

1 **Evolutionarily stable strategies for fecundity and**  
2 **swimming speed of fish**

3 **Michael J. Plank · Jonathan W.**  
4 **Pitchford · Alex James**

5  
6 the date of receipt and acceptance should be inserted later

7 **Abstract** Many pelagic fish species have a life history that involves producing  
8 a large number of small eggs. This is the result of a trade-off between fecun-  
9 dity and larval survival probability. There are also trade-offs involving other  
10 traits, such as larval swimming speed. Swimming faster increases the average  
11 food encounter rate but also increases the metabolic cost. Here we introduce  
12 an evolutionary model comprising fecundity and swimming speed as heritable  
13 traits. We show that there can be two evolutionary stable strategies. In en-  
14 vironments where there is little noise in the food encounter rate, the stable  
15 strategy is a low-fecundity strategy with a swimming speed that minimises  
16 the mean time taken to reach reproductive maturity. However, in noisy envi-  
17 ronments, for example where the prey distribution is patchy or the water is  
18 turbulent, strategies that optimise mean outcomes are often outperformed by  
19 strategies that increase inter-individual variance. We show that, when larval  
20 growth rates are unpredictable, a high-fecundity strategy is evolutionarily sta-  
21 ble. In a population following this strategy, the swimming speed is higher than  
22 would be anticipated by maximising the mean growth rate.

23 **Keywords** first passage time · fish egg size · fish growth rate · genetic  
24 algorithm · patchiness · stochastic growth

---

M. J. Plank  
School of Mathematics and Statistics, University of Canterbury, Christchurch 8140, New  
Zealand and Te Pūnaha Matatini, a New Zealand Centre of Research Excellence. E-mail:  
michael.plank@canterbury.ac.nz

J. W. Pitchford  
York Centre for Complex Systems Analysis, University of York, United Kingdom. E-mail:  
jon.pitchford@york.ac.uk

A. James  
School of Mathematics and Statistics, University of Canterbury, Christchurch 8140, New  
Zealand and Te Pūnaha Matatini, a New Zealand Centre of Research Excellence. E-mail:  
alex.james@canterbury.ac.nz

## 1 Introduction

Newborn larvae of pelagic spawning fish species face an extremely uncertain outlook. The median egg diameter of marine fish species is approximately 1.1 mm (Chambers and Leggett, 1996). These tiny eggs are abandoned by their parents in turbulent water (MacKenzie and Kiørboe, 1995), with a highly patchy prey distribution (Tsuda et al., 1993), spatiotemporal variations in abiotic factors like temperature and salinity (Jennings and Warr, 2003) and an abundance of predators. Most quickly perish – larval mortality rates as high as 42% per day have been recorded in Atlantic mackerel (Ware and Lambert, 1985) – but a lucky few reach reproductive maturity and contribute to the generation of spawners.

Most marine fish species have very high fecundity (Elgar, 1990). This high fecundity, high mortality life history skews the evolutionary pressures that operate on these populations because only the extreme tail of the fitness distribution contributes to the next generation. For this reason, the inter-individual variance in metrics such as the prey encounter rate can be a more important determinant of reproductive fitness than the mean (Pitchford et al., 2005).

Larval swimming speed is an important factor affecting the expected prey encounter rate (Chick and Van Den Avyle, 2000). There are trade-offs involving this trait: swimming faster will increase the prey encounter rate but will also increase energy expenditure. Previous models of swimming speed (Darowski et al., 1988; Pitchford et al., 2003) have focused on maximising the mean net rate of energy gain or mean growth rate. However, because only a tiny fraction of larvae reach reproductive maturity, the important part of the distribution of growth rates is the tail and focusing on optimising mean values may not produce representative results (Pitchford et al., 2005). In such circumstances, a strategy with a lower mean growth rate but a higher variance in the growth rate may be evolutionarily advantageous. This can occur if some fitness effects of a heritable trait are subject to higher demographic stochasticity (inter-individual variance) than others (Currey et al., 2007). Increasing swimming speed has an energetic cost that is approximately deterministic because it is a function of the energy required to overcome the drag force of the water (Pitchford et al., 2003). In contrast, the energetic benefit of swimming faster is stochastic because prey distributions are often very patchy (Duarte and Alcaraz, 1989).

The trade-offs between fecundity and egg size have been studied empirically and theoretically (Elgar, 1990; Winemiller and Rose, 1993; Andersen et al., 2008). Pelagic-spawning marine species tend to have very high fecundity and very small egg sizes, whereas demersal spawners and freshwater species typically produce fewer, larger eggs, possibly due to lower inter-larval variability (Duarte and Alcaraz, 1989). Models with a predetermined mortality rate cannot fully capture the trade-offs between high and low fecundity strategies because the mortality rate is a major factor influencing optimal life histories. We develop a model to investigate the evolutionarily stable strategy (ESS) for fish that captures trade-offs between fecundity, mortality, prey encounter rate

70 and metabolic cost in a stochastic environment. The model includes swim-  
 71 ming speed and fecundity as heritable traits. We explore evolutionarily stable  
 72 strategies for this combination of traits using two methods: (i) maximising  
 73 an analytical expression for reproductive fitness; (ii) simulating a genetic  
 74 algorithm. We show that high fecundity tends to be stable and that, in a noisy  
 75 environment, high swimming speeds can increase fitness despite reducing the  
 76 expected net growth rate.

