Does predation control adult sex ratios and longevities in marine pelagic copepods?

Hirst, AG; Bonnet, D; Conway, DVP; Kiorboe, T

For additional information about this publication click this link.
http://qmro.qmul.ac.uk/jspui/handle/123456789/1142

Does predation control adult sex ratios and longevities in marine pelagic copepods?

A. G. Hirst,[a,*] D. Bonnet,[b] D. V. P. Conway,[c] and T. Kiørboe[d]

[a] School of Biological and Chemical Sciences, Queen Mary University of London, London, U.K.
[b] Université Montpellier 2, Laboratoire Ecosystèmes Lagunaires, Montpellier, France
[c] Marine Biological Association of the United Kingdom, Plymouth, Devon, U.K.
[d] National Institute for Aquatic Resources, Oceanography Section, Technical University of Denmark, Charlottenlund, Denmark

Abstract

We assess the causes of adult sex ratio skew in marine pelagic copepods by examining changes in these ratios between the juveniles and adults, sexual differences in juvenile stage durations, and mortality rates of adults in the field and laboratory (when free from predators). In the field, late copepodite stages (CIV and CV) commonly have sex ratios that are either not significantly different from equity (1 : 1), or slightly male biased. By contrast, in adults, these ratios are commonly significantly biased toward female dominance. Sex ratio skews are therefore primarily attributable to processes in adults. Members of the non-Diaptomoidea have especially skewed adult ratios; in the members Oithonidae and Clausocalanidae this is not generated from differences between male and female adult physiological longevity (i.e., laboratory longevity when free of predators). In the genera *Acartia*, *Oithona*, and *Pseudocalanus*, we estimate that predation mortality contributed ≥ 69% of the field mortality rate in adult males, whereas in *Acartia*, *Oithona*, and *Calanus* adult females, this is ≥ 36%. We conclude that (1) adult sex ratio skew in pelagic copepods is primarily due to differential mortality of the sexes in the adult stage and not in juveniles, (2) mortality rates of adult *Acartia*, *Pseudocalanus*, and *Oithona* are dominated by predation mortality rather than physiological longevity (except under extreme food limitation), and (3) in *Pseudocalanus* and *Oithona*, elevated mortality rates in adult males to females is predominantly due to higher predation on males. Our work demonstrates that we now need to develop a more comprehensive understanding of the importance of feeding preferences in predators.

Copepods have separate sexes, and commonly the ratio of abundance in field populations is strongly skewed, with adult females outnumbering males (Hirst and Kiørboe 2002; Kiørboe 2006). According to Fisher's principle, at the point sex is determined, the ratio of males to females is expected to be 1 : 1 (Fisher 1930) or skewed to the sex in which the female invested least in the embryo. Evidence for sex-based differences in investment in copepod embryos is lacking, yet adult sex ratios are often highly skewed. This inequality is important because the mating success is dependent on the sex ratio (Kiørboe 2006, 2008), and the availability and density of males to fertilize females might be a limiting factor to population growth (Kiørboe 2007). Mating success can profoundly influence population dynamics and species success—hence, the need to understand the dynamics of such processes.

Great insights have recently been made in describing the importance of the sex ratio in population dynamics and linking sex skew with reproductive attributes (Kiørboe 2006). Kiørboe (2006) found that copepods that lack seminal receptacles have a sex ratio closer to 1 : 1 than do families that possess seminal receptacles. Repeat mating is necessary in the former to allow for the continued production of fertilized embryos because they cannot store sperm. Species that lack seminal receptacles include those in the genera Oncaea, and members of the superfamily Centropagoidea [henceforth, we use the corrected named for this superfamily, Diaptomoidea (Boxshall 2004)]. Included in the Diaptomoidea are the families Acartiidae, Candaciidae, Centropagidae, Diaptomidae, Fosshagenii-dae, Parapontellidae, Pseudodiaptomidae, Sulcanidae, Temoridae, and Tortanidae. Although Oncaea is not in the Diaptomoidea, given its lack of sperm-storing ability, we group it together with Diaptomoidea in our analyses. Those families that can store sperm (henceforth referred to as non-Diaptomoidea) can produce fertile eggs for a long period (possibly a lifetime) from a single mating (Marshall and Orr 1952; Ohtsuka and Huys 2001). Kiørboe (2006) attributed the greater sexual skew in the single-mating non-Diaptomoidea to a more risky mate search strategy of males, making them more vulnerable to predation. This risky behavior is traded off against the relatively greater reward in finding and fertilizing a female. Many non-Diaptomoidea also have reduced feeding rates in the males, which results in shorter physiological longevity compared with females (i.e., in the absence of predators, males simply have shorter lives than females), and this has also been postulated as a controlling difference in the mortality of the different sexes and in driving the strong sex ratio skew (Kiørboe 2008; Ohman and Hsieh 2008). The importance of each of these mechanisms (i.e., predation mortality on males from riskier mating behavior vs. reduced longevity from low feeding rates) has never been critically or widely assessed in the marine plankton. We have a poor understanding of the causes of mortality in the plankton, and yet this is fundamental if we are to appreciate and model the dynamics of marine planktonic populations. In this paper, we use the opportunity that field sex ratios provide to gain insight into the causes of mortality in the dominant mesozooplankton, the copepods.

Males tend to mature faster than females, and a population in growth phase will have more males arriving

---

* Corresponding author: a.g.hirst@qmul.ac.uk

at the adult stage, which will push the sex ratio toward male dominance. Once recruitment has stopped the adult ratio may then swing to females if these have a greater longevity, if they arrive later given their slower development rates, or both. These factors add to the temporal variability of the sex ratio and, together with poor count statistics, have made the discernment of underlying critical factors determining the ratios more difficult to examine (Kiørboe 2006). Other causes of a biased sex ratio might include environmental sex determination (ESD), wherein the environment alters the sex ratio (Irigoien et al. 2000). This has been demonstrated in the harpacticoid copepod *Tigriopus californicus* as a result of the temperature experienced during development and was shown not to be the result of differential mortality of the sexes (Voordouw and Anholt 2002). Sex (ratio) might therefore not be determined genetically in some harpacticoid copepods but, rather, be altered during the developmental process. By contrast, in the calanoid copepod *Acartia*, a chromosomal mechanism of sex determination has been reported, with males being heterogametic (XO) and females homogametic (XX) (Goswami and Goswami 1974; Lecher et al. 1995). A variety of mechanisms to explain ESD, which could act in different parts of the developmental life history, have been proposed (Gusmão and McKinnon 2009). Given these issues, we need to determine in which stage(s) the sex ratio skew arises in pelagic copepods.

Identifying where sex ratio skew arises (i.e., in juvenile or adult stages) will allow the likely causes of this skew to be identified. For example, equitable sex ratios in juveniles would suggest that these are unlikely to be biased at the point of inception. It will also give greater insight into ESD. Males and females of many genera are distinguishable morphologically in the late copepodite stages (e.g., from CIII or CIV), usually on the basis of segmentation, leg development, or the genital segment (Conway 2006). By contrast, in the Calanidae (e.g., *Calanus*, *Neocalanus*) no morphological sign of the sex is very reliable until the gonad rudiment gets well advanced on the route from anlagen to testis or ovary, typically in the CV stage. Unfortunately, there are very few accounts of simultaneous assessment of sex ratios across both juvenile and adult stages of copepods in the field. Males typically have shorter stage duration in CIV and CV than do females, which affects the apparent sex ratio. By quantifying these differences in development time, this cause of bias can in effect be removed.

In this paper we address the following questions: (1) Do juvenile sex ratios on average diverge from 1 : 1 in the field? (2) Can juvenile ratios explain adult sex ratio skews or do differential mortality (or longevity) rates of the sexes in the adults need to be invoked? (3) What are the relative contributions of physiological longevity and predation mortality to adult field mortality rates and adult sex ratios?

Methods

We compiled data on sex-specific stage duration and field mortality rates in copepods, and field data on abundance sex ratios in juvenile and adult stages from the published literature. We also made additional measurements where data are lacking. All data are available in electronic form as supplementary appendices.

Stage durations—That stage duration can vary between males and females, with males often having shorter durations, is well documented (Landry 1975; Uye et al. 1983; Jerling and Wooldridge 1991). Other than the seasonal effects that this might have on adult sex ratio skew, such differences also lead to skew in seasonally averaged sex ratios of juvenile stages because the sex with shorter stage durations will present comparatively reduced stage abundance, even with equal recruitment of males and females. We therefore need an assessment of juvenile stage duration differences between the sexes to make corrections. We compiled stage duration data from the published literature and only included measurements of stage durations when made under identical laboratory conditions for both sexes of a species and when animals were followed through the full stage (e.g., using median development times). Stage durations that were determined by use of the inverse of the molt rates of wild-caught animals were not included here because age-within-stages variation as a result of mortality (Hirst et al. 2005) or a cohort structure (Miller et al. 1984) can severely bias estimates of stage duration. Data were included from the following sources: Landry 1975, 1983; Uye et al. 1983; Kimoto et al. 1986; Jerling and Wooldridge 1991; Escribano and McLaren 1992; Ban 1994; Lee et al. 2003; Devreker et al. 2007.

Sex ratios across stages—We compiled data on the abundance ratios of the sexes across consecutive stages from juveniles to adults in marine epipelagic copepods as determined in the field. Sex ratios are binomial functions and, as such, they can be hampered by poor count statistics. To reduce the effects of poor count statistics and seasonal effects, we averaged data in studies in which multiple samples had been made over an annual cycle. Males and females commonly have distinctly different vertical distributions. We therefore included data only where sampling was designed to collect the entire population in an unbiased way. Our data are confined to studies on epipelagic species (Grainger 1959; Ferrari and Hayek 1990; Liang and Uye 1996a,b; 1997). Data from Crain and Miller (2000) for *Calanus finmarchicus* are also included; for CVs these were sexed by examining the development of ovaries and testes on older animals within this stage.

