THE SIGNIFICANCE OF FERTILIZATION

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A basic assumption in evolutionary biology and population dynamics is that eggs are always fertilized. The reproductive success of males is supposedly limited by the availability of females, while resources limit the reproductive success of females.

This is not necessarily true in the marine environment, where many species reproduce by external fertilization and eggs run the risk of never meeting a sperm in their lifetime. Important factors for successful fertilization are being in the vicinity of individuals of the opposite sex (population density), simultaneous spawning, male fecundity and sufficient diffusion or mixing.

Aspects of fertilization kinetics in *Macoma balthica* (L.) were studied by means of field observations, laboratory experiments and mathematical modeling. Our results suggest that fertilization is not always guaranteed for eggs and that females tune the size of their eggs to anticipated sperm concentrations. This is beneficial to the individual females, and they thereby lower their egg numbers at low sperm concentrations. Population dynamics could thus not only be directly affected by fertilization rate, but also indirectly by egg size adjustments.

Spawning induces spawning.
In the laboratory, spawning females inspire males as well as other females to also start to spawn. This effect will greatly enhance realized fertilization rates in the field. It is probably a pheromone released by the females or the eggs themselves that triggers spawning. Intriguingly, though, we also found that spawning in the field is spread out over a period of two months.

Not all males perform similarly.
Among 209 males induced to spawn by a temperature shock, the average number of spermatozoa released per male was 3.4.108, but the variation between males was enormous (Fig. 1). Size differences between the males partly cause this, but cannot explain all variation.

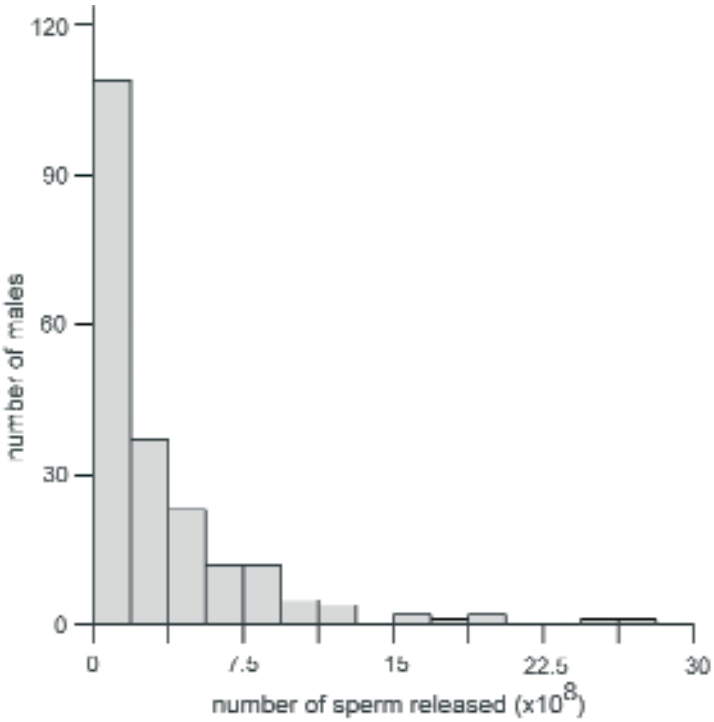


Fig. 1 – Some males spawn many sperm, but most very little.

Are all eggs fertilized?
In *Macoma balthica*, they are probably not. *Macoma balthica* occurs in a range of population densities: the majority of individuals live in densities below 100 per m^2 (Fig. 2). At high densities, more males will be spawning at the same time and so sperm limitation will be less severe than at low population densities. We estimated the relationship between sperm density and fertilization probability in lab experiments, and when we then assume that sperm is well mixed in

the water column in the field, we can make a rough prediction of fertilization probability for eggs in the field (Fig. 3). Because this prediction still contains many uncertainties, these probabilities must be interpreted with caution. Nevertheless, it is clear that fertilization depends very strongly on population density and is probably less (possibly much less) than 100%, given the conditions under which most *Macoma balthica* live.