## 77 2 Model

78 Larval fish grow as a result of encountering suitable prey and also have a  
 79 metabolic cost that increases with energy used swimming. We model the body  
 80 mass  $X(t)$  of an individual fish by a stochastic differential equation (SDE):

$$dX = rdt + \sigma dW, \quad X(0) = x_0 \quad (2.1)$$

81 (Pitchford et al., 2005), where  $W(t)$  is a standard Brownian motion. This  
 82 is a drift-diffusion process for body size with fixed mean growth rate  $r$  and  
 83 diffusivity  $\sigma^2$ . We assume that reproductive maturity is defined by reaching a  
 84 certain minimum body size  $x_m$ .

85 Pitchford and Brindley (2001) modelled foraging in a patchy environment  
 86 using Poisson processes for patch encounters and for prey encounters within a  
 87 patch. They calculated the mean and variance of the number of prey encounters  
 88 per unit time as functions of the average prey density, the patchiness and the  
 89 predator swimming speed. The mean number of prey encounters  $N_p$  during  
 90 a period of time  $\delta t$  is independent of the patchiness and is an approximately  
 91 linear function of the swimming speed  $v$ :

$$E(N_p) = (a + bv)\delta t,$$

92 where  $a$  and  $b$  are constants representing respectively the contribution of tur-  
 93 bulance to the encounter rate and the average prey density. Pitchford and  
 94 Brindley (2001) also showed that the variance in the number of prey encoun-  
 95 ters increases with the patchiness of the prey distribution. We therefore set

$$\text{Var}(N_p) = SE(N_p) = S(a + bv)\delta t,$$

96 where the constant  $S$  represents patchiness. For a homogeneous prey distribu-  
 97 tion, the number of encounters  $N_p$  is a Poisson random variable, which implies  
 98 that  $\text{Var}(N_p) = E(N_p)$  and hence  $S = 1$ . Increasingly patchy distributions of  
 99 the same mean density (e.g. sparse but highly densely populated patches of  
 100 prey) are represented by values of  $S$  greater than 1 (Pitchford and Brindley,  
 101 2001). Values of  $S$  less than 1 could also occur if there was a regular distribu-  
 102 tion of prey or a minimum handling time between successive encounters. All  
 103 prey encounters are assumed to result in an increase in predator body mass  
 104 of an equal amount  $x_p$ .

105 The larval fish experience an metabolic cost due to swimming. This is  
 106 assumed be deterministic and proportional to the Stokes drag, which in-  
 107 creases quadratically with swimming speed (Pitchford and Brindley, 2001).  
 108 The metabolic cost is assumed to result in a loss of body mass at rate

$$E_{\text{swim}} = cv^2.$$

109 According to the above assumptions, the mean net growth rate and the  
 110 diffusivity in Eq. (2.1) are

$$\begin{aligned} r(v) &= (a + bv)x_p - cv^2, \\ \sigma^2(v) &= S(a + bv)x_p^2. \end{aligned}$$

111 By a non-dimensionalisation of the variables  $X$ ,  $t$  and  $v$  (see Appendix), we  
 112 may rewrite

$$r(v) = \alpha + 2v - v^2, \quad (2.2)$$

$$\sigma^2(v) = s(\alpha + 2v), \quad (2.3)$$

113 where  $s = Sx_p/x_m$ ,  $\alpha = 4ac/(b^2x_p)$ , the initial mass is  $X(0) = x_0/x_m$  and the  
 114 maturity size is  $x_m = 1$ .

115 The time taken to reach maturity  $T_h$  is the first time that the body size  
 116  $X(t)$  exceeds  $x_m = 1$ . Since the growth process is stochastic,  $T_h$  is a random  
 117 variable, referred to as a first hitting time. For the stochastic process described  
 118 by Eq. (2.1), the first hitting time has as an inverse Gaussian distribution, with  
 119 cumulative density function (CDF)

$$P(T_h < t) = C(t; v, x_0) = 1 - \Phi\left(\frac{1 - x_0 - rt}{\sigma\sqrt{t}}\right) + e^{2r(1-x_0)/\sigma^2} \Phi\left(\frac{-1 + x_0 - rt}{\sigma\sqrt{t}}\right) \quad (2.4)$$

120 where  $\Phi$  is the CDF of the standard normal distribution  $N(0, 1)$  (Grimmett  
 121 and Stirzaker, 1992). Eq. (2.4) corresponds to the probability that a fish with  
 122 swimming speed  $v$  and mass-at-birth  $x_0$  will reach maturity by time  $t$ .

123 We assume that, on reaching maturity, a constant proportion  $p$  of the  
 124 parent's body mass is used to generate offspring, and that this mass is divided  
 125 evenly between all  $n$  offspring. Hence, the mass-at-birth of an individual whose  
 126 parent has fecundity  $n$  is  $x_0 = p/n$ .

127 The model therefore has three parameters: (i) the mean food intake rate  
 128 for a non-swimming larvae  $\alpha$ ; (ii) the proportion  $p$  of parental mass used for  
 129 reproduction; and (iii) the noise level  $s$ , which is the product of the prey  
 130 patchiness  $S$  and the mass of a prey item  $x_p$  relative to the maturity mass  $x_m$ .  
 131 We will set  $a = 0$  (and as a consequence  $\alpha = 0$ ) so that the expected encounter  
 132 rate for a non-swimming fish larvae is zero, and  $p = 0.2$ , and investigate a  
 133 range of noise levels  $s$ . Note that setting  $\alpha = 0$  does not remove noise from  
 134 the system; turbulence and spatial heterogeneity still play an important role  
 135 in promoting variability in realised encounter rates via the noise parameter  $s$ .  
 136 We have tested the effect of varying  $\alpha$  in the range 0 to 4 and  $p$  in the range  
 137 0.05 to 0.5 and this does not qualitatively change the results. Values for  $x_p/x_m$   
 138 could range from  $10^{-8}$  for the larvae of large species foraging on small prey  
 139 such as copepods, to  $10^{-4}$  for smaller species feeding on larger prey.

