



Resource and mate availability, and previous social experience modulate mate choice in the copepods *Acartia tonsa* and *Acartia hudsonica*



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ABSTRACT

Copepods, the most abundant metazoans in the oceans, exhibit sexual selection through mate choice. Mate choice may depend on resource and mate availability, mate quality, and the ability of an individual to assess potential mates. We measured the relative strength of mate choice for body size in male and female individuals of the copepod species *Acartia tonsa* and *Acartia hudsonica* as a function of food availability, encounter time, and previous social experience with the same and opposite sex. Mate choice in *A. tonsa* females depended on food availability and previous exposure to the opposite sex, whereas exposure to the opposite sex and encounter time affected mate choice in males. For *A. hudsonica*, previous social experience with the same and opposite sexes and encounter times were important for mate choice in females, and food availability and encounter time affected mate choice in males. The results suggest that mate choice responds to resource and mate availability, as well as social experience, but that the responses are species and sex-specific even within the same genus. Therefore, these copepods appear to have a flexible mate-sampling strategy that allows them to raise or lower their mate preferences in order to balance the benefits and costs associated with finding a desired mate.

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1. Introduction

Sexual selection, a form of natural selection due to differences in mating success (Darwin, 1871), can often explain a species' morphology, behavior, and population biology (Andersson, 1994). While sexual selection has been studied extensively in numerous terrestrial and even marine taxa, there have been few studies on pelagic copepods (Titelman et al., 2007; Ceballos and Kiørboe, 2010) even though they are the most abundant metazoans in the ocean. Copepods exhibit several behaviors that may be examples of sexual selection (i.e. precopulatory mate guarding, copulatory dances, mate coercion, and mating avoidance) (Titelman et al., 2007); moreover, the strength of sexual selection is likely different from one copepod species to the next since mating patterns vary among species (brood vs. free-spawn, single mating vs. obligate repeated mating to remain fertilized, feeding vs. non-feeding males, etc.). Thus, copepods may be informative for studies of sexual selection (Ceballos and Kiørboe, 2010).

Sexual selection, by way of mate choice, is starting to be recognized as important in the reproductive biology of pelagic copepods. Recent work has provided evidence that copepods may choose mates based on a variety of traits including size, age, and reproductive state. For instance, both sexes of *Acartia tonsa* prefer to mate with large mates (Ceballos and Kiørboe, 2010). Since size is heritable in copepods

(McLaren, 1976; McLaren and Corkett, 1978), and since larger individuals produce larger and more offspring, an individual can increase its fitness by mating with a large mate (Weatherhead and Robertson, 1979; Ceballos and Kiørboe, 2010). Similarly, both sexes of *Temora longicornis* mate preferentially with young individuals likely because offspring number and quality decrease with parental age (Ceballos and Kiørboe, 2011; Sichlau and Kiørboe, 2011). Additionally, males of many species (*A. tonsa*, *Acartia hudsonica*, *Oithona davisae*, and numerous parasitic copepods) distinguish between the reproductive states of females, and most mate with virgin females over those females that have already mated (Anstensrud, 1990, 1992; Heuch and Schram, 1996; Heuschele and Kiørboe, 2012; Burris and Dam, 2014). In summary, members of either sex or of both sexes simultaneously can choose for a specific trait and select among available mates.

While these studies are valuable in providing information about whether or not a trait is important for mate choice, relatively little work has been done in the field where mate choice is subjected to the effect of multiple time-dependent parameters. Mate choice in natural populations can change temporally depending on different ecological conditions as either more or less of the population is being selective (Emlen and Oring, 1977; Wilson and Hedrick, 1982; Jennions and Petrie, 1997; Forsgren et al., 2004). For instance, the strength of mate choice can vary simply because the potential benefits of mating with a particular mate are context-dependent and influenced by factors like the availability of mates (Shuster and Wade, 2003), the quality and variation in quality of those potential mates, and the ability of an individual to assess potential mates (Jennions and Petrie, 1997; Kokko and

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Monaghan, 2001; Shuster, 2007). As these conditions vary over time, the strength of mate choice will also likely vary. In field populations of copepods, these parameters can vary significantly between and within a season (Mauchline, 1998). Availability of potential mates, for instance, can be influenced by a number of population parameters, including population density and sex ratio. In coastal copepods, encounter rates can be very high during peak densities, when up to 30 potential mates may be encountered on a daily basis (Kiørboe, 2007). Since males can only mate about once a day and females remain fertilized for up to ten days (Ceballos and Kiørboe, 2010; Burris and Dam, 2014; Burris, unpublished data), these high densities exceed the mating needs of both sexes and likely allow individuals to be selective when choosing a mate. In contrast, at the beginning and end of the growing season for these populations, densities can be low enough that theoretically a potential mate is encountered only every few days (Heuschele et al., 2013). Here, the benefits of being selective may no longer exist, as copepods run the risk of not finding a mate, or experience increased costs as they search for another mate (Real, 1990). This inference is supported by numerous models (Hubbell and Johnson, 1987; Crowley et al., 1991; Kokko and Monaghan, 2001; Härdling and Kaitala, 2005; Kokko and Mappes, 2005; Heuschele et al., 2013).

