

Further analyses of the expected relationship between variability in reproductive rate and net recruitment rate based on life history trade-off models

Justin G. Cooke¹

ABSTRACT

Correlations between survival and recruitment rates are widely reported in the empirical and theoretical literature on life history strategies for birds, mammals and other animals. The sign of the correlations depends on the direction of the causal relationship. Experimental manipulation of reproductive rates tends to produce a negative correlation between survival and reproductive rates because the energy saved by not reproducing becomes available for maintenance of the adult. In contrast, variation in food availability tends to affect both survival and reproduction, such that they can be positively correlated. A simple trade-off model, where the individual chooses the amount of energy it allocates to reproduction to maximise its net reproductive rate, is extended to allow for stochastic variation in food availability between individuals and years. The model is used to compute predictions of the relationship between survival and reproduction. For the parameter sets considered, strong positive correlations are predicted. If these results are representative, they imply that true levels of variability in net recruitment rate in baleen whales may be substantially greater than would be inferred from considering only observed variability in reproductive rates under the assumption of invariant survival rates.

1. Introduction

The level of variability in net recruitment rate of baleen whales has been shown to be a potentially important factor in the estimation of MSY rates (maximum sustainable exploitation rates) of baleen whales from observed time series of abundance of recovering stocks (Cooke, 2007; IWC, 2010).

A recent Scientific Committee workshop (IWC, 2011a) examined a number of time series of different demographic parameters (mainly calving rates, proportions, or intervals) from baleen whale populations with a view to estimating typical levels of variability in baleen whale net recruitment rates.

A potentially important issue in this context is the relationship between the variability in reproductive rates and the variability in net recruitment rate. If variations in reproduction and survival are positively correlated, then the variability in net recruitment rate will be greater than the variability in reproductive rates alone; if variations in survival and reproduction are negatively correlated, the reverse applies (IWC 2011b).

There is a substantial literature on the issue of trade-offs or correlations between life history parameters (Stearns 1989, 1992; Roff 1992). In particular there are both empirical and theoretical results trade-offs in energy investment between reproduction and survival (Perrin and Sibly 1993), where in the case of mammals energy investment in reproduction includes lactation (Clutton-Brock *et al.* 1996; Rogowitz 1996).

The core question is how an animal allocates available resources between reproduction, on the one hand, and its own growth and maintenance on the other. With too little energy invested in reproduction, the animal will be outcompeted by conspecifics that invest more in reproduction; with

¹ Centre for Ecosystem Management Studies, Höllenbergr. 7, 79312 Emmendingen, Germany.
Email: jgc@cems.de

too much investment in reproduction at the expense of its own maintenance, the animal risks early death and reduced lifetime reproductive success (van Noordwijk and de Jong 1986).

Some of the literature on the issue is motivated by theoretical considerations, to understand the evolutionary pressures that have led to the diversity of life history strategies that we observe in nature: this has led to the concept of the evolutionary stable strategy (Hines, 1987). A practical spin-off from this question has been the derivation of expected relationships between life history parameters such that hard-to-observe parameters, such as natural mortality rates, can be inferred from more readily observable parameters such as somatic growth rates and age-specific fecundity (Myers and Dole, 1983).

Correlations between life history parameters can be of several kinds: correlations between parameters over populations; correlations over individuals within a population; and correlations over time within a population. The latter correlations are what primarily concern us here.

A common theme in the literature is the apparent discrepancies that have been observed between correlations between life history parameters that are observed naturally in the wild, and those that are observed in manipulation experiments, either in the laboratory or in the field (Reznick et al. 1990; Glazier 2007; Linden and Moller 1989).

It is important to pay attention to the direction of causation when analysing correlations. When reproduction is artificially suppressed, for example by removal of birds' eggs, survival of the parents tends to increase, as would be expected from the energy they save in not having to care for the brood (Dhondt 2001). Such experiments tend to yield an apparent negative correlation between survival and reproduction. Experiments involving the manipulation of food availability often show positive correlations between reproduction and survival: when food availability is increased, but not to satiation, both survival and reproduction are enhanced, and vice versa (Reznick et al. 1990).

