

Adaptive gamete allocation when fertilization is external and sperm competition is absent: Optimization models and evaluation using coral reef fish

Moshe Kiflawi*

Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA

ABSTRACT

I develop a series of optimization models of adaptive sperm allocation by external fertilizers when sperm competition is absent. The models differ with respect to either one or two of the following assumptions: the dependence of fertilization success on egg concentration; the optimization criteria (the maximization of per-spawn *vs* long-term average fitness); and the limiting factor on male reproduction (daily mate and sperm availability *vs* per-spawn mating costs). I propose that, *a priori*, these (and similar) models are often equally plausible. Consequently, strong inferences concerning the selective regime that led to the putative adaptation would be possible only upon the evaluation of conflicting predictions generated by the different models. I demonstrate this using published data on sperm allocation and fertilization success in pair-spawning coral reef fish.

Keywords: external fertilization, fish, optimization, sperm allocation.

INTRODUCTION

How should males allocate sperm over successive matings? The question is not simply one of apportionment, but rather an attempt to reach a deeper understanding of the selective pressures that shaped the evolution of male and female sexual strategies. Ejaculates containing millions of sperm can impose a non-trivial cost to male reproduction (Dewsbury, 1982). Moreover, sperm production rates can limit sperm availability, which, in turn, stand to limit both male and female reproductive success (Nakatsuru and Kramer, 1982; Pitnick and Markow, 1994; Levitan and Petersen, 1995). Adaptive, prudent allocation of limited or costly resources is often the expected outcome of selection. However, the underlying selective regime may vary.

Of the factors that stand to influence sperm allocation tactics, the effect of sperm competition is the most widely studied (e.g. Parker, 1990, 1993; Birkhead and Møller, 1992; Ball and Parker, 1996; Stockley *et al.*, 1997). The focus on sperm competition is not surprising given its significance as an evolutionary force and near ubiquitous occurrence

* Address all correspondence to Moshe Kiflawi, Institute of Evolution, University of Haifa, Mount Carmel, Haifa 31905, Israel.

Consult the copyright statement on the inside front cover for non-commercial copying policies.

(e.g. Smith, 1984). However, studies of mating systems that lack sperm competition may help address the following fundamental questions: (1) Is sperm allocation constrained by selection on female gamete allocation tactics? (2) Does selection act to maximize immediate or long-term average reproductive benefits? (3) Is sperm allocation dictated by sperm availability, or are male mating costs (in addition to sperm production) the governing factor?

Pelagic spawning, in which external fertilization follows the release of both eggs and sperm into the water column, is a common mode of reproduction in aquatic environments (Levitan, 1998). Two factors make pelagic spawners an excellent target for the study of the evolution of gamete allocation: first, external fertilization is generally believed to have preceded internal fertilization (e.g. Parker, 1984); second, external fertilization is not complicated by pregnancy initiation or female control of fertilization (Sivinski, 1984). Considerable effort has been devoted to the evolutionary implications of external fertilization in invertebrates (see Levitan, 1998, for a review). However, within most marine invertebrates, the spatial separation of mates at the time of spawning and a tendency to synchronize reproduction mean that gamete allocation is likely to be constrained by sperm competition and, using the same ejaculate, individual males can simultaneously fertilize several females. On the other hand, within pelagic spawning vertebrates (particularly coral reef fish), reproduction proceeds in close physical proximity (< 1 cm; Levitan and Petersen, 1995), with males accruing matings sequentially (i.e. one female per ejaculate). Hence, reef fish have been key in investigating the question that is the subject of this study (e.g. Shapiro *et al.*, 1994; Warner *et al.*, 1995).

The kinetics governing the fertilization process can play a significant role in shaping the sexual tactics of pelagic spawners (Denny and Shibata, 1989; Petersen, 1991; Shapiro and Giraldeau, 1996). Shapiro and Giraldeau (1996) proposed a conceptual model for adaptive sperm allocation tactics in pair-spawning external fertilizers when daily sperm production is limited. However, although invoking the rationale of the marginal value theorem (Charnov, 1976), their model is not developed explicitly and only implies a particular fertilization process (i.e. batch-size independent fertilization; see below for explanation). Thus, it falls short of providing the predictions needed for addressing questions such as those enumerated above. In this study, I develop a series of optimization models that are built around explicit formulations of the fertilization process. I propose that, often, there is no *a priori* reason to ignore any of the various assumptions made by these models, and that their conflicting predictions may be used to address the questions listed above.

I begin by presenting the conceptual framework for the fertilization models that form the basis of the sperm allocation models which I develop next. I then use published data to test predictions made by the allocation models, as they pertain to pair-spawning coral reef fish.

FERTILIZATION KINETICS

The relation between the proportion of spawned eggs that are fertilized (i.e. fertilization success, ϕ) and sperm concentration (S) is often depicted by a decelerating positive function of the form $1 - \exp(-kS)$, where k is a constant (Vogel *et al.*, 1982; see the Appendix). A qualitatively identical relation is described by a function of the form $X/(k + X)$, where k equals the value of X that produces a response equalling 50%. For mathematical tractability, I use the latter formulation to develop the allocation models presented below.

The degree to which spawned eggs compete for sperm may result in fertilization kinetics that are, at the extremes, either independent of egg concentration (E) or dependent on the per-spawn ratio of sperm to eggs (Vogel *et al.*, 1982; see the Appendix). I investigate both cases by depicting fertilization success as

$$\varphi = S/(k + S) \quad (1a)$$

or

$$\varphi = (S/E)/[k + (S/E)] \quad (1b)$$

Assuming that sperm and eggs released per spawn occupy a constant and overlapping unit volume, I use gamete concentrations and numbers interchangeably. Hereafter I refer to sperm and egg numbers as ejaculate and batch size, respectively. The constant k equals either the ejaculate size (equation 1a) or the ejaculate to batch size ratio (equation 1b) needed to achieve $\varphi = 50\%$, and subsumes gamete properties (e.g. egg cross-sectional area; see the Appendix) and environmental conditions (e.g. turbulence; Denny, 1988) that affect the success of external fertilization.

ALLOCATION MODELS: BACKGROUND

Male and female fitness are assumed to be linearly dependent on the number of eggs fertilized per unit reproductive effort (Φ_M and Φ_F , respectively):

$$\Phi_M = \varphi E/(C_M + S) \quad (2a)$$

$$\Phi_F = \varphi E/(C_F + E) \quad (2b)$$

C_M and C_F are the gamete-number equivalents of male and female per-spawn costs of obtaining a mating. Hence, the sums $(C_M + S)$ and $(C_F + E)$ depict male and female per-spawn reproductive efforts, respectively. The choice of gamete number as the unit of reproductive effort is one of convenience, and conveys the notion that both components (e.g. C_M and S) tap into the same energy reserve. I assume that both C_M and C_F are fixed within individuals (i.e. an individual's mating costs are independent of properties of its mates).

Providing no selection operates on female gamete allocation, ejaculate size is free to evolve independent of its consequences on female fitness. With males mating multiple times and with natural variation in batch size, selection on males may operate to maximize either their per-spawn fitness or their expected long-term average fitness; that is, max. $\varphi E/(C_M + S)$ or max. $\Sigma(\varphi E)/\Sigma(C_M + S)$, respectively (e.g. Tempelton and Lawlor, 1981). Per-spawn fitness maximization is possible when ejaculate size is constrained by C_M (see 'PS' models below). On the other hand, maximization of long-term average fitness is possible if ejaculate size is constrained by either C_M or by a finite daily sperm reserve (S_T). With C_M as the constraint, a solution is found using the marginal value theorem (Charnov, 1976; see 'MVT' models below). With S_T as the constraint, and assuming a fixed expected number of daily matings per male (N), the overall cost of mating ($NC_M + S_T$) is also fixed. Thus, the optimization objective becomes the maximization of the number of fertilized eggs (max. $\Sigma(\varphi E)$) and may be solved using the Lagrange multiplier method (e.g. Lloyd, 1988; see 'LMM' models below).

Neither PS nor MVT models place any restrictions on the expected number of daily matings per male. On the other hand, LMM models require that this number is predetermined by factors outside of the males' immediate control, for example by male vigour, female preference, the number and quality of competitors, the length of the daily reproductive period, and so on. These formulations differ from models that assume that N is traded-off with ejaculate size, given a fixed energy budget, and co-evolves with ejaculated size to maximize its product with the number of eggs fertilized per mating (e.g. Parker, 1993; Ball and Parker, 1996). It does not, however, imply that male energy allocation to reproduction is not under selection. Rather, trade-offs involving reproductive effort are simply implied by the fitness currency – that is, the number of eggs fertilized per unit reproductive effort or, in other words, the energetic efficiency of reproduction (see Shapiro and Giraldeau, 1996).

