o}{\partial t} &= 2\rho F_{on} (\hat{E}_n^i + \hat{E}_n^h - \hat{E}_o) - \mu_o^e \hat{E}_o - \hat{\gamma} \hat{E}_o S_o, \\ \frac{\partial \hat{S}_o}{\partial t} &= 2\rho F_{on} (\hat{S}_n^i + \hat{S}_n^h - \hat{S}_o) - \mu_o^s \hat{S}_o - \gamma E_o \hat{S}_o.\end{aligned}$$

The mutant's rates of fertilization through each sex are then

$$\begin{aligned}\hat{f}_{\text{female}} &= \hat{\gamma} [V_n (\hat{E}_n^i \tilde{S}_n^h + \hat{E}_n^h S_n^i + \hat{E}_n^h S_n^h) + (2\rho)^{-1} \hat{E}_o S_o], \\ \hat{f}_{\text{male}} &= \gamma [V_n (\tilde{E}_n^i \hat{S}_n^i + E_n^i \hat{S}_n^h + E_n^h \hat{S}_n^h) + (2\rho)^{-1} E_o \hat{S}_o].\end{aligned}$$

Its fitness is

$$\hat{w} = \frac{1}{2} (\hat{f}_{\text{female}} \hat{s} + \hat{f}_{\text{male}} s).$$

Pure Female Invades

Gamete densities near a mutant pure female are given by

$$\begin{aligned}\frac{\partial \hat{E}_n^i}{\partial t} &= I_e V_n^{-1} - F_{on} V_n^{-1} \hat{E}_n^i - \mu_n^e \hat{E}_n^i - \gamma \hat{E}_n^i \tilde{S}_n^f, \\ \frac{\partial \tilde{S}_n^f}{\partial t} &= F_{on} V_n^{-1} (S_o - \tilde{S}_n^f) - \mu_n^s \tilde{S}_n^f - \gamma (\hat{E}_n^i + \tilde{E}_n^f) \tilde{S}_n^f, \\ \frac{\partial \tilde{E}_n^f}{\partial t} &= F_{on} V_n^{-1} (E_o - \tilde{E}_n^f) - \mu_n^e \tilde{E}_n^f - \gamma \tilde{E}_n^f \tilde{S}_n^f.\end{aligned}$$

If we assume that once the mutant's gametes reach the open water, they are spread over a region of volume $(2\rho)^{-1}$, then we have

$$\begin{aligned}\frac{\partial \hat{E}_n^h}{\partial t} &= F_{\text{on}} V_n^{-1} (\hat{E}_o - \hat{E}_n^h) - \mu_n^e \hat{E}_n^h - \gamma \hat{E}_n^h (S_n^i + S_n^h), \\ \frac{\partial \hat{E}_o}{\partial t} &= 2\rho F_{\text{on}} (\hat{E}_n^i + \hat{E}_n^h - \hat{E}_o) - \mu_o^e \hat{E}_o - \gamma \hat{E}_o S_o.\end{aligned}$$

The mutant's rate of fertilization is then

$$\hat{f} = \gamma [V_n (\hat{E}_n^i \tilde{S}_n^f + \hat{E}_n^h S_n^i + \hat{E}_n^h S_n^h) + (2\rho)^{-1} \hat{E}_o S_o].$$

Her fitness is

$$\hat{w} = \frac{1}{2} \hat{f} s.$$

Pure Male Invades

Gamete densities near a mutant pure male are given by

$$\begin{aligned}\frac{\partial \hat{S}_n^i}{\partial t} &= I_s V_n^{-1} - F_{\text{on}} V_n^{-1} \hat{S}_n^i - \mu_n^s \hat{S}_n^i - \gamma \tilde{E}_n^m \hat{S}_n^i, \\ \frac{\partial \tilde{E}_n^m}{\partial t} &= F_{\text{on}} V_n^{-1} (E_o - \tilde{E}_n^m) - \mu_n^e \tilde{E}_n^m - \gamma \tilde{E}_n^m (\hat{S}_n^i + \tilde{S}_n^m), \\ \frac{\partial \tilde{S}_n^m}{\partial t} &= F_{\text{on}} V_n^{-1} (S_o - \tilde{S}_n^m) - \mu_n^s \tilde{S}_n^m - \gamma \tilde{E}_n^m \tilde{S}_n^m.\end{aligned}$$

If we assume that once the mutant's gametes reach the open water, they are spread over a region of volume $(2\rho)^{-1}$, then we have

$$\begin{aligned}\frac{\partial \hat{S}_n^h}{\partial t} &= F_{\text{on}} V_n^{-1} (\hat{S}_o - \hat{S}_n^h) - \mu_n^s \hat{S}_n^h - \gamma (E_n^i + E_n^h) \hat{S}_n^h, \\ \frac{\partial \hat{S}_o}{\partial t} &= 2\rho F_{\text{on}} (\hat{S}_n^i + \hat{S}_n^h - \hat{S}_o) - \mu_o^s \hat{S}_o - \gamma E_o \hat{S}_o.\end{aligned}$$

The mutant's rate of fertilization is then

$$\hat{f} = \gamma [V_n (\tilde{E}_n^m \hat{S}_n^i + E_n^i \hat{S}_n^h + E_n^h \hat{S}_n^h) + (2\rho)^{-1} E_o \hat{S}_o].$$

His fitness is

$$\hat{w} = \frac{1}{2} \hat{f} s.$$

Egg-Retaining Mutant Invades

Gamete densities near an egg-retaining mutant are given by

$$\begin{aligned}\frac{\partial \hat{E}_c^i}{\partial t} &= (1-d)(1-r)I_e V_c^{-1} - \mu_c^e \hat{E}_c^i - \gamma \hat{E}_c^i \tilde{S}_c^h, \\ \frac{\partial \tilde{S}_c^h}{\partial t} &= F_{nc} V_c^{-1} \tilde{S}_n^h - \mu_c^s \tilde{S}_c^h - \gamma (\hat{E}_c^i + \tilde{E}_c^h) \tilde{S}_c^h, \\ \frac{\partial \tilde{E}_c^h}{\partial t} &= F_{nc} V_c^{-1} \tilde{E}_n^h - \mu_c^e \tilde{E}_c^h - \gamma \tilde{E}_c^h \tilde{S}_c^h, \\ \frac{\partial \hat{S}_n^i}{\partial t} &= (1-d)rI_s V_n^{-1} - F_{on} V_n^{-1} \hat{S}_n^i - \mu_n^s \hat{S}_n^i - \gamma \tilde{E}_n^h \hat{S}_n^i, \\ \frac{\partial \tilde{E}_n^h}{\partial t} &= -F_{nc} V_n^{-1} \tilde{E}_n^h + F_{on} V_n^{-1} (E_o - \tilde{E}_n^h) - \mu_n^e \tilde{E}_n^h - \gamma \tilde{E}_n^h (\hat{S}_n^i + \tilde{S}_n^h), \\ \frac{\partial \tilde{S}_n^h}{\partial t} &= -F_{nc} V_n^{-1} \tilde{S}_n^h + F_{on} V_n^{-1} (S_o - \tilde{S}_n^h) - \mu_n^s \tilde{S}_n^h - \gamma \tilde{E}_n^h \tilde{S}_n^h.\end{aligned}$$