## 140 2.1 Fitness

141 In an equilibrium population in which all individuals have fecundity  $n$ , an  
 142 average proportion  $1/n$  of all offspring reach reproductive maturity. The as-  
 143 sumption of an equilibrium population size is reasonable over evolutionary  
 144 time scales. For example, this might represent a population whose sustainable  
 145 size is limited to some carrying capacity by the availability of suitable habitat  
 146 or the abundance of prey.

147 The fitness  $W(v, n)$  of a strategy with swimming speed  $v$  and fecundity  $n$   
 148 is defined by the expected time taken for a proportion  $1/n$  of the offspring to  
 149 reach maturity. Since the initial mass of offspring of a parent with fecundity  
 150  $n$  is  $x_0 = p/n$ , the expected time taken,  $t^*(v, n)$ , for a proportion  $1/n$  of the  
 151 parent's offspring to reach maturity is defined implicitly by

$$C(t^*; v, p/n) = 1/n.$$

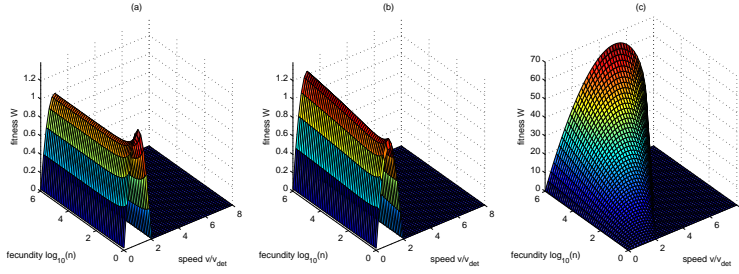
152 For given values of  $v$  and  $n$ , this equation was solved to find  $t^*$  using Matlab's  
 153 numerical root finder *fzero*. We define fitness  $W$  as inversely proportional to  
 154  $t^*$ :

$$W(v, n) = 1/t^*(v, n). \quad (2.5)$$

155 A resident strategy  $(v_r, n_r)$  is vulnerable to invasion by any mutant strategy  
 156  $(v, n)$  with a higher fitness. In this model formulation, the fitness of a given  
 157 strategy is independent of the strategies being followed by other individuals in  
 158 the population. An ESS is a strategy that cannot be invaded by any mutant  
 159 strategy (Maynard-Smith, 1982). In this context, an ESS is simply a strategy  
 160 with higher fitness than any other strategy.

## 161 2.2 Genetic algorithm

162 We simulated the evolution of swimming speed and fecundity using a sim-  
 163 ple genetic algorithm (GA). We assume an adult population of fixed size  $N$   
 164 and with swimming speed and fecundity traits  $(v_i, n_i)$ ,  $i = 1, \dots, N$ . For each  
 165 parent  $i$ , we create  $n_i$  offspring with traits  $(v_i + \phi_j, n_i e^{\psi_j})$ , where  $\phi_j$  and  $\psi_j$   
 166 ( $j = 1, \dots, n_i$ ) are independent normal random variables with mean zero and  
 167 variance  $\sigma_v^2$  and  $\sigma_n^2$  respectively. This represents normally distributed muta-  
 168 tions in swimming speed  $v$  and in log-fecundity  $\ln(n)$ . Both traits are restricted  
 169 to pre-defined ranges  $v_i \geq 0$  and  $1 \leq n_i \leq n_{\max}$ . If any trait values are gen-  
 170 erated outside the allowed range, they are adjusted to the closest allowable  
 171 value. The upper limit on fecundity is interpreted as a physiological limita-  
 172 tion on the minimum size for viable offspring ( $p/n_{\max}$ ); the effect of varying  
 173 the parameter  $n_{\max}$  will be investigated. The limitation of traits to defined  
 174 ranges is necessary numerically. The results show that this is not important  
 175 in terms of swimming speed (intermediate speeds are evolutionarily selected).  
 176 However, the evolutionary optimum for fecundity commonly lies at one of the  
 177 physiologically imposed limits, favouring either a strategy of "as many small  
 178 larvae as possible", or its opposite, depending on the selective environment.



**Fig. 1** Fitness calculated using Eq. (2.5) against speed and fecundity. (a) No noise ( $s = 0$ ), highest fitness occurs at fecundity  $n = 1$  and the deterministically optimum speed  $v = v_{\text{det}}$ . (b) Moderate noise ( $s = 0.001$ ), highest fitness occurs at maximum fecundity  $n = n_{\text{max}} = 10^6$  and the deterministically optimum swimming speed. (c) High noise ( $s = 0.4$ ), highest fitness occurs at maximum fecundity  $n = n_{\text{max}}$  and high swimming speed  $v > v_{\text{det}}$ .

179 The total number of offspring is  $\sum_{i=1}^N n_i$ . We sample the hitting times of  
 180 all offspring independently from the distribution in Eq. (2.4) and select the  
 181  $N$  individuals with the lowest hitting times to make up the next generation  
 182 of adults. Within these  $N$  individuals, we ignore any advantage to reaching  
 183 maturity earlier and assume that consecutive generations are non-overlapping.  
 184 This is the simplest selection choice for the GA. An ecological interpretation  
 185 would be a situation where there is a finite resource or limited space, to which  
 186 only the most successful  $N$  individuals have equal access. More complex selection  
 187 criteria could be included in the GA, based, for example, on a weighting of  
 188 the hitting time. However, this would be at the expense of introducing further  
 189 parameters, which would make the model more difficult to interpret.