Our synthesis revealed that relatively few studies have quantitatively assessed sex ratio across juvenile and adult stages; therefore, we made additional measurements. From February 2008 to January 2009 we sampled at the L4 station in the English Channel 10 nm southwest of Plymouth, U.K. (50°15′N, 04°13′W). A Working Package 2 (WP2) net with a mouth open area of 0.25 m² and mesh size of 200 μm was hauled vertically from close to the sea floor (water depth $\sim$ 55 m) to the surface. Samples were preserved and stored in 5% buffered formaldehyde. Approximately 150 randomly picked copepodite stages (CIV–adult) of each of the species *Paracalanus parvus*, *Pseudocalanus elongatus*, and *Acartia clausi* were initially

Table 1. Age survival parameters as determined by fitting a four-parameter logistic equation (Eq. 1) to experimental adult survival data for *Acartia clausi*. Incubation conditions for male and female copepods given, *see* text for further details.

Diaptomoidea *Acartia* species (sex)	Equation			Incubation conditions	
	α (SE)	T_{50} (SE)	r^2	Temperature (°C)	Food concentration (μg C L^{-1})
A. clausi (male)	3.83(0.36)	11.19(0.29)	0.993	20.0	1000
A. clausi (female)	2.32(0.23)	10.14(0.43)	0.992	20.0	1000
A. clausi (male)	17.95(0.83)	6.32(0.02)	1.000	20.0	0(starved)
A. clausi (female)	5.20(1.14)	6.62(0.33)	0.996	20.0	0(starved)

staged, sexed (according to Conway 2006), and enumerated. Additional individuals of each species were randomly picked so that at least 50 individuals of each stage in each species were examined. Sex ratios in each stage were then calculated from the total counts. In early 2008 *Acartia* was too rare to meet our counting standards and the results therefore discounted. In late 2008 and early 2009, large numbers of *Clausocalanus* and *Ctenocalanus* were present, making it problematic to accurately identify *Pseudocalanus* specimens; in these cases, sex ratio estimates were again not completed.

The proportion of males ($P_{i\text{male}}$) in stage i was determined as:

$$P_{i\text{male}} = \frac{A_{i\text{male}}}{A_{i\text{male}} + A_{i\text{female}}} \qquad (1)$$

where $A_{i\text{male}}$ and $A_{i\text{female}}$ are the abundance of females and males, respectively. The proportion female ($P_{i\text{female}}$) = 1 − $P_{i\text{male}}$. To account for differences in duration in the juvenile stages, the proportion of males was corrected with the use of stage-specific ratios of the duration of males to females (R_i). For CVI and CV, these ratios were estimated from our synthesis to be 0.75 and 0.80, respectively (*see* Fig. 1), and the duration-corrected proportion of males ($P_{i\text{male\_corrected}}$) is then

$$P_{i\text{male\_corrected}} = \frac{P_{i\text{male}}/R_i}{(P_{i\text{male}}/R_i) + P_{i\text{female}}} \qquad (2)$$

Stage-specific male proportions were tested to determine whether they were significantly different from 0.5 (i.e., equitable sex ratios) using one-sample *t*-tests.

Adult longevity under laboratory conditions—To quantify adult physiological longevity (i.e., longevity when free from predation), we compiled data on male and female adult longevity in the laboratory from published accounts. The initial search was based on the compilation of Hirst and Kiørboe (2002). The references they used were revisited, male and female data were compiled separately, and additional values from a more extensive and up-to-date search of the literature were added. Values for fed animals were separated from those under starved conditions. Temperature of incubation, the type of longevity measurement (e.g., mean, maximum, time to 50% dead), and the feeding conditions (cell types and concentrations) were included in the synthesis. Much of the data are from wild-collected adults of unknown age, which might therefore underestimate the full longevity of the adult; no corrections

were made for this. We also included our own data (*see* below), as well as data on six species of copepods (T. Kiørboe unpubl.) that were all obtained with copepods that had matured in the laboratory and thus were of known age. The data set contains 275 measurements, including the genera *Pseudocalanus*, *Centropages*, *Calanus*, *Acartia*, *Temora*, *Paracalanus*, *Calanoides*, *Triconia*, *Pseudodiaptomus*, *Eucalanus*, *Euterpina*, *Eurytemora*, *Oithona*, and *Oncaea*.

To supplement the data on adult longevity and to better define the age–survival relationship, in that it affects the mathematics of the relationship between physiological and total (field) longevity, we performed age–survival experiments for adult *A. clausi* as follows. Copepods were collected with gentle horizontal tows of a 200-μm mesh net (with solid cod end with filtering window) in coastal waters off Sète, France, in the Mediterranean in July 2009. Stage IV copepodites were sorted under binocular microscopes in a temperature-controlled room set at surface water temperature (20°C ± 0.5°C) and incubated individually in 40-mL plastic tubes. We initially incubated 300 animals. Phytoplankton (*Dunaliella tertiolecta*) was supplied at a concentration of 1000 μg C L^{-1}. Every other day, one third of the water in each container was replaced with fresh algal suspension, and every 8 d, the entire contents were changed. The stage of each animal was checked daily, and the day of molting to adulthood was noted. The viability of each adult was then determined each day, and the date of death was recorded. The longevity of each animal was therefore recorded from the point of molting to adult to the day it was found dead.

To determine the longevity of animals when starved, CV animals were fed in the same way as described above. Once an animal molted to adult, it was incubated in 0.25-μm filtered seawater, and filtered water was changed at the same frequency as described above.

A logistic curve was used to describe the fraction of animals surviving (S) as a function of age since molting to adult (t, days) as:

$$S = \frac{1}{1 + (t/T_{50})^{\alpha}} \qquad (3)$$

Where T_{50} is age (days) to which 50% of the animals survive, and α is a measure of the steepness of the curve (Table 1).

Adult mortality in the field—We compiled data on the field mortality rates of adult (or CV–adult) males and females from the literature (β_{field}). Ideally, we would just
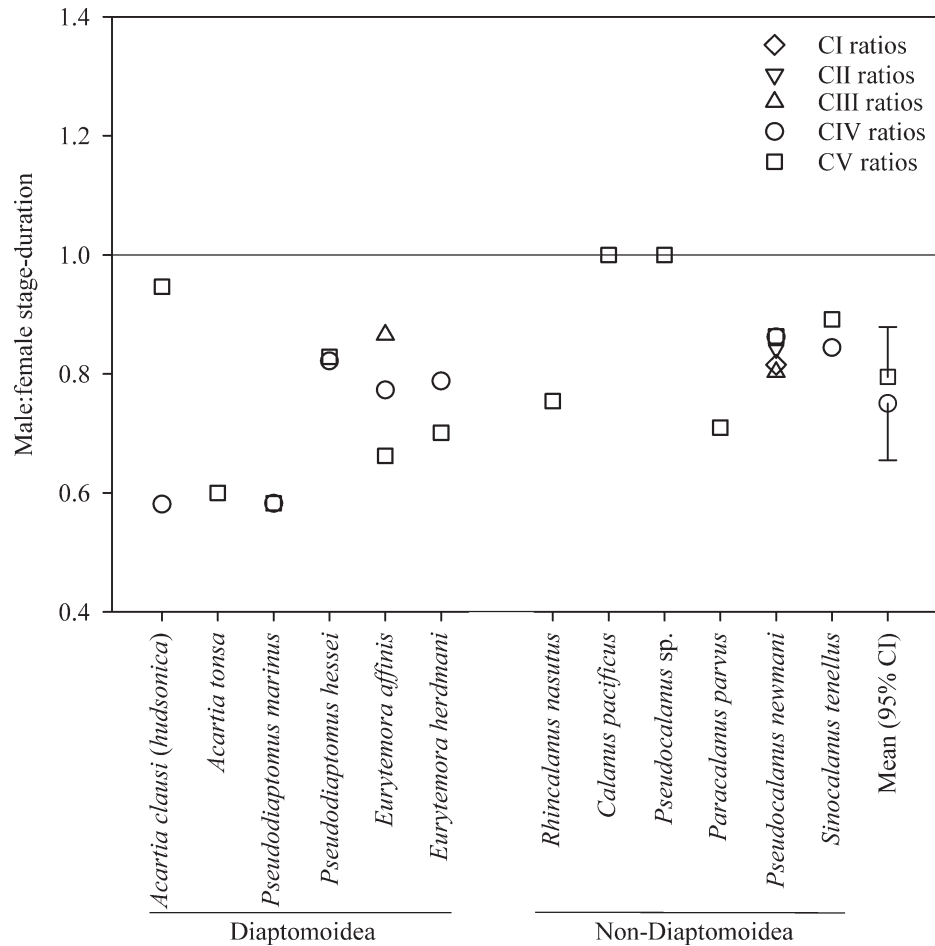
Fig. 1. Laboratory stage durations of male to female for a range of species. When more than one value has been determined (e.g., durations measured at more than one temperature), a simple arithmetic mean of each of the male to female durations is determined and plotted here. Averages across all species for the CIV and CV juvenile stages are indicted (error bars give ± 95% confidence intervals).

include adult mortality, but most data are for the stage pair because vertical methods can typically only be resolved at this level. We discuss the implications of this later. We focused our efforts on the four genera that dominate such estimates: *Acartia*, *Calanus*, *Oithona*, and *Pseudocalanus*. Water column temperatures for each mortality estimate were included in the synthesis and mortality rates standardizing to 15°C with a Q_{10} of 2.0 (Hirst and Kiørboe 2002). Mortality data were included for *Oithona similis* (Hirst and Ward 2008), *Calanus helgolandicus* (Hirst et al. 2007), *Pseudocalanus newmani* (Ohman and Wood 1996), *Acartia fancetti* (Kimmerer and McKinnon 1987), *A. clausi* (*husdonica*) (Landry 1978), and *Acartia californiensis* (Johnson 1981).

