

Thomas Kiørboe

Sex, sex-ratios, and the dynamics of pelagic copepod populations

Received: 6 September 2005 / Accepted: 14 December 2005 / Published online: 20 January 2006
© Springer-Verlag 2006

Abstract I examine how the population biology of pelagic copepods depends on their mating biology using field data and a simple demographic model. Among calanoid copepods, two distinct patterns emerge. Firstly, copepods that lack seminal receptacle and require repeated mating to stay fertilized have near equal adult sex ratios in field populations. Winter population densities are orders of magnitude less than the critical population density required for population persistence, but populations survive winter seasons as resting eggs in the sediment. Population growth in these species is potentially high because they have on average a factor of 2 higher egg production rates than other pelagic copepods. Secondly, other copepods require only one mating to stay fertile, and populations of these species have strongly female-skewed adult sex-ratios in field populations. Resting eggs have not been described within this group. Winter population sizes are well predicted by the critical density required for population persistence which, in turn, is closely related to the body-size-dependent mate-search capacity. Thus, the different requirements for mating lead in the first case to a more opportunistic reproductive strategy that implies rapid colonization of the pelagic during productive seasons, and in the second case to a strategy that allows maintenance of a pelagic populations during unproductive seasons. Positive density dependent population growth during periods of low population density ('Allee effect') amplifies population density variation during winter into the subsequent summer, thus explaining why summer densities appear to depend more on winter densities than on current growth opportunities in pelagic copepods.

Keywords Allee-effect · Critical population density · Mating behavior · Reproductive biology

Communicated by Ulrich Sommer

T. Kiørboe
Danish Institute for Fisheries Research, Kavalergaarden 6,
2920 Charlottenlund, Denmark
E-mail: tk@dfu.min.dk

Introduction

The dynamics of plankton populations may be constrained by a number of factors, including the physical environment, the availability of food, and the presence of predators. For populations of species that reproduces sexually, the dynamics may in addition be constrained by fertilization rate. In pelagic copepods, fertilization involves two processes: (1) mate encounter that depends on the ability of the mates to find one another and on the concentrations of males and females, and (2) mating that may involve coupling of the mates (precopula) and transfer of a spermatophore (copula). This study uses a simple demographic analysis, and established as well as recent insights in copepod mate-finding and mating behavior, to examine how fertilization may limit population growth and impact population composition (sex ratio) in pelagic copepods.

Mate finding represents a particular challenge in pelagic populations that operate in a 3-dimensional dilute environment where the chance of random encounter is small (Buskey 1998). Pelagic copepods have, however, evolved mechanisms to enhance mate encounter rates. These mechanisms include aggregation of ready-to-mate adults at certain depth strata (Hayward 1981; Tsuda and Miller 1998), adult swarming behavior (Ambler et al. 1996), and an ability of males to remotely locate receptive females. The latter in particular appears to apply to most pelagic copepods. Recent studies have for various species provided a mechanistic understanding of how hydromechanical and chemical mate-signalling allow males of millimeter-sized copepods to search tens of thousands of liters of water per day for females (Kiørboe and Bagøien 2005). Yet, the scarcity of adults at some times of the year may limit encounter and mating rates and, thus, constrain population growth rate.

Males can be limiting mating rates, even when potential encounter rates are high, by having a limited mating capacity. Courtship can in some species last many minutes (Kiørboe et al. 2005), and precopula,

where the mates cling to each other prior to copulation, may last up to several hours in calanoid copepods (Blades 1977; Gauld 1957) and up to several weeks in harpacticoid and poecilostomatoid copepods (Lazzaretto and Battaglia 1994). Mating capacity in pelagic copepods may also be limited by the spermatophore production rate. The few accounts available suggest that spermatophore production rate may be as low as 0.1–1 day⁻¹ (Ianora et al. 1999; Hopkins 1982). One can thus imagine situations in which male mating capacity becomes limiting.

The requirements for efficient mate finding and a high spermatophore production rate may be further emphasized in species that requires multiple matings. Many calanoid copepods of the superfamily Centropagoidea, within which the females of most species have no seminal receptacle (Ohtsuka and Huys 2001), appear to require repeated matings to stay fertile, up to one mating per batch of eggs produced (e.g., Katona 1975; Parrish and Wilson 1978; Ianora et al. 1989; Berger and Maier 2001). In contrast, most cyclopoid and non-centropagoidea calanoid copepods need to mate just once to remain fertilized for the rest of their life (e.g., Marshall and Orr 1952; Ohtsuka and Huys 2001; Berger and Maier 2001, and references therein).

Adult sex-ratios are typically skewed towards dominance of females in copepod field populations, potentially enhancing the extent of fertilization limitation. Since parental investment in each of the two sexes is equal, implying near-equal sex ratios at birth (Fishers rule: e.g., Fisher 1930; Charnov 1982), unequal sex-ratios imply differential mortality rates among the sexes. The pronounced and diverse patterns among field populations in adult sex-ratios across copepod families and seasons that has been reported (Mauchline 1998) may be related to the variability and asymmetry between genders in the reproductive value of one mating (resulting in one or several batches of eggs) and to other aspects of the mating biology, as well as having different impacts on fertilization limitation and population dynamics.

Fertilization limitation in natural populations may have several implications and become evident in various ways. One implication is that not all mature females are fertilized, thus limiting population growth rate. Such effects have been demonstrated for populations of pelagic copepods (Hopkins 1982; Williamson and Butler 1987). Another is that population growth rate may become positively dependent on the density of the population ('Allee effect'; Stephens et al. 1999), i.e. decreasing growth rate with decreasing density. This occurs at low population densities where mate encounters are rare. Finally, fertilization limitation implies that there is a critical minimum population size below which mate encounters are too rare to allow population maintenance and below which the population will go extinct (Gerritsen 1980). This, in turn, may constrain the distribution and diversity of pelagic copepods.

This paper offers a simple demographic analysis of fertilization limitation and population dynamics in

pelagic copepods. The analysis predicts how population properties, such as which fraction of the females are fertilized, the magnitude of fecundity, the adult sex ratio, and the critical population densities, depend on mating behavior. Whenever possible, I test model predictions against observations taken from the literature.

Demographic model

The following expands the demographic analysis of Gerritsen (1980) and Kiørboe and Sabatini (1994) by taking mating behavior into account. All considerations assume stable age-structure. Symbols are explained in Table 1.