### 190 3 Results

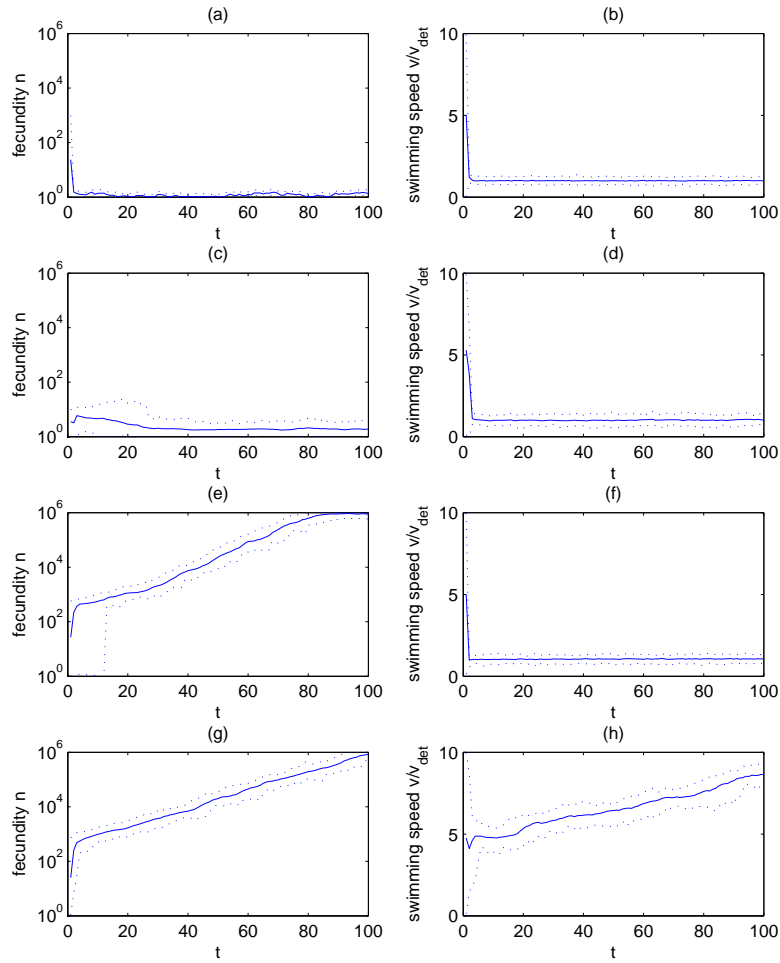
191 For fixed swimming speed  $v$ , fitness is a convex function of fecundity. There-  
 192 fore, the optimal fecundity is always either the minimum allowed fecundity (1)  
 193 or the maximum allowed fecundity ( $n_{\text{max}}$ ). Which of these two strategies has  
 194 the higher fitness depends on the level of noise. In a low noise ( $s \ll 1$ ) environ-  
 195 ment, the low fecundity strategy of having one large offspring is optimal. The  
 196 optimal swimming speed under these conditions is the one that maximises the  
 197 mean net growth rate in Eq. (2.2) (i.e. the deterministically optimum speed  
 198  $v_{\text{det}} = 1$ ). However, as the amount of noise increases, there is a tipping point  
 199 and, above that point, the optimal strategy is to have as many offspring as  
 200 physiologically possible. This can be understood intuitively as follows. In an  
 201 environment where everyone produces a large number of offspring, the larvae  
 202 all begin life at a very small size. Increasing the number of offspring causes a  
 203 negligible reduction in the initial larval size and, therefore, negligible change  
 204 in the hitting time distribution. So having more offspring is like getting more  
 205 lottery tickets for the same total cost.

206 Close to the tipping point between the low fecundity and high fecundity  
207 strategies, the optimal swimming speed is still close to the deterministic opti-  
208 mum. However, as the noise level  $s$  increases further, the optimal swim-  
209 ming speed increases above the deterministic optimum. This reduces the mean  
210 growth rate but, because the metabolic swimming cost is deterministic, it in-  
211 creases the variance of the growth rate. For high levels of noise, the optimal  
212 swimming speed can be several times larger than the deterministic optimum.  
213 In these cases, the mean growth rate is actually negative (i.e. mass lost due to  
214 the metabolic cost of swimming is greater than the mass gained from prey en-  
215 counters) but the increase in variance means that the individuals in the tail of  
216 the hitting-time distribution reach maturity more rapidly and therefore have  
217 higher fitness.

218 Each row of graphs in Fig. 2 shows a single simulation of the GA. The  
219 simulations shown are representative of the behaviour of the GA: there is  
220 variability among realisations in the time taken to converge, but the long-  
221 term behaviour is always the same for a given noise level  $s$  and given initial  
222 conditions. The results of the GA are consistent with the fitness functions in  
223 Fig. 1. The population converges to low fecundity ( $n = 1$ ) when noise is low  
224 (Fig. 2a, b) and to high fecundity ( $n = n_{\max}$ ) when noise is high (Fig. 2e-  
225 h). This finding is robust to changes to the value of  $n_{\max}$ , which only affect  
226 the time taken for the population to converge. At moderate noise levels, the  
227 population can get trapped in the local optimum at low fecundity (Fig. 2c, d).  
228 Whenever there is any noise ( $s > 0$ ), the low fecundity optimum (if it exists)  
229 is always local in the sense that fitness is eventually an increasing function of  
230 fecundity when fecundity is sufficiently high. The only thing that can make  
231 the low-fecundity strategy globally optimal is the physiological restriction on  
232 the maximum number of eggs.

