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Preface to the Themed Discussion on 'Mating biology of copepod crustaceans'

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PREFACE

In his book *The open sea: the world of plankton*, Sir Alister C. Hardy (1956) supported the estimate that copepod crustaceans probably outnumbered all other metazoans combined. They are undoubtedly among the most abundant animals on Earth, dominating the zooplankton community in the largest biome on Earth—the 1347 million km^3 of the open pelagic water column. A mean density of just one copepod per litre would suggest a total world population in the order of 1.35×10^{21}. Planktonic species are typically small, with a body length in the range of 0.5–10 mm, but they form a vital link in the marine food web, transferring enormous amounts of carbon to higher trophic levels. These tiny crustaceans were long regarded as passive members of the plankton, carried around at the mercy of water currents and feeding automatically as they swam. In the past two decades, however, our understanding of copepod behaviour has been revolutionized by the application of new techniques, particularly high speed video and ciné film, coupled with the recognition that they mostly operate within a low Reynolds number environment, dominated by viscous forces.

In meeting the imperatives of life in the plankton (finding and capturing food, locating a mate and avoiding predators), copepods exploit the special characteristics of the high viscosity, laminar flow regime they inhabit. Information flow in low Reynolds number environments is relatively predictable and the copepods take advantage of this in finding food particles in a nutritionally dilute medium, avoiding predators in a three-dimensional environment that lacks physical hiding places, and locating a mate when conspecific individuals may be separated by thousands of body lengths.

Currently there is great interest in copepod mating behaviour because it is the last of these behavioural imperatives to be understood in these small aquatic organisms. In the early 1980s, the paradigm of copepods as filter feeders was overturned by direct behavioural observation of copepods actively capturing individual algal cells (Alcaraz *et al*. 1980; Koehl & Strickler 1981; Paffenhöfer *et al*. 1982; Price *et al*. 1983). In the early 1990s, a greater understanding of mechanosensorily mediated copepod escape behaviour was gained, again by direct observation and experiment (Yen & Fields 1992; Hartline *et al*. 1996). Mating is now the focus of considerable research effort and the papers invited to form this issue bring together much of the latest work on mate location and mate recognition systems, in addition to new insights into the functional morphology of the copepod reproductive system and their sexually dimorphic sensory systems. The topic also has applied relevance since parasitic copepods (the sea lice of salmon: *Lepeophtheirus salmonis* and *Caligus elongatus*) are a major health hazard to farmed salmon (Boxshall & Defaye 1993), and interference with the chemosensory basis of mate location and mate recognition could provide information of great value in the development of novel control methods.

In some copepods, males are able to detect females at a distance and preliminary experimental evidence suggests that sex pheromones are involved, signalling the males of the presence of females (Katona 1973; Griffiths & Frost 1976; Uchima & Murano 1988). The investigation of this chemosensorily mediated behaviour is one of the central themes of this issue.

The improvements in techniques for directly observing copepods are outlined in this issue by Strickler. Progress in this field has been heavily dependent on technology, and the ability to observe copepods swimming freely in relatively large volumes of water has been the key to recent advances. The shift from high speed ciné film to sophisticated laser-illuminated 3D video recording systems has presented numerous problems and Strickler shows how these can be solved either by technical changes or by manipulation of the behaviour of the copepods. Doall *et al*., using this 3D video system, demonstrate that males of *Temora longicornis* follow the trails left by swimming females, overtake and mate with them. The males can detect trails up to 10 seconds old and successfully pursue females that are up to 60 body lengths away. Analysis of this mate tracking by Weissburg *et al*. indicates that the male copepod strongly relies on chemical cues. They regard the ability of *Temora* to track a 3D odour trail as unique, and possibly dependent upon the persistence of waterborne chemical signals created in low Reynolds number regimes.

The study by Van Duren *et al*. of swimming patterns in the same copepod, *T. longicornis*, reveals that females exhibit a different pattern of hops in the presence of chemical signals indicating the presence of males. Using laser sheet particle image velocimetry, Van Duren *et al*. investigate the possibility that these hops serve to create a hydrodynamical signal that increases encounter probability with potential males. Despite the short duration of this effect and the high energetic costs, this study represents the first indication that the female might play a more active role in attracting males.