Single mating, unlimited mating capacity

I consider first the simplest case where males are assumed to have an unlimited mating capacity and where females need to be mated just once. The net reproductive rate, R_0 , i.e. the average number of offspring per female that survive to adulthood in the next generation, can be computed from the survivorship, l_x , and the age-specific fecundity, m_x (number of fertilized eggs per female and day), as (x is age):

$$R_0 = \int_0^{\infty} l_x m_x dx. \quad (1)$$

I assume that eggs spawned freely in the water suffer from a constant mortality rate, δ_e , that post-hatched individuals suffer from a (lower) constant mortality rate, δ , and that eggs hatch at age τ ; then:

$$l_x = e^{-(\delta_e - \delta)\tau} e^{-\delta x}. \quad (2)$$

The fecundity, $m_x = 0$ for $x < \kappa$, where κ is the age of maturity. For $x > \kappa$:

$$m_x = f p_x, \quad (3)$$

where f is the fecundity of fertilized females (eggs per female per day), which is assumed age-independent, and p_x is the probability that a female has been mated at least once at age x . This probability depends on the ability of males to find females as well as on the concentration of mature males (C_M). The mate-finding capacity of a male can be expressed as a search volume rate, β (volume per time) (Kiørboe and Bagøien 2005). Females then encounter males at a rate βC_M and, assuming a Poisson process, the probability that a female has been mated at least once at age x is:

$$p_x = (1 - e^{-\beta C_M (x - \kappa)}). \quad (4)$$

Combining Eqs. 1, 2, 3 and 4 yields:

Table 1 Symbols used in this paper. Default values are for a field population of a small (~ 10 μg dry weight) generic broadcast-spawning copepod at 15°C

Symbol	Description	Units	Default value
C_M, C_F, C_T	Concentration of adult males (M), adult females (F), or adults (T)	m^{-3}	
f	Average fecundity of fertilized female	Eggs female $^{-1}$ day $^{-1}$	10
l_x	Survivorship at age x	–	
m_x	Fecundity at age x	Eggs female $^{-1}$ day $^{-1}$	
M	Mating rate	Matings female $^{-1}$ day $^{-1}$	
p_x	Probability of at least one mating at age x	–	
x	Age	Days	
α	Mating ‘handling time’	Days	0 or 1
β	Mate search volume rate	$\text{m}^3 \text{day}^{-1}$	0.1
δ_e	Egg mortality	Day $^{-1}$	1
δ	Post hatch mortality	Day $^{-1}$	0.1
κ	Age at maturity	Days	28
π	Adult sex ratio (male/female)	–	0.6
σ	Fraction of females fertilized at least once	–	
τ	Egg hatching time	Days	1
Φ	$e^{-\kappa\delta - (\delta_e - \delta)\tau} (f/\delta)$	Dimensionless	2.5

Values for fecundity, age at maturity, mortality rates, and sex-ratio were averages of these parameters as observed in field populations (corrected for temperature and body weight effects) and taken from Hirst and Kiørboe (2002), egg hatching time from Kiørboe and Sabatini (1994), and mate search volume rate from Kiørboe and Bagøien (2005). Apart from the mate search capacity, the parameters are almost independent of body size

$$R_0 = f e^{-(\delta_e - \delta)\tau} \int_{\kappa}^{\infty} e^{-\delta x} (1 - e^{-\beta C_M (x - \kappa)}) dx \Rightarrow$$

$$R_0 = e^{-\kappa\delta - (\delta_e - \delta)\tau} \frac{f}{\delta} \left(\frac{\beta C_M}{\delta + \beta C_M} \right) = \Phi \left(\frac{\beta C_T}{\delta + \delta/\pi + \beta C_T} \right), \quad (5)$$

where $\pi = C_M/C_F$ is the male/female sex-ratio of the adult population, $C_T = C_M + C_F$ is the concentration of adults, and $\Phi = e^{-\kappa\delta - (\delta_e - \delta)\tau} (f/\delta)$. (The above and all subsequent integrals were solved using software MATEMATICA). The requirement for population maintenance is that $R_0 \geq 2$. We can rearrange Eq. 5 to estimate the minimum concentration of males (C_M^*) or adults (C_T^*) required to allow population maintenance:

$$C_M^* = \frac{2\delta}{\beta(\Phi - 2)}, \quad (6)$$

$$C_T^* = \frac{2\delta(1 + \pi^{-1})}{\beta(\Phi - 2)}. \quad (6a)$$

The critical density decreases with increasing mate search capability (β) and fecundity (f) and decreasing mortality (δ, δ_e) and development time (κ, τ), and it depends also on the sex ratio (π).

One can also estimate the population growth rate, r , as:

$$r = \frac{\ln(R_0/2)}{T}, \quad (7)$$

where T is the generation time defined as:

$$T = \frac{\int_0^{\infty} x l_x m_x dx}{\int_0^{\infty} l_x m_x dx} = \kappa + \frac{1}{\delta} + \frac{1}{\beta C_T \pi / (\pi + 1) + \delta}. \quad (8)$$

It follows from Eqs. 5, 7 and 8 that the population growth rate, r , increases with adult population density;

that is, the population growth rate shows positive density dependence (Allee effect).

The fraction of fertilized females, σ , in a population can be estimated as:

$$\sigma = \frac{\int_{\kappa}^{\infty} p_x l_x dx}{\int_{\kappa}^{\infty} l_x dx} = \left[1 + \left(1 + \frac{\delta}{\beta C_T} \right) / \pi \right]^{-1}. \quad (9)$$

Multiple matings

Assume for simplicity that one mating per batch of eggs spawned is required, and that the batch of eggs is spawned only if the female has been mated since the last spawning event. Let t be the time-interval between spawning events, then the probability that mating has occurred in that time interval is:

$$p = (1 - e^{-\beta C_M t}) \quad (4a)$$

By replacing Eq. 4 with Eq. 4a we can again compute the net reproductive rate, the critical concentration for population maintenance, population growth rate, and the generation time (Table 2).

Limited mating capacity

There may be a limit to how many matings per unit time that a male copepod can undertake, both because each mating may take a substantial amount of time (min-days), or because of a limited spermatophore production capacity. Mating rate may be modelled by assuming a saturation Michaelis-Menten type kinetics (as also fre-

Table 2 Equations for mating strategies other than for those given in the text

Property	Symbol Eq. nos	Multiple matings, unlimited mating capacity of males	Single mating, limited mating capacity of males	Multiple matings, limited mating capacity of males
Probability of fertilization	p 4a, b, c	$[1 - \exp(-\beta C_T \pi / (1 + \pi))]$	$[1 - \exp(-\beta C_T \pi (x - \kappa) / (\pi + 1 + \alpha \beta C_T))]$	$[1 - \exp(-\beta C_T \pi / (\pi + 1 + \alpha \beta C_T))]$
Net reproductive rate	R_0 5a, b, c	$\exp(-\kappa \delta - (\delta_e - \delta) \tau) \times (f / \delta) \times (f / \delta) \times (1 - \exp(-\beta C_T \pi / (1 + \pi)))$	$\exp(-\kappa \delta - (\delta_e - \delta) \tau) \times (f / \delta) \times [\beta C_T \pi / ((\beta C_T \pi + \delta(1 + \alpha \beta C_T + \pi)) / 2(1 + \pi^{-1}) / ((\beta / \delta)(\Phi - 2) - 2\alpha \beta))]$	$\exp(-\kappa \delta - (\delta_e - \delta) \tau) \times (f / \delta) \times [1 - \exp(-\beta C_T \pi / (\pi + 1 + \alpha \beta C_T))]$
Critical concentration	C_T^* 6b, c, d	$-\ln[1 - (\delta / \Phi)] / (\pi + 1) / \beta \pi \tau$	$\kappa + (1 / \delta)$	$-\ln[1 - (\delta / \Phi)] / (\pi + 1) / [\beta \pi \tau + \alpha \beta \ln(1 - (\delta / \Phi))]$
Generation time	T 8a, b, c	$\kappa + (1 / \delta)$	$\kappa + (1 / \delta)$	$\kappa + (1 / \delta)$
Fraction fertilized	σ 9a, b, c	$[1 - \exp(-\beta C_T \pi / (1 + \pi))]$	$[1 - \exp(-\beta C_T \pi / (1 + \pi))]$	$\sigma = p = [1 - \exp(-\beta C_T \pi / (\pi + 1 + \alpha \beta C_T))]$