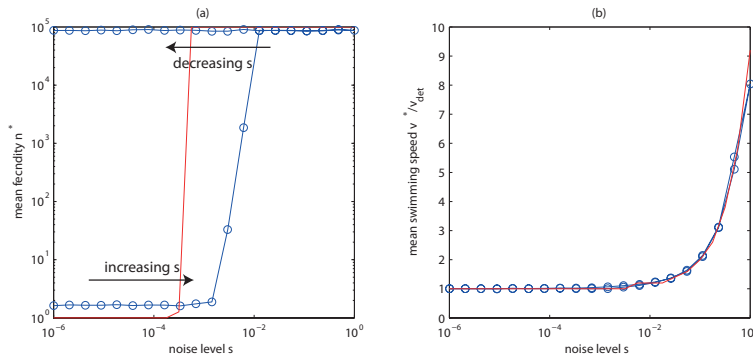
233 Figure 3 shows the optimal trait values according to the analytical model  
234 together with the mean trait values after 500 generations of the GA. The GA  
235 was run for a range of noise levels  $s$  and, for each new noise level, was initialised  
236 with the resulting population (i.e. same set of trait values) from the previous  
237 noise level. The noise level  $s$  was first increased in logarithmic increments  
238 from  $10^{-8}$  to 1 and then decreased back down to  $10^{-8}$ . This allows us to  
239 investigate bistability in the fecundity, which is indicated by the two branches  
240 of results in Fig. 3a. In the range of noise levels for which there are two  
241 branches, the population can evolve towards either the low fecundity ( $n \approx 1$ )  
242 or high fecundity ( $n \approx n_{\max}$ ) strategy, depending on the initial conditions.

243 The optimal swimming speed is largely independent of initial conditions  
244 and consistent with the predictions of the analytical model (Fig. 3b). At low  
245 noise levels, when the population is in the low-fecundity state, the swimming  
246 speed is close to the value that maximises the mean net growth rate in Eq.  
247 (2.2), referred to as the deterministically optimum speed. There is a range of  
248 intermediate noise levels (roughly  $10^{-4} < s < 10^{-2}$ ) for which the optimum  
249 strategy is high fecundity but the swimming speed is still close to the deter-  
250 ministic optimum. At high noise levels ( $s > 10^{-2}$ ), the optimum strategy is  
251 high fecundity and high swimming speed. As the noise level is subsequently



**Fig. 2** GA results showing the minimum, mean and maximum trait values of a population of  $N = 100$  individuals over time ( $t$  represents generation number). (a, b) No noise ( $s = 0$ ), population converges to fecundity  $n = 1$  and swimming speed  $v = v_{\text{det}}$ . (c, d, e, f) Moderate noise ( $s = 0.001$ ), population can converge to the local optimum at low fecundity (c), or to the global optimum at high fecundity (e), depending on initial conditions. (g, h) High noise ( $s = 1$ ), population always converges to the high fecundity optimum with  $v > v_{\text{det}}$ . Population size  $N = 100$ ; mutation size constants  $\sigma_n = 0.1$ ,  $\sigma_v = 0.1v_{\text{det}}$ ; maximum fecundity  $n_{\text{max}} = 10^6$ . Initial swimming speeds uniformly distributed in  $[0, 10v_{\text{det}}]$ . In (a, b, e-h) initial fecundity is log-uniformly distributed in  $[0, 1000]$ ; in (c, d) initial fecundity is log-uniformly distributed in  $[0, 10]$ .





**Fig. 3** Fecundity  $n$  and swimming speed  $v$  against noise level  $s$ . Blue curves show the trait values that maximise fitness as defined by Eq. (2.5); red circles show the mean population trait values after 100 generations of the GA. For each new noise level  $s$ , the GA was initialised with the trait values at the end of the previous simulation. Noise level was first increased in logarithmic increments from  $10^{-6}$  to 1 (labelled ‘increasing  $s$ ’) and then decreased in logarithmic decrements back down to  $10^{-6}$  (labelled ‘decreasing  $s$ ’). Black dotted line in (b) shows the deterministically optimum speed  $v = v_{\text{det}}$ . Population size  $N = 100$ ; mutation size constants  $\sigma_n = 0.1$ ,  $\sigma_v = 0.1v_{\text{det}}$ ; maximum fecundity  $n_{\text{max}} = 10^6$ .

252 reduced, the population remains trapped in the high-fecundity local optimum,  
 253 but the swimming speed evolves back down towards the deterministic op-  
 254 timum. In other words, the hysteresis observed in the population fecundity  
 255 (Fig. 3a) is not present in the population swimming speed (Fig. 3b).