If we assume that once the mutant's gametes reach the open water, they are spread over a region of volume $(2\rho)^{-1}$, then we have

$$\begin{aligned}\frac{\partial \hat{S}_n^h}{\partial t} &= F_{on} V_n^{-1} (\hat{S}_o - \hat{S}_n^h) - \mu_n^s \hat{S}_n^h - \gamma (E_n^i + E_n^h) \hat{S}_n^h, \\ \frac{\partial \hat{S}_o}{\partial t} &= 2\rho F_{on} (\hat{S}_n^i + \hat{S}_n^h - \hat{S}_o) - \mu_o^s \hat{S}_o - \gamma E_o \hat{S}_o.\end{aligned}$$

The mutant's rate of fertilization is then

$$\hat{f} = \gamma [V_c \hat{E}_c^i \tilde{S}_c^h + V_n (\tilde{E}_n^h \hat{S}_n^i + E_n^i \hat{S}_n^h + E_n^h \hat{S}_n^h) + (2\rho)^{-1} E_o \hat{S}_o].$$

Its fitness is

$$\hat{w} = \frac{1}{2} \hat{f} s.$$

Sperm-Retaining Mutant Invades

Gamete densities near a sperm-retaining mutant are given by

$$\begin{aligned}\frac{\partial \hat{S}_c^i}{\partial t} &= (1-d)rI_s V_c^{-1} - \mu_c^s \hat{S}_c^i - \gamma \tilde{E}_c^h \hat{S}_c^i, \\ \frac{\partial \tilde{E}_c^h}{\partial t} &= F_{nc} V_c^{-1} \tilde{E}_n^h - \mu_c^e \tilde{E}_c^h - \gamma \tilde{E}_c^h (\hat{S}_c^i + \tilde{S}_c^h), \\ \frac{\partial \tilde{S}_c^h}{\partial t} &= F_{nc} V_c^{-1} \tilde{S}_n^h - \mu_c^s \tilde{S}_c^h - \gamma \tilde{E}_c^h \tilde{S}_c^h, \\ \frac{\partial \hat{E}_n^i}{\partial t} &= (1-d)(1-r)I_e V_n^{-1} - F_{on} V_n^{-1} \hat{E}_n^i - \mu_n^e \hat{E}_n^i - \gamma \hat{E}_n^i \tilde{S}_n^h, \\ \frac{\partial \tilde{S}_n^h}{\partial t} &= -F_{nc} V_n^{-1} \tilde{S}_n^h + F_{on} V_n^{-1} (S_o - \tilde{S}_n^h) - \mu_n^s \tilde{S}_n^h - \gamma (\hat{E}_n^i + \tilde{E}_n^h) \tilde{S}_n^h, \\ \frac{\partial \tilde{E}_n^h}{\partial t} &= -F_{nc} V_n^{-1} \tilde{E}_n^h + F_{on} V_n^{-1} (E_o - \tilde{E}_n^h) - \mu_n^e \tilde{E}_n^h - \gamma \tilde{E}_n^h \tilde{S}_n^h.\end{aligned}$$

If we assume that once the mutant's gametes reach the open water, they are spread over a region of volume $(2\rho)^{-1}$, then we have

$$\begin{aligned}\frac{\partial \hat{E}_n^h}{\partial t} &= F_{on} V_n^{-1} (\hat{E}_o - \hat{E}_n^h) - \mu_n^e \hat{E}_n^h - \gamma \hat{E}_n^h (S_n^i + S_n^h), \\ \frac{\partial \hat{E}_o}{\partial t} &= 2\rho F_{on} (\hat{E}_n^i + \hat{E}_n^h - \hat{E}_o) - \mu_o^e \hat{E}_o - \gamma \hat{E}_o S_o.\end{aligned}$$

The mutant's rate of fertilization is then

$$\hat{f} = \gamma [V_c \tilde{E}_c^i \hat{S}_c^i + V_n (\hat{E}_n^i \tilde{S}_n^h + \hat{E}_n^h \tilde{S}_n^i + \hat{E}_n^h \tilde{S}_n^h) + (2\rho)^{-1} \hat{E}_o S_o].$$

Its fitness is

$$\hat{w} = \frac{1}{2} \hat{f} s.$$

Dioecious Sperm Casters

For a population of dioecious sperm casters, gamete densities are given by

$$\begin{aligned}\frac{\partial E_c^i}{\partial t} &= I_e V_c^{-1} - \mu_c^e E_c^i - \gamma E_c^i S_c^f, \\ \frac{\partial S_c^f}{\partial t} &= F_{nc} V_c^{-1} S_n^f - \mu_c^s S_c^f - \gamma E_c^i S_c^f, \\ \frac{\partial S_n^i}{\partial t} &= I_s V_n^{-1} - F_{on} V_n^{-1} S_n^i - \mu_n^s S_n^i, \\ \frac{\partial S_n^f}{\partial t} &= -F_{nc} V_n^{-1} S_n^f + F_{on} V_n^{-1} (S_o - S_n^f) - \mu_n^s S_n^f, \\ \frac{\partial S_n^m}{\partial t} &= F_{on} V_n^{-1} (S_o - S_n^m) - \mu_n^s S_n^m, \\ \frac{\partial S_o}{\partial t} &= \rho F_{on} (S_n^i + S_n^f + S_n^m - 2S_o) - \mu_o^s S_o.\end{aligned}$$