quently used to describe the functional response in ingestion rate to food density), hence:

$$\text{male-specific mating rate} = \frac{\beta C_F}{1 + \alpha \beta C_F}, \quad (10)$$

where α is the ‘handling time’, essentially either the inverse spermatophore production rate or the mating duration, whichever is the longest. We are rather interested in the specific rate at which females are mated, M , which is obtained by dividing with female concentration and multiplying with male concentration on both side, hence:

$$M = \frac{\beta C_M}{1 + \alpha \beta C_F} = \frac{\beta C_T \pi}{\pi + 1 + \alpha \beta C_T}. \quad (11)$$

We again distinguish between the situations with single and multiple matings. For single mating, the probability of a female being fertilized is:

$$p_x = \frac{(1 - e^{-M(x-\kappa)})}{[1 - \exp(-\beta C_T \pi (x - \kappa) / (\pi + 1 + \alpha \beta C_T))]} \quad (4b)$$

and for multiple matings it is:

$$p = (1 - e^{-Mt}) = [1 - \exp(-\beta C_T \pi t / (\pi + 1 + \alpha \beta C_T))]. \quad (4c)$$

As above, we replace Eq. 4 with either Eqs. 4b or 4c and then derive all the other properties of the population (Table 2).

Predictions and comparison with observations

The fraction of females fertilized

The most direct kind of evidence that the abundance or performance of males may be limiting fertilization of females stems from observations that the fraction of fertilized females in a population varies with the availability of males. Such observations have been provided for such different species as the huge oceanic copepod *Euchaeta norvegica*, that occurs at characteristic adult concentrations of 1 m^{-3} (Hopkins 1982; Fig. 1a), and the small freshwater copepod, *Diatomus pallidus*, that occurs at characteristic concentrations that are 3–4 orders of magnitude higher (Williamson and Butler 1987). The relationships for *Euchaete norvegica* between the fraction of fertilized females and adult sex ratio (Fig. 1a) or male abundance (Fig. 1b) suggest that in this species it is the mating ‘handling time’ (α) rather than mate search capacity (β) and male abundance (C_M) that limits fertilization rate in this species. From Eq. 9b in Table 2, it follows that for a species with limited mating capacity that requires just one mating, as applies to *E. norvegica*, fertilization frequency is independent of the density of adults (C_T) when $C_T \gg \delta / (1 + \alpha \delta) \beta$. If one assumes a ‘handling time’ (α) of 10 days in *E. norvegica* (spermatophore production rate is 0.1 day^{-1} , computed from

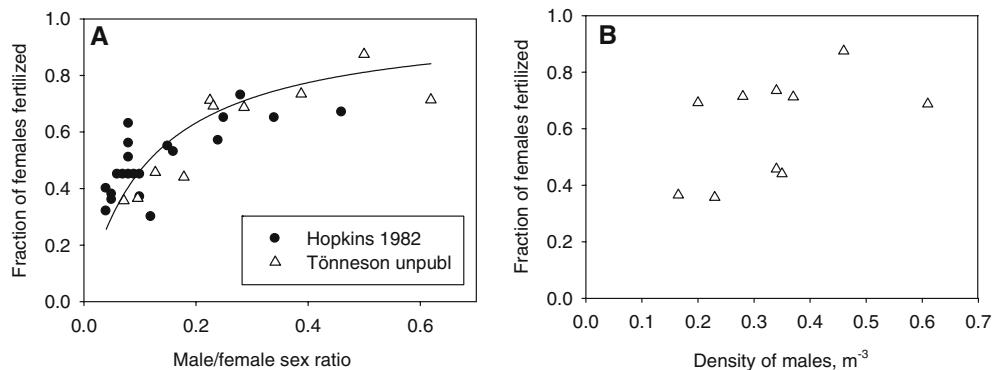


Fig. 1 *Euchaeta norvegica*. **a** The fraction of fertilized females (i.e. females carrying at least one spermatophore) as a function of adult male/female sex ratio in populations in a Scottish Sea loch (data from Hopkins 1982) and in the Skagerrak (unpublished data from Kajsa Tönneson, University of Gothenburg, Sweden). **b** Fraction of fertilized females as a function of the density of males (data from

the Skagerrak, K. Tönneson, unpublished data). The *line* in **a** is a fit of Eq. 9b in Table 2, where C_T is considered constant. In contrast to many other copepods, the females of *Euchaeta* spp. do not remove attached spermatophores (Ohtsuka and Huys 2001) and the presence or absence of a spermatophore is therefore a good indication of fertilization status

Hopkins 1982), an adult mortality rate ($\delta = 0.1 \text{ day}^{-1}$; Hirst and Kiørboe 2002) and a mate search volume rate ($\beta = 8 \text{ m}^3 \text{ day}^{-1}$; Kiørboe and Bagøien 2005) typical for copepods of this size (5 mm prosome length) then $\delta / (1 + \alpha\delta)\beta = 0.006 \text{ m}^{-3}$, which is much less typical adult densities (Fig. 1b).

Seminal receptacles

Another indirect piece of evidence that fertilization rate may be limiting is the presence of seminal receptacles in many species of calanoid copepods (all non-centropoagoida; Ohtsuka and Huys 2001). It is an advantage for a female to mate with multiple males in order to ensure a certain genetic variability among the offspring. However, in species where the female has seminal receptacles, one would expect all offspring to have one or at most two fathers (there are two genital openings), since once sperm has been added to a receptacle, the likelihood that another male can fertilize the female is substantially reduced (to zero?). The presence of seminal receptacles must therefore be considered an adaptation to male-encounter limitation, as the female can do with one or a few matings, and thus need only one or two encounters with males, in contrast to species lacking the capacity to store sperm.

Several aspects of the mating biology and population structure of pelagic copepods may be interpreted in the light of absence or presence of the capacity to store sperm in seminal receptacles. First, females with seminal receptacles have a lower requirement for mate-encounters than those without. Second, from the point of view of the male the reproductive value of each mating differs between the two mating systems: it is high in species with seminal receptacles because one mating may lead to many successive batches of eggs, and lower in species lacking seminal receptacles since one mating implies maybe only one batch of eggs. Thus, in species with

seminal receptacles, the two sexes have asymmetric ‘interests’ in mate encounters, while in species where the female lacks seminal receptacles, the sexes have more symmetric interests. This may lead to various degrees of asymmetry in behavior between the sexes.