Fertilization success affects both male and female fitness. Given batch-size dependent fertilization, the assumption that no selection operates on female gamete allocation becomes questionable. Hence, it is possible that both sexes adjust their per-spawn gamete expenditure in such a way that a female's investment (E) is optimal given the male is investing S , where S is the male's optimal value if the female is investing E – a Nash equilibrium (Maynard Smith, 1982). I investigate this possibility using a similar approach to that used, for example, in the analysis of the evolution of parental care (Clutton-Brock and Godfray, 1991).

The models I present below make predictions concerning four main relationships: (1) ejaculate size versus batch size; (2) fertilization success versus ejaculate size; (3) fertilization success versus batch size; and (4) fertilization efficiency versus batch size, where fertilization efficiency is defined as the number of fertilized eggs per spawned sperm ($\Omega = \varphi E/S$; Shapiro *et al.*, 1994). These relationships are of little biological interest; however, they do provide a basis with which to investigate the explanatory power of the various models. Moreover, although these relations are calculated for individuals, they are easily extendible to the among-male level. Extending the predictions would enable the examination of whether patterns viewed at the population level can confound inferences concerning allocation decisions that are selected for at the level of the individual. To allow for this extension, I further assume that mating is non-assortative. This restriction does not preclude mate choice; rather, it implies that no correlations exist between parameter values of mating partners.

ALLOCATION MODELS: FORMALIZATION AND PREDICTIONS

Batch-size independent fertilization (equation 1a)

Per-spawn fitness maximizers (PS1)

Setting $\partial\Phi_M/\partial S$ (see equation 2a) to zero and solving for S yields the optimal ejaculate size:

$$S^* = (kC_M)^{0.5} \quad (3)$$

The corresponding fertilization success (φ^*) and efficiency (Ω^*) can now be calculated as:

$$\varphi^* = 1/[1 + (k/C_M)^{0.5}] \quad (4)$$

and

$$\Omega^* = E/[k + (kC_M)^{0.5}] \quad (5)$$

Predictions

- *Within males.* Ejaculate size and fertilization success are independent of batch size (Fig. 1A and 1B, respectively), whereas fertilization efficiency increases linearly with increasing batch size. A significant relation between ejaculate size and both batch size and fertilization success is possible only if male mating costs covary positively with batch size.
- *Among males.* Variation in male mating costs introduces a positive relation between ejaculate size and fertilization success and weakens the relation between batch size and fertilization efficiency. Ejaculate size and fertilization success remain independent of batch size.

Long-term average fitness maximizers (MVT1)

The optimal ejaculate size of male i mating with female j (S_{ij}^*) is achieved when the male's marginal return ($\partial(\varphi_{ij}E_j)/\partial S_{ij}$) is the same for all the females with which it mates, and equals $\bar{\Phi}_{Mi}^*$, the number of eggs fertilized per unit reproductive effort, for an optimal male mating with an average female. With $\bar{E}$ equalling the expected average batch size and $S_{(\bar{E}i)}^* = (kC_{Mi})^{0.5}$ (see equation 3), we get:

$$\bar{\Phi}_{Mi}^* = \bar{E}/(k^{0.5} + C_{Mi}^{0.5})^2 \quad (6)$$

and

$$\partial(\varphi_{ij}E_j)/\partial S_{ij}|_{S=S^*} = [E_j k/(k + S_{ij}^*)^2] \quad (7)$$

Equating equations (6) and (7) and solving for S_{ij}^* yields

$$S_{ij}^* = [(kE_j/\bar{E})^{0.5} (k^{0.5} + C_{Mi}^{0.5})] - k \quad (8)$$

Note that, to satisfy $S_{ij}^* > 0$, equation (8) requires that males mate only with females that spawn batches larger than some critical value, namely $E_j > (k\bar{E}_i)/(k^{0.5} + C_{Mi}^{0.5})^2$.

Fertilization success (φ_{ij}^*) and efficiency (Ω_{ij}^*) are given by:

$$\varphi_{ij}^* = 1 - [(k\bar{E}_j/E_j)^{0.5}/(k^{0.5} + C_{Mi}^{0.5})] \quad (9)$$

and

$$\Omega_{ij}^* = (E\bar{E})^{0.5}/k + (kC_{Mi})^{0.5} \quad (10)$$

Predictions

- *Within males.* Ejaculate size increases, at a decelerating rate, with batch size (Fig. 2A). As a result, fertilization success will increase with batch size (Fig. 2B), although the relation will disappear once the effect of ejaculate size is controlled for. Fertilization efficiency increases with batch size. Note that although high male mating costs will cause fertilization success to be less sensitive to variation in ejaculate or batch size ($\partial^2\varphi/\partial C_M\partial E < 0$), it will also cause the disappearance of the relation between ejaculate size and batch size (e.g. $\partial^2 S/\partial C_M\partial E < 0$).

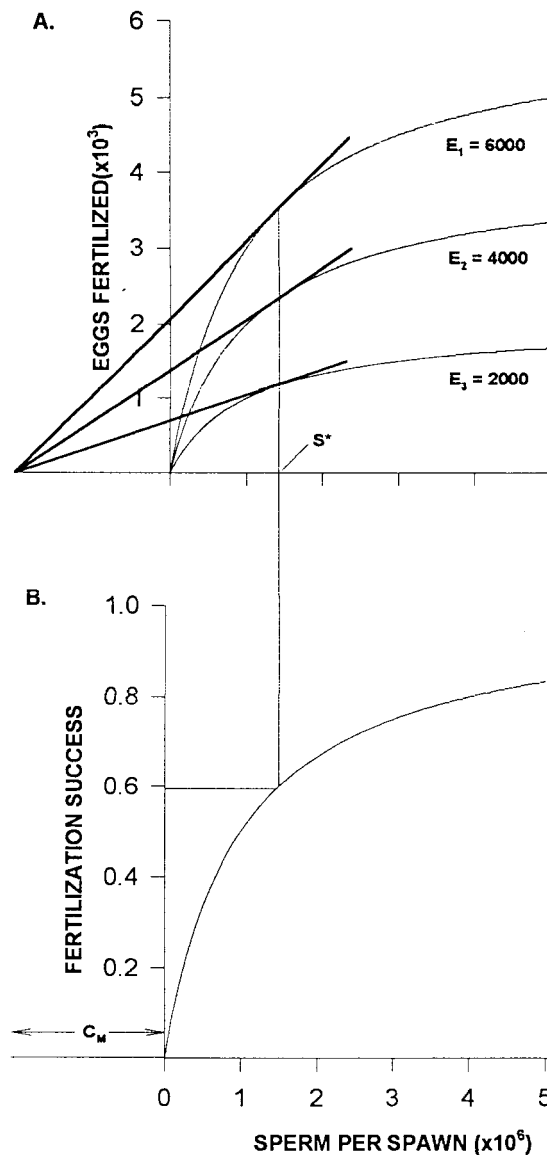


Fig. 1. Graphical depiction of PS1, where males are assumed to maximize their per-spawn fitness, and fertilization depends solely on sperm concentrations. The solid curves depict the effect of the number of sperm released per spawn on (A) the number of eggs fertilized and (B) fertilization success, given three different batch sizes (E). Solid tangents identify the optimal ejaculate size (S^*) that maximizes the number of fertilized eggs per unit reproductive effort ($C_M + S^*$, where C_M is male per-spawn mating cost). Accessory vertical and horizontal lines identify the corresponding fertilization success.

- *Among males.* Variation in male mating costs results in a positive, decelerating relation between fertilization success and ejaculate size. Concomitantly, this variation will weaken the relations between batch size and both ejaculate size and fertilization efficiency.

