

Optimal mate choice patterns in pelagic copepods

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Abstract The importance of sexual selection for the evolution, dynamics and adaptation of organisms is well known for many species. However, the topic is rarely studied in marine plankton, the basis of the marine food web. Copepods show behaviors that suggest the existence of sexually selected traits, and recent laboratory experiments identified some selected morphological traits. Here, we use a ‘life history-based’ model of sex roles to determine the optimal choosiness behavior of male and female copepods for important copepod traits. Copepod females are predicted to be choosy at population densities typically occurring during the main breeding season, whereas males are not. The main drivers of this pattern are population density and the difference in non-receptive periods between males and females. This suggests that male reproductive traits have evolved mainly due to mate competition. The model can easily be parameterized for other planktonic organisms, and be used to plan experiments about sexual selection.

Keywords Copepods · Pelagic · Sexual selection · Mate choice · Plankton

Introduction

Sexual selection is an important process for micro- and macro-evolution (Schluter 2001). It is studied extensively in vertebrates and terrestrial invertebrates, but rarely in marine organisms and especially not in plankton. This is astonishing given that marine plankton provides the basis of the marine food web, and that sexual selection are known to influence population dynamics (Kokko and Rankin 2006).

Copepods in particular have the highest accumulated biomass on earth compared to any other species group (Humes 1994). There are several indications of the presence of sexually selected behaviors in different species of copepods (Titelman et al. 2006). These include mate choice-related behaviors such as pre-copulatory mate guarding, copulatory dances, stroking, and mate escape behaviors. In *Pseudocalanus elongatus* (Kiørboe et al. 2004), *Oithona davisae* (Kiørboe 2007), and *Temora longicornis*, females apparently try to avoid matings by performing escape bouts (Doall et al. 1998), which suggests active mate avoidance behavior, which is a form of female mate choice. Recent studies have reported the first experimental evidence of mate choice in several copepod species. Both sexes of *Acartia tonsa* show a preference for large partners (Ceballos and Kiørboe 2010), which can increase the reproductive success of choosy individuals given the positive correlation of body size and offspring number. In *Oithona davisae*, young males and females are able to differentiate the age of potential partners, and are more likely to mate with young partners (Ceballos and

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Kjørboe 2011). Whether this is due to active mate choice or due to reduced mating capability in old individuals remains to be seen. Ali et al. (2009) found that the size of females of *Eudiaptomus graciloides* was inversely related to the number of attached spermatophores when caught in the field. Bigger females seem to be able to choose or escape males, while small females cannot. Thus, not only mate choice and mate competition but also mate coercion may play a role in copepod reproduction.

While the importance of sexual selection is widely recognized, a recent review questions our knowledge of the strength of sexual selection in different environments and conditions (Cornwallis and Uller 2010). Sexual selection is a context-dependent process (Jennions and Petrie 1997), driven by factors like the spatial and temporal distribution of mates (Shuster and Wade 2003), the quality distribution of potential partners, and the possibility to locate and assess mates (Jennions and Petrie 1997). In natural copepod populations, male and female densities vary between and within years, as well as between populations and species (Mauchline 1998). Encounter rates with potential mates are highly variable and depend not only on mate availability but also on physical conditions like water turbulence (Visser et al. 2009). The process of locating a mate is well studied in several species of copepods. Species like *T. longicornis* or *O. davisae* rely on pheromone cues released by the females to find mating partners (Kjørboe 2007; Doall et al. 1998; Yen et al. 1998). Others like *A. tonsa* use hydrodynamical cues for mate search (Bagøien and Kjørboe 2004). Typically, males take the active part of searching for females (e.g., Katona 1973), which may increase their mortality relative to the females (Hirst et al. 2010). The swimming pattern during mate search also varies between species and sexes, and is related to the feeding strategies: male copepods that cruise through the water when feeding, or do not feed at all, can search for mates all the time, while the males of ambush-feeding copepods must switch between feeding and mate searching, and adopt very high swimming velocities during search swimming (Kjørboe 2008). The mate availability, described by the operational sex ratio (OSR), is determined by the species-specific details of the reproductive biology such as the animal's ability to store sperm, the ability to remate, and the differential mortalities of males and females. In some species, adult sex ratios are close to be balanced, while in others, males can become a limiting factor for female reproduction (Kjørboe 2007).

The benefit of mate choice also depends on differences between potential mates, but unfortunately little is known about mate quality variation in copepods. Evolutionary fitness can be measured as the lifetime reproductive success of individuals relative to conspecifics. Offspring number is positively correlated with female and male body size in copepods (e.g., Smyly 1968; Maly 1973; Hylstøfte

Sichlau and Kjørboe 2011). We therefore suggest that the variance in body length within a population can serve as a proxy for the variance in fecundity, and thus for the potential benefits of being choosy.

Measuring the strength of sexual selection in copepod populations in the field and in the laboratory is difficult because the traits under selection are mostly unknown and the observations of mating behavior is only possible using video recordings. Therefore, we used a life history-based model (Kokko and Monaghan 2001) to explore how mate choosiness change with population density, mate quality, and length of the non-receptive period after matings ('time outs'). This allows us to compare the relative importance of these factors for the strength of sexual selection. Next, we used parameters on four pelagic copepod species to derive expected patterns of mate selectivity and sex roles in these species.