Mating and mate-finding are risky undertakings as they may increase the rate at which predators are encountered. There is, therefore, a trade-off between mate-finding on the one hand and predator avoidance on the other. The single-mating system may favor a more risky behavior of the males and, thus, a higher mortality rate, while in the multiple maters mortality rates would be more similar among the sexes. Mate-finding behavior has been described in only few species, so it is difficult to make a systematic comparison of behaviors between the two groups. However, the motility patterns, mate-finding and mating behavior of two representatives, *Pseudocalanus elongatus* (Kiørboe et al. 2005) with seminal receptacles, and *Acartia tonsa* (Bagøien and Kiørboe 2005) lacking seminal receptacles, may illustrate the point. In *P. elongatus*, motility patterns are radically different between the sexes: the female swims slowly along convoluted paths resembling a random walk (‘diffusive motility’), while the males cruise along much more straight tracks (‘ballistic motility’). The male swimming pattern increases his chance of finding a female, but obviously also elevates his risk of encountering a predator. Once a female has been encountered, the male engages in a convoluted ‘courtship’ behavior during which, for several minutes, he speeds around the female at very high velocity. The exact function of this behavior is unknown, but it may simply be that the male is examining the virgin status of the female. In *P. elongatus* and most other species in the single-mating group, the males do not feed (Ohtsuka and Huys 2001) and, thus, have a very limited number of spermatophores that they do not want to ‘waste’ on an already fertilized female. In any case, this further elevates the exposure of the male to predators. At the

opposite extreme, in *A. tonsa* the two sexes both swim in a diffusive manner, and mate pursuit and actual mating is concluded within a few seconds after mate encounter (Bagoien and Kiørboe 2005). Similar differences between single- and multiple-maters in mate-finding and mating behavior may apply more generally and would suggest differences in mortality patterns between the sexes. Such differences would become manifest as differences in adult sex-ratios.

Patterns in sex ratio

The sex-ratio in adult populations of pelagic copepods is typically biased towards dominance of females. Biased sex-ratios in the adult population are mainly due to differential mortality, with the adult sex-ratio being the inverse of the ratio of mortalities of the sexes. At birth or at the time the sex is determined, the sex-ratio must be 1:1 (Fisher's rule: Fisher 1930; Charnov 1982), or skewed towards the sex in which the female has invested the least. This might argue that sex-ratios should be biased towards males, if the typically smaller sizes of the males than the females (e.g. Maly and Maly 1999) reflect differences in egg sizes. The literature is rich in reports on adult sex ratios in pelagic copepod populations (Fig. 2; $n \sim 4,000$), but most reports are plagued by poor adult count statistics. Despite this variability, there are consistent differences in adult sex-

ratio between copepod families (Fig. 2), and in some cases also consistent seasonal patterns within species (Fig. 3). Among the 12 copepod families in Fig. 2, average sex-ratio varies between 0.15 and 1.1. Differences in sex ratio between the calanoid families (all but families 2 and 12 in Fig. 2) follow the phylogeny and differences in sexually dimorphic characters as described by, e.g., Ohtsuka and Huys (2001). Thus, the families with the least biased sex-ratios (families 7–11 in Fig. 2) all belong to the superfamily Centropagoidea that requires multiple matings. In contrast, those families with the female-skewed sex ratios (family numbers ≤ 6 in Fig. 2), including the non-calanoid Oithonidae, are able to reproduce continuously after just one mating. Thus, we do observe quite a distinct pattern in sex-ratios, which reflects differences in mortality rates between sexes and which is consistent with the above expectations: it is near 1:1 for species belonging to the Centropagoidea and strongly female-biased in others. In many of the latter, the males do not feed, thus providing a mechanistic—but not an evolutionary—explanation of their higher mortality rate.

Several early authors have noted that sex-ratios vary seasonally within species (Conover 1956; Moraítou-apostolopoulou 1972; Lee and McAlice 1979), although at this finer scale the often poor adult count statistics makes the data even noisier. If male mortalities are higher than female mortalities, we would in fact expect seasonal variations in sex-ratios that are functions of the

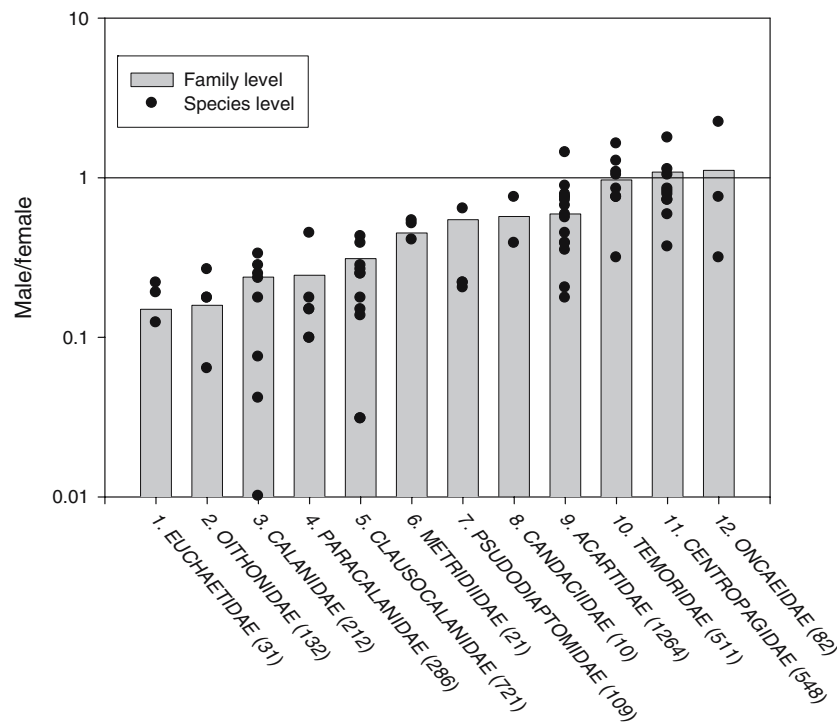


Fig. 2 Average male/female sex ratios in pelagic copepods from 12 families organized in order of increasing sex-ratio. Raw data compiled by Hirst and Kiørboe (2002). The numbers in parenthesis after family names give the total number of samples on which the

family-averaged ratios are based. Dots refer to average sex-ratios obtained in individual studies of individual species (each comprising many samples), and bars refer to family averages. The numbers in front of family names refer to family numbers as used in the text