An alternative possibility was discussed by IWC (2011b): if food availability varies during the reproductive cycle of a baleen whale, it is possible that a short period of food scarcity could lead to a failure to reproduce, but that the energy saved may lead to enhanced survival if conditions subsequently improve. In principle this could produce a negative relationship between survival and reproduction over a certain range. Variable predation on calves was mentioned as an additional factor that could result in a negative correlation between reproductive and survival rates.

In this paper, the model suggested by Cooke (2011) for the relationship between survival and reproductive rates, on the assumption that both are food-limited, is developed further to allow for inter-annual and inter-whale variability, and its predictions are explored over a wider range of parameters values, as recommended by IWC (2011b).

2. Model development

2.1. Deterministic model for an individual on a 1-year cycle

Suppose that in each year there is a ration y of energy available to the individual of which an amount x (where $0 \leq x < y$) can be invested in reproduction. For female adults, the survival rate of the calf depends on the invested energy x , and the survival rate of the mother depends on the remaining energy $y - x$. The total energy y is determined by environmental factors, but the part of this invested in reproduction can be optimised by the individual.

The factors of interest are S , the adult survival probability, and R , the effective reproductive rate. R is expressed in terms of the probability of raising a female calf that survives to maturity, so that the expected net recruitment rate is $S + R - 1$.

We would expect the relationship between available energy and survival to be roughly of the shape of the curves shown in Fig. 1, with diminishing returns at higher energy levels, but with survival rates of adults and calves possibly declining rapidly when the available energy drops below critical levels.

Curves of this shape can be modelled by:

$$S(x) = S_{\max} \exp\left(-\left(\frac{\alpha_S}{y-x}\right)^z\right) \quad (1)$$

$$R(x) = R_{\max} \exp\left(-\left(\frac{\alpha_R}{x}\right)^z\right) \quad (2)$$

where α_S and α_R are population-specific parameters and z is an exponent that is introduced to allow flexibility in the shape of the relationships. The values S_{\max} and R_{\max} denote the maximum survival rates of adults and offspring in times of plenty. The net recruitment rate is given by $r = S + R - 1$, and the maximum net recruitment rate is given by $r_{\max} = R_{\max} + S_{\max} - 1$.

If the individual “chooses” x optimally then two types of outcome are possible, depending on the total available energy y . For low values of y , the optimal choice is to set $x = 0$ and not to attempt reproduction ($R = 0$). For higher values of y , the optimal choice is at a local maximum that satisfies:

$$dR/dx + dS/dx = 0 \quad (3)$$

The globally optimum value of x can be determined for a given value of y , given values for the remaining parameters, as follows:

- (i) solve equation (3) for x in $0 < x < y$, if possible, to obtain a local maximum of $S + R$;
- (ii) calculate S for $x = 0$ (implying $R = 0$)
- (iii) choose either the value of $S+R$ at the local maximum, or the value of S at $x = 0$, whichever is the greater.

An example of the deterministic relationship between R , S and y for this model is shown by Cooke (2011), on the assumption that the individual chooses the value of x to maximise $S+R$.

2.2. Treatment of variability

Although we are primarily interested in variability between years, it may be important also to consider the effects of variation between individuals, in case this affects the model’s predictions with respect to inter-annual variability. We suppose that the variability in energy availability has both individual and year-specific components such that the energy available to individual i in year t is given by:

$$y_{it} = Y \exp(\sigma_T \gamma_t + \sigma_I \eta_i + \sigma_{IT} \varepsilon_{it})$$

where Y is the median energy availability, γ_t is an independently normally distributed annual residual, η_i is an independently normally distributed individual residual, and ε_{it} is an independently normally distributed year-specific individual residual. σ_T , σ_I and σ_{IT} are the standard deviations of the annual, individual and interaction variation. The model for individual variation can lie anywhere between the following extremes:

- (i) $\sigma_I = \sigma_{IT} = 0$ no individual variability
- (ii) $\sigma_I = 0$, $\sigma_{IT} > 0$: individual variability within a year, but individual residuals are not “remembered” from year to year
- (iii) $\sigma_I > 0$, $\sigma_{IT} = 0$: individual residuals persist throughout life (*i.e.* a weak individual remains weak for life).