These experimental studies are all based on coastal copepods but Tsuda & Miller developed a method for the observation of mate location behaviour in an oceanic copepod, *Calanus marshallae*. *Calanus* requires a relatively large volume of water within which females deposit a vertical pheromonal trail and males exhibit searching behaviour along primarily horizontal trajectories. Male pursuit behaviour and mate clasping are described here for the first time in an oceanic copepod.

The female genital system of *Temora* and related copepods within the superfamily Centropagoidea are the subject of detailed analysis by Barthélémy *et al*. They reveal that no members of this superfamily possess seminal receptacles, thus limiting the ability of females to store sufficient spermatozoa for multiple egg batches. Instead of a single mating with lifetime storage of spermatozoa, repeated mating may be necessary in these copepods and this appears to be reflected in their near-parity sex ratio.

Mate recognition, mediated by contact chemical signals, is the focus for the papers by Kelly *et al*. and Frey *et al*. Surface glycoproteins have been implicated in mating behaviour of the benthic copepod *Tigriopus japonicus*, and Kelly *et al*. show here that the attractiveness of females to males appears to be mediated via glycoproteins on the body surface of the females. These chemicals are species- and sex-specific, acting as contact pheromones. Using the propensity to engage in precopulatory mate guarding as a bioassay in two harpacticoid copepod species of the genus *Coullana*, Frey *et al*. investigate the effect of

lectin treatments on mate recognition. They find that mate recognition is inhibited by certain lectin treatments and conclude that the glycoproteins responsible for mate recognition with species of *Coullana* may be glycosylated with some monosaccharides from the N-acetylglucosamine group.

Precopulatory mate guarding also occurs in parasitic copepods. Hull *et al*. examine the competence of males for mating and their preference hierarchy for mate guarding partners. They confirm the existence of multiple mating in caligids and demonstrate both that males are more mobile than females and that they show greater levels of inter-host transfer. The rate of mating success in sea lice is considerably reduced by ablation of the distal tip of the antennules, the primary sensory interface between copepods and their environment.

The development of the array of sensors along the antennules in copepods is analysed by Boxshall & Huys. Sexual dimorphism typically appears late in development and commonly involves modification of the segments and setation elements of the antennule(s) used by the male for grasping the female during copulation. The identification of a common pattern of appearance of segments and setation elements for the Copepoda enabled changes in the male chemosensory system, associated with the attainment of sexual maturity, to be recognized. The chemosensory system of males in planktonic copepods is typically enhanced at the final moult either by the doubling of the aesthetascs on some segments, by the enlargement of existing aesthetascs or by the transformation of seta-like elements into aesthetasc-like elements. Oceanic copepods are more likely to exhibit enhancement of the chemosensory system than coastal or benthic forms.

Yen *et al*. present an important theoretical analysis of zooplankton behaviour in the aquatic environment, demonstrating that the low Reynolds number regime conserves distinct species-specific cues that can direct mate seeking in copepods. They show that, within small Komolgorov eddies where viscosity limits forces to molecular scales, pheromonal trails laid down by swimming females persist. Such signals are not ephemeral because the kinetic energy of the shearing forces is reduced and fluid motion is no longer effective in dissipating them. A new model of mate location in *Temora longicornis* is presented, based on the ability of the male to use its chemosensory and mechanosensory systems to discriminate between biologically formed mating trails and small-scale turbulence, and to recognize the presence of signal molecules left in the trail by conspecific females.

Brewer describes the hitherto unrecognized complexity of mate location behaviour in another small aquatic crustacean, *Daphnia pulicaria*. Several of the behaviour patterns they exhibit, such as scanning and the performance of area restricted spirals upon encounter are similar to those reported for diaptomid copepods and may be common to a larger group of zooplankton.

Together these papers show how copepods are able to increase their probability of encounter with a potential mate by exhibiting relatively sophisticated behaviour patterns. Males appear to rely heavily on distance chemoreception to bring them into close contact with the female but close range mate recognition may involve both short duration fluid mechanical signals and contact chemical signals. Mate choice and mate guarding may also be mediated by surface chemical signals, at least in benthic and parasitic copepods. Sensory modalities may be enhanced according to the balance of functional priorities across a range of stage-related behaviour patterns.

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