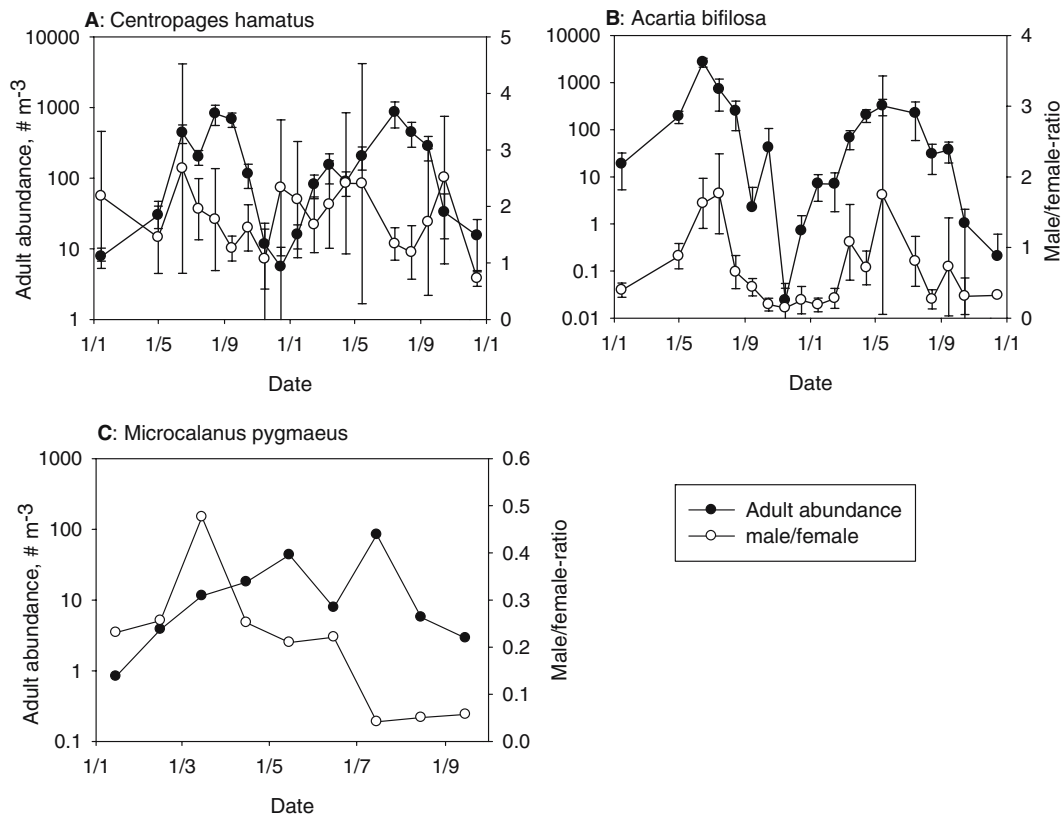


Fig. 3 Seasonal variation in male/female sex-ratio and adult density in the copepods *Centropages hamatus* (a) and *Acartia bifilosa* (b) during 2 years in the Kiel Bight, and of *Microcalanus*

pygmaeus during 1 year in Loch Striven. Kiel Bight data from Schnack (1978) and Loch Strieven data from Marshall (1949)

seasonal variation in population growth rate, with higher male:female sex-ratios during periods of population increase, and vice versa. A shorter development time of males than of females, as has been documented for several species (e.g., Smith and Lane 1985; Durbin et al. 2000), has a similar effect. Reviewing the reports compiled by Hirst and Kiørboe (2002, their Appendix C), particularly Marshall et al. (1934), Marshall (1949), Digby (1951), Schnack (1978), Goswami (1978), Kouwenberg (1993), and Liang and Uye (1996a, b, 1997) that all provide seasonal abundance and sex-ratio information reveals, in fact, such a pattern in some cases (Fig. 3). In other cases, no consistent pattern was found, possibly due to poor count statistics. A simple population dynamics model that incorporates differential mortality and development time between the sexes can largely reproduce the seasonal variation in adult abundances as well as the overall pattern in sex-ratio, but is unable to reproduce the magnitude of observed sex-ratio variation (Fig. 4). Other mechanisms of sex-ratio control may be invoked. There is circumstantial evidence that copepods of the family Calanidae may change sex in the course of development (Flemming 1985; Svensen and Tande 1999; Irigoien et al. 2000; Miller et al. 2005), as has been demonstrated in other copepods (see review by Miller et al. 2005), and that

sex-determination may be under environmental control (reviewed by Mauchline 1998). The pronounced seasonal variation in sex-ratio, exceeding the expectation based on a simple population dynamics model, makes further examination of sex-determination in pelagic copepods potentially rewarding.

Critical population size and density dependent population growth (Allee effect)

To estimate the densities of adult populations below which population growth becomes positively density dependent (Allee effect), as well as the minimum adult concentration that allows population maintenance, I initially use a set of default parameter values (mortality, fecundity, etc) for a generic but typical small broad-cast spawning pelagic copepod (Table 1). Depending on the mating behavior, critical adult densities for the generic copepod population are 10–40 m^{-3} (Fig. 5). Self-maintained populations are, thus, expected never to decrease to lower densities. Density dependent effects on population growth are evident at densities up to at least 1 order of magnitude higher (Fig. 5). The observation above that male/female sex ratios in many populations are lowest at the time of the year where population

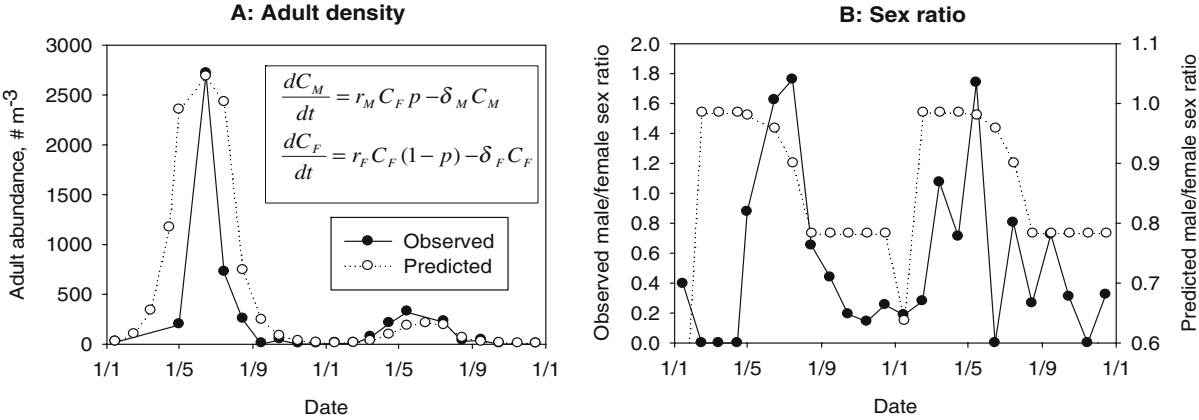


Fig. 4 *Acartia biflosa*. Observed and predicted seasonal variation in adult density (a) and male/female sex ratio (b) in Kiel Bight during a 2-year period. The population dynamics model (a) describes abundances of males (N_M) and females (N_F) as a function of the time-varying specific growth rate (r_M , r_F), time-varying mortalities of males (δ_M) and females (δ_F) and the fraction of males (p) and females ($1 - p$) in the population at sexual maturation. Differences in development time between the two sexes were

simulated as differences in growth rates. The seasonal pattern in specific mortalities and growth rates we taken from the observations for small neritic copepods of Kiørboe and Nielsen (1994) in a nearby coastal ecosystem, male-mortality was assumed to be twice the mortality of females, male development time 2/3 of female development time, and $p=0.55$. Abundance data for *Acartia biflosa* in Kiel Bight were taken from Schnack (1978). Note the different Y-axes scales of observed and predicted sex-ratios in (b)

densities are also at their lowest makes these estimates conservative. Copepods that require multiple matings and which have a limited mating capacity, such as would apply to most Centropagoidea, never attain positive growth rates independent of population density suggesting that this strategy is not feasible. This would suggest that copepods belonging to Centropagoidea would have higher realized egg production and/or development rates than other pelagic copepods. Re-analysing the data compiled by Hirst and Kiørboe (2002) in fact reveals that Centropagoidea copepods

have realised egg production rates that are significantly higher than other copepods, on average 14 versus 8 eggs female⁻¹ day⁻¹ for a 10 µg C copepod ($P < 0.05$; Fig. 6), sufficient to render the re-mating strategy feasible. Development rates are similar among the two groups.