For the results given in this paper, σ_I and σ_{IT} are interchangeable, because only 1-year breeding cycles are considered. The distinction is nevertheless retained, so that the model can later be extended to multi-year breeding cycles with energy storage between successive years.

2.3 Generation of results

Results are generated by drawing random deviates for the residuals γ_i, η_i for each individual and year, and computing R and S for each individual, on the assumption that each individual allocates energy to reproduction optimally for that individual. Within a year, values of R and S are averaged across individuals, and a single average (R, S) pair is plotted for each year.

2.4. Parameter values

Because the scaling of Y is arbitrary, we can without loss of generality fix $\alpha_S = 1$ such that only the ratio α_R/α_S is relevant.

The parameters of the model are: $S_{\max}, R_{\max}, \alpha_R/\alpha_S, z, \sigma_I, \sigma_T$ and Y .

The values of Y are chosen to yield three values of the mean net recruitment rate \bar{r} : (a) $\bar{r} = 0.8r_{\max}$; (b) $\bar{r} = 0.5r_{\max}$; (c) $\bar{r} = 0$. These three values correspond to a population: (a) at a low level, in good quality habitat, which is enjoying close to its maximum rate of increase; (b) at an intermediate level; and (c) at its carrying capacity (K), where the average net growth rate is zero.

The values explored for each of the remaining parameters are listed in Table 1.

In order to limit the number of combinations of parameter values to be examined, the parameter value combinations were selected according to a modified partial factorial design (Box *et al.* 2005), on the assumption that second and higher order interactions can be neglected, at least in an exploratory analysis. The parameter combinations selected (26 in total) are listed in Table 2.

3. Results and discussion

Figs 2a-z show the relationship between R and S for each set of parameter values. The correlation between R and S was also computed for each parameter and entered in the final column of Table 2.

The results show strong positive correlations between R and S for the parameter sets considered here. If these results are representative, they would imply that the net recruitment rate is considerably more variable than would be inferred from variations in reproductive rates alone, on the assumption of invariant survival rates.

REFERENCES

- Box G.E., Hunter J.S., Hunter W.G. 2005. *Statistics for Experimenters: Design, Innovation, and Discovery*, 2nd Edition. Wiley.
- Clutton-Brock T. H., Stevenson I. R., Marrow P., MacColl A. D., Houston A. I. and McNamara J. M. 1996. Population fluctuations, reproductive costs and life-history tactics in female soay sheep. *J. Animal Ecol.* 65(6):675-689.
- Cooke J.G. 2007. The influence of environmental variability on baleen whale sustainable yield curves. Paper SC/N07/MSYR1 presented to the MSYR workshop, November 2007.
- Cooke J.G. 2011. A note on the expected relationship between variability in reproductive rate and variation in net recruitment rate based on life history trade-off models. *J. Cetacean Res. Manage* 12 (Suppl.) :99-101.
- Dhondt A.A. 2001. Trade-offs between reproduction and survival in tits. *Ardea* 89(1)(Suppl.):155-166.