Materials and methods

Model

Life history-based model of sex roles

We consider a copepod mating system in which breeding occurs continuously and males and female alternate between being receptive ('time in') and non-receptive ('time out') to mating. During 'time in' phases (T_{IM} and T_{IF}), individuals are searching for mates and we assume search efficiency to be a function of swimming speed and detection range (see Table 1 for definition of parameters). The rate of encounter with potential mates also depends on population density. During the 'time out' (T_M and T_F), males are replenishing spermatophores and females use stored sperm to fertilize eggs. For simplicity, we assume that sperm from the first male to mate with a female fertilize all her eggs until his spermatophore is empty. Additional matings during this non-receptive period will hence be unsuccessful although males may try to attach spermatophores. The mortality rate may differ in 'time in' (μ_{IM} and μ_{IF}) and 'time out' (μ_M and μ_F), which, combined with different durations of the two states, causes sex-specific mortality rates in our model. As a result, the sex ratio may change through the breeding season. In nature, the adult sex ratio can be determined by several other factors besides differential mortality rates; for example, environmental sex determination (ESD) governed by food conditions (Fleminger 1985; Korpelainen 1990; Irigoien et al. 2000) or intersexuality (Gusmao and McKinnon 2009). The cost of breeding is a function of the mortality experienced in the 'time out' phase. For females, the cost of breeding, C_F , is:

Table 1 Variables and their meaning

Variable	Description	Unit
α	Primary male to female sex ratio	
β	Operational sex ratio	
σ	Variance in mate quality	mm
μ_F	Female mortality during ‘time out’	day ⁻¹
μ_M	Male mortality during ‘time out’	day ⁻¹
μ_{IF}	Female mortality during ‘time in’	day ⁻¹
μ_{IM}	Male mortality during ‘time in’	day ⁻¹
c	Mate choosiness	
C_F	Breeding cost for female	
C_M	Breeding cost for male	
F	Fitness of non-choosy individuals	
F_c	Fitness of choosy individuals	
D	Population density	ind l ⁻¹
L	Female body length	mm
M	Mate encounter rate	ind day ⁻¹
p_M, p_F	Proportion of accepted mates	
q_M, q_F	Increase in quality of mates by being choosy	
T_F	Female ‘time out’	days
T_M	Male ‘time out’	days
T_{IF}	Female ‘time in’	days
T_{IM}	Male ‘time in’	days
V	Mate search volume	L day ⁻¹
W	Lifetime reproductive success	
x_{mF}, x_{mM}	Mean length of mates	mm
x_{cF}, x_{cM}	Body length cut off	mm
x_{cmF}, x_{cmM}	Mean length of accepted mates	mm

$$c_F = \mu_F \frac{T_F}{(1 + \mu_F T_F)} \tag{1}$$

and for males, C_M ,

$$c_M = \mu_M \frac{T_M}{(1 + \mu_M T_M)} \tag{2}$$

As in the model of Kokko and Monaghan (2001), we use lifetime reproductive success as fitness measure. The number of offspring a female can produce per mating depends on the number of sperm the male transmits in each spermatophore. We assume sperm number to increase linearly with size of the male, and, similarly, that the number of eggs a female produces is a linear function of her length (Hylstofte Sichlau and Kiørboe 2011). We assume that the quality of mates increases linearly with body size (Ceballos and Kiørboe 2010; Hylstofte Sichlau and Kiørboe 2011), and that the length distribution of potential partners is defined by the mean x_m and the standard deviation σ . Individuals can choose to accept only the largest fraction p of the encountered mates, which give a higher mean length x_{cm} of accepted mates relative to the

population mean x_m . Using z-scores from a standard normal table we define a set of chosen proportions p , and calculate the associated cut off values x_c . The average length of a mating partner x_{cm} can be calculated by:

$$x_{cm} = x_m \sqrt{\frac{2}{\pi}} \frac{e^{\frac{(x_c - x_m)^2}{\sigma^2}}}{\text{erfc} \left(\frac{x_c - x_m}{\sqrt{2}\sigma} \right)} \tag{3}$$

where *erfc* is the complementary error function, and $x_c = z(p)\sigma + x_m$.

The fitness benefits from choosing a partner of length x is $F = ax$ given a linear increase in quality. a can be estimated as the slope of the fecundity–length relationship from experimental studies. If q is the relative increase in the quality of the offspring by receiving a fitness of $F_c = ax_{cm}$ compared to the fitness benefit from choosing randomly the population mean $F = ax_m$, then q will depend only on the ratio x_{cm}/x_m .

The length of the copepod also determines the encounter rate. The daily mate search volume V (L day⁻¹) is calculated using the relationship between female body length L_F (mm) and search volume (Kiørboe and Bagoien 2005).

$$V = 10^2 L_F^3 \tag{4}$$

The encounter rate per individual per day is the product of population density and search volume. In a population with equal numbers of males and females (adult sex ratio $\alpha = 1$), only half the encounters will be with a potential partner, hence $M = 0.5VD$.

The adult as well as the operational sex ratio (ratio of receptive males to receptive females) both become biased if mortality rates and length of the ‘time in’ and ‘time out’ periods differ between the sexes. The operational sex ratio, β , is then (Kokko and Monaghan 2001):

$$\beta = \frac{1}{2\mu_{IM}^2} \left[M^2 (\alpha C_F - C_M)^2 + 2\alpha\mu_{IF}\mu_{IM} + M(\alpha C_F - C_M) \sqrt{M^2 (\alpha C_F - C_M)^2 + 4\alpha\mu_{IF}\mu_{IM}} \right] \tag{5}$$

Female choice can invade if

$$C_F M \sqrt{\beta} > \mu_{IF} \frac{(1 - p_M q_M)}{(p_M (q_M - 1))} \tag{6}$$

and male choice can invade if

$$C_M \frac{M}{\sqrt{\beta}} > \mu_{IM} \frac{(1 - p_F q_F)}{(p_F (q_F - 1))} \tag{7}$$

We determine the invasiveness of mate choice strategies for different combinations of population densities, variance in quality, search mortalities and ‘time outs’. For each parameter combination, we first calculate the lifetime reproductive success W of all strategies. Female fitness is calculated according to Kokko and Monaghan (2001) as

$$W_F = \frac{p_M q_M M \sqrt{\beta}}{(\mu_{IF} + \mu_{IF} \mu_F T_F + \mu_F T_F p_M M \sqrt{\beta})} \quad (8)$$

and male fitness by

$$W_M = \frac{p_F q_F M / \sqrt{\beta}}{(\mu_{IM} + \mu_{IM} \mu_M T_M + \mu_M T_M p_F M / \sqrt{\beta})} \quad (9)$$

Then, we determine the W_{\max} among all mate choosiness levels (p from 0.1 to 1), and use the correspondent p as the optimal choosiness level strategy for each scenario.