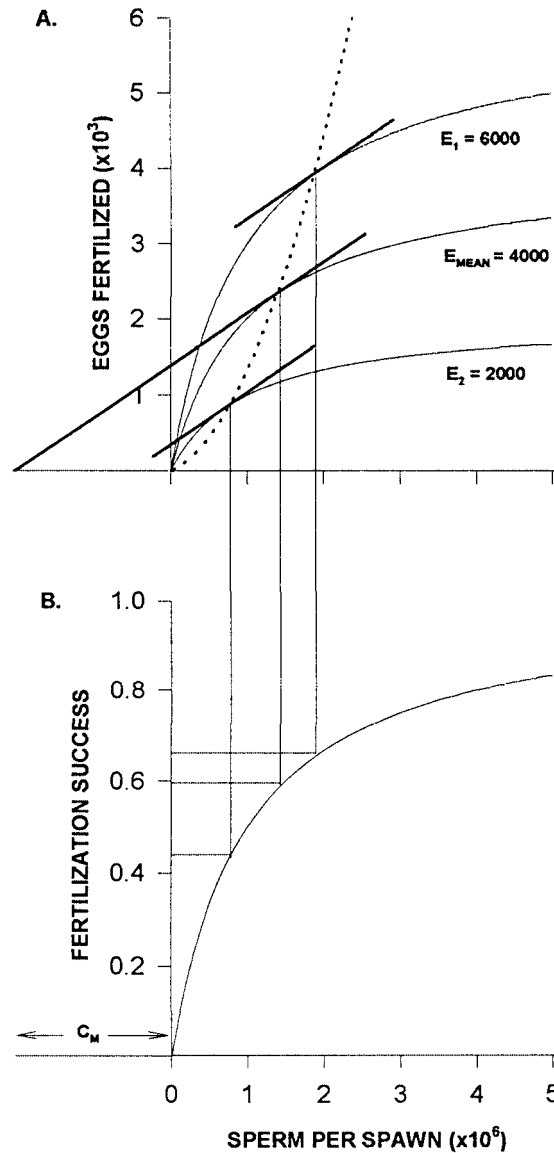


Fig. 2. Graphical depiction of MVT1, where males are assumed to maximize their long-term average fitness, and fertilization depends solely on sperm concentrations. The basic plots are as in Fig. 1. The slope of the dotted line corresponds to fertilization efficiency.

Fertilization success is independent of batch size once the effect of ejaculate size is statistically removed.

Long-term average fitness maximizers with finite sperm reserves (LMM1)

Let P_{ij} represent the proportion of male i 's daily sperm reserve (S_{Ti}) allocated to a female spawning E_j eggs. The optimal proportion (P_{ij}^*) depends on the batch-size frequency

distribution of all the females with which the male expects to mate (N_i). The Lagrange multiplier method provides values of P_{ij}^* that maximize $\Sigma \varphi_{ij} E_j$, given S_{Ti} and N_i . Specifically, these are the values that equalize the marginal returns ($\partial(\varphi_{ij} E_j)/\partial S_{ij}$) across all mated females, subject to the constraint that

$$N_i \sum_j f_j P_{ij} = 1$$

where f_j is the proportion of females spawning batches of size E_j . Unfortunately, no simple analytical solution exists in this case, which is, therefore, not fully explored. Predictions are based on numerical solutions obtained using Mathcad, SE 6.0.

Predictions

- *Within males.* Same as MVT1.
- *Among males.* Variation in male daily sperm reserves or expected number of mates can generate a positive decelerating relationship between fertilization success and ejaculate size.

Batch-size dependent fertilization (equation 1b)

Per-spawn fitness maximizers (PS2)

Setting $\partial \Phi_M / \partial S$ (see equation 2a) to zero and solving for S yields the optimal ejaculate size of male i mating with female j :

$$S_{ij}^* = (k E_j C_{Mi})^{0.5} \quad (11)$$

Fertilization success (φ_{ij}^*) and efficiency (Ω_{ij}^*) can now be calculated as:

$$\varphi_{ij}^* = 1/[1 + (k E_j / C_{Mi})^{0.5}] \quad (12)$$

and

$$\Omega_{ij}^* = 1/[k + (k C_{Mi} / E_j)^{0.5}] \quad (13)$$

Predictions

- *Within males.* Ejaculate size and fertilization efficiency increase, at a decelerating rate, with batch size. Conversely, fertilization success decreases with batch and ejaculate size (Fig. 3).
- *Among males.* With batch size and male mating costs having opposing effects on fertilization success (equation 12), relatively large among-male variation in C_M (as compared with variation in E) will cause a positive relation between ejaculate size and fertilization success to emerge at the population level. The negative relation between batch size and fertilization success will persist, even after the effect of ejaculate size is statistically removed. Ejaculate size and fertilization efficiency will increase with batch size.

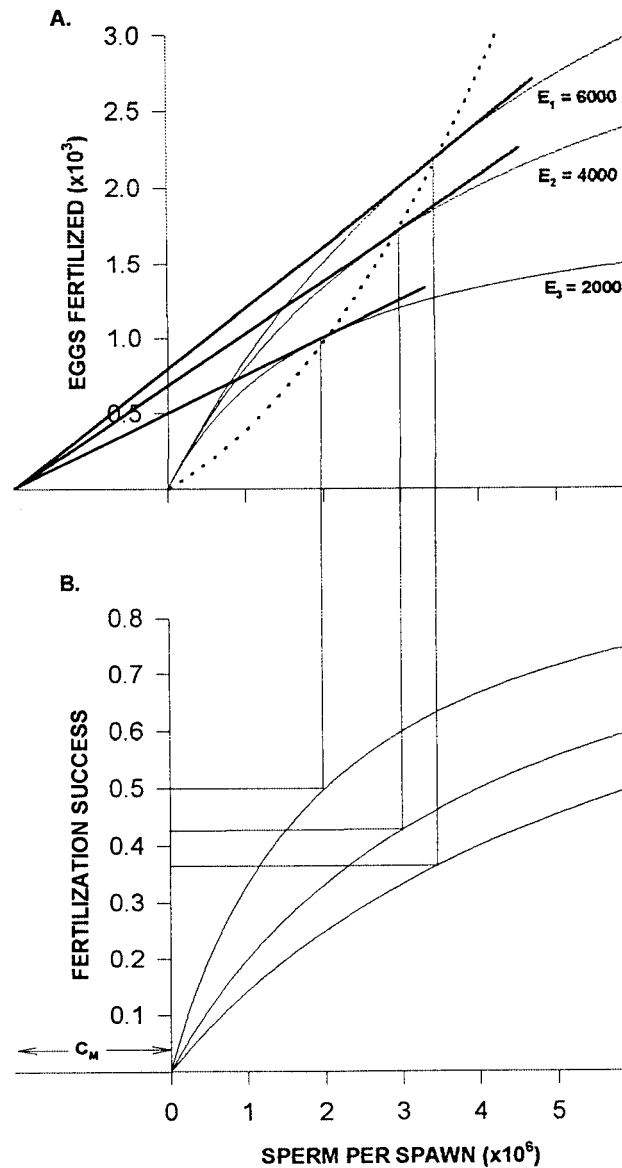


Fig. 3. Graphical depiction of PS2, where males are assumed to maximize their per-spawn fitness, and fertilization depends on the per-spawn sperm to egg ratio. Plots are as in Fig. 2.

Long-term average fitness maximizers (MVT2)

Given that the optimal ejaculate size of male i , when mating with the average female, results in $\bar{\Phi}_{Mi}^*$ fertilized eggs per unit reproductive effort, the optimal ejaculate size when mating with female j is:

$$S_{ij}^* = E_j [(k/\bar{\Phi}_{Mi}^*)^{0.5} - k] \quad (14)$$

because

$$\partial(\varphi_{ij}E_j)/\partial S_{ij}|_{S=S^*} = E_j^2 k / (kE_j + S_i^*)^2 = \bar{\Phi}_{Mi}^*$$

Note that $\bar{\Phi}_{Mi} < 1/k$ is always true, preventing S_{ij}^* from taking values smaller than zero. The ensuing fertilization success (φ_{ij}^*) and efficiency (Ω_{ij}^*) are given by:

$$\varphi_{ij}^* = 1 - (k\bar{\Phi}_{Mi}^*)^{0.5} \quad (15)$$

and

$$\Omega_{ij}^* = [1 - (k\bar{\Phi}_{Mi}^*)^{0.5}] / [(k/\bar{\Phi}_{Mi}^*)^{0.5} - k] \quad (16)$$

Predictions

- *Within males.* Ejaculate size is a linear function of batch size, anchored at the origin. As a result, fertilization success will be constant – that is, independent of ejaculate and batch size (Fig. 4). Fertilization efficiency is independent of batch size.
- *Among males.* Variation in C_M , which is relatively larger than that in batch size, will lead to the emergence of a positive relation between ejaculate size and fertilization success (Fig. 5A). Ejaculate size is a linear function of batch size, with an intercept at or below the origin (Fig. 5B), but not above (i.e. as S^* is a saturative function of C_M , for any value of E). Fertilization success and efficiency remain independent of batch size.