Typical population densities are strongly body-size-dependent and we thus need to consider effects of size on the critical population density. Neither fecundity, mortality, egg hatching or development times depend strongly on body size in pelagic copepods (Huntley and Lopez 1992; Hirst and Kiørboe 2002; Kiørboe and

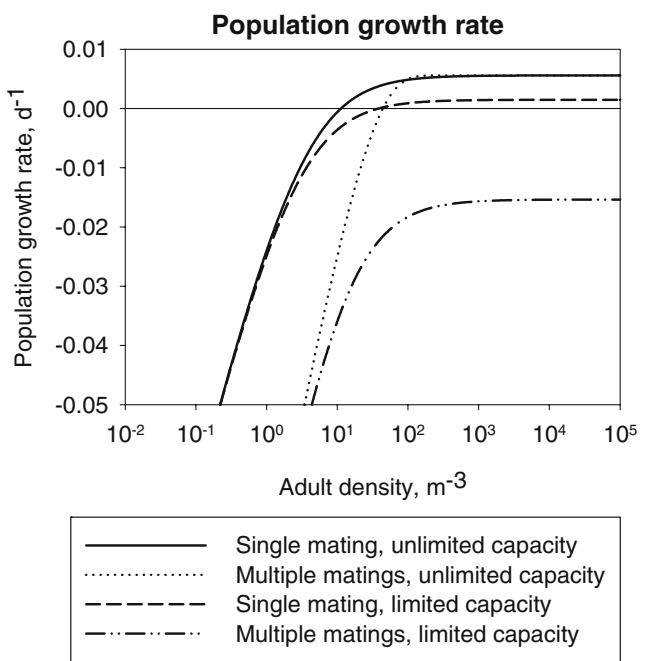


Fig. 5 Predicted population growth rate as a function of adult density for various mating strategies. The default parameters in Table 1 have been assumed

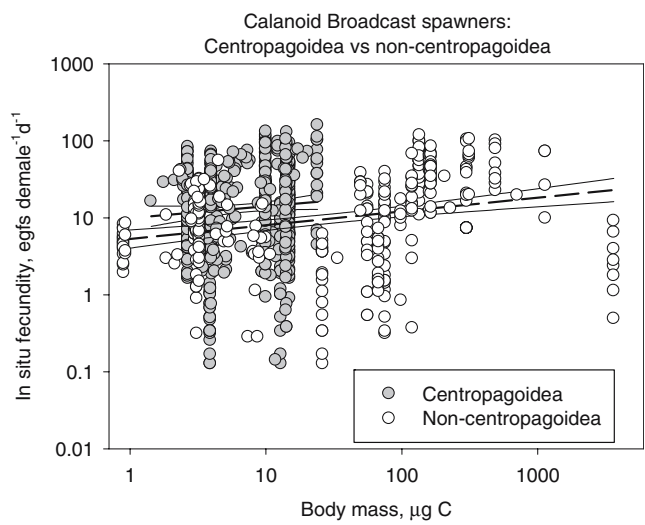


Fig. 6 In situ fecundities as a function of body mass of calanoid broadcast spawning copepods either belonging to or not belonging to the superfamily Centropagoidea. Observed fecundities have been converted to fecundities at 15°C assuming a $Q_{10}=1.3$ (Hirst and Kiørboe 2002). Data taken from the compilation of Kiørboe and Hirst (2002). The regression lines have non-overlapping confidence limits and are, thus, statistically different from one another

Sabatini 1995) and the strongest size effect is through mate-searching capability (β). Kiørboe and Bagøien (2005) found β to scale approximately with female length cubed. Using their relation for β as a function of female size leads to estimated critical adult abundances that are largely consistent with seasonal minimum abundances of adult male copepods in the North Sea when one assumes the most relaxed mating behavior (one mating required, mating capacity unlimited) (Fig. 7). The more restrictive mating behaviors lead to higher critical concentrations that appear inconsistent with the observed low winter concentrations of copepods that require multiple mating (Fig. 7). Critical concentrations also depend strongly on the realized fecundity, development time, and in particular mortality rate, and are in general 1–2 orders of magnitude higher in species requiring multiple mating than in those where one mating is sufficient (Fig. 8). Many copepods appear to overwinter as late copepodites rather than as adult, thus relaxing the requirement for dense adult populations during winter. This applies, however, mainly to copepods in the single-mating group (e.g. *Calanus* spp. and *Pseudocalanus* spp.) and is not pronounced—if occurring at all—among the multiple maters (e.g. *Acartia* spp., *Centropages* spp., *Temora* spp.)

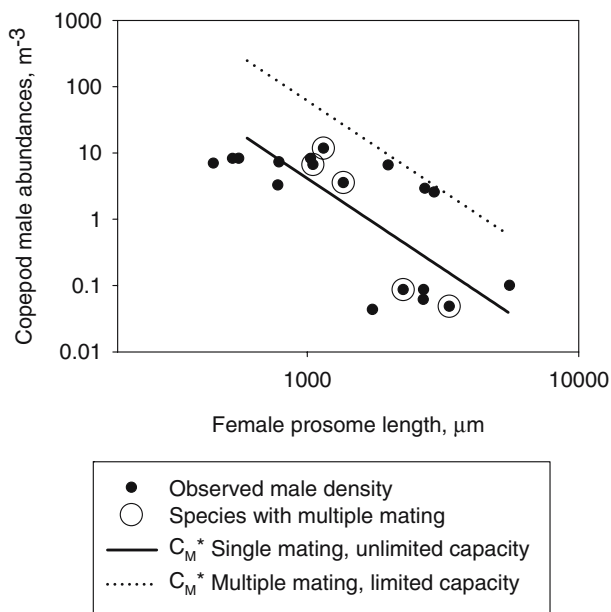


Fig. 7 Predicted critical concentrations and observed late winter concentrations of adult male copepods as a function of female size. Default parameters (Table 1) have been assumed for the predicted critical concentrations assuming two contrasting mating strategies, except that mate search volume rate β ($\text{m}^3 \text{ day}^{-1}$) was varied with female prosome length (L , mm) according to $\beta = 0.10 \times L^{2.73}$ (Kiørboe and Bagøien 2005). The plotted male abundances were provided by Peter Munk (Danish Institute for Fisheries Research) and were computed from depth-integrated samples taken by pump ($1,000 \text{ l min}^{-1}$) or Midwater Isak Kitt trawl from the surface to within 10 m of the bottom in the Skagerrak and NE North Sea during March–April, when copepod population abundances are at their seasonal minimum

(Mauchline 1998). Thus, without over-interpreting the above considerations and the observations in Fig. 7, they do suggest that copepod population sizes of ‘single-maters’ do not fall to below the critical density in the North Sea and, thus, typically can persist as self-maintained populations, whereas multiple-maters appear to rely on a different population survival mechanism than assumed in the analysis. One such mechanism could be survival as resting eggs in the sediment. Mauchline (1998) lists 47 species of marine pelagic copepods in which resting eggs have been found. All these species belong to the centropagoidea that require multiple mating. It is unknown whether all multiple maters can produce resting eggs, but the analysis would suggest so.

