

## Geographic divergence of gamete recognition systems in two species in the sea urchin genus *Strongylocentrotus*

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Two closely related species in the camarodont sea urchin family Strongylocentrotidae, *Strongylocentrotus pallidus* and *Strongylocentrotus droebachiensis*, have circumpolar ranges with overlapping depth distributions and spawning seasons. Both species show genetic differences between Europe and the Pacific in the nuclear sperm binding gene, and *S. droebachiensis* also differs in mitochondrial DNA. Gamete recognition systems of allopatric populations may or may not have drifted apart, but are unlikely to have diverged by reinforcing selection. Geographic divergence in gamete compatibility may illustrate mutational biases and variability and hence possible initial stages of reproductive isolation.

We carried out fertilisation experiments with both species' gametes from Norway and from the Eastern Pacific Ocean. Serially diluted sperm were added to egg suspensions in factorial designs, and fertilisation success was assessed by counting the proportion of cleaving embryos. To separate the specificity of the acrosome reaction from subsequent sperm-egg binding steps, a subsample of sperm was pre-activated by performing the last dilution step in diluted egg jelly from conspecific females. Fertilisation successes were compared by logistic regression ANCOVAs over five, 4-fold sperm dilutions for each cross. The graphs shown here illustrate fertilisation success for one sperm concentration only.

Sperm from Pacific populations fertilise a higher proportion of eggs from the same ocean than of Atlantic eggs, while Atlantic *S. droebachiensis* sperm fertilise eggs from either population equally well (Fig. 1). The cross between *S. pallidus* sperm and *S. droebachiensis* eggs is much more successful than the reciprocal cross (Strathmann, 1981) (Figs. 2, 3). Pre-treating sperm with homologous egg jelly increases fertilisation success dramatically between species in both directions. This is in contrast to other species combinations in this same genus, where the acrosome reaction occurs non-specifically and sperm binding is species-specific (Minor *et al.*, 1991). The poor compatibility of Pacific *S. droebachiensis* sperm with Atlantic *S. droebachiensis* eggs can not be remedied by pretreat-

ing the sperm with egg jelly (Fig. 2). Within this species, the ability for the subsequent sperm-binding step may have diverged between oceans. In contrast, the low fertilisation success of Pacific *S. pallidus* sperm on Atlantic *S. droebachiensis* eggs can be augmented by acrosome-reacting them (Fig. 3), i.e. the heterospecific cross discloses a functional divergence of the egg

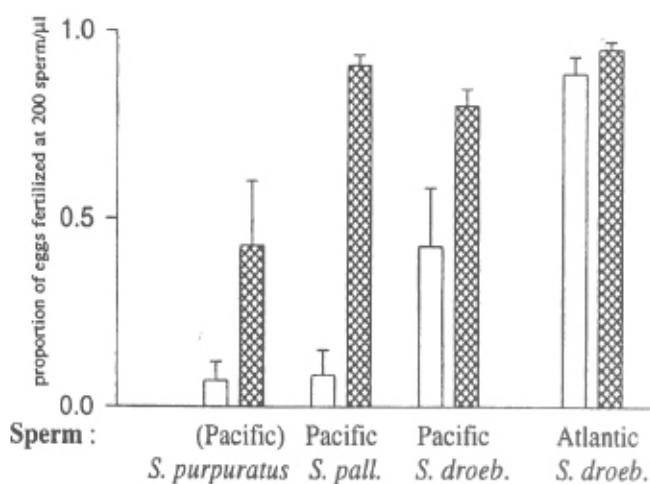


Figure 1 Fertilisation success of *Strongylocentrotus droebachiensis* eggs from Atlantic (open bars) and Pacific (cross-hatched bars) females.

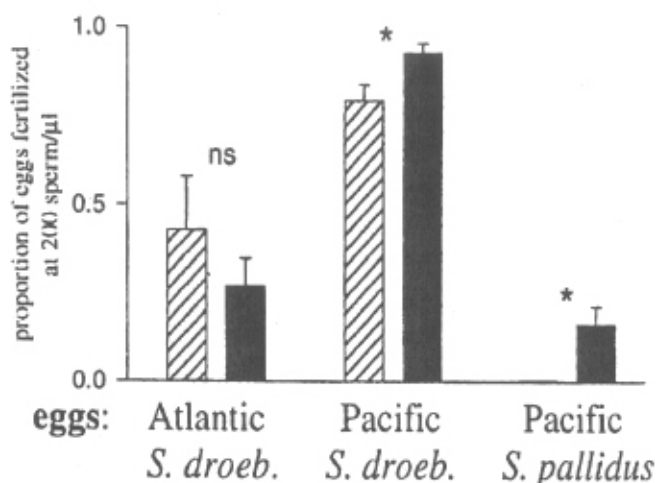


Figure 2 Sperm from Pacific *Strongylocentrotus droebachiensis*, used plain (hatched bars) or pre-activated with conspecific egg jelly (filled bars).

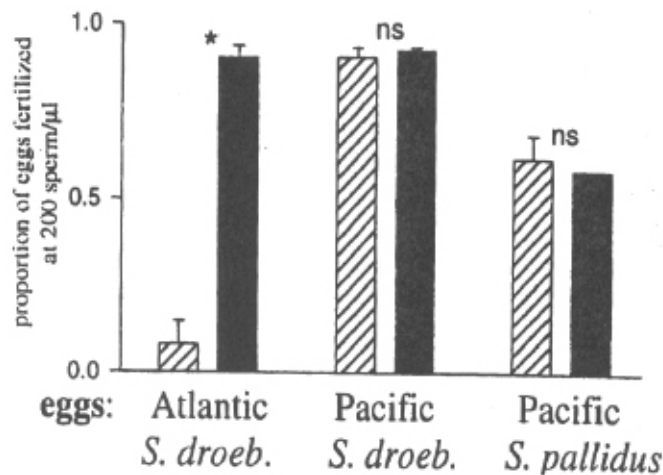


Figure 3 Sperm from Pacific *Strongylocentrotus pallidus*, used plain (hatched bars) or pre-activated with conspecific egg jelly (filled bars).

jelly/acrosome reaction system between populations.

This study has uncovered asymmetries in fertilisation compatibility not only between species but also between allopatric populations, as well as in the interaction between eggs and sperm and between egg-jelly coats and sperm. Gametic reproductive barriers are complex, and the relative order and speed of their formation is unpredictable.

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## References

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