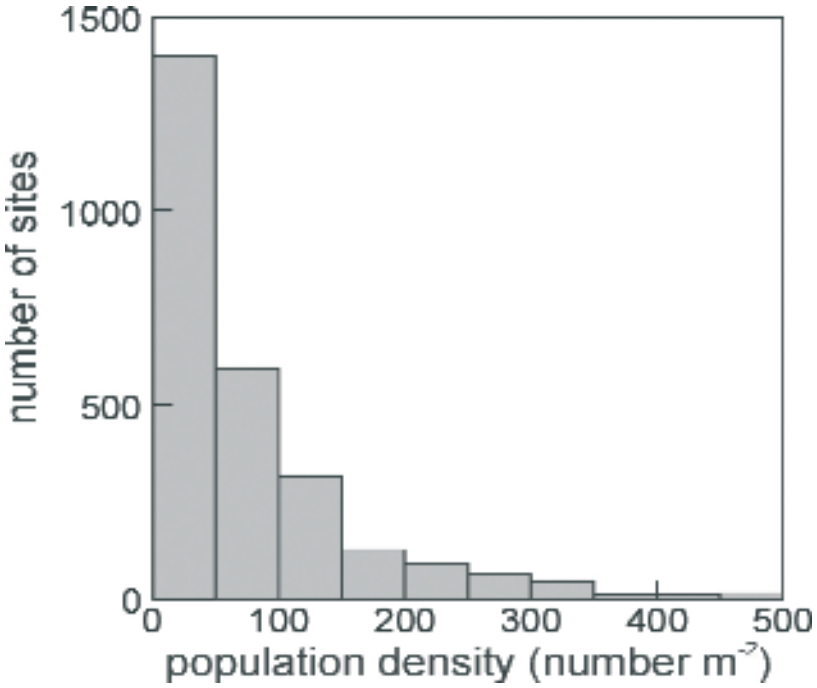


Fig. 2 – Variation in population density of *Macoma balthica* (>10 mm) in the western Dutch Wadden Sea among 2724 sites in 2000 (data: Jan van Gils, NIOZ).

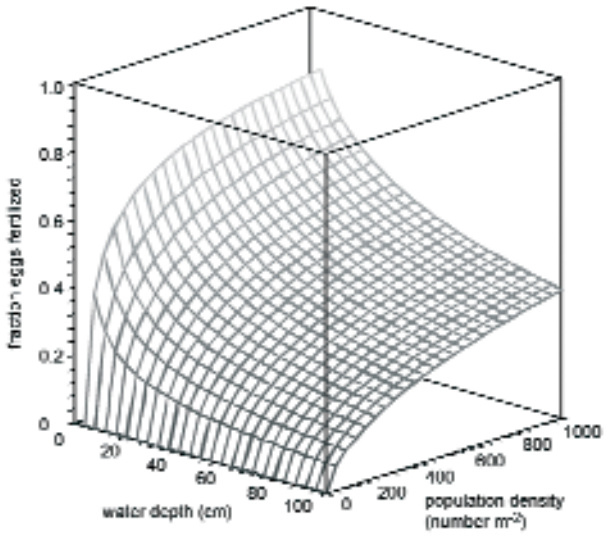


Fig. 3 – Predicted probability for eggs to be fertilized at different population densities and different water depths, under the assumptions that gametes are well-mixed through the water column and spawning is fully synchronized.

Egg size: females anticipate and adjust.

Could it be useful to females to increase the size of their eggs when sperm are in short supply, so that the eggs become a larger target for sperm? This has been suggested earlier, and our analysis of a generalized model shows that it is true under a wide range of possible circumstances. And indeed, data on *Macoma balthica* suggest that it really happens in the field (Fig.

4). The correlation with population density is so strong (a 10% increase in egg diameter means a 25% increase in egg volume and thus about 25% fewer eggs) that it might be expected to impact recruitment success.