## 256 Discussion

257 The trade-off between producing many small eggs or fewer large ones has been  
 258 investigated empirically (Duarte and Alcaraz, 1989; Elgar, 1990) and theoret-  
 259 ically (Winemiller and Rose, 1993; Andersen et al., 2008). Stochasticity in the  
 260 growth trajectories of fish larvae is clearly a major factor in the high-fecundity  
 261 life histories of many marine fish species (Pitchford et al., 2005). In this pa-  
 262 per, we have explored the interplay between fecundity and another heritable  
 263 trait, larval swimming speed. We have shown that, in low-noise environments,  
 264 the evolutionarily stable strategy is to swim at the speed that maximises the  
 265 mean net growth rate, which is a balance between the prey encounter rate and  
 266 the metabolic cost. This is the result of a simple deterministic optimisation.  
 267 In high-noise environments, it becomes advantageous to swim faster than the  
 268 deterministic optimum. This reduces the mean net growth rate, but increases  
 269 the variance, and thereby increases the likelihood of having at least one off-  
 270 spring reach reproductive maturity. The evolutionarily stable swimming speed  
 271 was estimated in two ways, which gave the same results: (i) by minimising  
 272 the expected time taken for at least one offspring to reach maturity; (ii) by  
 273 simulating the evolution of a population using a genetic algorithm.

274 Considering the huge difference in size between the larvae and adults of  
275 most marine fish species, there is remarkably little variation in egg mass, with  
276 many species producing eggs close to 1 mg (Ware and Lambert, 1985; Ri-  
277 jnsdorp and Ibelings, 1989; Chambers and Waiwood, 1996; Mendiola et al.,  
278 2006). This suggests that there may be physiological constraints that prevent  
279 production of viable eggs much smaller than this. For example, hydrodynamic  
280 factors severely limit the ability of small larvae to obtain an adequate food  
281 supply (China and Holzman, 2014). There is a strong correlation between an  
282 individual’s reproductive effort (total mass of eggs produced) and its fecun-  
283 dity (Duarte and Alcaraz, 1989), suggesting that, given an increase in biomass  
284 available for reproduction, adult fish produce more eggs rather than larger  
285 eggs. These empirical observations are consistent with our model assumption  
286 that there is a maximum number of offspring that can be produced in a single  
287 spawning bout, corresponding to a minimum egg size.

288 The FishBase database ([www.fishbase.org](http://www.fishbase.org)) is the principal repository for  
289 fish data, while the most comprehensive experimental study of larval swim-  
290 ming speed is Fisher et al. (2005). Of the 62 identified species studied by Fisher  
291 et al. (2005), FishBase provides fecundity estimates for four species: *Lutjanus*  
292 *carponotatus* (speed 52 cm/s, fecundity 7,074–748,959); *Oxymonacanthus lon-*  
293 *girostris* (speed 31.1 cm/s, fecundity 200–300); *Dascyllus aruanus* (speed 24  
294 cm/s, fecundity 1,500–2,000); *Plectropomus leopardus* (speed 31.5 cm/s, fecun-  
295 dity 457,900) (fecundity data extracted using rfishbase). The two species with  
296 the fastest swimming larvae (*L. carponotatus* and *P. leopardus*) have fecundi-  
297 ties 2-3 orders of magnitude larger than the other two species.

298 This is consistent with our theoretical predictions for this long-standing  
299 evolutionary problem, but cannot be regarded as corroboration due to the  
300 small sample size. The quoted speeds are for settlement-stage juvenile fish and  
301 are based on measurements of maximum sustainable swimming speed; this is  
302 used as a proxy for foraging speed, but may mask other factors (Fisher and  
303 Leis, 2010). Moreover, empirical observations may reveal other differences in  
304 swimming and behaviour, involving for example diurnal changes in activity  
305 (Fisher and Bellwood, 2003). It is plausible that variations in swimming speed  
306 and movement behaviour will result in increasing variance in the context of the  
307 model developed here, and may thereby convey fitness benefits in a turbulent  
308 environment. Fish larvae also exhibit other traits: for example, some species  
309 possess oil globules which act as initial energy reserves (Fisher et al., 2007) and  
310 vary with body size and reproductive strategy. These are presumably subject  
311 to selection. The model presented here could be extended to account for this  
312 trait, possibly using simple descriptions of seasonality and unpredictability in  
313 the underlying food supply (James et al., 2003; Burrow et al., 2011).

314 We have presented results for a specific model of larval growth and mortal-  
315 ity in Eq. (2.1). This simple model assumes a constant average growth rate ( $r$ )  
316 and ignores density-dependent effects, such as competition for food or habi-  
317 tat, group defence against predators and cannibalism. In reality, interactions  
318 among individuals may be a function of relative body size, which could affect  
319 trade-offs involving fecundity. The model assumes there is no parental care:

320 this is reasonable for most pelagic marine species, although there are some  
321 species that invest substantial effort into care of offspring (Duarte and Al-  
322 caraz, 1989). The model also ignores the substantial changes in the abundance  
323 and size of prey as an individual fish grows to maturity (Benoît and Rochet,  
324 2004). An advantage of this simple model is that it only has a small number of  
325 parameters: the mean food encounter rate for stationary larvae, the proportion  
326 of parental mass used for reproduction, and the level of noise in the food en-  
327 counter rate. The first two of these parameters were found not to have a major  
328 impact on evolutionarily stable outcomes. The noise level was shown to be a  
329 product of the patchiness of the prey distribution and the ratio of the mass of  
330 a prey item to the maturity mass. The reason for the latter effect is that, when  
331 fewer prey encounters are required to reach maturity, there is a higher prob-  
332 ability of an individual offspring reaching maturity much faster than average.  
333 Patchy prey distributions have been argued to promote high-risk, high-reward  
334 strategies (Pitchford and Brindley, 2001).