Conclusions

Two conditions—among several others—are important for the success of a species in a particular region, i.e. population survival during unproductive periods (e.g. winter), and rapid population growth when and where conditions are favorable. As demonstrated by the demographic analysis, fertilization limitation may constrain populations in both respects. A number of specific features (seminal receptacles, fecundity, resting eggs) appear to represent adaptations in pelagic copepods to reduce fertilization limitation. Two main strategies that are related to the presence or absence of seminal receptacles emerge from this analysis.

Those species where the females have seminal receptacles are particularly prone to population collapse, since they presumably lack the possibility of producing resting eggs and will have to survive low production seasons in the water column. The sufficiency of a single mating relaxes the need for females to encounter many males. For the males, the reproductive value of one mating is high and males with a behavior geared towards high encounter rates with females at the sacrifice of feeding and predator avoidance are favored. Females may remain fertile after just one or two matings and a more predator-safe behavior with less emphasis on mate encounter is favored. The consequently lower male/female sex ratio and the lower realised egg production rates in these species result in lower potential growth rates during favorable periods, but reduce the risk of population collapse.

The requirement for repeated mating in other copepods (Centropagoidea) implies higher fecundities than in single-maters and requires, apparently, survival of winter seasons as resting eggs in the sediment to make the strategy feasible. The higher fecundities allow higher potential population growth rates during favorable periods. Consequently these populations may grow faster and be released from constraints imposed by fertilization limitation and mate-search inefficiency, may rapidly colonize the pelagic in spring, and may build up larger population sizes during summer.

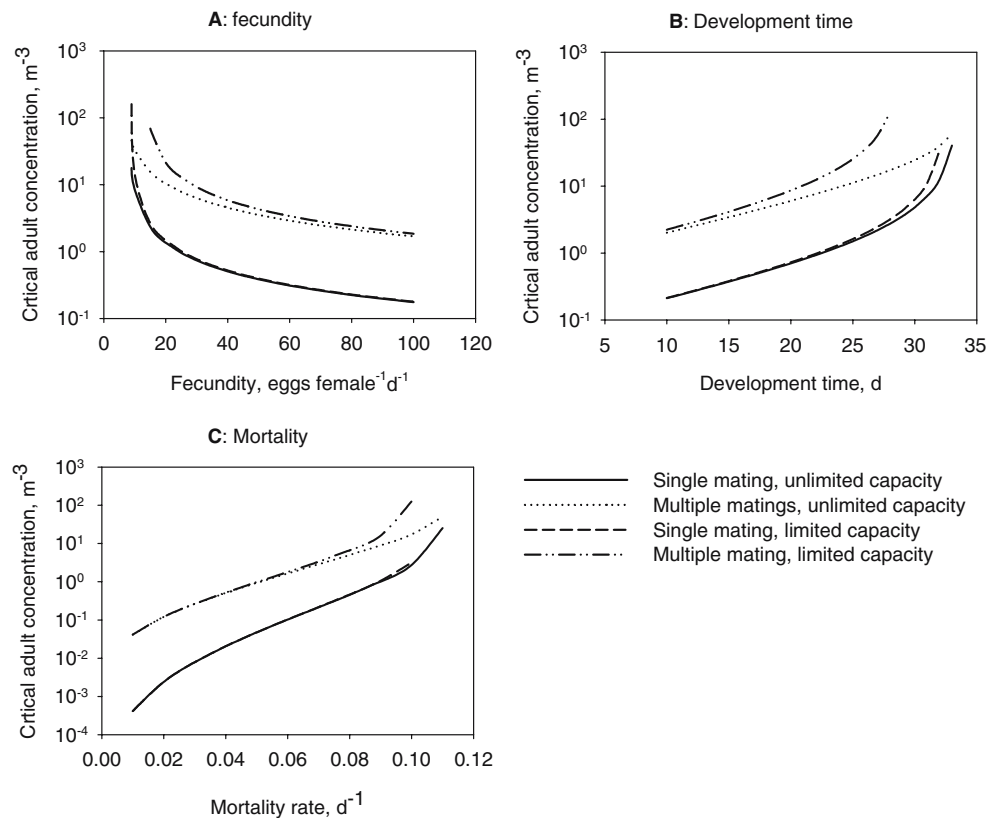


Fig. 8 Critical adult abundances as a function of mating behavior and **a** fecundity, **b** development time, and **c** mortality rate. Except for the parameters varying, default parameters (Table 1) have been

assumed and egg mortality has been assumed to be 1/10 of post hatch mortality

The demographic analysis and the field observations suggest that population sizes of pelagic copepods come close to critical sizes during certain periods of the year (Fig. 7), and definitely within the range where population growth becomes positively density dependent (Allee effect). Allee effects are rarely documented in marine populations (Gascoigne and Lipicus 2004), but pelagic copepods may offer an example. Positive density dependent population growth during winter implies that variations in winter densities would become amplified—not dampened—in the subsequent summer. This may explain why summer population sizes of pelagic copepods in the North Atlantic are more related to winter population sizes than to the immediate or recent growth conditions (Colebrook 1985; Smetacek and Pollehne 1986), and how the winter variations in population density can persist through many months and maybe several generations despite high ($\sim 0.1 \text{ day}^{-1}$) but variable mortality rates.

Acknowledgements The study was supported by a grant from the Danish National Science Research Council (21-01-0549). Kajsa Tønneson and Peter Munk gave permission to use their unpublished data, and Sigrid Schnack-Schiel supplied the original data from Schnack (1978). Ellen Toby, George Jackson and Andy Visser helped solve equations. Christian Jørgensen and Øyvind Fiksen provided essential comments to the manuscript. I thank them all.

References

- Ambler JW, Broadwater SA, Buskey EJ, Peterson JO (1996) Mating behaviour in swarms of *Dioithona oculata*. In: Lenz PH, Hartline DK, Purcell JE, MacMillan DL (eds) Zooplankton: sensory ecology and physiology. Gordon and Breach, Basel, pp 287–299
- Bagøien E, Kjørboe T (2005) Blind dating—mate finding in planktonic copepods. III. Hydromechanica communication in *Acartia tonsa*. Mar Ecol Prog Ser (in press)
- Berger I, Maier G (2001) The mating and reproductive biology of the freshwater planktonic calanoid copepod *Eudiaptomus gracilis*. Freshw Biol 46:787–794
- Blades PI (1977) Mating behavior of *Centropages typicus* (Copepoda: Calanoida). Mar Biol 40:57–64
- Buskey EJ (1998) Components of mating behaviour in planktonic copepods. J Mar Syst 15:13–21
- Charnov EL (1982) The theory of sex allocation. Princeton University Press, Princeton, p 355
- Colebrook JM (1985) Continuous plankton records: overwintering and annual fluctuations in the abundance of zooplankton. Mar Biol 84:261–265
- Conover RJ (1956) Oceanography of Long Island Sound, 1952–1954. VI. Biology of *Acartia clausi* and *A. tonsa*. Bull Bingham Oceanogr Coll 15:156–233
- Digby PSB (1951) The biology of the small planktonic copepods of Plymouth. J Mar Biol Assoc UK 29:393–438
- Durbin EG, Garrahan PT, Casas MC (2000) Abundance and distribution of *Calanus finmarchicus* in the Georges Bank during 1995 and 1996. ICES J Mar Sci 57:1664–1685