The average rate of fertilization in the population is then

$$f = \gamma V_c E_c^i S_c^f.$$

Average fitness is

$$w = \frac{1}{2} f s.$$

Female with Different Egg Size Invades

Gamete densities near a mutant female with different egg size are given by

$$\begin{aligned}\frac{\partial \hat{E}_c^i}{\partial t} &= \hat{I}_e V_c^{-1} - \mu_c^e \hat{E}_c^i - \hat{\gamma} \hat{E}_c^i \tilde{S}_c^f, \\ \frac{\partial \tilde{S}_c^f}{\partial t} &= F_{nc} V_c^{-1} S_n^f - \mu_c^s \tilde{S}_c^f - \hat{\gamma} \hat{E}_c^i \tilde{S}_c^f.\end{aligned}$$

The mutant's fertilization rate is then

$$\hat{f} = \hat{\gamma} V_c \hat{E}_c^i \tilde{S}_c^f.$$

Her fitness is

$$\hat{w} = \frac{1}{2} \hat{f} \hat{s}.$$

Hermaphrodite Invades

Gamete densities near a mutant hermaphrodite with sex allocation \hat{r} are given by

$$\begin{aligned} \frac{\partial \hat{E}_c^i}{\partial t} &= (1-d)(1-\hat{r})I_c V_c^{-1} - \mu_c^e \hat{E}_c^i - \gamma \hat{E}_c^i \tilde{S}_c^h, \\ \frac{\partial \tilde{S}_c^h}{\partial t} &= F_{nc} V_c^{-1} S_n^f - \mu_c^s \tilde{S}_c^h - \gamma \hat{E}_c^i \tilde{S}_c^h, \\ \frac{\partial \hat{S}_n^i}{\partial t} &= (1-d)\hat{r}I_s V_n^{-1} - F_{on} V_n^{-1} \hat{S}_n^i - \mu_n^s \hat{S}_n^i. \end{aligned}$$

If we assume that once the mutant's gametes reach the open water, they are spread over a region of volume ρ^{-1} , then we have

$$\begin{aligned} \frac{\partial \hat{S}_c^f}{\partial t} &= F_{nc} V_c^{-1} \hat{S}_n^f - \mu_c^s \hat{S}_c^f - \gamma \hat{E}_c^i \hat{S}_c^f, \\ \frac{\partial \hat{S}_n^f}{\partial t} &= -F_{nc} V_n^{-1} \hat{S}_n^f + F_{on} V_n^{-1} (\hat{S}_o - \hat{S}_n^f) - \mu_n^s \hat{S}_n^f, \\ \frac{\partial \hat{S}_n^m}{\partial t} &= F_{on} V_n^{-1} (\hat{S}_o - \hat{S}_n^m) - \mu_n^s \hat{S}_n^m, \\ \frac{\partial \hat{S}_o}{\partial t} &= \rho F_{on} (\hat{S}_n^i + \hat{S}_n^f + \hat{S}_n^m - 2\hat{S}_o) - \mu_o^s \hat{S}_o. \end{aligned}$$

The mutant's fertilization rate is then

$$\hat{f} = \gamma V_c (\hat{E}_c^i \tilde{S}_c^h + E_c^i \hat{S}_c^f)$$

Its fitness is

$$\hat{w} = \frac{1}{2} \hat{f} \hat{s}$$

Egg-Releasing Female Invades

Gamete densities near a mutant egg-releasing female are given by

$$\begin{aligned} \frac{\partial \hat{E}_n^i}{\partial t} &= I_c V_n^{-1} - F_{on} V_n^{-1} \hat{E}_n^i - \mu_n^e \hat{E}_n^i - \gamma \hat{E}_n^i \tilde{S}_n^f, \\ \frac{\partial \tilde{S}_n^f}{\partial t} &= F_{on} V_n^{-1} (S_o - \tilde{S}_n^f) - \mu_n^s \tilde{S}_n^f - \gamma \hat{E}_n^i \tilde{S}_n^f. \end{aligned}$$

If we assume that once the mutant's gametes reach the open water, they are spread over a region of volume ρ^{-1} , then we have

$$\begin{aligned}\frac{\partial \hat{E}_c^f}{\partial t} &= F_{nc} V_c^{-1} \hat{E}_n^f - \mu_c^e \hat{E}_c^f - \gamma \hat{E}_c^f S_c^f, \\ \frac{\partial \hat{E}_n^f}{\partial t} &= -F_{nc} V_n^{-1} \hat{E}_n^f + F_{on} V_n^{-1} (\hat{E}_o - \hat{E}_n^f) - \mu_n^e \hat{E}_n^f - \gamma \hat{E}_n^f S_n^f, \\ \frac{\partial \hat{E}_n^m}{\partial t} &= F_{on} V_n^{-1} (\hat{E}_o - \hat{E}_n^m) - \mu_n^e \hat{E}_n^m - \gamma \hat{E}_n^m (S_n^i + S_n^m), \\ \frac{\partial \hat{E}_o}{\partial t} &= \rho F_{on} (\hat{E}_n^i + \hat{E}_n^f + \hat{E}_n^m - 2\hat{E}_o) - \mu_o^e \hat{E}_o - \gamma \hat{E}_o S_o.\end{aligned}$$

The mutant's fertilization rate is then

$$\hat{f} = \gamma [V_c \hat{E}_c^f S_c^f + V_n (\hat{E}_n^i S_n^i + \hat{E}_n^f S_n^f + \hat{E}_n^m S_n^i + \hat{E}_n^m S_n^m) + \rho^{-1} \hat{E}_o S_o].$$

Her fitness is

$$\hat{w} = \frac{1}{2} \hat{f} s.$$

Hermaphroditic Sperm Casters

For a population of hermaphroditic sperm casters, gamete densities are given by

$$\begin{aligned}\frac{\partial E_c^i}{\partial t} &= (1-d)(1-r)I_c V_c^{-1} - \mu_c^e E_c^i - \gamma E_c^i S_c^h, \\ \frac{\partial S_c^h}{\partial t} &= F_{nc} V_c^{-1} S_n^h - \mu_c^s S_c^h - \gamma E_c^i S_c^h, \\ \frac{\partial S_n^i}{\partial t} &= (1-d)rI_s V_n^{-1} - F_{on} V_n^{-1} S_n^i - \mu_n^s S_n^i, \\ \frac{\partial S_n^h}{\partial t} &= -F_{nc} V_n^{-1} S_n^h + F_{on} V_n^{-1} (S_o - S_n^h) - \mu_n^s S_n^h, \\ \frac{\partial S_o}{\partial t} &= 2\rho F_{on} (S_n^i + S_n^h - S_o) - \mu_o^s S_o.\end{aligned}$$