Results

Stage durations—Where the sexes have been separated (typically from the CIV stage), juvenile males typically have shorter stage duration than the females (Fig. 1), with the duration ratios of males commonly being between 0.7 and 0.9 times those of the females. Only in 2 of 23 comparisons

do males have stage duration equal to females (for CV in *Calanus pacificus* and *Pseudocalanus* sp.). The ratios of male to female durations for Diaptomoidea and non-Diaptomoidea broadly overlap and were merged. The mean male to female stage duration ratios are 0.75 in CIV (± 0.095, 95% CI) and 0.80 in CV (± 0.084, 95% CI) (Fig. 1). These mean values are used in subsequent analyses to remove the effect of sex-specific differences in stage durations on the field sex ratios.

Sex ratio across stages—Field data on sex ratios across consecutive stages for various species are given in Fig. 2. This includes the data collected over an annual cycle at L4 off Plymouth (*see* Fig. 3). Sex ratios vary a great deal between locations and through seasons, as is observable in the wide scatter of grey lines that link sex ratios across stages on any one sampling point (Fig. 2). The pattern in average sex ratios is clear, with the sex ratios across juvenile stages almost always being either not significantly different from equitable (i.e., male proportion = 0.5) or with male bias. Correcting juvenile stages for differences in the duration of males and females makes only minor differ-
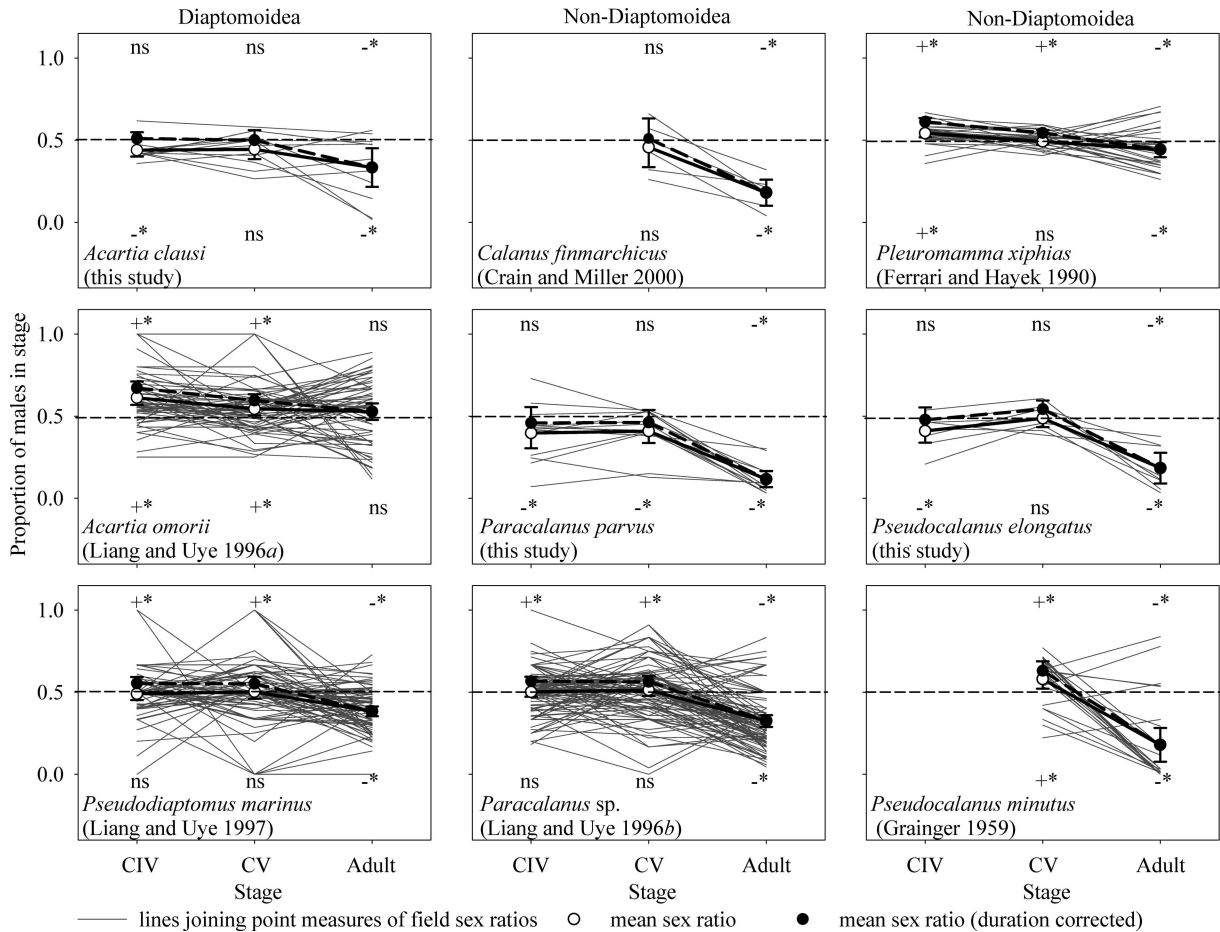
Fig. 2. Proportion in each stage that are male [male abundance/(male abundance + female abundance)] as derived from field abundances. Each thin grey line joins data simultaneously collected at a single sampling event in a study. Mean values are given for each stage (open circles, joined by heavy solid line) and after correcting for the different stage duration of juvenile males and females (filled circles, joined by heavy dashed lines). Error bars give ± 95% confidence intervals. Asterisks denotes where the male proportion is significantly different from 0.5, with a plus sign when higher and a minus sign when lower; ns indicates not significant. Those results for duration-corrected abundances are at the top of each graph; those for non-corrected abundances at the bottom.

ences to the pattern of changes in sex ratio across stages and does not alter the general conclusion; average sex ratios are most commonly near equitable (i.e., in the duration-corrected CV stage, the male proportion is not significantly different from 0.5 in *A. clausi*, *Pseudodiamptomus marinus*, *C. finmarchicus*, *Paracalanus* sp., *Pleuromamma xiphias*, and *P. elongatus*), with male domination in the remaining juveniles (i.e., *Acartia omorii*, *P. parvus*, and *Pseudocalanus minutus*). By contrast, sex ratios in adults are significantly biased toward females (as assessed from a one-sample *t*-test comparison against a value of 0.5, with significance set at $p < 0.05$) in all but one of the cases we tested (*A. omori*; *see* Fig. 2). In four of the nine cases examined here, the proportion of males is ~ 0.5 in CV but < 0.25 in adults. Variation in sex ratio among the three species examined in the English Channel showed no consistent seasonal pattern (Fig. 3).

Adult longevity—Data for adult longevity are separated into male and female and into Diaptomoidea (including *Oncaea*) and non-Diaptomoidea. Adult longevities from fed laboratory investigations expressed as a function of

temperature (Fig. 4) show significant ($p < 0.05$) negative relationships (i.e., longevity declines as temperature increases) in the case of females of non-Diaptomoidea and Diaptomoidea, and for males of the Diaptomoidea. The regression through the females and males of the Diapto-moidea have similar slopes of −0.034 and −0.025, respectively, which are somewhat lower than those of male and female non-Diaptomoidea, which is −0.011 for females and not significant in the case of males. Male and female Diaptomoidea have similar physiological longevities. Comparing slopes and intercepts with analysis of co-variance (ANCOVA), we find that males and females of the Diaptomoidea have intercepts and slopes that are not significantly (ns) different from one another ($p > 0.05$, ns). In the non-Diaptomoidea, males and females have slopes that are not significantly different ($p > 0.05$, ns) but intercepts that are ($p < 0.05$), confirming the shorter average lifespan of their males.