- Glazier, D.S. 2007. Trade-offs between reproductive and somatic (storage) investments in animals: a comparative test of the Van Noordwijk and De Jong model. *Evolutionary Ecology* 13(6):539-555.
- Hines W.G.S. 1987. "Evolutionary stable strategies: a review of basic theory". *Theoretical Population Biology* 31 (2): 195–272.
- IWC. 2011a. Report of the 3rd inter-sessional workshop on the review of MSYR for baleen whales. *J. Cetacean Res. Manage.* 12(Suppl.): 399-412.
- IWC. 2011b. Report of the subcommittee on the Revised Management Procedure. *J. Cetacean Res. Manage.* 12(Suppl.): 89-116.
- Linden M, Moller AP. 1989. Cost of reproduction and covariation of life history traits in birds. *Trends Ecol. Evol.* 6:183–85
- Myers R.A. and Doyle R.W. 1983. Predicting natural mortality rates and reproduction-mortality trade-offs from fish life history data. *Can. J. Fish. and Aq. Sci.* 40(5): 612-620.
- Perrin N. and Sibley R.M. 1993. Dynamic models of energy allocation and investment. *Annual Reviews of Ecology and Systematics* 24:379-410.
- Reznick D.N. 1992. Measuring the costs of reproduction. *Trends Ecol. Evol.* 7:42–45
- Reznick D.N, Bryga H, Endler JA. 1990. Experimentally-induced life history evolution in a natural population. *Nature* 346:357–59
- Rogowitz G.L. 1996. Trade-offs in energy allocation during lactation. *Am. Zool.* 36:197–204
- Roff D.A. 1992. *The Evolution of Life Histories*. New York: Chapman & Hall. 535 pp.
- Stearns S.C. 1989. Trade-offs in life history evolution. *Funct. Ecol.* 3:259-48
- Stearns S.C. 1992. *The Evolution of Life Histories*. Oxford, UK: Oxford Univ. Press. 249 pp.

TABLES

Table 1. List of parameters and alternative values.

Table 2. Combinations of parameter values used to generate the results shown in Figs 2a-z.

FIGURES

Fig. 1. Curves of potential relationships between effective reproductive success and energy invested in reproduction (analogous curves for the energy/survival relationship).

Figs 2a-z. Scatter plots of S (survival rate) versus R (recruitment rate) generated from the model for each parameter combination. Each point corresponds to the average (across individuals) of S and R in a given year.

Table 1. List of parameters and alternative values.

Symbol	Name	Values			Description
S_{\max}	Smax	0.95	0.99		
R_{\max}	Rmax	0.05	0.10		
α_R/α_S	a	0.5	1.0	2.0	See equations 1,2
z	z	1.0	2.0	5.0	Exponent: linear; moderate curvature; severe curvature
σ_I	sI	0.0	0.5		Individual residual for available energy
σ_T	sT	0.5	1.0		Annual residual for available energy
σ_{IT}	sIT	(not used)			Individual residual by year (not used)
\bar{r}/r_{\max}	r_rmax	0.8	0.5	0.0	Ratio of mean net recruitment to max value: depleted stock; intermediate; stock at K