The average rate of fertilization in the population is then

$$f = 2\gamma V_c E_c^i S_c^h.$$

Average fitness is

$$w = \frac{1}{2} f s.$$

Mutant with Different Egg Size Invades

Gamete densities near a mutant hermaphrodite with different egg size are given by

$$\begin{aligned}\frac{\partial \hat{E}_c^i}{\partial t} &= (1-d)(1-r)\hat{I}_c V_c^{-1} - \mu_c^e \hat{E}_c^i - \hat{\gamma} \hat{E}_c^i \hat{S}_c^h, \\ \frac{\partial \hat{S}_c^h}{\partial t} &= F_{nc} V_c^{-1} \hat{S}_n^h - \mu_c^s \hat{S}_c^h - \hat{\gamma} \hat{E}_c^i \hat{S}_c^h, \\ \frac{\partial \hat{S}_n^i}{\partial t} &= (1-d)rI_s V_n^{-1} - F_{on} V_n^{-1} \hat{S}_n^i - \mu_n^s \hat{S}_n^i.\end{aligned}$$

If we assume that once the mutant's gametes reach the open water, they are spread over a region of volume $(2\rho)^{-1}$, then we have

$$\begin{aligned}\frac{\partial \hat{S}_c^h}{\partial t} &= F_{nc} V_c^{-1} \hat{S}_n^h - \mu_c^s \hat{S}_c^h - \gamma E_c^i \hat{S}_c^h, \\ \frac{\partial \hat{S}_n^h}{\partial t} &= -F_{nc} V_n^{-1} \hat{S}_n^h + F_{on} V_n^{-1} (\hat{S}_o - \hat{S}_n^h) - \mu_n^s \hat{S}_n^h, \\ \frac{\partial \hat{S}_o}{\partial t} &= 2\rho F_{on} (\hat{S}_n^i + \hat{S}_n^h - \hat{S}_o) - \mu_o^s \hat{S}_o.\end{aligned}$$

The mutant's rates of fertilization through each sex are then

$$\begin{aligned}\hat{f}_{\text{female}} &= \hat{\gamma} V_c \hat{E}_c^i \hat{S}_c^h, \\ \hat{f}_{\text{male}} &= \gamma V_c E_c^i \hat{S}_c^h.\end{aligned}$$

Its fitness is

$$\hat{w} = \frac{1}{2} (\hat{f}_{\text{female}} \hat{s} + \hat{f}_{\text{male}} s).$$

Pure Female Invades

Gamete densities near a mutant pure female are given by

$$\begin{aligned}\frac{\partial \hat{E}_c^i}{\partial t} &= I_c V_c^{-1} - \mu_c^e \hat{E}_c^i - \gamma \hat{E}_c^i \hat{S}_c^f, \\ \frac{\partial \hat{S}_c^f}{\partial t} &= F_{nc} V_c^{-1} \hat{S}_n^h - \mu_c^s \hat{S}_c^f - \gamma \hat{E}_c^i \hat{S}_c^f.\end{aligned}$$

The mutant's rate of fertilization is then

$$\hat{f} = \gamma V_c \hat{E}_c^i \hat{S}_c^f.$$

Her fitness is

$$\hat{w} = \frac{1}{2} \hat{f} \hat{s}.$$

Pure Male Invades

Gamete densities near a mutant pure male are given by

$$\frac{\partial \hat{S}_n^i}{\partial t} = I_s V_n^{-1} - F_{on} V_n^{-1} \hat{S}_n^i - \mu_n^s \hat{S}_n^i.$$

If we assume that once the mutant's gametes reach the open water, they are spread over a region of volume $(2\rho)^{-1}$, then we have

$$\begin{aligned} \frac{\partial \hat{S}_c^h}{\partial t} &= F_{nc} V_c^{-1} \hat{S}_n^h - \mu_c^s \hat{S}_c^h - \gamma E_c^i \hat{S}_c^h, \\ \frac{\partial \hat{S}_n^h}{\partial t} &= -F_{nc} V_n^{-1} \hat{S}_n^h + F_{on} V_n^{-1} (\hat{S}_o - \hat{S}_n^h) - \mu_n^s \hat{S}_n^h, \\ \frac{\partial \hat{S}_o}{\partial t} &= 2\rho F_{on} (\hat{S}_n^i + \hat{S}_n^h - \hat{S}_o) - \mu_o^s \hat{S}_o. \end{aligned}$$

The mutant's rate of fertilization is then

$$\hat{f} = \gamma V_c E_c^i \hat{S}_c^h.$$

His fitness is

$$\hat{w} = \frac{1}{2} \hat{f} \hat{s}.$$

Egg-Releasing Mutant Invades

Gamete densities near an egg-retaining mutant are given by

$$\begin{aligned} \frac{\partial \hat{E}_n^i}{\partial t} &= (1-d)(1-r) I_c V_n^{-1} - F_{on} V_n^{-1} \hat{E}_n^i - \mu_n^c \hat{E}_n^i - \gamma \hat{E}_n^i \tilde{S}_n^h, \\ \frac{\partial \hat{S}_n^i}{\partial t} &= (1-d) r I_s V_n^{-1} - F_{on} V_n^{-1} \hat{S}_n^i - \mu_n^s \hat{S}_n^i, \\ \frac{\partial \tilde{S}_n^h}{\partial t} &= F_{on} V_n^{-1} (S_o - \tilde{S}_n^h) - \mu_n^s \tilde{S}_n^h - \gamma \hat{E}_n^i \tilde{S}_n^h. \end{aligned}$$

If we assume that once the mutant's gametes reach the open water, they are spread over a region of volume $(2\rho)^{-1}$, then we have

$$\begin{aligned} \frac{\partial \hat{E}_c^h}{\partial t} &= F_{nc} V_c^{-1} \hat{E}_n^h - \mu_c^e \hat{E}_c^h - \gamma \hat{E}_c^h \hat{S}_c^h, \\ \frac{\partial \hat{S}_c^h}{\partial t} &= F_{nc} V_c^{-1} \hat{S}_n^h - \mu_c^s \hat{S}_c^h - \gamma E_c^i \hat{S}_c^h, \\ \frac{\partial \hat{E}_n^h}{\partial t} &= -F_{nc} V_n^{-1} \hat{E}_n^h + F_{on} V_n^{-1} (\hat{E}_o - \hat{E}_n^h) - \mu_n^c \hat{E}_n^h - \gamma \hat{E}_n^h (S_n^i + S_n^h), \\ \frac{\partial \hat{S}_n^h}{\partial t} &= -F_{nc} V_n^{-1} \hat{S}_n^h + F_{on} V_n^{-1} (\hat{S}_o - \hat{S}_n^h) - \mu_n^s \hat{S}_n^h, \\ \frac{\partial \hat{E}_o}{\partial t} &= 2\rho F_{on} (\hat{E}_n^i + \hat{E}_n^h - \hat{E}_o) - \mu_o^e \hat{E}_o - \gamma \hat{E}_o S_o, \\ \frac{\partial \hat{S}_o}{\partial t} &= 2\rho F_{on} (\hat{S}_n^i + \hat{S}_n^h - \hat{S}_o) - \mu_o^s \hat{S}_o. \end{aligned}$$