Mean longevities of fed and starved males and females corrected to 15°C are compared in Fig. 5. Fed females of the non-Diaptomoidea species live on average 34.2 d (± 5.17, 95% CI), whereas males have a significantly shorter
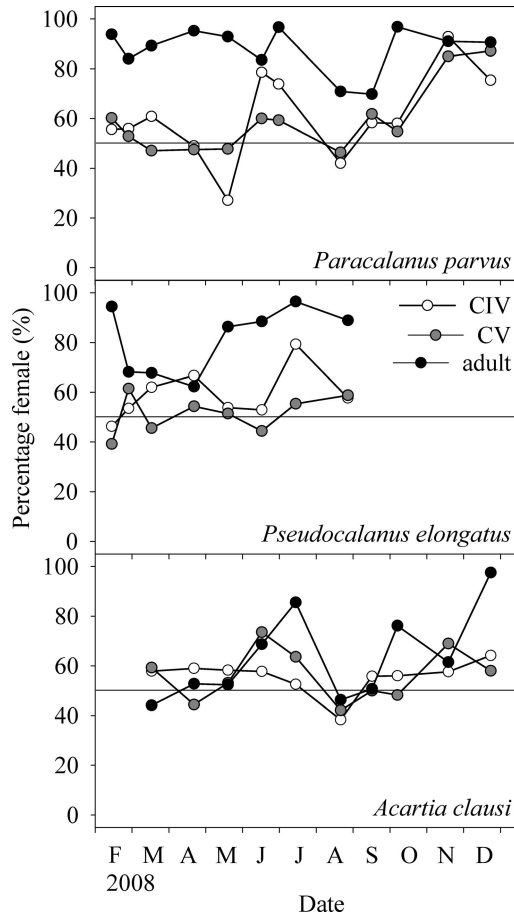
Fig. 3. Sex ratios across juvenile and adult stages (CIV–Adult) for three copepods collected over an annual cycle at the L4 station. Values in the juveniles have been corrected to allow for longer duration of females (*see* text for details).

life span of 19.0 d ($\pm$ 9.27, 95% CI). Female non-Diaptomoidea have a significantly greater life expectancy than do the females of the Diaptomoidea (*t*-test, $t = 3.30$, df = 153, $p = 0.001$). Reduced feeding rates in male non-Diaptomoidea might be the cause of their shorter life expectancy. By contrast, in the Diaptomoidea (in which the males do feed), the longevity is virtually identical in males and females at 24.1 ($\pm$ 2.59, 95% CI) and 21.6 d ($\pm$ 4.53, 95% CI), respectively. When starved, the mean longevity of female non-Diaptomoidea is reduced by 59% of the average fed value, to just 14.1 days ($\pm$ 2.10, 95% CI), which is significantly different from the fed value (*t*-test, $t = 7.02$, df = 132, $p < 0.001$). Unfortunately, data are insufficient to compare males between fed and starved conditions in the non-Diaptomoidea because we have data for only one species of the latter.

The age–survival curves for *A. clausi* males and females, both when fed and starved, are presented in Fig. 6. An exponential survival curve, indicative of age-independent mortality, does not describe the data well, whereas a logistic curve well describes the male and female survival data when both fed and starved. This suggests that the mortality rate increases with age.

Figure 7 summarizes laboratory longevity and sex ratio observations from the field. Expected male : female sex ratios from laboratory observations were computed from longevity data as the ratio of male to female longevity. Field sex ratios are much more female biased in the non-Diaptomoidea families Oithonidae and Clausocalanidae than those based on laboratory longevities, suggesting in these cases that physiology alone cannot explain the sex-differentiated mortalities in the field and that males have higher mortality rates than females from causes other than physiology.

Discussion

We have data on nine species in which sex ratios are tracked across juvenile to adult stages (Figs. 2, 3). Although sex ratios are highly variable both seasonally and spatially, the average values demonstrate clearly where sex ratio biases are predominantly generated and how these change stage by stage. Average sex ratios are not usually highly skewed in the juvenile stages. In several cases, males dominate slightly before the adult stage. The male to female ratio typically then declines from the CV stage to adult; hence, we can attribute most sex ratio skew as a result of processes in the adult stage itself. The decline is slight in some species (*P. xiphias* and *A. omorii*) and dramatic in others; for example, in *P. parvus*, *P. elongatus*, *P. minutus*, and *C. finmarchicus*, the proportion of males in the stage more than halves between CV and adult. In both *P. parvus* and *P. minutus*, the proportion of males in CV is ~ 0.5 (once corrected for duration) but < 0.18 in the adults, a significant difference. In the species for which we have data, the adult skew is therefore primarily not attributable to sex ratio skew in juveniles (Fig. 2); consequently, we expect adult males to have greater mortality rates than females (be this from physiological limits on age or predation). If the sex ratios of juveniles recruiting to adult are 1 : 1, then adult sex ratios are estimates of the ratio of adult longevities and indicative of differences in mortalities between sexes.

Although we are in no way implying that intersex (sex change) and ESD are not important in early life stages, we find little evidence to suggest this is a major driver of the change we observe across the late stages (CV–adult). We found no evidence of intersex in *P. elongatus*, *A. clausi*, and *P. parvus* at L4. When late-stage copepodites change sex, this is typically demonstrated by morphological abnormalities of the genital segment and P5, and such indicators were never found in our sampling program at L4. Indeed, many field reports of intersex give occurrence as being in the low single-digit percentages (Hirst 1996; Gusmão and McKinnon 2009). An exception is Liang and Uye (1996*b*, pg. 226), who state that "Specimens with intersex characteristics were found in 12 [out of 85] samples for 2.5% to 23% of adult females"; their data are included in our Fig. 2. This observation might very slightly affect our results only in the very unlikely case that sex changes occurred between CV and the adult stage and that animals showing intersex were then assigned to being female (hence contributing to the sex ratio shift observed).
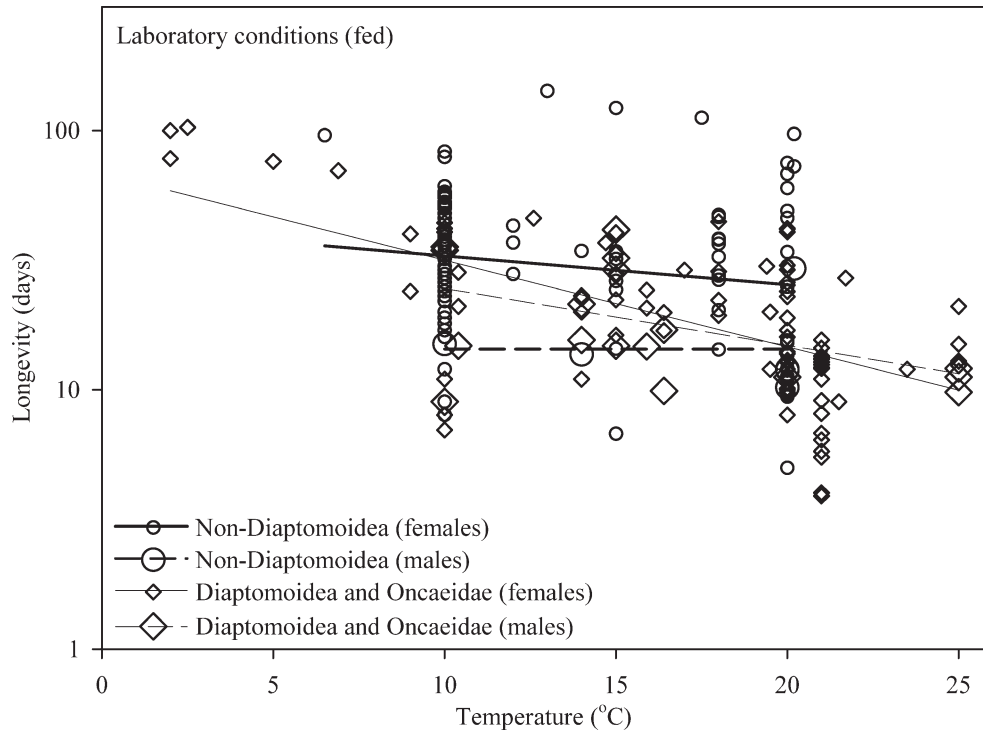
Fig. 4. Laboratory longevity (*P*, days) of adult females and males when fed, as a function of incubation temperature (*T*, °C). Animals are separated into Diaptomoidea (with inclusion of Oncaeidae) and the non-Diaptomoidea. Regressions are described by the equations: non-Diaptomoidea females: $\log P = -0.011T + 1.628$ ($r^2 = 0.027$, $n = 105$, $p < 0.05$); non-Diaptomoidea males: $\log P = -0.00003T + 1.158$ ($r^2 = 0.5 \times 10^{-6}$, $n = 6$, $p > 0.05$, ns); Diaptomoidea females: $\log P = -0.034T + 1.838$ ($r^2 = 0.343$, $n = 91$, $p < 0.001$); Diaptomoidea males: $\log P = -0.025T + 1.645$ ($r^2 = 0.245$, $n = 19$, $p < 0.05$).

Physiological mortality—In the Diaptomoidea, the male to female sex ratios derived from fed physiological longevities is 0.90, in the field the sex ratio is 0.73 (± 0.22, 95% CI; Fig. 7b). Field sex ratios suggest adult females have greater life expectancy than males, but this is much more marked in many of the non-Diaptomoidea families. Sex ratios predicted from physiological longevity fall within the range of the field values in the Diaptomoidea genera (Fig. 7a), although in the Pseudodiaptomidae, the laboratory longevities suggest sex ratios at the very upper limit of the field values. By contrast, in the non-Diaptomoidea families Oithonidae and Clausocalanidae, field sex ratios are much more heavily skewed than physiological longevity differences can explain.

Many families within the non-Diaptomoidea have males with reduced or atrophied mouthparts and with lower feeding rates than the females. For example, in the Euchaetidae, all males appear to have atrophied mouth parts, whereas in Calanidae, Clausocalanidae, and Paracalanidae, only some genera or some species of some genera have atrophied mouth parts (G. Boxshall unpubl.). This lack of feeding might result in shortened life expectancy (physiological longevity) because reserves become exhausted, and this could explain differences in physiological longevity between the sexes. Indeed, this has been attributed as one of the causes of their greater sex ratio skew (Kiørboe 2006; Ohman and Hsieh 2008). Unfortu-

nately, data on longevity in males and females are still too insufficient across a range of non-Diaptomoidea families to make a widespread conclusion for this group. However, in the families in which we are able to examine this, Oithonidae and Clausocalanidae (Fig. 7), differences in physiological longevity are too small to explain the stronger sex skew of adults in the field.