Long-term average fitness maximizers with finite sperm reserves (LMM2)

Evoking a finite daily sperm reserve (S_T) and a predictable daily number of mates (N), the optimal ejaculate size is given by $S_{Ti}P_{ij}^*$, where P_{ij}^* is the optimal proportion of S_{Ti} that male i should allocate to each female spawning a batch of size j . Unlike the case with LMM1, a simple analytical solution exists for P_{ij}^* when fertilization success is dependent on batch size. Letting f_j equal the proportion of females spawning batches of size E_j , optimal ejaculate size is given by

$$S_{ij}^* = S_{Ti} \frac{E_j}{N_i \sum_j f_j E_j} \quad (17)$$

Note that this solution implies that males need not have knowledge of the frequency of E_j , but only of the average batch size of the females with which they mate ($\bar{E} = \sum f_j E_j$). Fertilization success (φ_{ij}^*) and efficiency (Ω_{ij}^*) may now be written as:

$$\varphi_{ij}^* = \frac{S_{Ti}/N_i \bar{E}}{k + S_{Ti}/N_i \bar{E}} \quad (18)$$

and

$$\Omega_{ij}^* = \frac{1}{k + S_{Ti}/N_i \bar{E}} \quad (19)$$

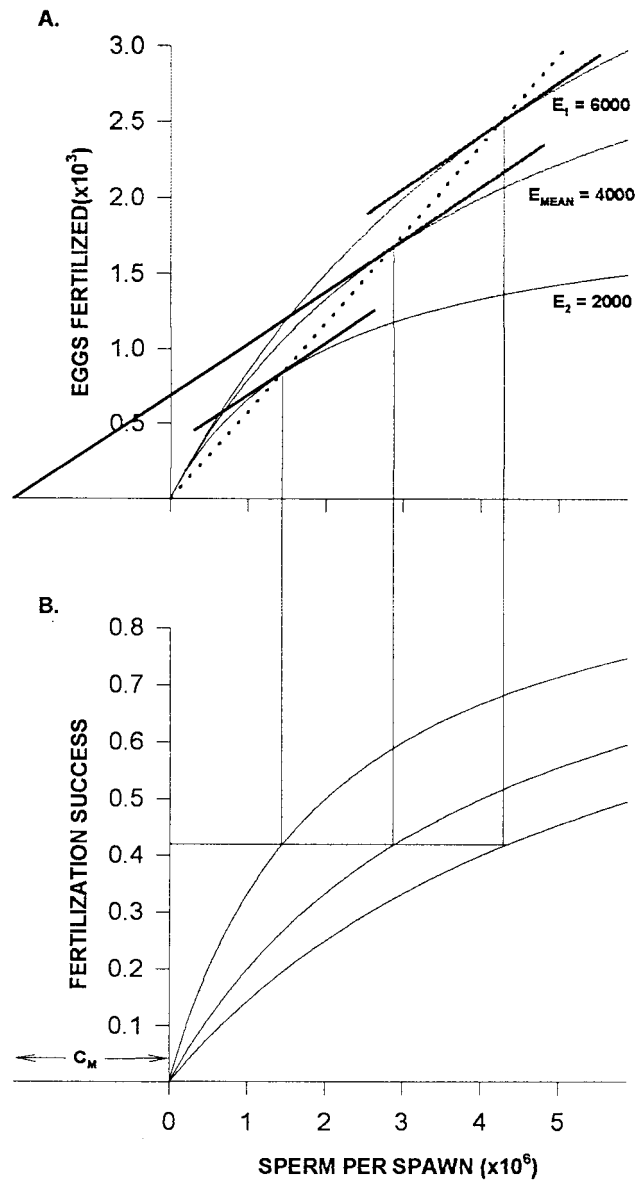


Fig. 4. Graphical depiction of MVT2, where males are assumed to maximize their long-term average fitness, and fertilization depends on per-spawn sperm to egg ratio. Plots are as in Fig. 2.

Predictions

- *Within males.* Same as MVT2.
- *Among males.* Variation in S_T or N can lead to the emergence of a positive relation between ejaculate size and fertilization success (Fig. 5A). With ejaculate size proportional to the ratio of S_T and N , however, the emergence and strength of this positive relation will

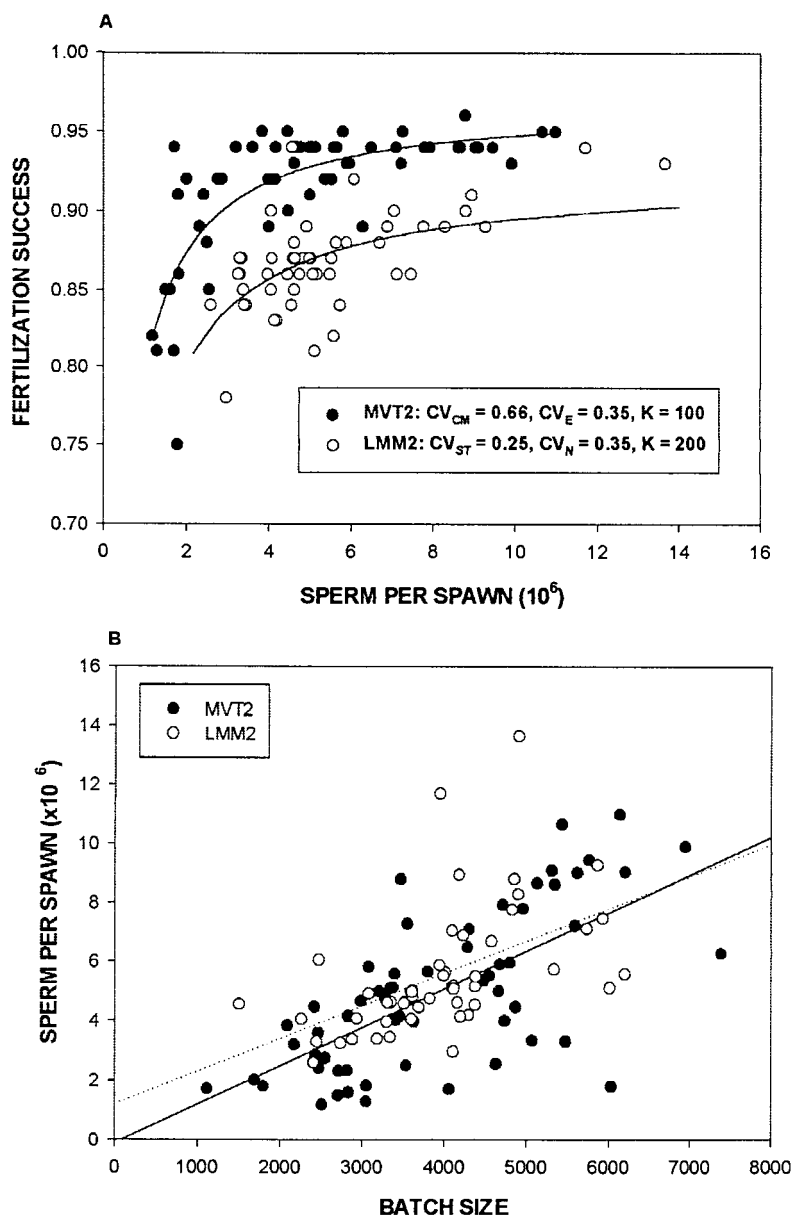


Fig. 5. The expected among-male relation between (A) ejaculate size and fertilization success and (B) batch and ejaculate size, as predicted by MVT2 and LMM2. MVT2 (●): the coefficient of variation in male mating costs (CV_{CM}) is larger than that in batch size (CV_E). Sixty values of C_M were randomly drawn from a normal distribution (mean $\pm$ standard deviation: $8 \times 10^7 \pm 5 \times 10^7$) and randomly paired with 60 values of E (4000 ± 1500) using Microsoft Excel 6.0. LMM2 (○): the coefficient of variation in the expected number of mates (CV_N ; 80 ± 30) is larger than in sperm-reserve size (CV_{ST} ; $4 \times 10^8 \pm 10^8$). The two variables are positively correlated ($r = 0.73$) and are randomly paired with batch sizes drawn from a normal distribution (4000 ± 1000). K is the ratio of sperm to eggs required to achieve $\phi = 50\%$.

depend on (1) the relative variation in S_T , N and E and (2) the strength of the correlation between S_T and N . The apparent dependence of ejaculate size on S_T and N will be similarly sensitive to the variation and correlation structure of these variables. Ejaculate and batch sizes will covary positively. Providing the coefficient of variation of N is larger than that of S_T , and the two variables covary weakly and positively, a linear regression of S on E can result in a positive y-intercept (Fig. 5B). Fertilization success and efficiency will be independent of batch size.