The mutant's rate of fertilization is then

$$\hat{f} = \gamma[V_c(\hat{E}_c^h S_c^h + E_c^i \hat{S}_c^h) + V_n(\hat{E}_n^i \hat{S}_n^h + \hat{E}_n^h S_n^i + \hat{E}_n^h S_n^h) + (2\rho)^{-1} \hat{E}_o S_o].$$

Its fitness is

$$\hat{w} = \frac{1}{2} \hat{f} s.$$

Dioecious Egg Casters

For a population of dioecious egg casters, gamete densities are given by

$$\begin{aligned} \frac{\partial S_c^i}{\partial t} &= I_s V_c^{-1} - \mu_c^s S_c^i - \gamma E_c^m S_c^i, \\ \frac{\partial E_c^m}{\partial t} &= F_{nc} V_c^{-1} E_n^m - \mu_c^e E_c^m - \gamma E_c^m S_c^i, \\ \frac{\partial E_n^i}{\partial t} &= I_e V_n^{-1} - F_{on} V_n^{-1} E_n^i - \mu_n^e E_n^i, \\ \frac{\partial E_n^f}{\partial t} &= F_{on} V_n^{-1} (E_o - E_n^f) - \mu_n^e E_n^f, \\ \frac{\partial E_n^m}{\partial t} &= -F_{nc} V_n^{-1} E_n^m + F_{on} V_n^{-1} (E_o - E_n^m) - \mu_n^e E_n^m, \\ \frac{\partial E_o}{\partial t} &= \rho F_{on} (E_n^i + E_n^f + E_n^m - 2E_o) - \mu_o^e E_o. \end{aligned}$$

The average rate of fertilization in the population is then

$$f = \gamma V_c E_c^m S_c^i.$$

Average fitness is

$$w = \frac{1}{2} f s.$$

Female with Different Egg Size Invades

Gamete densities near a mutant female with different egg size are given by

$$\frac{\partial \hat{E}_n^i}{\partial t} = \hat{I}_e V_n^{-1} - F_{on} V_n^{-1} \hat{E}_n^i - \mu_n^e \hat{E}_n^i.$$

If we assume that once the mutant's gametes reach the open water, they are spread over a region of volume ρ^{-1} , then we have

$$\begin{aligned} \frac{\partial \hat{E}_c^m}{\partial t} &= F_{nc} V_c^{-1} \hat{E}_n^m - \mu_c^e \hat{E}_c^m - \hat{\gamma} \hat{E}_c^m S_c^i, \\ \frac{\partial \hat{E}_n^f}{\partial t} &= F_{on} V_n^{-1} (\hat{E}_o - \hat{E}_n^f) - \mu_n^e \hat{E}_n^f, \\ \frac{\partial \hat{E}_n^m}{\partial t} &= -F_{nc} V_n^{-1} \hat{E}_n^m + F_{on} V_n^{-1} (\hat{E}_o - \hat{E}_n^m) - \mu_n^e \hat{E}_n^m, \\ \frac{\partial \hat{E}_o}{\partial t} &= \rho F_{on} (\hat{E}_n^i + \hat{E}_n^f + \hat{E}_n^m - 2\hat{E}_o) - \mu_o^e \hat{E}_o. \end{aligned}$$

The mutant's rate of fertilization is then

$$\hat{f} = \hat{\gamma} V_c \hat{E}_c^m S_c^i.$$

Her fitness is

$$\hat{w} = \frac{1}{2} \hat{f} \hat{s}.$$

Hermaphrodite Invades

Gamete densities near a mutant hermaphrodite with sex allocation \hat{r} are given by

$$\begin{aligned} \frac{\partial \hat{S}_c^i}{\partial t} &= (1-d) \hat{r} I_s V_c^{-1} - \mu_c^s \hat{S}_c^i - \gamma \tilde{E}_c^h \hat{S}_c^i, \\ \frac{\partial \tilde{E}_c^h}{\partial t} &= F_{nc} V_c^{-1} E_n^m - \mu_c^e \tilde{E}_c^h - \gamma \tilde{E}_c^h \hat{S}_c^i, \\ \frac{\partial \hat{E}_n^i}{\partial t} &= (1-d)(1-\hat{r}) I_c V_n^{-1} - F_{on} V_n^{-1} \hat{E}_n^i - \mu_n^e \hat{E}_n^i. \end{aligned}$$

If we assume that once the mutant's gametes reach the open water, they are spread over a region of volume ρ^{-1} , then we have

$$\begin{aligned} \frac{\partial \hat{E}_c^m}{\partial t} &= F_{nc} V_c^{-1} \hat{E}_n^m - \mu_c^e \hat{E}_c^m - \gamma \hat{E}_c^m S_c^i, \\ \frac{\partial \hat{E}_n^r}{\partial t} &= F_{on} V_n^{-1} (\hat{E}_o - \hat{E}_n^r) - \mu_n^e \hat{E}_n^r, \\ \frac{\partial \hat{E}_n^m}{\partial t} &= -F_{nc} V_n^{-1} \hat{E}_n^m + F_{on} V_n^{-1} (\hat{E}_o - \hat{E}_n^m) - \mu_n^e \hat{E}_n^m, \\ \frac{\partial \hat{E}_o}{\partial t} &= \rho F_{on} (\hat{E}_n^i + \hat{E}_n^r + \hat{E}_n^m - 2\hat{E}_o) - \mu_o^e \hat{E}_o. \end{aligned}$$