Model parameterization

We assume a primary adult male to female sex ratio α (when individuals are entering the adult phase) of 1. In natural copepod populations, sex ratios are often skewed, which may be due to differential mortality during the adult stage, e.g., by predation and senescence (Hirst and Kiørboe 2002), or other factors such as environmental sex determination (Korpelainen 1990). In the model, we assume that augmented male mortality during mate search ('time in', T_{IM}) is the main reason for a female-biased sex ratio in the population. As a result, changes in sex ratio always come along with changes in search costs, which could potentially reduce male choosiness. In the general analysis, we therefore also consider the optimal choosiness level when males have lower search costs than females (Figs. 1, 2).

To test whether males and females of certain copepod species should be choosy, we parameterized the model using species-specific values as listed in Table 2. Most values are taken from the primary literature, while some originate from recent experiments performed on-board R/V "DANA" during a cruise in the North Sea. Information about natural mortality rates in copepods is rare and difficult to assess from field data (Hirst and Kiørboe 2002). Therefore, we had to rely on data compiled from several studies (Hirst et al. 2010). We used 'overall' mortality rates from the primary literature for female 'time in' and 'out', as well as male 'time out'. We then adjusted the male's mortality during time in so that calculated adult sex ratios (ASR) matched the ones found in natural populations at common population densities. This is done assuming that it is mainly male copepods that are taking the active and dangerous task of searching for mates (e.g., Katona 1973, Tsuda and Miller 1998). The ASR is approximated using the relative times spend 'out' and 'in' and the corresponding mortality rates.

$$ASR = \frac{\mu_{IF} \frac{T_{IF}}{(T_{IF}+T_F)} + \mu_F \frac{T_F}{(T_{IF}+T_F)}}{\mu_{IM} \frac{T_{IM}}{(T_{IM}+T_M)} + \mu_M \frac{T_M}{(T_{IM}+T_M)}} \quad (10)$$

The 'time-in' of females T_{IF} and males T_{IM} are the inverse of the encounter rate with perceptive partners, which in turn is a function of the operational sex ratio β

$$T_{IF} = \frac{1}{p_M M \sqrt{\beta}} \quad (11)$$

and

$$T_{IM} = \frac{1}{p_F M / \sqrt{\beta}}. \quad (12)$$

We calculated the choosiness for a range of combinations of population densities, time-outs and degrees of variation of the partner population. For each species, we analyzed the effect of different variation (σ) in the partner's quality on the direction and strength of sexual selection, as these vary during the breeding season. We standardized the approach using the coefficient of variation (CV) in mate quality to be able to compare between species. The values of CV ranged from 0.01 to 0.1, as observed in natural populations (see Table 2). We define mate choosiness as $c = (1-p)$ when p is the accepted proportion of the partner population.

Results

Main drivers of sexual selection

We predict that mate choice in pelagic copepods follows the common pattern where females are choosy and males mate with the first receptive female they find (Figs. 1, 2). Population density and the 'time out' of females are the main determinants of the strength of female mate choice in copepods within a biologically relevant parameter space. If population densities are low or the 'time out' of females approaches that of males, females become less choosy (Fig. 1a, b). Both factors influence the number of receptive mates, which in turn ultimately limits the potential for sexual selection.

Male limitation will reduce female choosiness at low encounter rates. Female-biased sex ratios, due to high mate searching costs in males, have a limited effect on female choosiness in our model (Fig. 1c). At the same time, mate searching costs have little effect on male choosiness (Fig. 2c), and remain low even when search mortality of males falls below that of females. Longer female 'time outs' compared to males reduces the time of females to encounter a male with developed spermatophores. Once