Field mortality and sex ratio: role of predation—In the field, physiological mortality combines with all other mortality causes (disease, predation, parasites) to yield field mortality rates. In this paper, we make the assumption that the main cause after accounting for physiology (and the effect of food on physiological longevity) is predation. With knowledge of physiological mortality or longevity and estimates of field mortality, it is possible to estimate predation mortality (including all other sources of mortality in the field) for the adult stages. Our laboratory observations suggest that physiological mortality rate is not age independent but rather changes with age. Some species approach a near constant lifespan (i.e., individuals die at a common age, e.g., *A. clausi* under starved conditions; Fig. 7a). Indeed, the logistic curve is used here because it suggests a constant lifespan that is normally distributed around a mean. Data similar to those reported herein for six other species of pelagic copepods show similar and additional adult age–survival patterns, ranging from near
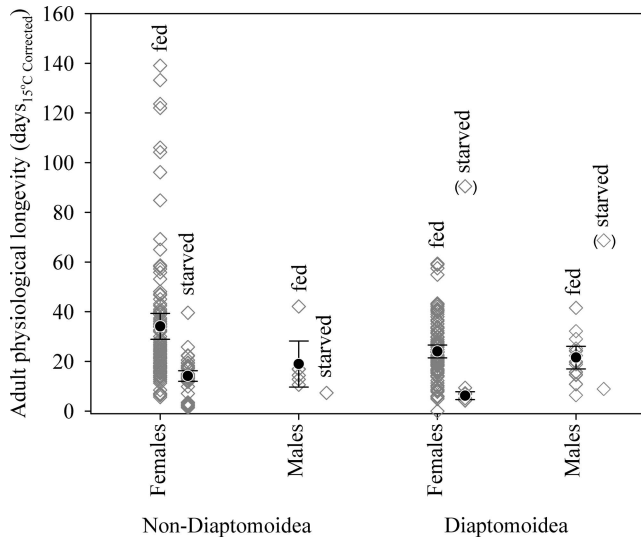
Fig. 5. Adult physiological longevities in the laboratory under fed and starved conditions. Data divided by sex and into Diaptomoidea (and Oncaeidae) and non-Diaptomoidea. Open diamonds give individual data points, closed circles give means (error bars denote ± 95% confidence interval). Means only determined when $n > 1$. All values have been corrected to 15°C assuming a Q_{10} of 0.5 (Hirst and Kiørboe 2002). The two values in brackets are for the Oncaeidae *Triconia canadensis* (from Nishibe 2005), which have been excluded from the means and confidence intervals.

age-independent physiological mortality over physiological mortality increasing with age to an almost constant life span (T. Kiørboe unpubl.). For the field data we have collected, we do not know what physiological mortality pattern would apply; therefore we have computed predation mortality under two extreme assumptions. Assuming age-independent predation mortality and a constant physiological lifespan (P_{lab}; i.e., a similar physiological lifespan across all individuals when free of predators) yields (Kiørboe 2008),

$$P_{field} = (1 - e^{-\beta_{pred}P_{lab}})/\beta_{pred} \cong \frac{1}{\beta_{field}} \qquad (4a)$$

where average longevity in the field (P_{field}) is approximated by the inverse average field mortality rate of adult stages. P_{lab} is the average physiological longevity in the laboratory (days). Alternatively, assuming age independence of both predation and physiological mortality yields (Hirst and Kiørboe 2002):

$$\beta_{pred} = \beta_{field} - (1/P_{lab}) \qquad (4b)$$

The resulting estimates of predation (β_{pred}) vs. physiological mortality rates for the four genera for which we have sex-specific field mortality rates are shown in Table 2 and Fig. 8.

Field mortality rates are generally higher or much higher than physiological mortality rates, and males have greater field mortality rates on average than the females. Applying the laboratory physiological longevities under fed conditions to the model shown in Eq. 4a, we estimate predation
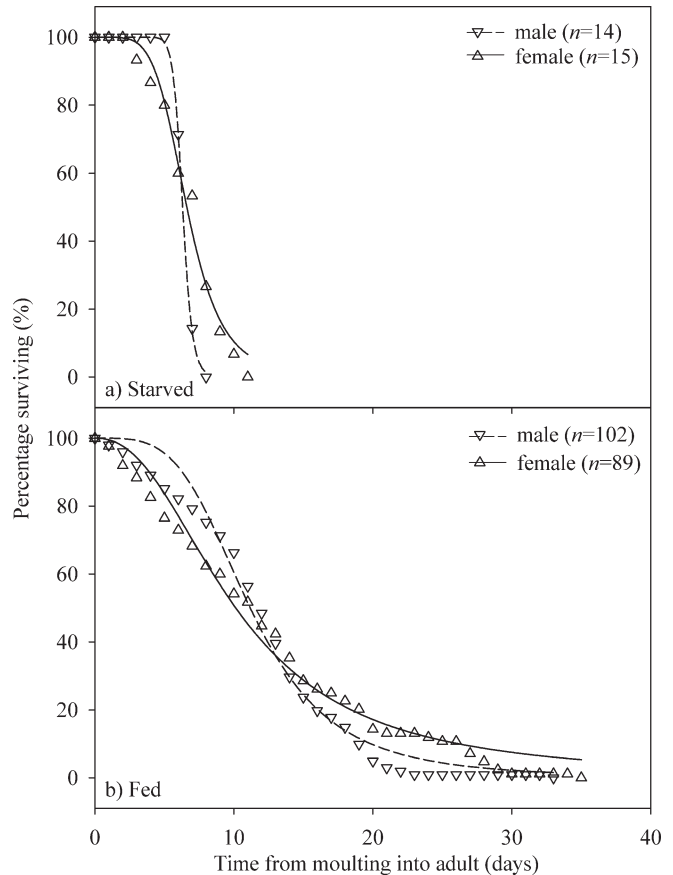

Fig. 6. *Acartia clausi* age survival curves of animals from the point they molt into the adult stage. Data are for (a) starved and (b) fed conditions (*see* text for details). *n* values denote the number of animals incubated.

mortality to make a major contribution to the total field mortality rates, accounting for ≥ 61% in male and female *Acartia*, *Pseudocalanus*, and *Oithona* and in the females of *Calanus*; indeed, in most of these cases, predation accounts for ≥ 95% of the field mortality (*see* Fig. 8; Table 2). This suggests that, in these cases, physiological longevity on average has a minor role in controlling field mortality (i.e., animals do not commonly die of old age). Applying starved longevities (as an extreme, i.e., over emphasizing the role of physiological longevity over predation mortality), we are able to estimate the minimum contribution of predation mortality to field rates. In these cases, predation mortality is estimated to account for 0% of total mortality in females of *Oithona* and *Pseudocalanus* but 73% in the females of both *Calanus* and *Acartia* (Table 2). In male *Oithona*, predation contributes an estimated 82% of the field mortality.

Applying the model shown in Eq. 4b to determine predation mortality rates, the contribution to total field mortality is reduced. In all cases examined, except *Pseudocalanus* females, the contribution of predation mortality to the total is ≥ 36%, and in five of the seven cases, this value is ≥ 69% (applying fed physiological longevities). In four of the six cases examined using starved physiological longevities, predation mortality was estimated to contribute ≥ 44% of the field mortality.
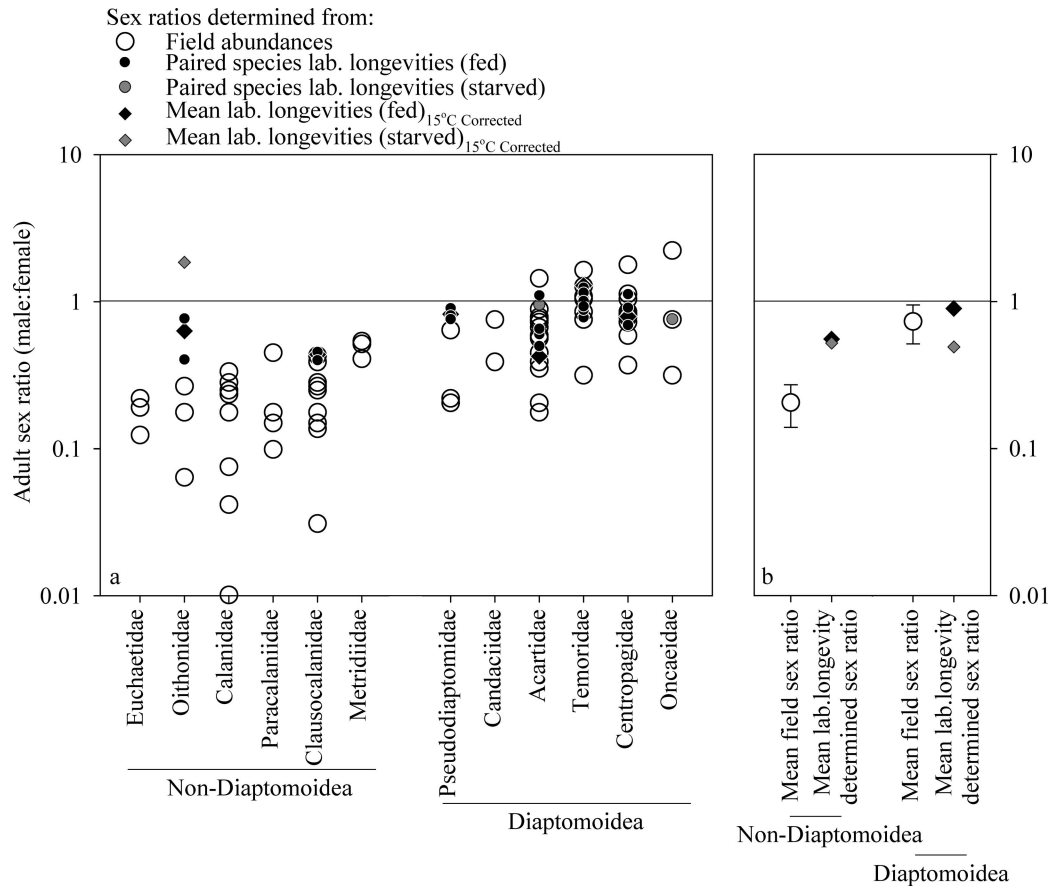
Fig. 7.   (a) Field adult sex ratios (data from Hirst and Kiørboe [2002] plot adapted from Kiørboe [2006]). Sex ratios from paired laboratory longevities in which males and females in a single study are kept under the same food and temperature conditions (fed—black diamonds, starved—grey diamonds). Sex ratios from family mean laboratory longevities (corrected to 15°C) of males and females (fed—black circles, starved—grey circle). (b) Mean field sex ratio (error bars give ± 95% confidence intervals) for Diaptomoidea and non-Diaptomoidea (from data given in panel a), together with sex ratios derived from the laboratory longevities.