Co-evolved gamete release tactics, given batch-size dependent fertilization

With selection operating on both male and female gamete allocation, the number of possible models is large, as sex-specific constraints need not be the same. For brevity, I develop only the simplest possible model (PS3) in which both males and females are assumed to be per-spawn fertilization fitness maximizers.

Setting $\partial\Phi_F/\partial E$ to zero (see equation 2b) and solving for E yields the optimal batch size (E_{ji}^*) of female j mating with male i :

$$E_{ji}^* = (S_i C_{Fj}/k)^{0.5} \quad (20)$$

Note that no solution exists for E^* under batch-size independent fertilization. Optimal ejaculate size (S^*) is given by equation (11). Both S^* and E^* are local maxima, with $\partial^2\Phi_M/\partial S^2 < 0$ and $\partial^2\Phi_F/\partial E^2 < 0$ under all reasonable parameter values (as a reminder, Φ refers to the per-spawn number of eggs fertilized per unit reproductive effort). Substituting equation (11) into equation (20) and vice versa yields two expressions that describe ejaculate and clutch sizes that maximize Φ_M and Φ_F simultaneously:

$$S_{ESSij} = k^{1/3} C_{Mi}^{2/3} C_{Fj}^{1/3} \quad (21a)$$

$$E_{ESSji} = C_{Mi}^{1/3} C_{Fj}^{2/3}/k^{1/3} \quad (21b)$$

The evolutionary stability of S_{ESS} and E_{ESS} is depicted graphically in Fig. 6. Fertilization success and efficiency can now be seen to depend on the ratio of the sex-specific costs of mating:

$$\phi_{ESSij} = (C_{Mi}/C_{Fj})^{1/3} [k^{1/3} + (C_{Mi}/C_{Fj})^{1/3}] \quad (22)$$

and

$$\Omega_{ESSij} = 1/[k + k^{2/3}(C_{Mi}/C_{Fj})^{1/3}] \quad (23)$$

Predictions

- *Within males.* Variation in female mating costs will cause ejaculate size to increase with batch size ($\partial E_{ESS}/\partial C_F > \partial S_{ESS}/\partial C_F > 0$). Fertilization success will decrease with increasing batch and ejaculate size ($\partial\phi_{ESS}/\partial C_F < 0$), while fertilization efficiency will increase ($\partial\Omega_{ESS}/\partial C_F > 0$).
- *Among males.* For a female mating with males that vary with respect to C_M , fertilization success should increase with ejaculate size ($\partial\phi_{ESS}/\partial C_M > 0$). As a result, among-male patterns of fertilization success will depend on the relative variation in C_M and C_F . For example, if the coefficient of variation in C_M is much larger than that in C_F , a positive

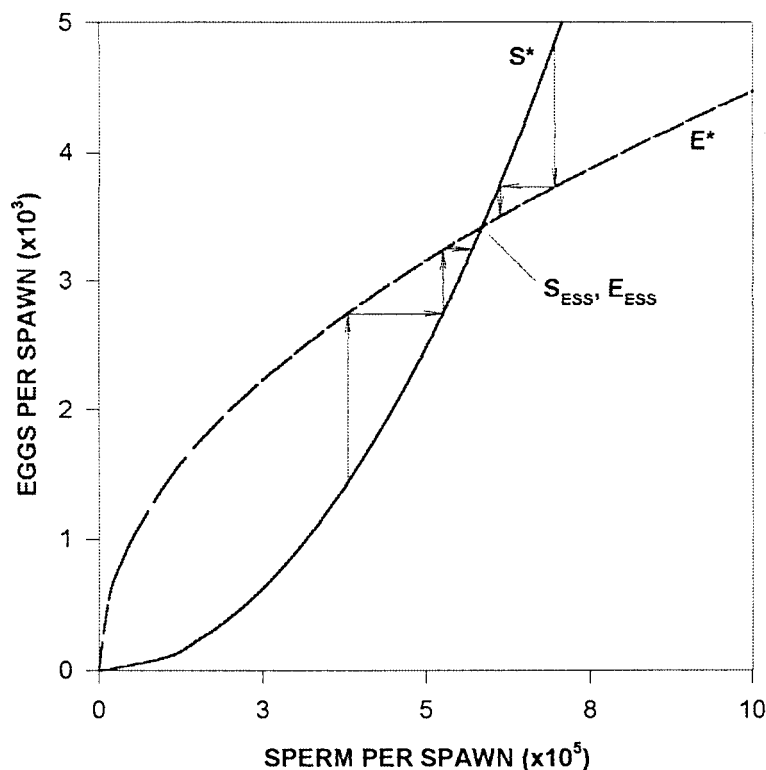


Fig. 6. Graphical depiction of the evolutionary stability of male and female gamete allocation, when selection is assumed to operate on their per-spawn fitness (PS3). The two curves depict each sex's best response to the number of gametes released by its mate (solid: S^* as a function of E ; dashed: E^* as a function of S). The point at which the two curves intersect represents the ejaculate and batch sizes that maximize male and female fitness simultaneously (S_{ESS} and E_{ESS} , respectively). The stability of the strategy pair is indicated by the arrow sequences.

relation will emerge between ejaculate size and fertilization success. Fertilization success will appear to increase with batch size, whereas fertilization efficiency will appear to decrease.

DISCUSSION

Evolutionary biologists using optimality theory assume an adaptive answer to the problem they address, so that they may establish whether a particular adaptive process can generate the observed 'solution' (Parker and Maynard Smith, 1990). Identification of a likely adaptive process involves inference pertaining to the relevant constraints on selection (physiological, physical, etc.), as well as the fitness measure under selection. It is these key elements – as they apply to the evolution of male gamete allocation tactics in the absence of sperm competition – that I attempt to evaluate. Specifically, postulating that ejaculate size is at equilibrium under selection, I attempt to isolate the most plausible adaptive scenario from a number of alternatives.

The alternative models presented above differ in what are general constraints: (1) the fertilization kinetics invoked (i.e. batch-size dependence *vs* independence); (2) the fitness measure being maximized (i.e. immediate *vs* long-term average fitness); and (3) the factor limiting male reproduction (i.e. sperm availability or male costs of mating). While constructed with externally fertilizing aquatic organisms in mind, the models may be of broader relevance. The adaptive process they address, as well as its outcome, presumably formed the background against which internal fertilization has evolved. Under specific circumstances, they may even apply to internal fertilizers. Moreover, the constraints I examine need not be restricted to systems lacking sperm competition, although I resort to such systems to simplify analyses.

In the absence of *a priori* reasons to ignore any of the contingencies that are possible given the above alternatives, all must be examined. Despite mutually exclusive assumptions, some of the models overlap in their predictions (Table 1). Thus, the remaining question is, how close can we come to identify the selective forces that shape gamete allocation tactics? To exemplify this point, I test the various models using published data on pair-spawning reef fish – specifically, the bluehead wrasse, *Thalassoma bifasciatum*, and the backtooth parrotfish, *Sparisoma radians* – for which the positive relation between ejaculate and batch size has been proposed to reflect adaptive sperm allocation (e.g. Shapiro *et al.*, 1994). These data are summarized in Table 2, and enumerated observations are hereafter abbreviated as ‘obs. i’.

Table 1. Summary of the major relations predicted by the different models of this study, both within and among males, and the corresponding empirical patterns. Ejaculate size, batch size and fertilization success and efficiency are depicted, in turn, by S , E , φ and Ω . Plus (+) and minus (–) signs refer to positive or negative relations, with the subscripts L, D and A signifying whether the relation is linear, decelerating or accelerating, respectively; ‘n’ denotes no relation. b_x refers to the x-intercept

	Batch-size independent			Batch-size dependent		
	PS1	PS3	MVT1/LMM1	PS2	MVT2/LMM2	Observed
Within						
$S=f(E)$	n	$+_D, b_x=0$	$+_D, b_x>0$	$+_D, b_x=0$	$+_L, b_x=0$	$+_?, b_x=?$
$\varphi=f(S)$	n	–	$+_D$	–	n	n
$\varphi=f(E)$	n	–	+ or n*	–	n	?
$\Omega=f(E)$	$+_L$	+	$+_D$	$+_D$	n	?
Among						
$S=f(E)$	n	$+_A, b_x=0$	$+_D, b_x>0$	$+_D, b_x=0$	$+_L, b_x=0$	$+_?, b_x=?$
$\varphi=f(S)$	+	$+_D$	$+_D$	$+_D^{\S}$	$+_D^{\S}$	$+_D$
$\varphi=f(E)$	n	$+^{\ddagger}$	+ or n*	–	n	n
$\Omega=f(E)$	+	$-^{\ddagger}$	+	+	n	+

* Controlling for effect of S

$\ddagger$ Providing $CV_{CM} > CV_{CF}$ (CV = coefficient of variation).