Table 2 Input values for species-specific patterns

Variable	Description	<i>Temora longicornis</i>	Source	<i>Acartia tonsa</i>	Source	<i>Oithona davisae</i>	Source	<i>Pseudocalanus elongatus</i>	Source
T_F	'Time out' of females, the time females are unavailable to the mating market (days)	14	Hylstoftie and Kjørboe (2011)	20	Wilson and Parrish (1971)	40	40 days as <i>Oithona</i> normally mates just once Uchima (1985)	30	From Corckett and McLaren (1969) for <i>P. minutus</i> (Conservative) assumption
T_M	'Time out' of males. The time males need to produce a new spermatophore (days)	0.2	DANA cruise ^a	1	Ceballos and Kjørboe (2010)	0.4	Ceballos and Kjørboe (2011) (max male mating capacity 2.5 day ⁻¹)	1	(Conservative) assumption
μ_F	Mortality rate during time out of females. (day ⁻¹)	0.1 (0.007–0.300)	Hirst and Kjørboe (2002) Appendix	0.06–0.33 0.217	Landry (1978), Hirst et al. (2010)	0.1	Hirst and Kjørboe (2002)	0.023	Average mortality reported in Möllmann and Köster (2002)
μ_M	Mortality rate during time out of males. (day ⁻¹)	0.1 (0.007–0.300)	Hirst and Kjørboe (2002) Appendix	0.06–0.33 0.239	Landry (1978), Hirst et al. (2010)	0.1	Hirst and Kjørboe (2002)	0.023	Average mortality reported in Möllmann and Köster (2002)
μ_{IF}	Mortality rate of receptive females (day ⁻¹)	0.1 (0.007–0.300)	Hirst and Kjørboe (2002) Appendix	0.217	Hirst et al. (2010)	0.1	Hirst and Kjørboe (2002)	0.023	Average mortality reported in Möllmann and Köster (2002)
μ_{IM}	Mortality rate of searching males (day ⁻¹)	0.1	Estimated ^b	0.1	Estimated ^b	0.5	Estimated ^b	0.75	Estimated ^b
χ_{mF}	Mean body length of the female population (mm)	0.9	DANA cruise 2010 ^c	0.83	0.83 (0.004 SE) Buskey et al. (2002)	0.331	Uye and Sano (1995)	1.074	Renz et al. (2008) from Figure 4
σ_F	SD of the length of the female population (mm)	0.09	DANA cruise 2010 ^c	0.02	Buskey et al. (2002)	0.0076	Uye and Sano (1995) from Figure 5	0.0759	Renz et al. (2008) from Figure 4
χ_{mM}	Mean body length of the male population (mm)	0.83	DANA cruise 2010 ^c	0.78	Buskey et al. (2002)	0.300	Assumed to be around the same size as females	0.8207	Renz et al. (2008) from Figure 4
σ_M	SD of the length of the male population (mm)	0.08	DANA cruise 2010 ^c	0.036	0.78 (0.009 SE) Buskey et al. (2002)	0.001	Assumed to be around the same size as females	0.0672	Renz et al. (2008) from Figure 4
D	Population density (individuals L ⁻¹)	0.019–0.1 0–40	DANA cruise 2010	3 (0–10)	Lee and McAlice (1979)	4.4–300	Uye and Sano (1995)	0–120	Renz et al. (2008)
α	Adult sex ratio at the onset of maturity	1	Hirst et al. (1999) Hirst et al. (2010)	1	Hirst et al. (2010)	1	Hirst et al. (2010)	1	Hirst et al. (2010)
ASR	Observed adult sex ratios in the field. Average (range)	1.125 (0.75–1.63)	Hirst and Kjørboe (2002)	0.39–1.44	Hirst and Kjørboe (2002)	0.22	Uye and Sano (1995) (at max pop. density)	0.27	Hirst and Kjørboe (2002) original data: Digby (1950)
ASR targeted	Value of ASR that was used to estimate the mortality of males while searching	1.0		1.0		0.20		0.30	

^a Field-caught single males were incubated in bottles for 24 h with 10 females, and the number of free-floating and attached spermatophores counted
^b We adjusted the male's mortality during time in so that calculated adult sex ratios (ASR) matched the ones found in natural populations at common population densities (ASR targeted)
^c The prosome lengths of field-caught copepods from 5 stations in the North Sea were measured from digital photographs using a dissecting microscope

Fig. 1 Optimal female mate choosiness level (mean \pm SD) taken over all other factor combinations as a function of **a** population density, **b** duration of female non-receptivity (time out), **c** male searching mortality, and **d** CV of male quality. Constant parameter values: $T_M = 1$ day; $\mu_M, \mu_F, \mu_{IF} = 0.1 \text{ day}^{-1}$; $\alpha = 1$; male and female length = 1.0 mm. Varied parameter values: $\mu_{IM} = 0.05\text{--}0.55 \text{ day}^{-1}$, CV of male quality = 0.01–0.13, $T_F = 1\text{--}3$ days; $D = 0.001\text{--}10.03 \text{ ind L}^{-1}$