The mutant's rate of fertilization is then

$$\hat{f} = \gamma V_c (\tilde{E}_c^h \hat{S}_c^i + \hat{E}_c^m S_c^i).$$

Its fitness is

$$\hat{w} = \frac{1}{2} \hat{f} \hat{s}.$$

Sperm-Releasing Male Invades

Gamete densities near a mutant sperm-releasing male are given by

$$\begin{aligned} \frac{\partial \hat{S}_n^i}{\partial t} &= I_s V_n^{-1} - F_{on} V_n^{-1} \hat{S}_n^i - \mu_n^s \hat{S}_n^i - \gamma \tilde{E}_n^m \hat{S}_n^i, \\ \frac{\partial \tilde{E}_n^m}{\partial t} &= F_{on} V_n^{-1} (E_o - \tilde{E}_n^m) - \mu_n^e \tilde{E}_n^m - \gamma \tilde{E}_n^m \hat{S}_n^i. \end{aligned}$$

If we assume that once the mutant's gametes reach the open water, they are spread over a region of volume ρ^{-1} , then we have

$$\begin{aligned}\frac{\partial \hat{S}_c^m}{\partial t} &= F_{nc} V_c^{-1} \hat{S}_n^m - \mu_c^s \hat{S}_c^m - \gamma E_c^m \hat{S}_c^m, \\ \frac{\partial \hat{S}_n^r}{\partial t} &= F_{on} V_n^{-1} (\hat{S}_o - \hat{S}_n^r) - \mu_n^s \hat{S}_n^r - \gamma (E_n^i + E_n^f) \hat{S}_n^r, \\ \frac{\partial \hat{S}_n^m}{\partial t} &= -F_{nc} V_n^{-1} \hat{S}_n^m + F_{on} V_n^{-1} (\hat{S}_o - \hat{S}_n^m) - \mu_n^s \hat{S}_n^m - \gamma E_n^m \hat{S}_n^m, \\ \frac{\partial \hat{S}_o}{\partial t} &= \rho F_{on} (\hat{S}_n^i + \hat{S}_n^r + \hat{S}_n^m - 2\hat{S}_o) - \mu_o^s \hat{S}_o - \gamma E_o \hat{S}_o.\end{aligned}$$

The mutant's rate of fertilization is then

$$\hat{f} = \gamma [V_c E_c^m \hat{S}_c^m + V_n (\tilde{E}_n^m \hat{S}_n^i + E_n^i \hat{S}_n^r + E_n^f \hat{S}_n^r + E_n^m \hat{S}_n^m) + \rho^{-1} E_o \hat{S}_o].$$

His fitness is

$$\hat{w} = \frac{1}{2} \hat{f} s.$$

Hermaphroditic Egg Casters

For a population of hermaphroditic egg casters, gamete densities are given by

$$\begin{aligned}\frac{\partial S_c^i}{\partial t} &= (1-d)rI_c V_c^{-1} - \mu_c^s S_c^i - \gamma E_c^h S_c^i, \\ \frac{\partial E_c^h}{\partial t} &= F_{nc} V_c^{-1} E_n^h - \mu_c^e E_c^h - \gamma E_c^h S_c^i, \\ \frac{\partial E_n^i}{\partial t} &= (1-d)(1-r)I_c V_n^{-1} - F_{on} V_n^{-1} E_n^i - \mu_n^e E_n^i, \\ \frac{\partial E_n^h}{\partial t} &= -F_{nc} V_n^{-1} E_n^h + F_{on} V_n^{-1} (E_o - E_n^h) - \mu_n^e E_n^h, \\ \frac{\partial E_o}{\partial t} &= 2\rho F_{on} (E_n^i + E_n^h - E_o) - \mu_o^e E_o.\end{aligned}$$

The average rate of fertilization in the population is then

$$f = 2\gamma V_c E_c^h S_c^i.$$

Average fitness is

$$w = \frac{1}{2} f s.$$

Mutant with Different Egg Size Invades

Gamete densities near a mutant with different egg size are given by

$$\begin{aligned}\frac{\partial \hat{S}_c^i}{\partial t} &= (1-d)\hat{H}_s V_c^{-1} - \mu_c^s \hat{S}_c^i - \gamma \tilde{E}_c^h \hat{S}_c^i, \\ \frac{\partial \tilde{E}_c^h}{\partial t} &= F_{nc} V_c^{-1} E_n^h - \mu_c^e \tilde{E}_c^h - \gamma \tilde{E}_c^h \hat{S}_c^i, \\ \frac{\partial \hat{E}_n^i}{\partial t} &= (1-d)(1-\hat{r})\hat{I}_c V_n^{-1} - F_{on} V_n^{-1} \hat{E}_n^i - \mu_n^e \hat{E}_n^i.\end{aligned}$$

If we assume that once the mutant's gametes reach the open water, they are spread over a region of volume $(2\rho)^{-1}$, then we have

$$\begin{aligned}\frac{\partial \hat{E}_c^h}{\partial t} &= F_{nc} V_c^{-1} \hat{E}_n^h - \mu_c^e \hat{E}_c^h - \hat{\gamma} \hat{E}_c^h \hat{S}_c^i, \\ \frac{\partial \hat{E}_n^h}{\partial t} &= -F_{nc} V_n^{-1} \hat{E}_n^h + F_{on} V_n^{-1} (\hat{E}_o - \hat{E}_n^h) - \mu_n^e \hat{E}_n^h, \\ \frac{\partial \hat{E}_o}{\partial t} &= 2\rho F_{on} (\hat{E}_n^i + \hat{E}_n^h - \hat{E}_o) - \mu_o^e \hat{E}_o.\end{aligned}$$

The mutant's rates of fertilization through each sex are then

$$\begin{aligned}\hat{f}_{\text{female}} &= \hat{\gamma} V_c \hat{E}_c^h \hat{S}_c^i \\ \hat{f}_{\text{male}} &= \gamma V_c \tilde{E}_c^h \hat{S}_c^i.\end{aligned}$$

Its fitness is

$$\hat{w} = \frac{1}{2} (\hat{f}_{\text{female}} \hat{s} + \hat{f}_{\text{male}} s).$$

Pure Female Invades

Gamete densities near a mutant pure female are given by

$$\frac{\partial \hat{E}_n^i}{\partial t} = I_c V_n^{-1} - F_{on} V_n^{-1} \hat{E}_n^i - \mu_n^e \hat{E}_n^i.$$