$\S$ Providing $CV_{CM} > CV_E$ or, in the case of LMM2, $CV_N > CV_{ST}$.

Table 2. Key observations regarding the mating behaviour, sperm allocation and fertilization success in two species of externally fertilizing, pair-spawning reef fish, *Thalassoma bifasciatum* and *Sparisoma radians*

1. Daily spawning is restricted to a short period of time, about 110 min for *T. bifasciatum*¹ and 30–60 min for *S. radians*⁴
2. Females release their daily egg production in a single spawn^{1,4}
3. Batch size is positively correlated with female size²
4. Males spawn repeatedly^{1,4} and at a predictable rate^{3,4} during daily spawning periods
5. Males do not exhibit sperm depletion across successive spawns^{1,2,4}
6. Ejaculate size increases with batch size, both within and among males^{2,4}
7. Fertilization success increases with ejaculate size among males,^{3,4} but not necessarily within males⁶
8. Among males, fertilization success is independent of batch size^{3,4}
9. Among males, fertilization efficiency increases with batch size^{2,4}
10. Male daily sperm reserves and mating frequencies are positively correlated^{3,4}
11. Male daily mating rate is negatively correlated with ejaculate size and fertilization success; the size of mated females is independent of male daily mating rates³
12. Pair spawning is non-assortative, at least in *T. bifasciatum*⁵

¹ Petersen *et al.* (1992), ² Shapiro *et al.* (1994), ³ Warner *et al.* (1995), ⁴ Marconato and Shapiro (1996), ⁵ Van den Berghe and Warner (1989), ⁶ Yoshikawa (1992).

Sperm allocation in pair-spawning reef fish

Fertilization success in reef fish has been suggested, either explicitly or implicitly, to be batch-size independent (Petersen, 1991; Shapiro and Giraldeau, 1996), but has not been examined empirically. A first approximation of the kinetics that govern the fertilization process may be obtained by parameterizing four variables in the biologically explicit model of Vogel *et al.* (1982): sperm life span, sperm swimming speed, egg cross-sectional area and egg concentration. For pelagic spawning fish, examination of these variables suggests batch-size independent fertilization kinetics, but also exposes the potential for substantial deviations from the assumptions of Vogel *et al.* (see the Appendix). In the absence of direct support for or against batch-size dependent or independent fertilization, I examine both contingencies.

Two of the models that maximize per-spawn fitness (PS1 and PS2) seem to fail in identifying the constraints on sperm allocation in reef fish. Assuming batch-size independent fertilization and constant male mating costs, PS1 fails to predict the positive within-male relation between batch size and ejaculate size (obs. 6). While a positive correlation between male mating costs and expected batch size will produce the observed relation, I am unaware of any evidence in support of such a correlation. Similarly, under batch-size dependent fertilization, the negative within-male relation between fertilization success and ejaculate size predicted by PS2 lacks unequivocal empirical support: Yoshikawa (1992) describes a positive relation for one male *T. bifasciatum*, a marginally significant positive relation for a second, one negative relation and two cases with no relation at all (obs. 7). Arguably, however, failure to detect a significant pattern may be due to low statistical power, providing weak grounds for refuting the hypothesis.

The lack of a constant within-male relationship between ejaculate size and fertilization success (Yoshikawa, 1992) is consistent with batch-size dependent fertilization (models

MVT2 and LMM2; Table 1). However, as mentioned above, the supporting data are somewhat limited ($n = 5$ fish). The issue of batch-size dependence may also be addressed by studying the among-male relationship between ejaculate and batch size. Under batch-size independent fertilization, ejaculate size is expected to be a positive decelerating function of batch size. On the other hand, if fertilization is batch-size dependent, the relationship is expected to be linear, possibly with a positive y-intercept (LMM2). Large variation in the empirical relation, however, makes a clear distinction difficult (e.g. fig. 2 of Shapiro *et al.*, 1994, and of Marconato and Shapiro, 1996).

A third distinction between batch-size dependent and independent fertilization is found in the relation between batch size and fertilization efficiency. Only models invoking batch-size independence (MVT1 and LMM1) predict the observed positive relationship. Yet, at least with *S. radians*, the significant increase in efficiency exists only between small females (i.e. small batch sizes) and medium or large females (Marconato and Shapiro, 1996). This pattern can easily emerge if male regulation of sperm release (Rasotto and Shapiro, 1998) is poor at low ejaculate sizes (i.e. when fertilizing small batches), such that more sperm is released than is optimal. A similar situation will arise if a minimum ejaculate size (i.e. sperm concentration), which is larger than the optimal response to small batch size, is required for the initiation of fertilization (e.g. Shapiro and Giraldeau, 1996; fig. 4 in Marconato *et al.*, 1997).

A distinction between the alternative constraints on gamete allocation tactics of long-term average fitness maximizers – costs of sperm production and mate acquisition (C_M ; MVT models) versus predetermined number of matings (N) and limited daily sperm reserves (S_T ; LMM models) – appears equally elusive (Table 1). Under the latter set of constraints, the among-male relation between ejaculate size and fertilization success (obs. 7) is conditional on variation in S_T and/or N . With S_T and N positively correlated (obs. 10) and having opposing effects (equations 17 and 18), the one with the largest coefficient of variation will drive the relation between S^* and ϕ . In *T. bifasciatum*, a greater than ten-fold increase in the number of daily matings is associated with an average 4.3-fold increase in daily sperm production (Warner *et al.*, 1995). As expected, among males, ejaculate size and N are indeed negatively associated (obs. 11, Table 1).

MVT models, on the other hand, make no direct predictions relating to sperm reserves (S_T) or the expected number of daily matings per male (N). Moreover, these models imply that optimal ejaculate size is independent of both S_T and N . However, if N covaries negatively with male per-spawn mating costs (C_M), MVT models could also be seen as predicting the negative effect of N on ejaculate size and fertilization success. Were such a correlation reflective of a causative relationship between C_M and N (e.g. $C_M \propto [\text{territory defence costs}]/N$), empirical manipulation of N would be confounded by consequent changes in C_M . Hence, such manipulations (cf. Shapiro and Giraldeau, 1995, p. 22) would have little power to discriminate between the two models based solely on the observed relation between ejaculate size and N . A distinction should be possible by examining the relationship between ejaculate size and S_T , once the (apparent) effect of N is statistically or empirically controlled. Whether C_M and N are functionally dependent or independent (i.e. correlates of a third variable such as male vigour), MVT models predict that S and S_T be either independent or negatively associated, whereas LMM models predict a positive relation in both cases.

The optimization of sperm allocation results in a sexual conflict, as females mating with 'optimal' males experience less than perfect fertilization success. An evolutionarily stable

resolution of the conflict is possible if fertilization is batch-size dependent and, for example, both sexes maximize per-spawn fitness (Fig. 6). However, that females tend to release their daily egg production in a single spawning (obs. 2), coupled with the positive correlation between batch size and female body size (obs. 3), seems to invalidate PS3. As is the case with two other models of co-evolved gamete allocation (in which males are assumed to behave according to MVT2 and LMM2, while females maximize their per-spawn fitness; not shown), PS3 predicts that the positive relationship between female body size and batch size is the result of a similar relationship between body size and the cost of obtaining a mating (C_F ; see equation 21b). This prediction is clearly counter-intuitive, and probably wrong. It is much more plausible that, at least for small fish such as *T. bifasciatum* and *S. radians*, batch size is limited by physiological or anatomical constraints (e.g. storage space).

Possible implications

Comparing how PS models perform in relation to MVT and LMM models can inform us of what is maximized by selection and, indirectly, of the capacity of individuals to establish mean resource quality. To the extent that selection is operating on the number of eggs fertilized per unit reproductive effort, per-spawn fitness maximization appears an unlikely target of selection. Although this finding may seem intuitive, it is not self-evident given our lack of *a priori* knowledge of male capacity to ascertain the expected mean batch size, as required of long-term average fitness maximizers. Pair-spawning reef fish seem to possess such a capacity, and to allocate sperm in a manner that maximizes long-term average fitness.