Because we predominantly have used physiological longevities on animals collected from the wild in this study, whose exact age was unknown, this would have led to an underestimation of physiological longevity and, hence, an underestimation of the importance of predation mortality. Our results are therefore conservative with regard to the contribution of predation to field mortality. Many of our mortality rates that have been used in this analysis are for CV–adult stages combined, rather than adults alone, because many vertical life table approaches typically can only resolve mortality for a stage pair and not a single stage. If the CV mortality rates are comparable to the adult rates, then our results will be unaffected. If, however, the CV mortality rates are less than adult rates, we will have underestimated the adult mortality rates (by applying the CV–adult rates) and hence underestimated the total contribution made by predation mortality. Indeed, mortality rates in preceding stages (e.g., CIV–CV) are typically the same or lower than those across CV–adult (Johnson 1981; Ohman et al. 2004; Hirst and Ward 2008). Again, our results therefore appear to be conservative with regard to estimating the contribution of predation to the field mortality rate. In conclusion, with the species for which we have data, it appears likely that predation is important

to (and often dominates) adult mortality, except when food concentrations are very low, regardless of which model we apply to describe longevity (Eqs. 4a or 4b).

Field mortality rates are often higher in males than in females. In *Acartia* (the only Diaptomoidea examined), the male–female differences are not significant (*t*-test, $t = 0.69$, $df = 122$, $p = 0.49$), but the males of *Calanus*, *Oithona*, and *Pseudocalanus* have substantially greater mortality rates than the females (Ohman and Wood 1996; Hirst et al. 2007; Hirst and Ward 2008). In these species, the male mortality rates are higher than female rates by a factor of 2.3, 6.3, and 32, respectively. Our solution for the contribution that predation makes to adult mortality suggests that the higher rates of predation mortality in males over females are more marked in *Oithona* and *Pseudocalanus*, but not in *Acartia* (Fig. 8). This result suggests that the biased sex ratios in *Oithona* and *Pseudocalanus* could commonly be due to different mortalities between the sexes.

Adult *Oithona* males have mortality rates similar to those of male *Acartia* and *Calanus* (Fig. 8). By contrast, *Oithona* females have much lower rates than their own males and the females of *Calanus* and *Acartia*. The estimated predation mortality rate in males of *Oithona* is an order of magnitude greater than in the females. This

Table 2.　Average physiological longevity (P, days) in the laboratory (under fed and starved conditions) and field mortality rates (β_{field}, d^{-1}) of four copepod genera. These are combined according to Eqs. 4a and b to estimate predation mortality (β_{pred}, d^{-1}). The percentage that predation mortality contributes to the field mortality rate ($\beta_{pred}\%\beta_{field}$) is presented in the final column. In the final column, a negative value is returned in the case of starved female *Oithona* and *Pseudocalanus*; this is set at 0%. Ranges have been determined using the 95% confidence intervals of P and β_{field}. Physiological longevities and field mortality rates have been corrected to 15°C using Q_{10}s of 0.5 and 2.0, respectively (Hirst and Kiørboe 2002). Results are presented in Figs. 8 and 9.

| Species	Sex	Condition	P (d), mean (±95% CI)	β_{field} (d^{-1}), mean (±95% CI)	β_{pred} (d^{-1}), mean(range) 4a	4b	Mean $\beta_{pred}\%\beta_{field}$ 4a	4b
Diaptomoidea								
Acartia	Male	Fed	13.3(±2.3)	0.239(±0.049)	0.227(0.151–0.285)	0.164(0.099–0.224)	95	69
	Female	Fed	31.3(±4.7)	0.217(±0.042)	0.217(0.173–0.259)	0.185(0.137–0.231)	100	85
Acartia	Male	Starved	8.9(—)	0.239(±0.049)	0.198	0.127	83	53
	Female	Starved	8.3(±2.1)	0.217(±0.042)	0.159(0.027–0.237)	0.097(0.0137–0.163)	73	45
Non-diaptomoidea								
Calanus	Male	Fed	—	0.252(±0.014)	—	—	—	—
	Female	Fed	53.6(±22.1)	0.108(±0.005)	0.108(0.098–0.113)	0.089(0.071–0.100)	100	82
Oithona	Male	Fed	22.6(±12.8)	0.279(±0.076)	0.279(0.162–0.355)	0.235(0.101–0.327)	100	84
	Female	Fed	35.7(±16.5)	0.044(±0.021)	0.027(−0.077–0.063)	0.016(−0.029–0.046)	61	36
Pseudocalanus	Male	Fed	11.7(±2.1)	0.744(±0.107)	0.744(0.668–0.820)	0.659(0.533–0.779)	100	89
	Female	Fed	26.8(±3.3)	0.023(±0.007)	0.023(−0.031–0.059)	−0.014(−0.266–0.003)	100	0
Calanus	Male	Starved	—	0.252(±0.014)	—	—	—	—
	Female	Starved	16.6(±1.5)	0.108(±0.005)	0.079(0.064–0.091)	0.048(0.037–0.058)	73	44
Oithona	Male	Starved	7.4(—)	0.279(±0.076)	0.228	0.144	82	52
	Female	Starved	4.0(±2.7)	0.044(±0.021)	−0.712(−3.966–0.221)	−0.206(−0.746–0.083)	0	0
Pseudocalanus	Male	Starved	—	0.744(±0.107)	—	—	—	—
	Female	Starved	14.6(±1.7)	0.023(±0.007)	−0.130(−0.203–0.079)	−0.045(−0.062–0.031)	0	0
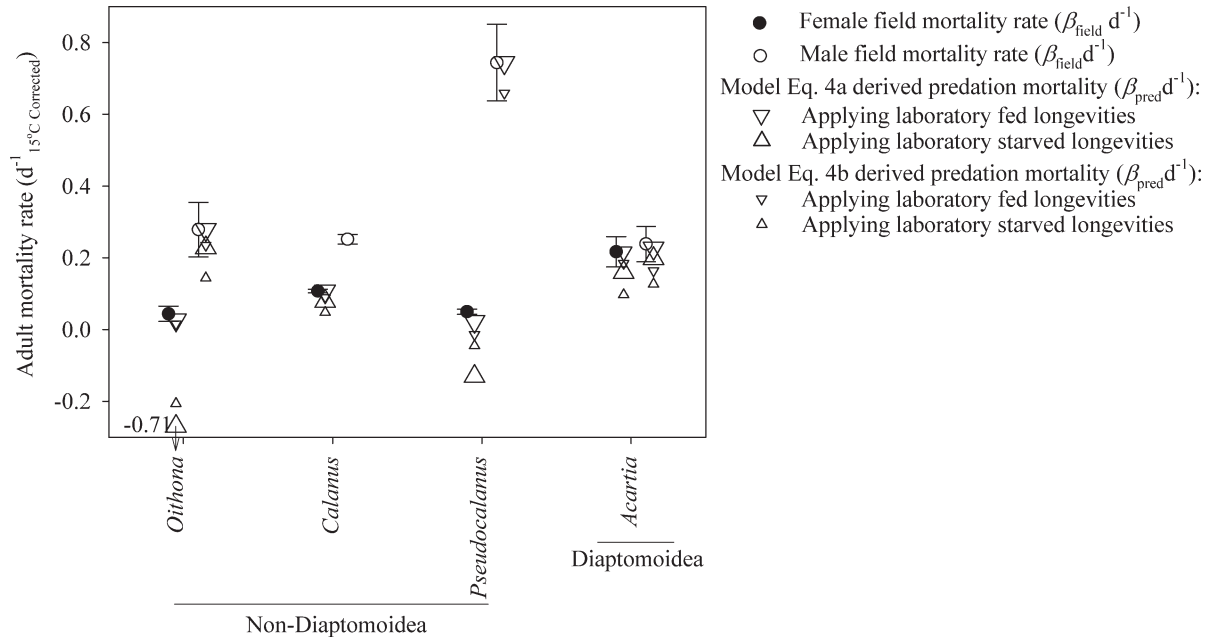
Fig. 8. Mean field mortality rates (β_{field}, d^{-1}) of adult female and male copepods corrected to 15°C (error bars give ± 95% confidence intervals) for the genera *Oithona*, *Calanus*, *Pseudocalanus*, and *Acartia*. Estimated predation mortality rates (β_{pred}, d^{-1}) are given when applying fed and starved laboratory physiological longevities to Eqs. 4a and b. Values as presented in Table 2.

suggests that *Oithona* females are able to avoid predation more effectively than in these two other genera while the males live a risky life. Differences in behavior between the sexes has been observed (Kiørboe 2008), *Oithona* females hang motionless for long periods and thereby reduce hydromechanical disturbance and encounter rates with predators (Eiane and Ohman 2004; Hirst and Ward 2008). *Pseudocalanus* males demonstrate especially high mortality rates, and our models suggest that predation contributes much of this (Figs. 8, 9). Kiørboe and Bagøien (2005) have observed that motility patterns are radically different between male and female *P. elongatus*. Females swim slowly along convoluted paths resembling a random walk, whereas males cruise along straight tracks, a motility pattern that increases the risk of encountering a predator. Furthermore, once a female has been encountered, the male engages in "courtship" behavior, during which he speeds around the female at very high velocity for several minutes (Kiørboe et al. 2005). This might expose the males to predators.