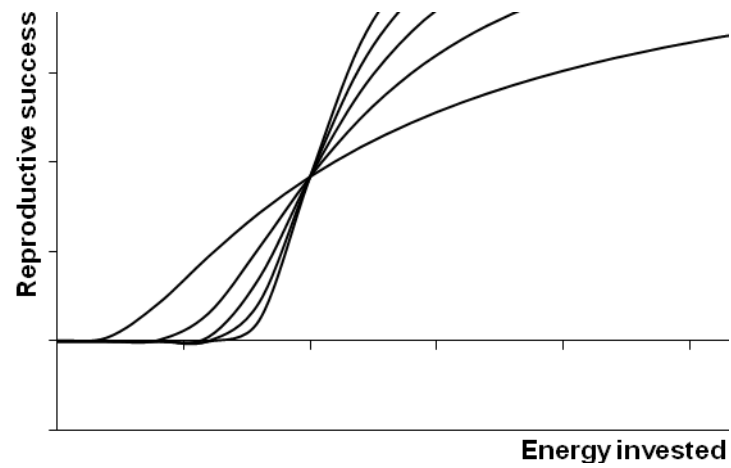
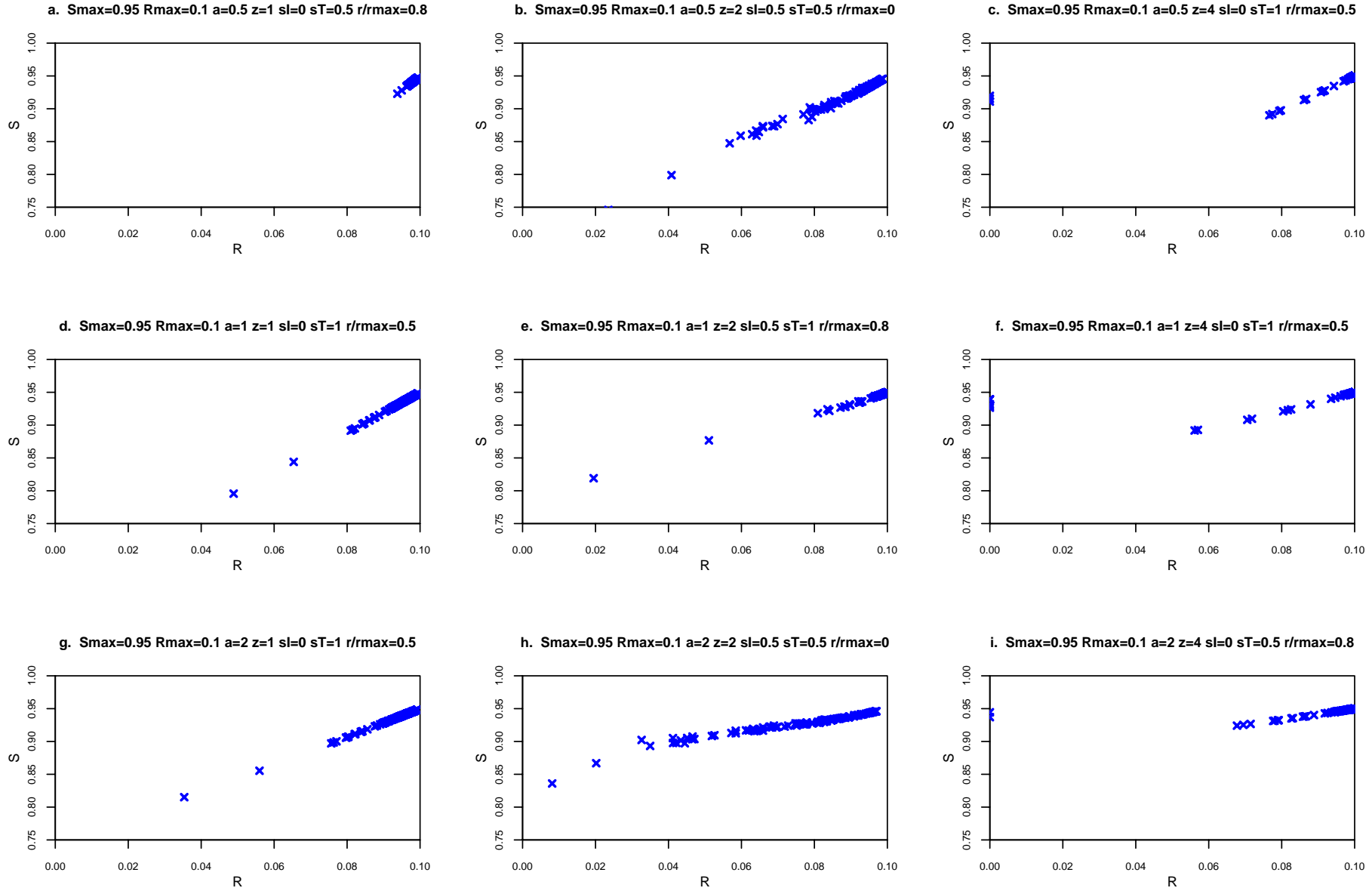