335 The evolutionary stability of a high-fecundity strategy is robust to changes  
336 in model assumptions. For example, if both the mean and variance in the  
337 growth rate are proportional to size, rather than simply constant, Eq. (2.1)  
338 describes the logarithm of size and, for a given initial mass, results in the same  
339 hitting-time distribution. The trade-off between fecundity and initial mass re-  
340 sults in slightly different fitness landscapes (Fig. 1), but the switch from low  
341 fecundity, slow swimming to high fecundity, fast swimming with increasing  
342 noise still occurs. When a resident population is following a high-fecundity  
343 strategy, egg size is by definition very small. A mutant with the same total  
344 reproductive effort but higher fecundity experiences little disadvantage from  
345 the further decrease in egg size, but benefits from having a greater number  
346 of tickets in the lottery of larval growth and survival. This effect is clearly  
347 at work in the genetic algorithm results in Fig. 2e, h, which show a steady  
348 evolution in the direction of increasing fecundity, consistent with empirical  
349 observation (Duarte and Alcaraz, 1989). Physiological and hydrodynamic fac-  
350 tors are likely to put a lower limit on viable egg size (Leviton, 1993; China  
351 and Holzman, 2014), and we hypothesise that producing eggs around this size  
352 will be evolutionarily stable in many cases. An exception to this would be if  
353 there is sensitive dependence of larval survival on egg size, even at very small  
354 egg sizes. This could occur if the hatchlings' mass-specific growth rate is low  
355 relative to their mortality rate (Houde, 1997; Law et al., 2014).

356 In the model, we assumed that fish reproduce only once on reaching ma-  
357 turity and then die. In reality, mature fish of large species have a relatively  
358 low mortality rate and can survive for several years and undergo multiple re-  
359 productive bouts. The genetic algorithm could be generalised to include this  
360 by allowing non-overlapping generations. This would increase the advantage of  
361 having offspring reach maturity at an early age because this will allow multiple  
362 spawning bouts and lead to a faster increase in representation in the gene pool.  
363 This may enhance the selection pressure for high-risk, high-reward strategies  
364 like the one identified in this model, because there would be even greater  
365 benefit to having offspring in the extreme tail of the growth rate distribution.

366 We chose to study larval swimming speed because it is a variable trait  
 367 that is a key determinant of prey encounter rate. But our results illustrate a  
 368 wider point: when a particular trait has a combination of deterministic and  
 369 stochastic effects, its optimal value will depend on the level of stochasticity  
 370 (Currey et al., 2007). Optimising mean values, like the mean growth rate, is  
 371 not likely lead to an evolutionarily stable strategy when stochastic effects are  
 372 strong and when only a small fraction of offspring reach reproductive maturity.

## 373 Appendix

374 We define dimensionless variables

$$\hat{X} = \frac{X}{x_m}, \quad \hat{t} = \frac{t}{t_{\text{ref}}}, \quad \hat{v} = \frac{v}{v_{\text{det}}},$$

375 where  $t_{\text{ref}} = 4cx_m/(b^2x_p^2)$  and  $v_{\text{det}} = bx_p/(2c)$ , which is the swimming speed that maximises  
 376 the expected growth rate, i.e. the deterministic optimum. Then Eq. (2.1) becomes

$$d\hat{X} = \hat{r}d\hat{t} + \hat{\sigma}d\hat{W},$$

377 where

$$\hat{r} = \frac{4ac}{b^2x_p} + 2\hat{v} - \hat{v}^2,$$

$$\hat{\sigma}^2 = S \frac{x_p}{x_m} \left( \frac{4ac}{b^2x_p} + 2\hat{v} \right)$$

378 and  $\hat{W} = W/t_{\text{ref}}^{1/2}$  is a standard Brownian motion with respect to dimensionless time  $\hat{t}$ . The  
 379 initial condition in the new variables is  $\hat{X}(0) = x_0/x_m$  and the fish reaches maturity when  
 380  $\hat{X} = 1$ . Dropping the hats, this is equivalent to Eq. (2.1) with the growth rate and diffusivity  
 381 given in Eqs. (2.2) and (2.3).

## 382 References

- 383 Andersen, K. H., Beyer, J., Pedersen, M., Andersen, N. G., and Gislason, H. (2008). Life-  
 384 history constraints on the success of the many small eggs reproductive strategy. *Theoret-*  
 385 *ical Population Biology*, 73(4):490–497.
- 386 Benoît, E. and Rochet, M.-J. (2004). A continuous model of biomass size spectra governed by  
 387 predation and the effects of fishing on them. *Journal of Theoretical Biology*, 226(1):9–21.
- 388 Burrow, J. F., Horwood, J. W., and Pitchford, J. W. (2011). The importance of variable  
 389 timing and abundance of prey for fish larval recruitment. *Journal of Plankton Research*,  
 390 page fbr015.
- 391 Chambers, R. C. and Leggett, W. C. (1996). Maternal influences on variation in egg sizes  
 392 in temperate marine fishes. *American Zoologist*, 36(2):180–196.
- 393 Chambers, R. C. and Waiwood, K. G. (1996). Maternal and seasonal differences in egg sizes  
 394 and spawning characteristics of captive Atlantic cod, *Gadus morhua*. *Canadian Journal*  
 395 *of Fisheries and Aquatic Sciences*, 53(9):1986–2003.
- 396 Chick, J. H. and Van Den Avyle, M. J. (2000). Effects of feeding ration on larval swimming  
 397 speed and responsiveness to predator attacks: implications for cohort survival. *Canadian*  
 398 *Journal of Fisheries and Aquatic Sciences*, 57(1):106–115.
- 399 China, V. and Holzman, R. (2014). Hydrodynamic starvation in first-feeding larval fishes.  
 400 *Proceedings of the National Academy of Sciences*, 111(22):8083–8088.