This leads us to next address whether the feeding rates and preferences of the predators of copepods tallies with higher predation mortality on the males. There is experimental evidence of sex-specific selection of copepods by predators in freshwater (Maly 1970; Hairston et al. 1983) and marine and brackish systems. Reviewing the marine and brackish literature, we find the following accounts. Landry (1978) observed that three-spine sticklebacks (*Gasterosteus aculeatus*), herring (*Clupea harengus*), and yellow-shiner perch (*Cymatogaster aggregata*) in Jakle's Lagoon, Washington, typically had more adult female *Acartia hudsonica* than males in their stomachs, whereas there was no consistent preference in smelt (*Hypomesus pretiosus*) (Landry 1978). Greater selection of females over

males was observed in Baltic herring (*C. harengus membras*) for *Eurytemora affinis*, *Acartia* sp., and *Temora longicornis*, but little difference between sexes was observed when feeding on *P. elongatus* (Viitasalo et al. 2001). Females of *Eurytemora* spp. were also found to be more frequent in the stomachs of Baltic herring (*C. harengus membras*) from Bothnia Bay (Sandstrom 1980), whereas no preference was found for either of the sexes of *Eurytemora* in sticklebacks (*G. aculeatus*; Vuorinen et al. 1983) or larval striped bass (*Morone saxatilis*; Meng and Orsi 1991). Johnson (1990) found greater selection for the females of adult *A. californiensis* and *A. clausi* over their respective males in northern anchovy (*Engraulis mordax mordax*), surf smelt (*H. pretiosus pretiosus*), and top smelt (*Atherinops affinis affinis*) collected in Yaquina Bay, Oregon. By contrast, males of *A. clausi* were eaten at three times the rate of females in *Sagitta elegans* (Alvarez-Cadena 1993), whereas Saito and Kiørboe (2001) found that males of *A. clausi* were cleared at a rate of up to an order of magnitude greater than similarly sized females by this chaetognath. Finally, there was no preference on the basis of prey sex in the scyphozoan *Chrysaora quinquecirrha* (Suchman and Sullivan 1998) when fed *Acartia tonsa*.

To summarize, although visual predation by fish is biased toward taking females in many cases (or no apparent preference), feeding by mechanoreception in *Sagitta* is strongly biased toward male consumption, with no clear preference in the single jellyfish study. So, does predation control adult sex ratios and longevities in marine pelagic copepods? The indirect approach we have adopted here suggests that sex skew arises predominantly in adults, that predation on the adults is a major contributor to field mortality, and that predation mortality is found to generate much of the sex ratio skew in
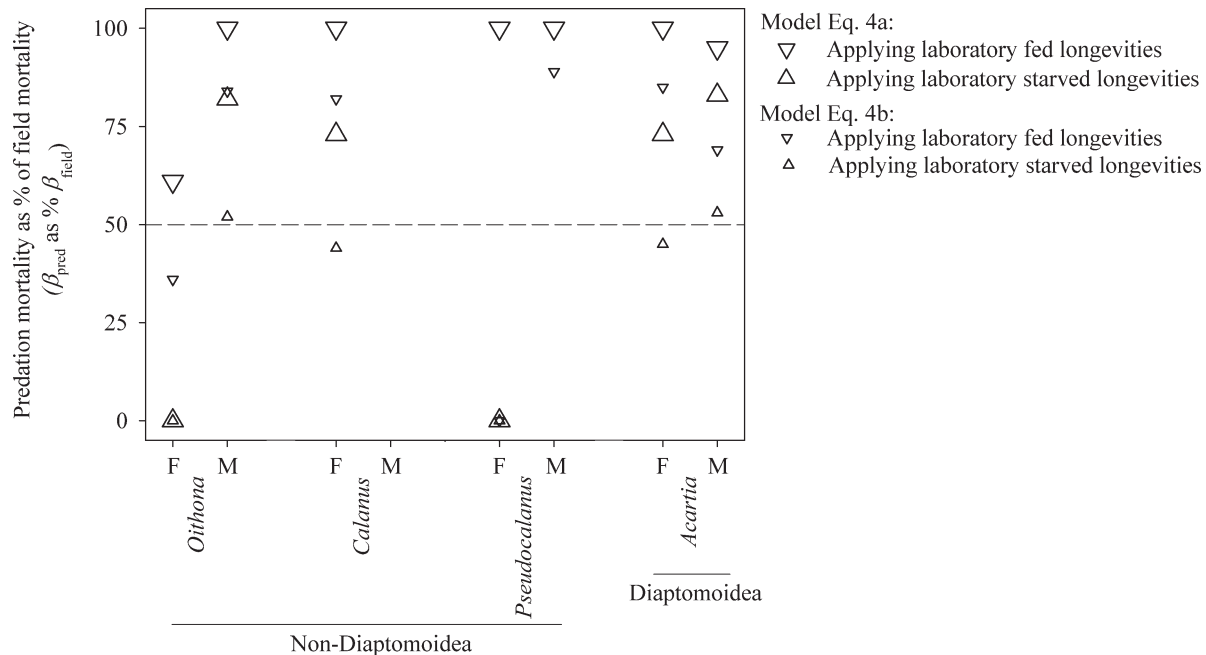
Fig. 9. Predation mortality as a percentage of field mortality of adult female and male copepods for the genera *Oithona*, *Calanus*, *Pseudocalanus*, and *Acartia*. Rates are determined applying field mortality estimates and mean physiological longevities under fed and starved conditions (all data first corrected to 15°C, *see* Methods) to Eqs. 4a and b. Values as presented in Table 2. Dashed horizontal line represents where predation mortality accounts for 50% of the total field mortality.

Pseudocalanus and *Oithona*. At present, however, we lack a comprehensive understanding of the relative importance of the different predator guilds in marine systems and the degree to which they differentially select male and female copepods. We need such data to unequivocally show that the males are indeed consumed at greater rates than the females. Quantitative data on cause of death, including predation, disease, and toxic diets (Avery et al. 2008), and novel methods to make such assessments (Tang et al. 2006) are a necessary next step if we are to make progress in what is a critical aspect of mesozooplankton population dynamics.

Sex ratios provide us with a unique opportunity to investigate sex-specific mortality and to link this with behavior and physiology. Although there are relatively few estimates of field mortality rates in copepods (*see* review of Hirst and Kiørboe 2002), there are a large number of adult sex ratio estimates. Because sex ratios are especially skewed in the families Euchaetidae, Oithonidae, and Calanidae (Fig. 7), these are excellent groups to next examine whether skewed field mortality rates are linked with asymmetric behavior and predation in the field (Tsuda and Miller 1998; Miller et al. 2005; Kiørboe 2008).

References

ÁLVAREZ-CADENA, J. N. 1993. Feeding of the chaetognath *Sagitta elegans* Verrill. Estuar. Coast. Shelf Sci. **36:** 195–206, doi:10.1006/ecss.1993.1013

AVERY, D., K. J. K. ALTLAND, AND H. G. DAM. 2008. Sex-related differential mortality of a marine copepod exposed to a toxic dinoflagellate. Limnol. Oceanogr. **53:** 2627–2636.

BAN, S. 1994. Effect of temperature and food concentration on post-embryonic development, egg production and adult body size of calanoid copepod *Eurytemora affinis*. J. Plankton Res. **16:** 721–735, doi:10.1093/plankt/16.6.721

BOXSHALL, G. A. 2004. An introduction to copepod diversity. The Ray Society.

CONWAY, D. V. P. 2006. Identification of the copepodite developmental stages of twenty-six North Atlantic copepods. Occasional Publications. Marine Biological Association of the United Kingdom 21, 27 p.

CRAIN, J. A., AND C. B. MILLER. 2000. Detection of sex and sex ratio in *Calanus finmarchicus* early stage fifth copepodites. ICES J. Mar. Sci. **57:** 1773–1779, doi:10.1006/jmsc.2000.0979

DEVREKER, D., S. SOUISSI, J. FORGET-LERAY, AND F. LEBOULENGER. 2007. Effects of salinity and temperature on the post-embryonic development of *Eurytemora affinis* (Copepoda: Calanoida) from the Seine estuary: A laboratory study. J. Plankton Res. **29:** i117–i133, doi:10.1093/plankt/fbl071

EIANE, K., AND M. D. OHMAN. 2004. Stage-specific mortality of *Calanus finmarchicus*, *Pseudocalanus elongatus* and *Oithona similis* on Fladen Ground, North Sea, during a spring bloom. Mar. Ecol. Prog. Ser. **268:** 183–193, doi:10.3354/meps268183

ESCRIBANO, R., AND I. A. MCLAREN. 1992. Testing hypotheses of exponential growth and size-dependent molting rates in two copepod species. Mar. Biol. **114:** 31–39.