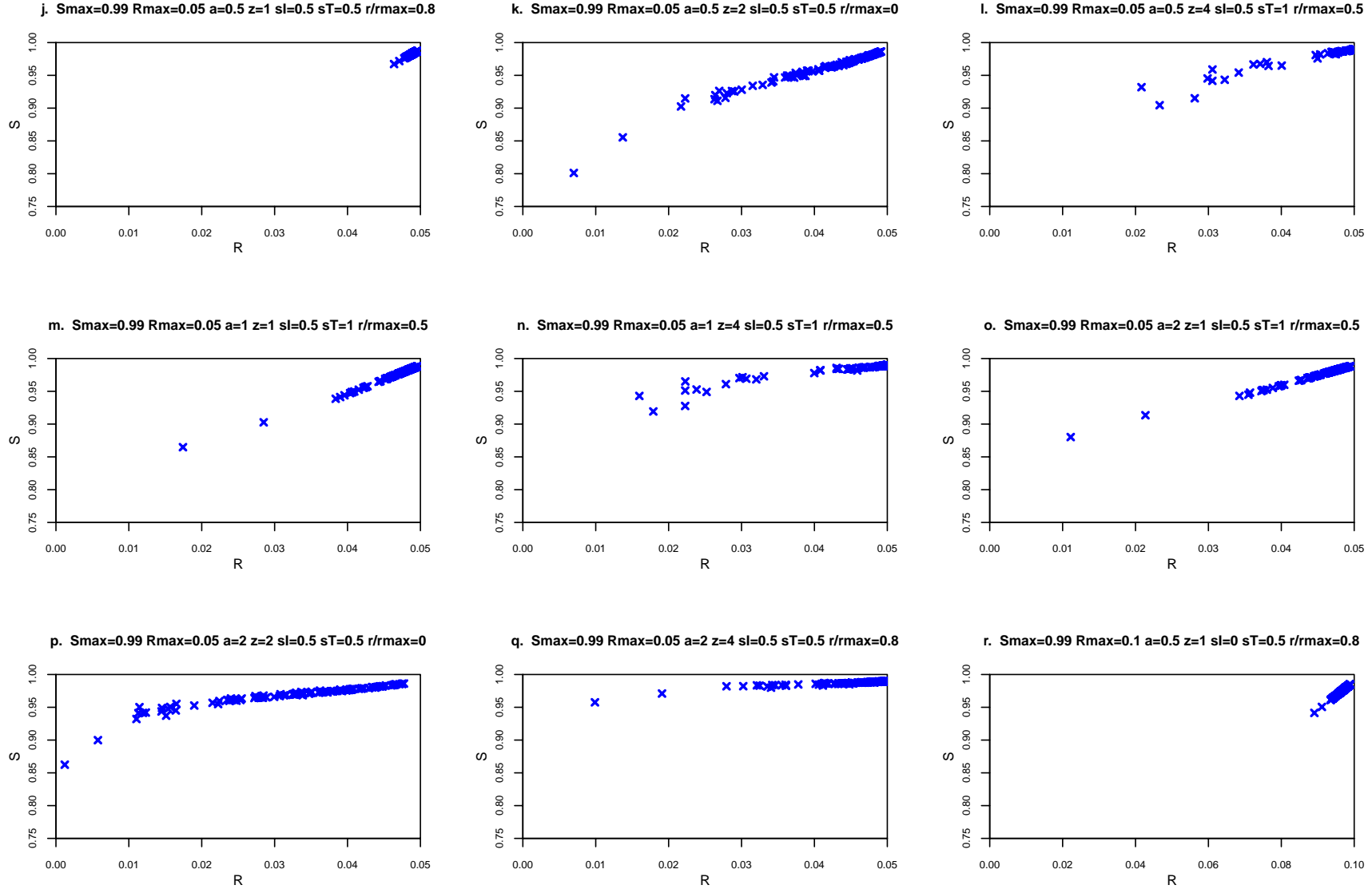