Sperm allocation may be constrained either by finite sperm reserves, or by the costs associated with the acquisition of mating opportunities. This statement does not imply that fertilization success may not be sperm-limited, but rather addresses the potential reasons for such a limitation. Which of the two constraints is, in fact, relevant can prescribe the options available to females to counter male gamete allocation tactics that result in less-than-perfect fertilization (i.e. in addition to encouraging sperm competition; e.g. Ball and Parker, 1996). As suggested by Shapiro and Giraldeau (1996), females can act to reduce the mating opportunities of the male with which they mate, providing sperm and mate availability (S_T and N , respectively) delimit ejaculate size. This option is not available with male mating costs (C_M) as the constraining factor, unless C_M and N are causally related. On the other hand, providing male mating costs constrain sperm allocation, females can act to increase these costs (e.g. by prolonging courtship), thus eliciting larger ejaculates and higher fertilization success rates. Unfortunately, the data available for pair-spawning fish are insufficient to distinguish between the two putative constraints. Moreover, my analysis highlights the need for precise understanding of male mating costs before the two may be unequivocally teased apart.

The question of whether fertilization follows batch-size dependent or independent kinetics would be best addressed empirically. However, logistic and practical constraints can make a direct assessment unfeasible. My evaluation of the model of Vogel *et al.* (1982; see the Appendix) is an attempt at an indirect appraisal of the fertilization process, as it may pertain to externally fertilizing fish. As a first approximation, the evaluation suggests batch-size independent kinetics, previously invoked with little justification (e.g. Petersen, 1991; Shapiro and Giraldeau, 1996). However, in the Appendix I also discuss possible deviations from the model of Vogel *et al.*, which could result in batch-size dependent

kinetics. By comparing the performance of models such as MVT1 (or LMM1) with that of MVT2 (or LMM2), I seek further insight into the fertilization process. I suggest that the available data can be interpreted as supportive of batch-size dependence (Table 1), contrary to expectations based on the model of Vogel *et al.*, and that ignoring this possibility in externally fertilizing fish could be premature.

One important consequence of the true nature of the fertilization process is the possibility for co-evolved male and female gamete allocation tactics. An evolutionarily stable batch size is possible only if fertilization is batch-size dependent. Yet, even if fertilization is indeed batch-size dependent, my analysis suggests that co-evolved tactics are unlikely when females mate once daily (i.e. when females maximize per-spawn fitness). Rather, co-evolved tactics may be restricted to large species, where E_{ESS} is likely to be smaller than the largest possible batch that females can produce or store, and where females exhibit multiple daily mating (i.e. maximize long-term average fitness). It is noteworthy, however, that various advantages to multiple female mating, other than in terms of fertilization success, are possible (e.g. Yasui, 1998).

Attempts to use patterns observed at the population level to infer constraints or processes that operate at the level of the individual may lead to erroneous conclusions if the appropriate sources of variation are not controlled for. For example, among-male variation in mating costs will produce a decelerating positive relation between ejaculate size and fertilization success (Fig. 5A), where none is expected under the constraints invoked in MVT2 (Fig. 4B). Similarly, the relative magnitude of among-male variation in the expected number of mates (N) and the size of sperm reserves (S_T), as well as the strength of their correlation, could lead to conflicting conclusions regarding the relation between ejaculate size and a male's number of mates. As the relevant sources of among-male variation are not always clear at the onset, it would appear that studies of individuals are more likely to elucidate the evolutionary scenarios of interest.

In conclusion, it is clear that optimization of gamete allocation by external fertilizers may proceed under different constraints. My analysis of pair-spawning reef fish exemplifies the need to consider competing hypotheses before any strong inferences can be made.

ACKNOWLEDGEMENTS

I am grateful to H. Kaplan for helpful discussions, to D.R. Levitan, T. Yoshikawa and C.W. Petersen for copies of their manuscripts, and to D. Albrecht, P. Andrews, D. Goulet, L. Green, A. Kodric-Brown, K. Rich and J. Rosenfield for helpful comments. Suggestions made by A. Sih, D.Y. Shapiro and C.W. Petersen greatly improved the quality of the manuscript. While writing, I was a guest of A. Genin (The H. Steinitz Marine Biology Laboratory of Eilat, Israel), for whose generosity I am greatly indebted.

REFERENCES

- Amanze, D. and Iyengar, A. 1990. The micropyle: A sperm guidance system in teleost fertilization. *Development*, **109**: 495–500.
- Ball, M. and Parker, G.A. 1996. Sperm competition games: External fertilization and 'adaptive' infertility. *J. Theor. Biol.*, **180**: 141–150.
- Birkhead, T.R. and Møller, A.P. 1992. *Sperm Competition in Birds*. London: Academic Press.
- Charnov, E.L. 1976. Optimal foraging, the marginal value theorem. *Theor. Pop. Biol.*, **9**: 129–136.

- Clutton-Brock, T. and Godfray, C. 1991. Parental investment. In *Behavioral Ecology, An Evolutionary Approach* (J.R. Krebs and N.B. Davies, eds), pp. 234–262. Oxford: Blackwell.
- Denny, M.W. 1988. *Biology and the Mechanics of the Wave-swept Environment*. Princeton, NJ: Princeton University Press.
- Denny, M.W. and Shibata, M.F. 1989. Consequences of surf-zone turbulence for settlement and external fertilization. *Am. Nat.*, **134**: 859–889.
- Dewsbury, D.A. 1982. Ejaculate cost and male choice. *Am. Nat.*, **119**: 601–610.
- Ginzburg, A.S. 1968. *Fertilization in Fishes and the Problem of Polyspermy*. Jerusalem: Israel Program of Scientific Translation.
- Jamieson, B.G.M. 1991. *Fish Evolution and Systematics: Evidence from Spermatozoa*. Cambridge: Cambridge University Press.
- Kiflawi, M., Mazeroll, A.I. and Goulet, D. 1998. Does mass spawning enhance fertilization in coral reef fish? A case study of the brown surgeonfish. *Mar. Ecol. Prog. Ser.*, **172**: 107–114.
- Lahnsteiner, F. and Patzner, R.A. 1998. Sperm motility in the marine teleosts *Boops boops*, *Diplodus sargus*, *Mullus barbatus* and *Trachurus mediterraneus*. *J. Fish Biol.*, **52**: 726–742.
- Levitan, D.R. 1998. Sperm limitation, gamete competition, and sexual selection in external fertilizers. In *Sperm Competition and Sexual Selection* (T.R. Birkhead and A.P. Møller, eds), pp. 173–215. Orlando, FL: Academic Press.
- Levitan, D.R. and Petersen, C.W. 1995. Sperm limitation in the sea. *Trends Ecol. Evol.*, **6**: 228–231.
- Lloyd, D.G. 1988. A general principle for the allocation of limited resources. *Evol. Ecol.*, **2**: 175–187.
- Marconato, A. and Shapiro, D.Y. 1996. Sperm allocation, sperm production and fertilization rates in the bucktooth parrotfish. *Anim. Behav.*, **52**: 971–980.
- Marconato, A., Shapiro, D.Y., Petersen, C.W., Warner, R.R. and Yoshikawa, T. 1997. Methodological analysis of fertilization rate in the bluehead wrasse *Thalassoma bifasciatum*: Pair versus group spawns. *Mar. Ecol. Prog. Ser.*, **161**: 61–70.
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- Nakatsuru, K. and Kramer, D.L. 1982. Is sperm cheap? Limited male fertility and female choice in the lemon tetra (Pisces, Characidae). *Science*, **216**: 753–755.
- Parker, G.A. 1984. Sperm competition and the evolution of animal mating strategies. In *Sperm Competition and the Evolution of Animal Mating Systems* (R.L. Smith, ed.), pp. 1–60. Orlando, FL: Academic Press.
- Parker, G.A. 1990. Sperm competition games: Raffles and roles. *Proc. R. Soc. Lond. B*, **242**: 120–126.
- Parker, G.A. 1993. Sperm competition games: Sperm size and sperm number under adult control. *Proc. R. Soc. Lond. B*, **253**: 255–262.
- Parker, G.A. and Maynard Smith, J. 1990. Optimality theory in evolutionary biology. *Nature*, **348**: 27–33.
- Petersen, C.W. 1991. Sex allocation in simultaneous hermaphrodites. *Am. Nat.*, **138**: 650–667.
- Petersen, C.W., Warner, R.R., Cohen, S., Hess, H.C. and Sewell, A.T. 1992. Variable pelagic fertilization success: Implications for mate choice and spatial patterns of mating. *Ecology*, **73**: 391–401.
- Pitnick, S. and Markow, T.A. 1994. Male gamete strategies: Sperm size, testes size, and the allocation of ejaculate among successive mates by the sperm-limited fly *Drosophila pachea* and its relatives. *Am. Nat.*, **143**: 785–819.
- Rasotto, M.B. and Shapiro, D.Y. 1998. Morphology of gonoducts and male genital papilla in the bluehead wrasse: Implications and correlates on the control of gamete release. *J. Fish Biol.*, **52**: 716–725.
- Robertson, D.R. 1996. Egg size in relation to fertilization dynamics in free-spawning tropical reef fishes. *Oecologia*, **108**: 95–104.