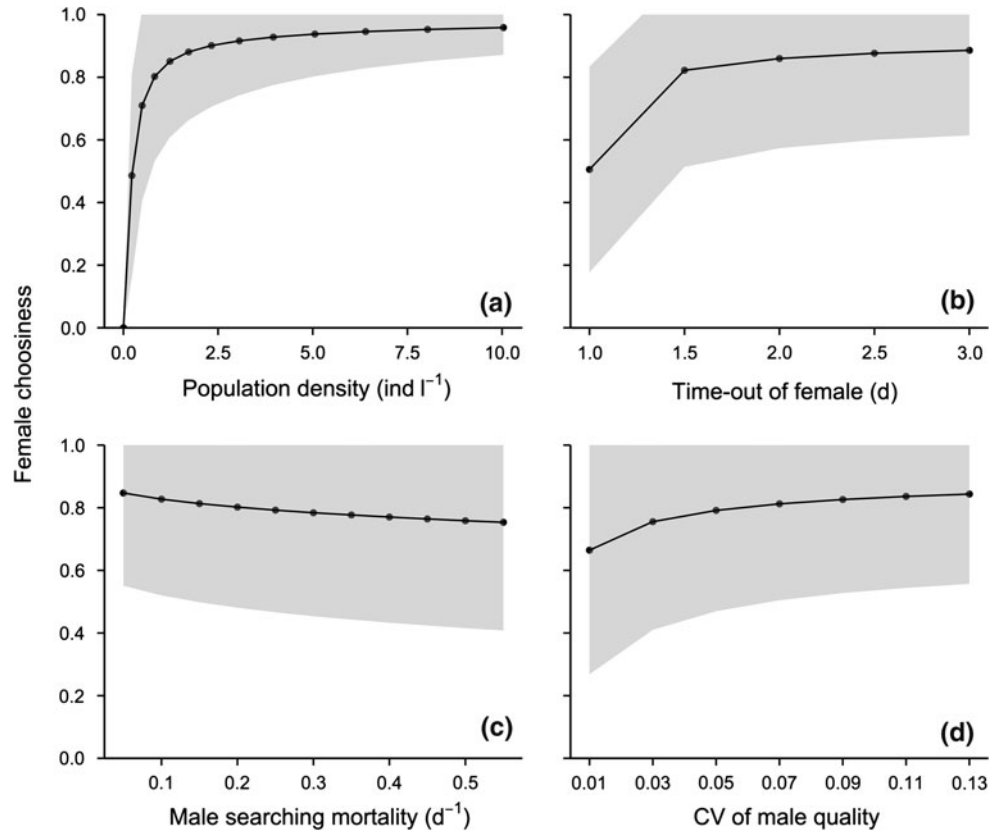
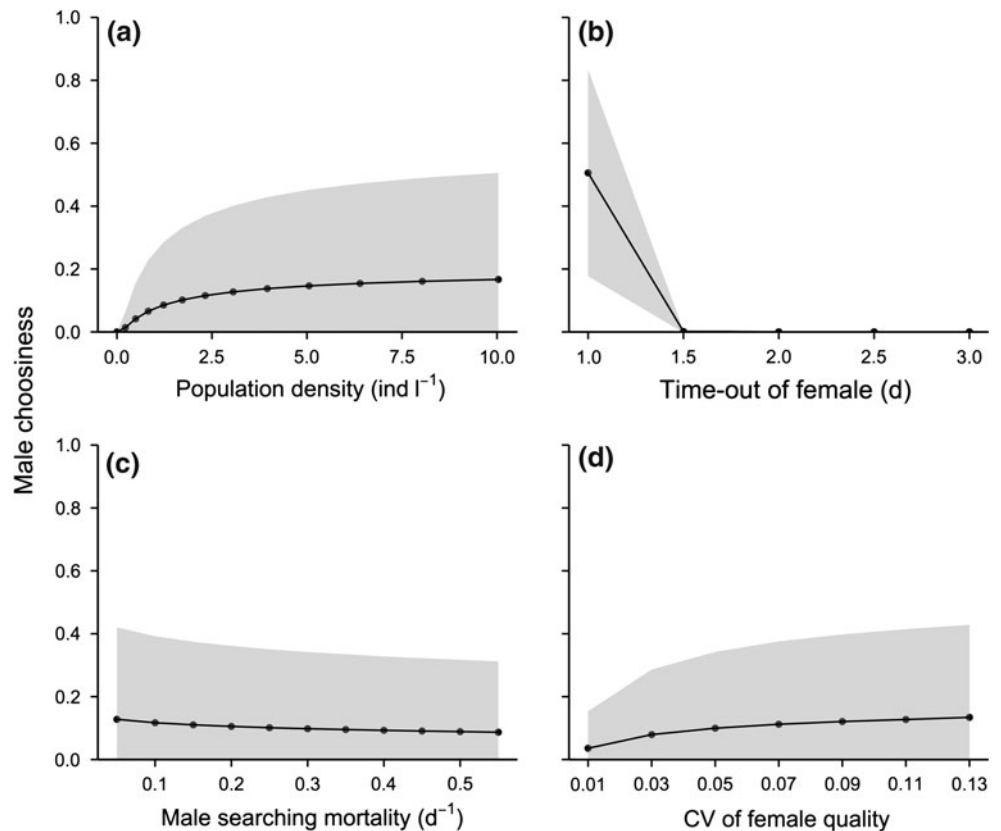


Fig. 2 Optimal male choosiness level (mean \pm SD) taken over all other factor combinations as a function of **a** population density, **b** duration of female non-receptivity (time out), **c** male searching mortality, and **d** CV of male quality. Constant parameter values: $T_M = 1$ day; $\mu_M, \mu_F, \mu_{IF} = 0.1 \text{ day}^{-1}$; $\alpha = 1$; male and female length = 1.0 mm. Varied parameter values: $\mu_{IM} = 0.05\text{--}0.55 \text{ day}^{-1}$, CV of female quality = 0.01–0.13, $T_F = 1\text{--}3$ days; $D = 0.001\text{--}10.03 \text{ ind L}^{-1}$



there are enough potential mates, the variance in mate quality determines the strength of mate choice (Fig. 1d). Obviously, if there is no variance in mate quality, then individuals would not be choosy. However, it is reasonable to assume that there will always be at least some variance in mate quality in natural populations.

The larger differences in ‘time-out’ between males and females suppress any male choosiness (Fig. 2b). Only if male and female ‘time outs’ are similar, may other factors lead to the expression of male choice. However, in copepods, male time outs are always shorter than those of females (see Table 2), hence male choice is unlikely to evolve in natural copepod populations.

Species-specific patterns

In Fig. 3, we show optimal choosiness values for different degrees of variance in mate quality and population densities for four different species, which represent different mating strategies. For all four species, the model predicts that males should not be choosy, which is primarily caused by the time out difference between males and females. *Temora longicornis*, *Acartia tonsa*, and *Pseudocalanus elongatus* show similar female choosiness patterns, characterized by choosiness at low population densities ($<0.25 \text{ ind L}^{-1}$). *P. elongatus* is the biggest of all four tested species, which means that high encounter rates can be maintained even at very low population densities. In contrast to that, *O. davisae*, the smallest species, is predicted to be choosy only if population densities are higher ($<10 \text{ ind L}^{-1}$) and the variance in mate quality is more important in determining the strength of selection.

Discussion

General points

Encounter rates, variance in mate quality, and difference in time outs are the main determinants of the strength of sexual selection in this model (Kokko and Monaghan 2001). The variation in the first two factors is big within and between copepod populations and species, assuming that differences in body length represent differences in quality within species. Our study shows a general pattern in copepods with choosy females and non-choosy males.