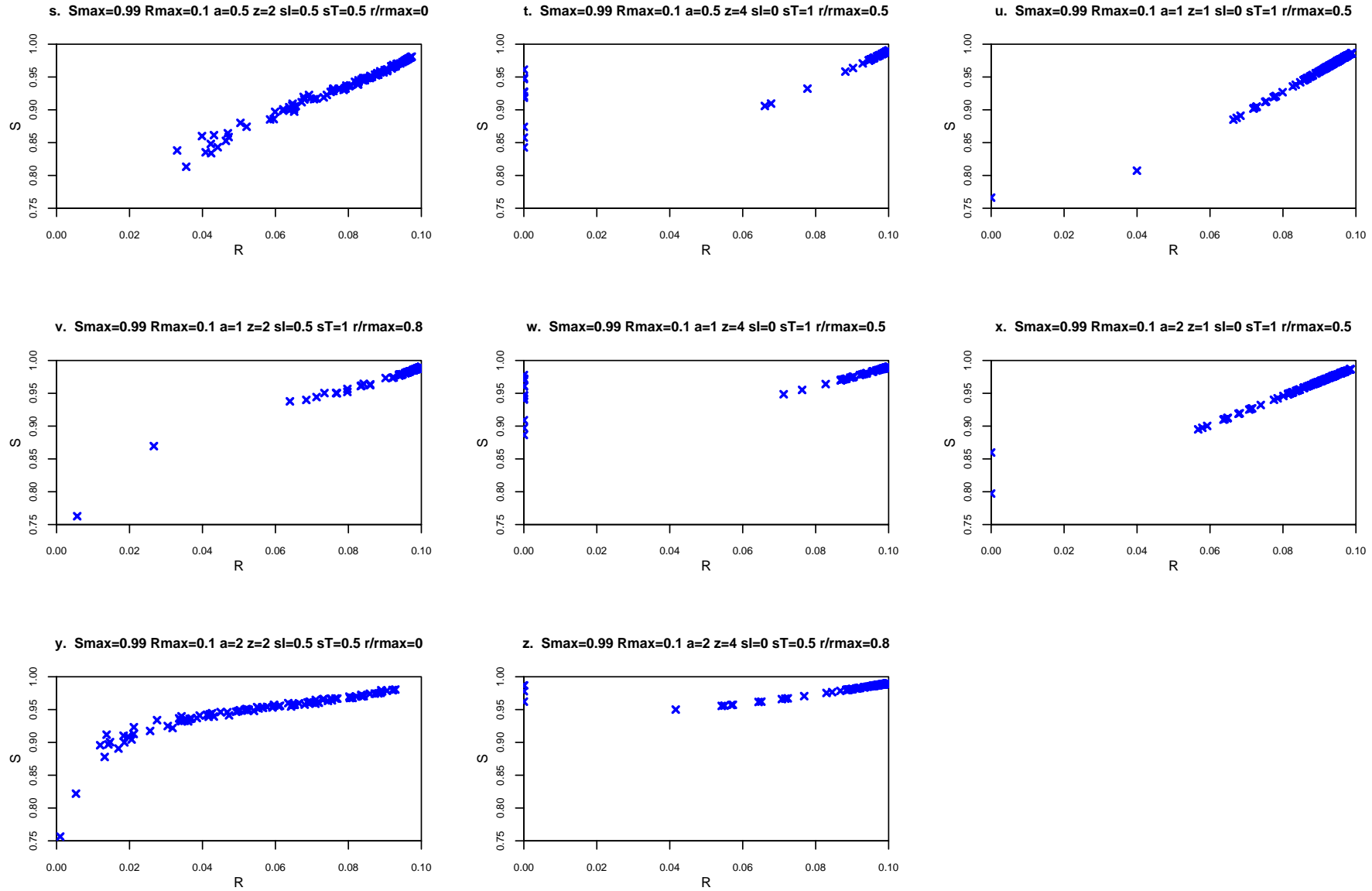
Fig. 1. Curves of potential relationships between effective reproductive success and energy invested in reproduction (analogous curves for the energy/survival relationship).



Figs 2a-z. Scatter plots of S (survival rate) versus R (recruitment rate) generated from the model for each parameter combination. Each point corresponds to the average (across individuals) of S and R in a given year



Figs 2a-z. Scatter plots of S (survival rate) versus R (recruitment rate) generated from the model for each parameter combination. Each point corresponds to the average (across individuals) of S and R in a given year



Figs 2a-z. Scatter plots of S (survival rate) versus R (recruitment rate) generated from the model for each parameter combination. Each point corresponds to the average (across individuals) of S and R in a given year