- Rothchild, B.J. and Osborn, T.R. 1988. Small-scale turbulence and plankton contact rates. *J. Plankton Res.*, **10**: 465–474.
- Shapiro, D.Y. and Giraldeau, L.-A. 1996. Mating tactics in external fertilizers when sperm is limited. *Behav. Ecol.*, **7**: 19–23.
- Shapiro, D.Y., Marconato, A. and Yoshikawa, T. 1994. Sperm economy in a coral reef fish, *Thalassoma bifasciatum*. *Ecology*, **75**: 1334–1344.
- Sivinski, J. 1984. Sperm in competition. In *Sperm Competition and the Evolution of Animal Mating Systems* (R.L. Smith, ed.), pp. 85–115. Orlando, FL: Academic Press.
- Smith, R.L., ed. 1984. *Sperm Competition and the Evolution of Animal Mating Systems*. Orlando, FL: Academic Press.
- Stockley, P., Gage, M.J.G., Parker, G.A. and Møller, A.P. 1996. Coevolution of female reproductive biology and ejaculate characteristics in fish. *Proc. R. Soc. Lond. B*, **263**: 451–458.
- Stockley, P., Gage, M.J.G., Parker, G.A. and Møller, A.P. 1997. Sperm competition in fishes: The evolution of testis size and ejaculate characteristics. *Am. Nat.*, **149**: 933–954.
- Templeton, A.R. and Lawlor, L.R. 1981. The fallacy of the averages in ecological optimization theory. *Am. Nat.*, **117**: 390–393.
- Van den Berghe, E.P. and Warner, R.R. 1989. The effects of mating system on male mate choice in a coral reef fish. *Behav. Ecol. Sociobiol.*, **24**: 409–415.
- Vogel, H., Cizhak, G., Chang, P. and Wolf, W. 1982. Fertilization kinetics of sea urchin eggs. *Math. Biosci.*, **58**: 189–216.
- Warner, R.R., Shapiro, D.Y., Marconato, A. and Petersen, C.W. 1995. Sexual conflict: Males with highest mating success convey the lowest fertilization benefits to females. *Proc. R. Soc. Lond. B*, **262**: 135–139.
- Yasui, Y. 1998. The ‘genetic benefits’ of female multiple mating reconsidered. *Trends Ecol. Evol.*, **13**: 246–250.
- Yoshikawa, T. 1992. Efficient sperm use in a coral reef fish. MSc thesis, University of Puerto Rico, Mayagüez.

APPENDIX: FERTILIZATION KINETICS IN PELAGIC SPAWNING FISH

Vogel *et al.* (1982) proposed a model to predict the fertilization success (i.e. the proportion of exposed eggs that are fertilized) of external fertilizers, when (1) eggs and sperm are found in overlapping, homogenous suspensions, (2) the volume occupied by the gametes is constant over time and (3) chemotactic attraction of spermatozoa by eggs is absent.

The kinetics that form the basis for Vogel and co-workers’ (1982) fertilization model are used to calculate the average number of potential fertilizing sperm, λ , encountering each egg. Given λ , fertilization success (ϕ) is then estimated by the Poisson probability of an egg being encountered by at least one potential fertiliser: $\phi = 1 - e^{-\lambda}$. The extent to which λ depends on the concentration of eggs released per spawn is determined by the product of four variables: sperm swimming speeds; the life span of sperm, defined as the *average* time sperm retain their capacity to fertilize once released into the water; egg cross-sectional area; and egg concentration. A product significantly smaller than 1 implies that eggs do not compete for sperm and fertilization is limited by sperm longevity (i.e. most sperm do not encounter an egg within their life span). Hence, gamete encounter rates and fertilization success would be insensitive to egg concentration. At the other extreme, a product greater than 1 signifies gamete encounter rates, and hence fertilization kinetics, that are proportional to the ratio of per-spawn sperm to egg concentrations. Below I attempt to differentiate between these extremes using parameter estimates compiled from the published literature.

The mean curvilinear swimming speeds of motile sperm, 10 s after initiation of motility, of four Mediterranean species (*Boops boops*, *Diplodus sargus*, *Mullus barbatus* and *Trachurus mediterraneus*) range between 0.12 and 0.16 mm·s⁻¹ (Lahnsteiner and Patzner, 1998, who also note the limited

knowledge of sperm motility in marine teleosts). Comparable speeds have been recorded in freshwater species (e.g. $0.139 \pm 0.085 \text{ mm} \cdot \text{s}^{-1}$; mean ± 1 standard deviation, $n = 9$ species; *sensu* Ginzburg, 1968, table 23). In both cases, swimming speed appears to decline significantly within the life span of the sperm (Ginzburg, 1968; Lahnsteiner and Patzner, 1998). I use $0.14 \text{ mm} \cdot \text{s}^{-1}$ as a rough estimate.

It is generally accepted that the duration of sperm motility (i.e. longevity) reflects fertilization ability or viability (i.e. 'life span' *sensu* Vogel *et al.*, 1982; see Ginzburg, 1968). Stockley *et al.* (1996) compiled longevity measures for the sperm of 14 species of freshwater fish, averaging just over a minute ($64 \pm 25 \text{ s}$, $n = 12$; two species with longevities greater than 4 min were not included). Sperm longevity in freshwater species is often shorter than in marine species (Ginzburg, 1968; Jamieson, 1991). However, ejaculates of *T. bifasciatum* and the brown surgeonfish, *Acanthurus nigrofasciatus*, achieve 50% of their maximal fertilization capacity at roughly 5 s and 25 s, respectively (Petersen *et al.*, 1992; Kiflawi *et al.*, 1998). A putative trade-off between sperm longevity and swimming speed (see Ball and Parker, 1996; but see also Stockley *et al.*, 1997) may be partially responsible for the relatively short longevities in these coral reef species. Moreover, sperm may lose their viability before they stop moving, making motility a maximum estimate of viability. I use 20 s as a first approximation of sperm life span.

Robertson (1996) provides egg volume measurements for 24 species of pelagic spawning reef fish (members of the Labridae, Scaridae and Serranidae) that translate to a mean cross-sectional area of $0.3 \pm 0.08 \text{ mm}^2$. As for batch sizes, females of the two species examined in this study rarely spawn batches in excess of ~6000 eggs. Marconato and Shapiro (1996) estimated the volume of water occupied by the sperm of *S. radians* 10 s after spawning as 14–65 ml. For pair-spawning *T. bifasciatum*, Shapiro *et al.* (1994) judged the sperm cloud at the moment of release as slightly smaller than 20 ml. Assuming that eggs and sperm overlap within the gamete cloud, I use 0.2 mm^{-3} as a rough estimate of mean egg concentration.

Multiplying the above parameter estimates yields a value below 1 ($0.14 \text{ mm} \cdot \text{s}^{-1} \times 20 \text{ s} \times 0.3 \text{ mm}^2 \times 0.2 \text{ mm}^{-3} = 0.168$), suggesting a fertilization process that is essentially independent of the number of eggs spawned. However, substantial deviations from the underlying assumptions of Vogel and co-workers' (1982) model seem likely. For example, in most cases, fish sperm can penetrate an egg only through a small (about 5–10 μm diameter) section of the membrane called the micropyle (e.g. Amanze and Iyengar, 1990). Consequently, egg cross-sectional area may overestimate the target of sperm. On the other hand, evidence exists to suggest that fish eggs secrete substances that can enhance sperm motility in their immediate vicinity and that lead to the concentration of sperm around the micropyle (Ginzburg, 1968; Amanze and Iyengar, 1990). Such 'chemoattraction' will act as if to increase the effective cross-sectional area of eggs.

Turbulence, such as that generated by the discharge of gametes and the swimming movements of spawning fish, may lead to further deviations. First, turbulence can increase the relative velocity of any two suspended particles, thereby increasing their encounter rate beyond that expected solely on the basis of swimming speeds (e.g. Rothchild and Osborn, 1988). Second, turbulence results in eddy diffusivity of suspended particles, reducing their concentration over time (Denny, 1988). Were most eggs to be fertilized immediately after spawning (e.g. Kiflawi *et al.*, 1998), the egg-concentration estimate used above may underestimate mean concentrations at fertilization. Moreover, a dissipating gamete cloud could include pockets of relatively high concentrations of unfertilized eggs that compete locally for sperm. Such localized competition would result in a fertilization process that is batch-size dependent.