Variation in sex ratio can also influence mate availability, and thus mate choice, by changing the density of members of the opposite sex as well as that of the same sex (Kokko and Rankin, 2006). Competition and aggression among individuals of the abundant sex for mating opportunities with the rarer sex is reported in some copepod species (see Ahnesjö et al., 1993). In this case, mate choice may be influenced by previous exposure to members of the same sex prior to mating. Moreover, copepod sex ratios vary considerably over the season and are often highly skewed toward females (review: Kiørboe, 2007). Therefore, individuals may adjust mate choice in response to the rate at which they encounter other individuals of the same sex. Many animal species across many taxa vary their choice of mate according to their previous social experience. For instance, a high-quality female that encounters a low-quality female may become more selective in her initial choice of a mate, since she may have a lower risk of failing to mate (Petrie and Hunter, 1993).

Similarly, mating preferences are influenced by the variation in trait quality between potential mates in a number of invertebrate species (Hebets, 2003; Dukas, 2005; Fincke et al., 2007; Hebets and Vink, 2007). In this case, a female's decision to mate may be influenced by the quality of the previous male she has encountered. When male size is variable, a female may refuse small males since the potential benefits of mating with a large male are much greater (Parker, 1983; Getty, 1995; Real, 1990). Conversely, females may be less selective in choosing a mate when male body size varies little. There is little information on variation in mate quality in copepods, but body size has been shown to be an important trait for mate choice in *A. tonsa* (Ceballos and Kiørboe, 2010) and *A. hudsonica* (Burris, unpublished data). Copepod body size is a relatively easy trait to measure, and is variable within and between seasons in copepod populations, by up to a factor of two in field populations (Berggreen et al., 1988; Dam and Peterson, 1991; Arendt et al., 2005). Body size can be used as a proxy for mate quality since it reflects reproductive potential: female fecundity and spermatophore size are positively correlated with adult size in copepods (Kiørboe and Hirst, 2008; Ceballos and Kiørboe, 2010). Additionally, size may indicate 'good genes' (Andersson, 1994) by reflecting the ability to obtain food: adult size is related to juvenile feeding rates (Arendt et al., 2005). Body size can be influenced in field populations by a number of factors, including temperature and food availability (Durbin et al., 1992). Therefore, variance in body size, in addition to mate availability, may be important in determining the strength of mate choice in these copepods.

Finally, in addition to trait quality, the short-term condition of an individual also influences mate choice in invertebrates. For instance, hungry females mate less selectively and often more frequently than

well-fed females in a number of insects (Proctor, 1991; Poulin, 1994; Simmons, 1994). Copepods likely experience instances of food limitation in the field (Berggreen et al., 1988; Durbin et al., 1992; Müller-Navarra and Lampert, 1996; Gulati and Demott, 1997; Sterner and Schulz, 1998). Therefore, changes to food availability may also influence mate choice in these copepods.

Individuals make mate choices. Yet, there have been no experimental studies on how changes to population-level parameters may impact individual-mate choice in pelagic copepods. In the present study, variation in mate-choice strength was measured experimentally in the lab as the availability and quality of potential mates were manipulated in two pelagic copepod species, *A. tonsa* and *A. hudsonica*. The effect of resource (food) availability on mate choice was also studied. In particular, we manipulated four variables: the amount of time before two potential mates were allowed to encounter one another (a proxy for population density), the presence/absence of an individual of the same sex of either low or high quality before mating, the presence/absence of an individual of the opposite sex of either low or high quality before mating, and food availability. We hypothesized that both sexes would be less selective (i.e., mate more often) as the time between encounters increased. In addition, we predicted that those held with another individual will be less selective (mate more frequently) than those held alone, and that copepods held with similarly sized copepods would mate less readily than those held with smaller copepods. Finally, we predicted that under limiting-food conditions, male and female mating preferences would become weaker.

2. Methods

2.1. Maintenance of copepods

Live animals were collected by surface tows off of Groton Long Point, Long Island Sound, USA (Latitude: 41.3271 N, Longitude: 72.00150 W) using a conical plankton net with a 200- μ m mesh and solid cod end. Tows were conducted each year in October for *A. tonsa* and April for *A. hudsonica*; adults were sorted from the tows and kept at 15 °C (the water temperature in the field) in an environmental chamber on a 12:12 light:dark cycle and fed on a standard diet of the diatom *Thalassiosira weissflogii* and the green flagellate *Tetraselmis* sp. (>700 μ g C L⁻¹; 50% of each by carbon). Algae were grown at 18 °C as semi-continuous cultures on F/2 medium (Guillard, 1975). Every week, eggs were separated from adults and raised to adulthood under the same conditions, so that differently aged cohorts could be obtained.

2.2. Mate pairing of copepods

In all experiments, individuals were sorted as juveniles by sex, placed in pretreatment conditions for up to 24 h, then paired with an optimally sized partner for 24 h, and finally, checked for mating (Box 1).

All individuals, whether to be tested or used in pre-treatments or as potential mates, were sorted by sex as stage C4 juveniles from the same cohort and held either individually in 70 mL petri dishes or with individuals of the same sex in 8 L containers, depending upon the experiment, and fed as above. Within 24 h of maturation, each copepod was photographed using a camera mounted on a dissecting microscope and its prosome length (a correlate for body size as per Mauchline, 1998) was measured to 1/1000 of a millimeter, using the program ImageJ. Copepods were paired so that the average body size for each sex was the same for each treatment. During the measurement phase, individuals were held alone in a well of a 12-well plate with high-food solution as above (about 6 mL). For any pre-treatment that lasted more than 2 h (i.e. food availability treatments, density treatments), individuals were transferred to 70 mL petri dishes with replete food. If pre-treatment lasted for more than 24 h, then water and food were changed each day. Pre-treatment conditions are explained for each experimental variable in the next section.

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