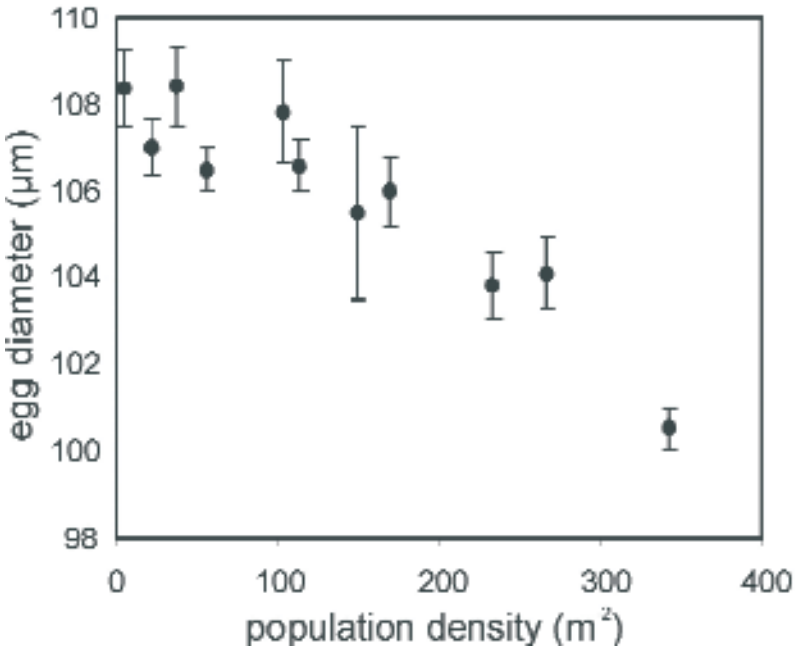
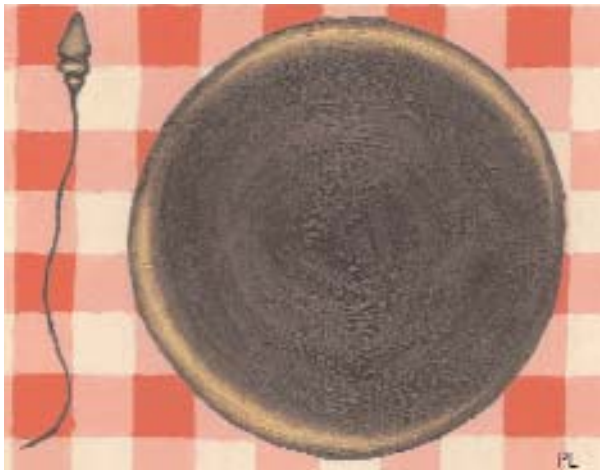


Fig. 4 – Egg size of *Macoma balthica* in the western Dutch Wadden Sea correlates well with population density (egg size data: partly from P. Honkoop and J. van der Meer, 1997, Mar. Ecol. Progr. Ser. 149; density data: partly from J. Beukema and R. Dekker).

The future.
The large variation in recruitment success of benthic marine invertebrates is still for the most part unexplained. To quantitatively investigate the influence of the factor fertilization, several parts of our models and empirical relationships will require more consideration. It will be essential to establish whether the egg size — population density correlation is causal. Also, the effect of egg size on fertilization probability and embryo survival will need to be quantified. The fact that spawning is stretched out over a time span of two months is still a mystery, because one would expect the animals to synchronize their spawning efforts to avoid eggs remaining unfertilized. Could bet-hedging on unpredictable pelagic conditions play a role, and could this increase sperm limitation even further?

A combination between analytical optimization models, mechanistic models of larval growth and of diffusion and dispersal of gametes in moving water, laboratory experiments with spawning populations and transplantation experiments in the field should bring us closer to quantitative answers. And, ideally, methods should be designed to study fertilization in the field that can cope with the turbulent, turbid and unpredictable nature of the soft-sediment tidal environment.



Egg ans sperm cell of *Macoma balthica*