- 401 Currey, J. D., Pitchford, J. W., and Baxter, P. D. (2007). Variability of the mechanical  
402 properties of bone, and its evolutionary consequences. *Journal of The Royal Society*  
403 *Interface*, 4(12):127–135.
- 404 Darowski, K., Takashima, F., and Law, Y. (1988). Bioenergetic model of planktivorous  
405 fish feeding, growth and metabolism: theoretical optimum swimming speed of fish larvae.  
406 *Journal of Fish Biology*, 32(3):443–458.
- 407 Duarte, C. M. and Alcaraz, M. (1989). To produce many small or few large eggs: a size-  
408 independent reproductive tactic of fish. *Oecologia*, 80(3):401–404.
- 409 Elgar, M. A. (1990). Evolutionary compromise between a few large and many small eggs:  
410 comparative evidence in teleost fish. *Oikos*, 59:283–287.
- 411 Fisher, R. and Bellwood, D. R. (2003). Undisturbed swimming behaviour and nocturnal  
412 activity of coral reef fish larvae. *Marine Ecology Progress Series*, 263:177–188.
- 413 Fisher, R. and Leis, J. M. (2010). Swimming speeds in larval fishes: from escaping predators  
414 to the potential for long distance migration. In *Fish locomotions: An eco-ethological*  
415 *perspective*, chapter 11, pages 333–373. Science Publishers.
- 416 Fisher, R., Leis, J. M., Clark, D. L., and Wilson, S. K. (2005). Critical swimming speeds  
417 of late-stage coral reef fish larvae: variation within species, among species and between  
418 locations. *Marine Biology*, 147(5):1201–1212.
- 419 Fisher, R., Sogard, S. M., and Berkeley, S. A. (2007). Trade-offs between size and energy  
420 reserves reflect alternative strategies for optimizing larval survival potential in rockfish.  
421 *Marine Ecology Progress Series*, 344:257–270.
- 422 Grimmett, G. and Stirzaker, D. (1992). *Probability and random processes*. Oxford Univ  
423 Press.
- 424 Houde, E. D. (1997). Patterns and consequences of selective processes in teleost early life  
425 histories. In *Early life history and recruitment in fish populations*, chapter 6, pages  
426 173–196. Springer.
- 427 James, A., Pitchford, J. W., and Brindley, J. (2003). The relationship between plankton  
428 blooms, the hatching of fish larvae, and recruitment. *Ecological Modelling*, 160(1):77–90.
- 429 Jennings, S. and Warr, K. J. (2003). Environmental correlates of large-scale spatial variation  
430 in the  $\delta^{15}\text{N}$  of marine animals. *Marine Biology*, 142(6):1131–1140.
- 431 Law, R., Plank, M. J., and Kolding, J. (2014). Balanced exploitation and coexistence of  
432 interacting, size-structured, fish species. *Fish and Fisheries*.
- 433 Levitan, D. R. (1993). The importance of sperm limitation to the evolution of egg size in  
434 marine invertebrates. *American Naturalist*, 141:517–536.
- 435 MacKenzie, B. R. and Kjørboe, T. (1995). Encounter rates and swimming behavior of pause-  
436 travel and cruise larval fish predators in calm and turbulent laboratory environments.  
437 *Limnology and Oceanography*, 40(7):1278–1289.
- 438 Maynard-Smith, J. (1982). *Evolution and the theory of games*. Cambridge University Press.
- 439 Mendiola, D., Alvarez, P., Cotano, U., Etxebeste, E., and de Murguía, A. M. (2006). Effects  
440 of temperature on development and mortality of atlantic mackerel fish eggs. *Fisheries*  
441 *Research*, 80(2):158–168.
- 442 Pitchford, J. W. and Brindley, J. (2001). Prey patchiness, predator survival and fish recruit-  
443 ment. *Bulletin of Mathematical Biology*, 63(3):527–546.
- 444 Pitchford, J. W., James, A., and Brindley, J. (2003). Optimal foraging in patchy turbulent  
445 environments. *Marine Ecology Progress Series*, 256:99–110.
- 446 Pitchford, J. W., James, A., and Brindley, J. (2005). Quantifying the effects of individual  
447 and environmental variability in fish recruitment. *Fisheries Oceanography*, 14(2):156–160.
- 448 Rijnsdorp, A. D. and Ibelings, B. (1989). Sexual dimorphism in the energetics of reproduc-  
449 tion and growth of North Sea plaice, *Pleuronectes platessa* L. *Journal of Fish Biology*,  
450 35(3):401–415.
- 451 Tsuda, A., Sugisaki, H., Ishimaru, T., Saino, T., and Sato, T. (1993). White-noise-like  
452 distribution of the oceanic copepod *Neocalanus cristatus* in the subarctic North Pacific.  
453 *Mar. Ecol. Prog. Ser.*, 97:39–46.
- 454 Ware, D. M. and Lambert, T. C. (1985). Early life history of atlantic mackerel (*Scomber*  
455 *scombrus*) in the southern Gulf of St. Lawrence. *Canadian Journal of Fisheries and*  
456 *Aquatic Sciences*, 42(3):577–592.
- 457 Winemiller, K. O. and Rose, K. A. (1993). Why do most fish produce so many tiny offspring?  
458 *American Naturalist*, 142:585–603.