While information about male mating rates are rare, the few which have been reported show that males are able to produce and deploy more than one spermatophore per day (Ceballos and Kiørboe 2011; Ceballos et al., unpublished data; Ianora et al. 1999), whereas females do not need to be remated for several days or never during their lifetime (i.e., Ceballos and Kiørboe 2011; Hylstoftte and Kiørboe 2011;

Wilson and Parrish 1971). Therefore, especially at high population densities, females of all species are predicted to be choosy. At such densities, even a low variance in the quality of potential mates is sufficient to favor choosy females (Fig. 1). However, a combination of low population density and low variance in quality will increase the costs of being choosy and exceed the possible gains of having offspring from high quality partners.

Species and strategies

Based on differences in their feeding behavior, we might expect costs of mate search to vary in the four copepod species. Copepods that move while feeding (*T. longicornis* and *A. tonsa*) can simultaneously search for mates, while ambush-feeders (*O. davisae*) need to spend dedicated time searching for mates (Kiørboe 2008). Assuming that movement increases encounters with predators through increased hydrodynamic signals and encounter speeds, the latter may face an elevated mortality risk when engaging in mate search (Kiørboe and Visser 1999). Our analysis, however, predicts only small differences in female choosiness among the four copepod species (Fig. 2). Adult males of *P. elongatus* do not feed at all and hence devote all their efforts to mate searching (Corkett and McLaren 1978), but our analysis indicates that females can still afford high mate choosiness even at low population densities.

As in the general analysis, the body size of a species, which determines its encounter rate (Eq. 4), and the variance in mate quality are the most important factors determining the strength of mate choice. At low population densities, small copepods like *O. davisae* should be less choosy than the larger copepod species. Due to their small size, encounter rates are drastically reduced compared to bigger species. However, the abundance of planktonic organisms generally varies inversely with their size (Sheldon et al. 1972; Rodriguez and Mullin 1986), and typical densities of *O. davisae* can approach 300 individuals per liter (Uye and Sano 1995). This means that typical population densities exceed by far the threshold densities that are predicted for female choosiness in our model. Hence, higher population densities balance the reduction of search capacity due to the smaller size, and the intensity of female mate choice can be expected to be similarly high in small and big copepods (Fig. 3).

The role of males

It is remarkable that copepod males are not predicted to be choosy in natural conditions, despite their costly investment in spermatophores. In laboratory experiments, males showed choosiness for large-sized females (Ceballos and Kiørboe 2010). In agreement, male choosiness is predicted

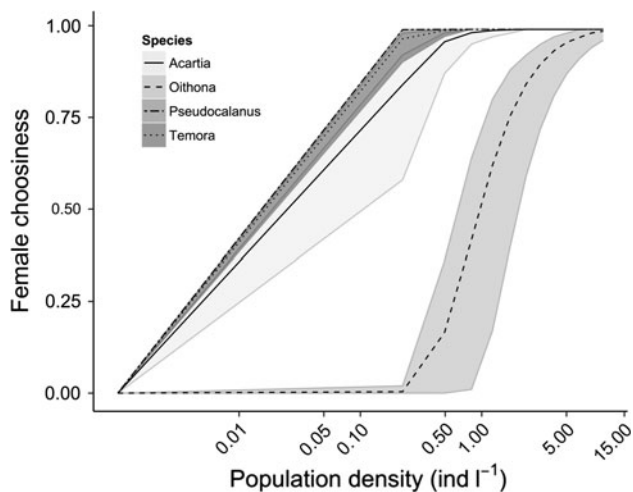


Fig. 3 Female mate choosiness in four copepod species (*Acartia tonsa*, *Temora longicornis*, *Oithona davisae*, *Pseudocalanus elongatus*) as a function of population density (presented on a log scale to the base 10). Female choosiness is expressed as the optimal fraction of the male population to mate (mean \pm upper and lower choosiness limits). Parameter values are taken from Table 2. Varied parameter values: CV of male quality = 0.01–0.10

by our model at the skewed ASR in the experiments by Ceballos and Kiørboe (2010) (Fig. 4). The model assumes a constant resupply of potential partners, which is not given in the experiment of Ceballos and Kiørboe (2010). The males' hesitation to mate in the experiment might indicate the insufficient knowledge acquisition about potential partners.

The difference of choosiness in the laboratory versus field populations suggests that competition among males for the few rare receptive females in natural populations

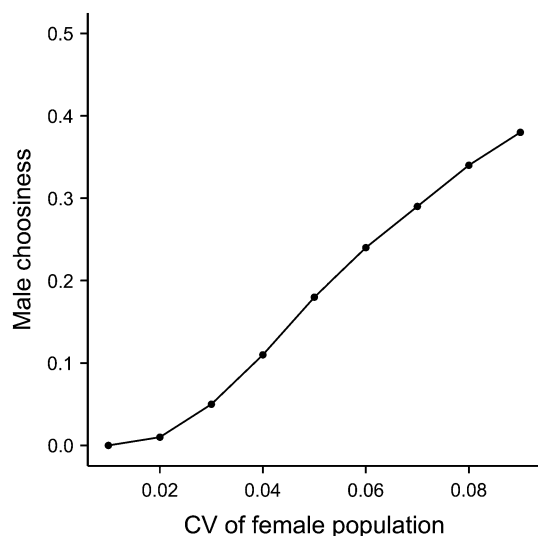


Fig. 4 The optimal male choosiness levels for the experimental conditions described in Ceballos and Kiørboe (2010), which consisted of 4 females and 1 male of *Acartia tonsa* in a 69-ml bottle

overrides mate choice. Hence, distinctive morphological structures of males might have evolved to coerce matings, as suggested by Ali et al. (2009).

Our results show that the intensity of sexual selection and the 'critical density' for the onset of mate choice depends on the variance of quality and the ASR of the male population. Choosing larger males gives females a reproductive advantage (Hylstoft and Kiørboe 2011), as this leads to increased nauplii production in females.

Unfortunately, in population studies, information about male abundance and size is often not reported. Hence, the past and present focus on female traits in plankton ecology may neglect a crucial point of their reproductive biology and, thus, also for the understanding of copepod population dynamics.

