Sole Pheromones: "What we have here is a failure to communicate"?

Pheromones are an important, but understudied, facet of reproduction in many animals. What we know about pheromones in fish mostly comes from freshwater species. However, many economically important species are marine. One such is the Senegalese sole (*Solea senegalensis*), a species of increasing value in the aquaculture industry. For reasons that are not yet clear, fish-farmers have to rely on wild-caught males for reproduction; hatchery-bred males are just not up to the job. One possible explanation is a break-down in communication between the sexes during reproduction. To assess this, it is necessary first to understand how these fish communicate normally; what are their reproductive pheromones, how are they released and detected, and what are their biological effects?

Urine has been identified as a vehicle for pheromone release in several freshwater species. However, marine fish produce much less urine. Therefore, we considered other possible routes of release; the most obvious being the faeces. In fish, pheromones are detected by the olfactory system; fish have surprisingly sensitive noses. One way of assessing a possible pheromone is testing whether the fish can smell it; the method used was recording of the electro-olfactogram, or EOG, from the olfactory epithelium in response to urine and faeces from males and females, both mature and immature, and from both wild-caught and hatchery-bred fish. Also, one possible role of reproductive pheromones was tested; the ability to increase circulating levels of FSH (follicle stimulating hormone; an important hormone in the physiological regulation of reproduction).

The olfactory system of the sole was found to be highly sensitive to both urine and faeces. Interestingly, the strength of the EOG response depended not only on the sex and maturity of the donor, an *a priori* requisite for reproductive pheromones, but also on the sex and maturity of the receiver. This suggests a complex system of chemical communication in these fish involving more than one compound released by each sex, and the ability to detect these compounds depending on the presence of certain olfactory receptors which, in turn, are differentially expressed in each sex and/or at the appropriate stage of sexual maturation. That the urine from mature females, at least, contains reproductive pheromones was confirmed by its ability to stimulate an increase in circulating FSH levels in males. Finally, and contrary to expectations, the olfactory potency of urine taken from wild-caught fish proved to be *less* potent than that from hatchery-bred fish, despite living under similar conditions and being fed the same diet.

Taken together, these results are indicative of a complex process of chemical communication between the sexes during reproduction in the sole. Both the odorants they produce and release - putative pheromones - and the ability to detect them depend on both their sex and reproductive status. Furthermore, there are clear differences - quantitative or qualitative we do not yet know - between the odorants released by wild-caught and hatchery-bred fish. However, to fully understand if - and how - defects in this communication system are responsible for the poor reproductive

performance of hatchery-bred males, then the compounds involved - the pheromones - and their receptors need to be identified, and their physiological and behavioural roles established Clearly, this means a lot more work!

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