If we assume that once the mutant's gametes reach the open water, they are spread over a region of volume $(2\rho)^{-1}$, then we have

$$\begin{aligned}\frac{\partial \hat{E}_c^h}{\partial t} &= F_{nc} V_c^{-1} \hat{E}_n^h - \mu_c^e \hat{E}_c^h - \hat{\gamma} \hat{E}_c^h \hat{S}_c^i, \\ \frac{\partial \hat{E}_n^h}{\partial t} &= -F_{nc} V_n^{-1} \hat{E}_n^h + F_{on} V_n^{-1} (\hat{E}_o - \hat{E}_n^h) - \mu_n^e \hat{E}_n^h, \\ \frac{\partial \hat{E}_o}{\partial t} &= 2\rho F_{on} (\hat{E}_n^i + \hat{E}_n^h - \hat{E}_o) - \mu_o^e \hat{E}_o.\end{aligned}$$

The mutant's rate of fertilization is then

$$\hat{f} = \gamma V_c \hat{E}_c^h \hat{S}_c^i.$$

Her fitness is

$$\hat{w} = \frac{1}{2}\hat{f}s.$$

Pure Male Invades

Gamete densities near a mutant pure male are given by

$$\begin{aligned}\frac{\partial \hat{S}_c^i}{\partial t} &= I_s V_c^{-1} - \mu_c^s \hat{S}_c^i - \gamma \tilde{E}_c^h \hat{S}_c^i \\ \frac{\partial \tilde{E}_c^h}{\partial t} &= F_{nc} V_c^{-1} E_n^h - \mu_c^e \tilde{E}_c^h - \gamma \tilde{E}_c^h \hat{S}_c^i\end{aligned}$$

The mutant's rate of fertilization is then

$$\hat{f} = \gamma V_c \tilde{E}_c^h \hat{S}_c^i.$$

His fitness is

$$\hat{w} = \frac{1}{2}\hat{f}s.$$

Sperm-Releasing Mutant Invades

Gamete densities near a sperm-releasing mutant are given by

$$\begin{aligned}\frac{\partial \hat{E}_n^i}{\partial t} &= (1-d)(1-r)I_e V_n^{-1} - F_{on} V_n^{-1} \hat{E}_n^i - \mu_n^e \hat{E}_n^i, \\ \frac{\partial \hat{S}_n^i}{\partial t} &= (1-d)rI_s V_n^{-1} - F_{on} V_n^{-1} \hat{S}_n^i - \mu_n^s \hat{S}_n^i - \gamma \tilde{E}_n^h \hat{S}_n^i, \\ \frac{\partial \tilde{E}_n^h}{\partial t} &= F_{nc} V_n^{-1} (E_o - \tilde{E}_n^h) - \mu_n^e \tilde{E}_n^h - \gamma \tilde{E}_n^h \hat{S}_n^i.\end{aligned}$$

If we assume that once the mutant's gametes reach the open water, they are spread over a region of volume $(2\rho)^{-1}$, then we have

$$\begin{aligned}\frac{\partial \hat{E}_c^h}{\partial t} &= F_{nc} V_c^{-1} \hat{E}_n^h - \mu_c^e \hat{E}_c^h - \gamma \hat{E}_c^h \hat{S}_c^i, \\ \frac{\partial \hat{S}_c^h}{\partial t} &= F_{nc} V_c^{-1} \hat{S}_n^h - \mu_c^s \hat{S}_c^h - \gamma E_c^h \hat{S}_c^h, \\ \frac{\partial \hat{E}_n^h}{\partial t} &= -F_{nc} V_n^{-1} \hat{E}_n^h + F_{on} V_n^{-1} (\hat{E}_o - \hat{E}_n^h) - \mu_n^e \hat{E}_n^h, \\ \frac{\partial \hat{S}_n^h}{\partial t} &= -F_{nc} V_n^{-1} \hat{S}_n^h + F_{on} V_n^{-1} (\hat{S}_o - \hat{S}_n^h) - \mu_n^s \hat{S}_n^h - \gamma (E_n^i + E_n^h) \hat{S}_n^h, \\ \frac{\partial \hat{E}_o}{\partial t} &= 2\rho F_{on} (\hat{E}_n^i + \hat{E}_n^h - \hat{E}_o) - \mu_o^e \hat{E}_o, \\ \frac{\partial \hat{S}_o}{\partial t} &= 2\rho F_{on} (\hat{S}_n^i + \hat{S}_n^h - \hat{S}_o) - \mu_o^s \hat{S}_o - \gamma E_o \hat{S}_o.\end{aligned}$$

The mutant's rate of fertilization is then

$$\hat{f} = \gamma[V_c(\hat{E}_c^h S_c^i + E_c^h \hat{S}_c^h) + V_n(\tilde{E}_n^h \hat{S}_n^i + E_n^i \hat{S}_n^h + E_n^h \hat{S}_n^h) + (2\rho)^{-1} E_o \hat{S}_o].$$

Its fitness is

$$\hat{w} = \frac{1}{2} \hat{f} s.$$

Appendix B from J. M. Henshaw et al., “Local Gamete Competition Explains Sex Allocation and Fertilization Strategies in the Sea” (Am. Nat., vol. 184, no. 2, p. E32)

Choice of Parameters

In the robustness analysis, we generated parameter values randomly for each trial. Here we present the range of values from which each parameter was chosen (table B1). We also justify our choice of ranges for scaling exponents. These exponents determine the allometric relationships between body size, population density, and pumping ability and between egg size and fertilization efficiency. Lastly, we consider two parameters that were not varied randomly: the gamete budget coefficient k_M and the volume of a fertilization cavity V_c .

Body Size B

In the first series of trials, we chose the logarithm of body size $\log_{10}B$ from the range (1,7) according to a uniform distribution. We stratified the randomization so that $\log_{10}B$ was in the range $(i, i + 1)$ exactly 200 times for each integer $i = 1, \dots, 6$. In the second series of trials, we compared behavior at fixed body sizes of $B = 10^2$ and $B = 10^4$ in one half of the trials and at $B = 10^4$ and $B = 10^6$ in the other half.

Population Density ρ

Larger-bodied species tend to live at lower population densities. In studies of single taxa taken over large geographic areas, scaling of population density in body size is surprisingly consistent, with a scaling exponent usually near -0.75 (Damuth 1987; White et al. 2007). Scaling relationships measured over local areas show both more varied relationships and poorer fits, although aquatic systems appear to be more consistent than terrestrial ones (Marquet et al. 1990; Cyr et al. 1997; White et al. 2007). In the vast majority of cases, scaling exponents of population density to body size lie between -1 and -0.5 . Consequently, we assume that

$$\rho = k_\rho B^{a_\rho}, \quad (\text{B1})$$

with $-1 < a_\rho < -0.5$.