- Fisher RA (1930) The genetical theory of natural selection. Oxford University Press, London
- Flemming A (1985) Dimorphism and sex change in copepods of the family Calanidae. *Mar Biol* 88:273–294
- Gascoigne J, Lipcius RN (2004) Allee effects in marine systems. *Mar Ecol Prog Ser* 269:49–59
- Gauld DT (1957) Copulation in calanoid copepods. *Nature* 180:510
- Gerritsen J (1980) Sex and parthenogenesis in sparse populations. *Am Nat* 115:718–742
- Goswami SC (1978) Developmental stages, growth and sex ratio in *Pseudodiaptomus binghami* Sewell (Copepoda: Calanoida). *Indian J Mar Sci* 7:103–109
- Hayward TL (1981) Mating and the depth distribution of an oceanic copepod. *Limnol Oceanogr* 26:374–377
- Hirst AG, Kjørboe T (2002) Mortality of marine planktonic copepods: global rates and patterns. *Mar Ecol Prog Ser* 230:195–209
- Hopkins CCE (1982) The breeding biology of *Euchaete norvegica* (Boeck) (Copepoda, Calanoida) in Loch Etive, Scotland—assessment of breeding intensity in terms of seasonal cycles in the sex-ratio, spermatophore attachment, and egg-sac production. *J Exp Mar Biol Ecol* 60:91–102
- Huntley ME, Lopez MDG (1992) Temperature-dependent production of marine copepods—a global synthesis. *Am Nat* 140:201–242
- Ianora A, Dicarlo BS, Mascellaro P (1989) Reproductive biology of the planktonic copepod *Temora stylifera*. *Mar Biol* 101:187–197
- 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
- Irigoin X, Obermüller B, Head RN, Harris RP et al (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
- Katona SK (1975) Copulation in the copepod *Eurytemora affinis* (Poppe, 1880). *Crustaceana* 28:89–95
- Kjørboe T, Bagøien E (2005) Motility patterns and mate encounter rates in planktonic copepods. *Limnol Oceanogr* 50:1999–2007
- Kjørboe T, Nielsen TG (1994) Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. I. Copepods. *Limnol Oceanogr* 39:493–507
- Kjørboe T, Sabatini M (1994) Reproductive and life cycle strategies in egg-carrying cyclopoid and free-spawning calanoid copepods. *J Plankton Res* 16:1353–1366
- Kjørboe T, Sabatini M (1995) The scaling of fecundity, growth and development in planktonic copepods. *Mar Ecol Prog Ser* 120:285–298
- Kjørboe T, Bagøien E, Thygesen UH (2005) Blind dating—mate finding in planktonic copepods. II. The pheromone cloud of *Pseudocalanus elongatus*. *Mar Ecol Prog Ser* 300:117–128
- Kouwenberg JHM (1993) Sex ratio of calanoid copepods in relation to population composition in the northwestern Mediterranean. *Crustaceana* 64:281–299
- Lazzaretto FF, Battaglia B (1994) Reproductive behaviour in the harpacticoid copepod *Tigriopus fulvus*. *Hydrobiologia* 292/293:229–234
- Lee WY, McAlice BJ (1979) Seasonal succession and breeding cycles of three species of *Acartia* (Copepoda: Calanoida) in a Maine estuary. *Estuaries* 2:228–235
- Liang D, Uye S (1996a) Population dynamics and production of the planktonic copepods in a eutrophic inlet of the Inland Sea of Japan. III. *Acartia omori*. *Mar Biol* 125:109–117
- Liang D, Uye S (1996b) Population dynamics and production of the planktonic copepods in a eutrophic inlet of the Inland Sea of Japan. III. *Paracalanus* sp. *Mar Biol* 127:219–227
- Liang D, Uye S (1997) Seasonal reproductive biology of the egg-carrying calanoid copepod *Pseudodiaptomus marinus* in a eutrophic inlet of the Inland Sea of Japan. *Mar Biol* 128:409–414
- Maly EJ, Maly MP (1999) Body size and sexual size dimorphism in calanoid copepods. *Hydrobiologia* 391:173–179
- Marshall SM (1949) On the biology of the small copepods in Loch Striven. *J Mar Biol Assoc UK* 28:45–122
- Marshall SM, Orr AP (1952) On the biology of *Calanus finmarchicus*. VII. Factors affecting egg production. *J Mar Biol Assoc UK* 30:527–547
- Marshall SM, Nicholls AG, Orr AP (1934) On the biology of *Calanus finmarchicus*. V. Seasonal distribution, size, weight and chemical composition in Loch Striven in 1933, and their relation to the phytoplankton. *J Mar Biol Assoc UK* 19:793–827
- Mauchline J (1998) The biology of calanoid copepods. *Adv Mar Biol* 33:1–710
- Miller CB, Crain JA, Marcus NH (2005) Seasonal variation of male-type antennular setation in female *Calanus finmarchicus*. *Mar Ecol Prog Ser* 301:217–229
- Moraïtou-Apostolopoulou M (1972) Sex ratio in the pelagic copepods *Temora stylifera* Dana and *Centropages typicus* Krøyer. *J Exp Mar Biol Ecol* 8:83–87
- Ohtsuka S, Huys R (2001) Sexual dimorphism in calanoid copepods: morphology and function. *Hydrobiologia* 453/454:441–466
- Parrish KK, Wilson DF (1978) Fecundity studies on *Acartia tonsa* (Copepoda: Calanoida) in standardized culture. *Mar Biol* 46:65–81
- Schnack SB (1978) Seasonal change of zooplankton in Kiel Bay. III. Calanoid copepods. *Kiel Meeresforsch* 4:201–209
- Smetacek V, Pollehne F (1986) Nutrient cycling in pelagic systems: a reappraisal of the conceptual framework. *Ophelia* 26:401–428
- Smith SL, Lane PVZ (1985) Laboratory studies of the marine copepod *Centropages typicus*: egg production and development rates. *Mar Biol* 85:153–162
- Stephens PA, Sutherland WJ, Freckleton RP (1999) What is the Allee effect. *Oikos* 87:185–190
- Svensen C, Tande K (1999) Sex change and female dimorphism in *Calanus finmarchicus*. *Mar Ecol Prog Ser* 176:93–102
- Tsuda A, Miller CB (1998) Mate-finding behaviour in *Calanus marshallae* frost. *Phil Trans R Soc Lond B* 353:713–720
- Williamson CE, Butler NM (1987) Temperature, food and mate limitation of copepod reproductive rates: separating the effects of multiple hypotheses. *J Plankton Res* 9:821–836