Multiple mating and mate choice

Our model assumes that females are not able to use sperm for fertilization from a new male until they run out of sperm from the previous male (e.g., Blades 1977; Anstensrud 1990). While this is the common view in copepodology, it might not hold true for all copepods, as females with several attached spermatophores have been observed in various species (Ali et al. 2009; J.H., personal observation). It is, however, not known whether copepod females can simultaneously use sperm from different males to fertilize their eggs. Females of several insect species are known to engage in multiple matings and receive sperm from several males (Arnqvist and Nilsson 2000). This could make females less choosy when accepting mates, and shift mate choice to later stages in the mating process, for example through cryptic female choice.

Multiple matings can, however, come at additional costs. In fruit flies, the seminal gland products that are transferred during the mating increase female mortality (Fowler and Partridge 1989; Chapman et al. 1995). In the copepod *T. longicornis*, the repeated exposure to males reduces the longevity of the females (Hylstoft and Kiørboe 2011). Females could therefore benefit from escaping male mating attempts. Such a behavior was used to explain the increased number of spermatophores attached to smaller in comparison to bigger *E. graciloides* females (Ali et al. 2009). Multiple matings are thus a possibility that, on the one hand, might lead to reduced precopulatory female choice, and the evolution of post-copulatory cryptic female choice on sperm from different males (Jennions and Petrie 2000), while, on the other hand, copepod females would still benefit of being choosy, if the act of mating itself reduces female fitness either through the transfer of seminal substances or increased predation risk during coupling.

Conclusion

Our study is the first to use a modeling approach to determine the direction and strength of sexual selection by mate choice in planktonic copepods. It predicts strong female choice at typical copepod population densities that occur during the breeding season. Males are predicted to not be choosy under natural conditions. This suggests that the evolution of reproductive traits in males is mainly driven by competition between males for mating opportunities, which can lead to mate guarding tactics as observed in some harpacticoid copepod species (Burton 1985; Shimanaga and Shirayama 2005). Female choosiness can delay the onset of reproduction, and at the same time increase the quality and quantity of offspring, and shows that the link between the relative male and female densities and population densities can be more complicated than previously thought. More knowledge about the behavioral plasticity of mating decisions to changes in mate availability is needed. Our model can facilitate the planning of experimental approaches to sexual selection in copepods and other planktonic organisms.

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References

- Ali AK, Primicerio R, Folstad I, Liljedal S, Berge J (2009) Morphological correlates of mating frequency and clutch size in wild caught female *Eudiaptomus graciloides* (Copepoda: calanoida). *J Plankton Res* 31:389–397
- Anstensrud M (1990) Mating strategies of two parasitic copepods [(*Lernaeocera branchialis* (L.)(Pennellidae) and *Lepeophtheirus pectoralis* (Müller)(Caligidae)] on flounder: polygamy, sex-specific age at maturity and sex ratio. *J Exp Mar Biol Ecol* 136:141–158
- Arnqvist G, Nilsson T (2000) The evolution of polyandry: multiple mating and female fitness in insects. *Anim Behav* 60:145–164
- Bagøien E, Kiørboe T (2004) Blind dating - mate finding in planktonic copepods. III. Hydromechanical communication in *Acartia tonsa*. *Mar Ecol Prog Ser* 300:129–133
- Blades P (1977) Mating behavior of *Centropages typicus* (Copepoda: calanoida). *Mar Biol* 40:57–64
- Burton RS (1985) Mating system of the intertidal copepod *Tigriopus californicus*. *Mar Biol* 86:247–252
- Buskey E, Lenz P, Hartline D (2002) Escape behavior of planktonic copepods in response to hydrodynamic disturbances: high speed video analysis. *Mar Ecol Prog Ser* 235:135–146
- Ceballos S, Kiørboe T (2010) First evidences of sexual selection by mate choice in marine zooplankton. *Oecologia* 164:627–635
- Ceballos S, Kiørboe T (2011) Senescence and sexual selection in a pelagic copepod. *PLoS ONE* 6:e18870
- Chapman T, Liddle L, Kalb J, Wolfner M, Partridge L (1995) Cost of mating in *Drosophila melanogaster* females is mediated by male accessory-gland products. *Nature* 373:241–244
- Corkett CJ, McLaren IA (1969) Egg production and oil storage by the copepod *Pseudocalanus* in the laboratory. *J Exp Mar Biol Ecol* 3:90–105
- Corkett CJ, McLaren IA (1978) The biology of *Pseudocalanus*. *Adv Mar Biol* 15:1–231
- Cornwallis CK, Uller T (2010) Towlatter faces a significantly elevated ards an evolutionary ecology of sexual traits. *Trends Ecol Evol* 25:145–152
- Digby PSB (1950) The biology of the small planktonic copepods of Plymouth. *J Mar Biol Assoc UK* 29:393–438
- Doall M, Colin S, Strickler J, Yen J (1998) Locating a mate in 3D: the case of *Temora longicornis*. *Philos Trans R Soc Lond B* 353:681–689
- Fleminger A (1985) Dimorphism and possible sex change in copepods of the family Calanidae. *Mar Biol* 88:273–294
- Fowler K, Partridge L (1989) A cost of mating in female fruitflies. *Nature* 338:760–761
- Gusmao LFM, McKinnon AD (2009) Sex ratios, intersexuality and sex change in copepods. *J Plankton Res* 31:1101–1117
- Hirst A, Kiørboe T (2002) Mortality of marine planktonic copepods: global rates and patterns. *Mar Ecol Prog Ser* 230:195–209
- Hirst AG, Shearer M, Williams JA (1999) Annual pattern of calanoid copepod abundance, prosome length and minor role in pelagic carbon flux in the Solent, UK. *Mar Ecol Prog Ser* 177:133–146
- Hirst A, Bonnet D, Conway D, Kiørboe T (2010) Does predation control adult sex ratios and longevity in marine pelagic copepods? *Limnol Oceanogr* 55:2193–2206
- Humes AG (1994) How many copepods? *Hydrobiologia* 292–293:1–7
- Hylstoft Sichelau M, Kiørboe T (2011) Age- and size-dependent mating performance and fertility in a pelagic copepod, *Temora longicornis*. *Mar Ecol Prog Ser* 442:123–132
- Ianora A, Miralto A, Buttino I, Romano G, Poulet SA (1999) First evidence of some dinoflagellates reducing male copepod fertilization capacity. *Limnol Oceanogr* 44:147–153
- Irgoien X, Obermüller B, Head RN, Harris RP, Rey C, Hansen BW, Hygum BH, Heath MR, Durbinal EG (2000) The effect of food on the determination of sex ratio in *Calanus spp.*: evidence from experimental studies and field data. *ICES J Mar Sci* 57:1752–1763
- Jennions MD, Petrie M (1997) Variation in mate choice and mating preferences: a review of causes and consequences. *Biol Rev* 72:283–327
- Jennions MD, Petrie M (2000) Why do females mate multiply? A review of the genetic benefits. *Biol Rev Cambridge Philos Soc* 75:21–64
- Katona SK (1973) Evidence for sex pheromones in planktonic copepods. *Limnol Oceanogr* 18:574–583
- Kiørboe T (2007) Mate finding, mating, and population dynamics in a planktonic copepod *Oithona davisae*: there are too few males. *Limnol Oceanogr* 52:1511–1522
- Kiørboe T (2008) Optimal swimming strategies in mate-searching pelagic copepods. *Oecologia* 155:179–192
- Kiørboe T, Bagoien E (2005) Motility patterns and mate encounter rates in planktonic copepods. *Limnol Oceanogr* 50:1999–2007
- Kiørboe T, Visser AW (1999) Predator and prey perception in copepods due to hydromechanical signals. *Mar Ecol Prog Ser* 179:81–95
- Kiørboe T, Bagoien E, Thygesen U (2004) Blind dating—mate finding in planktonic copepods. II. The pheromone cloud of *Pseudocalanus elongatus*. *Mar Ecol Prog Ser* 300:117–128
- Kokko H, Monaghan P (2001) Predicting the direction of sexual selection. *Ecol Lett* 4:159–165