Water Flow in the Fertilization Cavity F_{nc}

In sessile or slow-moving benthic species, water flow into the fertilization cavity has two potential causes. First, ambient currents flow over the organism. Second, many organisms actively pump water, often as part of their feeding behavior (Bishop and Pemberton 2006). In organisms dominated by ambient currents, we can assume that water flows through the fertilization cavity via an entrance region that is perpendicular or oblique to the current. In this case, the rate of flow will be proportional to the area of the entrance region. Assuming isometry of the fertilization cavity, this results in a scaling relationship of the form

$$F_{nc} = k_f B^{a_f}, \quad (\text{B2})$$

with an exponent of $a_f = 0.67$.

For organisms that actively pump water, we assume for simplicity that gametes are filtered out of the water via one or more cylindrical filtration pipes. Suppose that each pipe has length L and radius a . By the Hagen-Poiseuille equation (Spurk and Aksel 2008), the pressure drop Δp required to pump water through such a pipe at a rate of F'_{nc} obeys

$$\Delta p \propto \frac{L F'_{nc}}{a^4}. \quad (\text{B3})$$

The power required to maintain this pressure drop is given by $P' = F'_{nc} \Delta p$, and so this implies that

$$F'_{nc} \propto \sqrt{\frac{a^4 P'}{L}}. \quad (\text{B4})$$

Let us write $P = nP'$ for the total power requirement. Then the total water flow through n pipes is given by

$$F_{nc} = nF'_{nc} \propto \sqrt{\frac{na^4P}{L}}. \quad (\text{B5})$$

If filtration of gametes can only happen along the boundary surface of pipes, then pipe radius should be independent of body size (Vogel 1981). In this case, the number of pipes increases as $B^{2/3}$ and their lengths increase as $B^{1/3}$. Consequently, we have $F_{nc} \propto (B^{1/3}P)^{1/2}$.

Let us now consider the allometry of P , the total power devoted to pumping water. If organisms devote a fixed proportion of their metabolism to pumping, then P will increase in proportion to total metabolic rate. Empirical studies of the allometry of metabolism in marine organisms suggest that scaling exponents almost always lie in the range of 0.6 to 1.0 (Patterson 1992; Glazier 2005). Taking these estimates gives us a scaling exponent for water flow of $0.47 \leq a_f \leq 0.67$ if the radius of pipes is independent of body size. Larger scaling exponents are expected if pipe radius increases with body size.

Empirical studies on the allometry of pumping rate and body size have most often focused on suspension-feeding bivalves. These studies have found that most scaling exponents lie between 0.6 and 0.75 (Riisgård 2001), which is in broad agreement with the range calculated above. To ensure the full range of natural variation is covered for both passive and active organisms, we consider scaling exponents in the range $0.5 < a_f < 0.8$. In this range, water flow increases with body size but at a rate that is less than isometric.

Fertilization Efficiency γ

The efficiency of fertilization depends on how fast gametes move and on how close they must be for fertilization to occur. Suppose that the movement of sperm relative to eggs is approximately Brownian with a diffusion coefficient of δ and that fertilization occurs when sperm approach within a distance r of an egg. Then the gamete encounter coefficient is given by (Dusenbery 2009)

$$\gamma = 4\pi r\delta. \quad (\text{B6})$$

Suppose first that gametes must be in direct contact for fertilization to occur and that they have no mechanism to detect and swim toward opposite-type gametes. If we approximate eggs as spheres of volume m_e then the detection distance r is simply equal to the egg's radius. Consequently,

$$r = \sqrt[3]{\frac{3}{4\pi}m_e^{1/3}}. \quad (\text{B7})$$

In most species, however, fertilization rates are improved through chemotaxis: eggs produce pheromones, while sperm can detect and swim toward higher pheromone concentrations (Kaupp et al. 2008). Chemotaxis improves fertilization rates by increasing the detection distance.

Theoretical calculations suggest that if a fixed proportion of egg metabolism is devoted to pheromone production, then detection distance could increase in proportion to egg volume (Dusenbery 2011). There is, however, an upper limit to the detection distance that can be achieved by diffusion of pheromones. This is because, under natural conditions, turbulence disrupts diffusion over larger scales. It is difficult to estimate the scale on which turbulent effects will become important and little is known about pheromone transport under field conditions (Grasso 2001). In the absence of more detailed estimates, we assume that detection distance obeys the relationship

$$r = k_r \cdot (m_e)^{a_r}, \quad (\text{B8})$$

with $1/3 < a_r < 1$. This range includes the extreme cases where no pheromones are produced and where pheromone diffusion is unaffected by turbulent flow. It also includes more realistic cases where turbulence disrupts pheromone signals over larger scales. Assuming that egg speed is independent of egg size, this means that fertilization efficiency is related to egg size by

$$\gamma = k_\gamma \cdot (m_e)^{a_\gamma}, \quad (\text{B9})$$

with $1/3 < a_\gamma < 1$.

Gamete Budget Coefficient k_M and Volume of Fertilization Cavity V_c

Two parameters were not varied randomly. First, the gamete budget coefficient k_M determines the ratio of gamete

production to body size, according to the relationship $M = k_m B$. Since varying this coefficient is equivalent to changing the scale on which body size is measured, we left it fixed at $k_m = 10^{-4}$ for all trials.

Second, the volume of a fertilization cavity V_c must be sufficient to hold the maximum volume of gametes that an individual retains at any one time. Since M is the volume of gametes produced per unit time, this maximum is given by M/μ , where μ is the mortality rate of retained gametes. We set

$$V_c = M/\mu_c^e \tag{B10}$$

for all individuals, regardless of sex. This means that fertilization cavities are the same size in females, males, and hermaphrodites. It also ensures that the volume of fertilization cavities increases isometrically with body size.

Table B1. Parameter ranges for robustness analysis

Parameter	Value chosen uniformly from
d	(0,.2)
α	(.1,1)
a_γ	(1/3,1)
a_p	(-1,-.5)
a_F	(.5,.8)
	Log ₁₀ of value chosen uniformly from
B	(1,7)
F_{on}	(1,3)
V_n	(3,5)
m_s	(-5,-3)
μ_n^s	(-6,-4)
μ_n^s	(-4,-2)
μ_L	(-3,-2)
k_γ	(0,2)
k_p	(-6,-4)
k_F	(-1,1)

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