- Kokko H, Rankin D (2006) Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philos Trans R Soc Lond B* 361:319–334
- Korpelainen H (1990) Sex ratios and conditions required for environmental sex determination in animals. *Biol Rev Cambridge Philos Soc* 65:147–184
- Landry MR (1978) Population dynamics and production of a planktonic marine copepod, *Acartia clausii*, in a small temperate lagoon on San Juan Island, Washington. *Int Rev Ges Hydrobiol* 63:77–119
- Lee WY, McAlice B (1979) Seasonal succession and breeding cycles of three species of *Acartia* (Copepoda: calanoida) in a Maine estuary. *Estuar Coast* 2:228–235
- Maly EJ (1973) Density, size, and clutch of two high altitude diaptomid copepods. *Limnol Oceanogr* 18:840–848
- Mauchline J (1998) The biology of calanoid copepods. Academic, London
- Möllmann C, Köster F (2002) Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. *J Plankton Res* 24:959–977
- Renz J, Mengedoht D, Hirche H (2008) Reproduction, growth and secondary production of *Pseudocalanus elongatus* Boeck (Copepoda, Calanoida) in the southern North Sea. *J Plankton Res* 30:511–528
- Rodriguez J, Mullin MM (1986) Relation between biomass and body weight of plankton in a steady state oceanic ecosystem. *Limnol Oceanogr* 31:361–370
- Schluter D (2001) Ecology and the origin of species. *Trends Ecol Evol* 16:372–380
- Sheldon RW, Prakash A, Sutcliffe WH Jr (1972) The size distribution of particles in the ocean. *Limnol Oceanogr* 17:327–340
- Shimanaga M, Shirayama Y (2005) Precopulatory mate guarding of interstitial *Phyllopodopsyllus* sp. (Copepoda: harpacticoida) in Otsuchi Bay, Northeastern Japan. *Benthos Res* 60:39–40
- Shuster SM, Wade MJ (2003) Mating systems and strategies. Princeton University Press, Princeton
- Smyly WJP (1968) Number of eggs and body size in the freshwater copepod *Diaptomus gracilis* Sars in the English Lake District. *Oikos* 19:323–338
- Titelman J, Varpe Ø, Eliassen S, Fiksen Ø (2006) Copepod mating: chance or choice? *J Plankton Res* 29:1023–1030
- Tsuda A, Miller C (1998) Mate-finding behaviour in *Calanus marshallae* Frost. *Philos Trans R Soc Lond B* 353:713–720
- Uchima M (1985) Copulation in the marine copepod *Oithona davisae*. I. Mate discrimination. *Bull Plankton Soc Jpn* 32:23–30
- Uye S, Sano K (1995) Seasonal reproductive biology of the small cyclopoid copepod *Oithona davisae* in a temperate eutrophic inlet. *Mar Ecol Prog Ser* 118:121–128
- Visser AW, Mariani P, Pigolotti S (2009) Swimming in turbulence: zooplankton fitness in terms of foraging efficiency and predation risk. *J Plankton Res* 31:121–133
- Wilson D, Parrish K (1971) Remating in a planktonic marine calanoid copepod. *Mar Biol* 9:202–204
- Yen J, Weissburg M, Doall M (1998) The fluid physics of signal perception by mate-tracking copepods. *Philos Trans R Soc Lond B* 353:787–804