FERRARI, F. D., AND L. A. C. HAYEK. 1990. Monthly distributions of sex and asymmetry in a looking-glass copepod, *Pleuromamma xiphias*, off Hawaii. J. Crustac. Biol. **10:** 114–127, doi:10.2307/1548674

FISHER, R. A. 1930. The genetical theory of natural selection. Oxford Univ. Press.

GOSWAMI, U., AND S. C. GOSWAMI. 1974. Cytotaxonomical studies on some Calanoid copepods. Nucleus 17: 109–113.

GRAINGER, E. H. 1959. The annual oceanographic cycle at Igloolik in the Canadian Arctic. 1. The zooplankton and physical and chemical observations. J. Fish. Res. Board Can. 16: 453–501.

GUSMÃO, L. F. M., AND A. D. MCKINNON. 2009. Sex ratios, intersexuality and sex change in copepods. J. Plankton Res. 31: 1101–1117, doi:10.1093/plankt/fbp059

HAIRSTON, N. G., JR., W. E. WALTON, AND K. T. LI. 1983. The causes and consequences of sex-specific mortality in a freshwater copepod. Limnol. Oceanogr. 28: 935–947, doi:10.4319/lo.1983.28.5.0935

HIRST, A. G. 1996. Towards a biological model of Southampton Water. Ph.D. thesis. Univ. of Southampton, United Kingdom.

———, D. BONNET, AND R. P. HARRIS. 2007. Seasonal dynamics and mortality rates of Calanus helgolandicus over two years at a station in the English Channel. Mar. Ecol. Prog. Ser. 340: 189–205, doi:10.3354/meps340189

———, AND T. KIØRBOE. 2002. Mortality of marine planktonic copepods: Global rates and patterns. Mar. Ecol. Prog. Ser. 230: 195–209, doi:10.3354/meps230195

———, W. T. PETERSON, AND P. ROTHERY. 2005. Errors in juvenile copepod growth rate estimates are widespread: Problems with the moult rate method. Mar. Ecol. Prog. Ser. 296: 263–279, doi:10.3354/meps296263

———, AND P. WARD. 2008. Spring mortality of the cyclopoid copepod Oithona similis in polar waters. Mar. Ecol. Prog. Ser. 372: 169–180, doi:10.3354/meps07694

IRIGOIEN, X., AND OTHERS. 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, doi:10.1006/jmsc.2000.0960

JERLING, H. L., AND T. H. WOOLDRIDGE. 1991. Population dynamics and estimates of production for the calanoid copepod Psuedodiaptomus hessei in a warm temperate estuary. Estuar. Coast. Shelf. Sci. 33: 121–135, doi:10.1016/0272-7714(91)90002-S

JOHNSON, J. K. 1981. Population dynamics and cohort persistence of Acartia californiensis (Copepoda: Calanoida) in Yaquina Bay, Oregon. Ph.D. thesis, Oregon State Univ.

KIMMERER, W. J., AND A. D. MCKINNON. 1987. Growth, mortality, and secondary production of the copepod Acartia tranteri in Westernport Bay, Australia. Limnol. Oceanogr. 32: 14–28, doi:10.4319/lo.1987.32.1.0014

KIMOTO, K., S.-I. UYE, AND T. ONBE. 1986. Growth characteristics of a brackish-water Calanoid copepod Sinocalanus tenellus in relation to temperature and salinity. Bull. Plankton Soc. Jpn. 33: 43–57.

KIØRBOE, T. 2006. Sex, sex-ratios, and the dynamics of pelagic copepod populations. Oecologia 148: 40–50, doi:10.1007/s00442-005-0346-3

———. 2007. Mate finding, mating, and population dynamics in a planktonic copepod Oithona davisae: There are too few males. Limnol. Oceanogr. 52: 1511–1522.

———. 2008. Optimal swimming strategies in mate-searching pelagic copepods. Oecologia 155: 179–192, doi:10.1007/s00442-007-0893-x

———, AND E. BAGØIEN. 2005. Motility patterns and mate encounter rates in planktonic copepods. Limnol. Oceanogr. 50: 1999–2007, doi:10.4319/lo.2005.50.6.1999

———, ———, AND U. H. THYGESEN. 2005. Blind dating–mate finding in planktonic copepods. II. The pheromone cloud of Pseudocalanus elongatus. Mar. Ecol. Prog. Ser. 300: 117–128, doi:10.3354/meps300117

LANDRY, M. 1975. The relationship between temperature and the development of life stages of the marine copepod Acartia clausi Giesbr. Limnol. Oceanogr. 20: 854–857, doi:10.4319/lo.1975.20.5.0854

LANDRY, M. R. 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, doi:10.1002/iroh.19780630106

———. 1983. The development of marine calanoid copepods with comments on the isochronal rule. Limnol. Oceanogr. 28: 614–624, doi:10.4319/lo.1983.28.4.0614

LECHER, P., D. DEFAYE, AND P. NOEL. 1995. Chromosomes and nuclear DNA of Crustacea. Invertebr. Reprod. Dev. 27: 85–114.

LEE, H.-W., S. BAN, T. IKEDA, AND T. MATSUISHI. 2003. Effect of temperature on development, growth and reproduction in the marine copepod Pseudocalanus newmani at satiating food conditions. J. Plankton Res. 25: 261–271, doi:10.1093/plankt/25.3.261

LIANG, D., AND S. UYE. 1996a. Population dynamics and production of the planktonic copepods in a eutrophic inlet of the Inland Sea of Japan. II. Acartia omorii. Mar. Biol. 125: 109–117, doi:10.1007/BF00350765

———, AND ———. 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, doi:10.1007/BF00942106

———, AND ———. 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, doi:10.1007/s002270050106

MALY, E. J. 1970. The influence of predation on the adult sex ratios of two copepod species. Limnol. Oceanogr. 15: 566–573, doi:10.4319/lo.1970.15.4.0566

MARSHALL, S. M., AND A. P. ORR. 1952. On the biology of Calanus finmarchicus. VII. Factors affecting egg production. J. Mar. Biol. Assoc. U. K. 30: 527–547, doi:10.1017/S0025315400012959

MENG, L., AND J. J. ORSI. 1991. Selective predation by larval striped bass on native and introduced copepods. Trans. Am. Fish. Soc. 120: 187–192, doi:10.1577/1548-8659(1991)120<0187:SPBLSB>2.3.CO;2

MILLER, C. B., J. A. CRAIN, AND N. H. MARCUS. 2005. Seasonal variation of male-type antennular setation in female Calanus finmarchicus. Mar. Ecol. Prog. Ser. 301: 217–229, doi:10.3354/meps301217

———, M. E. HUNTLEY, AND E. R. BROOKS. 1984. Post-collection molting rates of planktonic, marine copepods: Measurements, applications, problems. Limnol. Oceanogr. 29: 1274–1289, doi:10.4319/lo.1984.29.6.1274

NISHIBE, Y. 2005. The biology of the oncaeid copepods (Poecilostomatoida) in the Oyashio region, western subarctic Pacific: its community structure, vertical distribution, life cycle and metabolism. Ph.D. thesis. Univ. of Hokkaido, Japan.

OHMAN, M. D., K. EIANE, E. G. DURBIN, J. A. RUNGE, AND H.-J. HIRCHE. 2004. A comparative study of Calanus finmarchicus mortality patterns at five localities in the North Atlantic. ICES J. Mar. Sci. 61: 687–697, doi:10.1016/j.icesjms.2004.03.016

———, AND C.-H. HSIEH. 2008. Spatial differences in mortality of Calanus pacificus within the California Current system. J. Plankton Res. 30: 359–366, doi:10.1093/plankt/fbm110

———, AND S. N. WOOD. 1996. Mortality estimation for planktonic copepods: Pseudocalanus newmani in a temperate fjord. Limnol. Oceanogr. 41: 126–135, doi:10.4319/lo.1996.41.1.0126

OHTSUKA, S., AND R. HUYS. 2001. Sexual dimorphism in calanoid copepods: Morphology and function. Hydrobiologia **453/454:** 441–466, doi:10.1023/A:1013162605809

SAITO, H., AND T. KIØRBOE. 2001. Feeding rates in the chaetognath *Sagitta elegans*: Effects of prey size, prey swimming behaviour and small-scale turbulence. J. Plankton Res. **23:** 1385–1398, doi:10.1093/plankt/23.12.1385

SANDSTRÖM, O. 1980. Selective feeding by Baltic herring. Hydrobiologia **69:** 199–207, doi:10.1007/BF00046793

SUCHMAN, C. L., AND B. K. SULLIVAN. 2000. Effect of prey size and vulnerability of copepods to predation by the scyphomedusae *Aurelia aurita* and *Cyanea* sp. J. Plankton Res. **22:** 2289–2306.

TANG, K. W., C. S. FREUND, AND C. L. SCHWEITZER. 2006. Occurrence of copepod carcasses in the lower Chesapeake Bay and their decomposition by ambient microbes. Estuar. Coast. Shelf. Sci. **68:** 499–508, doi:10.1016/j.ecss.2006.02.021

TSUDA, A., AND C. B. MILLER. 1998. Mate-finding behaviour in *Calanus marshallae* Frost. Philos. Trans. R. Soc. Lond. B Biol. Sci. **353:** 713–720, doi:10.1098/rstb.1998.0237

UYE, S., Y. IWAI, AND S. KASAHARA. 1983. Growth and production of the inshore marine copepod *Pseudodiaptomus marinus* in the central part of the Inland Sea of Japan. Mar. Biol. **73:** 91–98, doi:10.1007/BF00396289

VIITASALO, M., J. FLINKMAN, AND M. VIHERLUOTO. 2001. Zooplanktivory in the Baltic Sea: A comparison of prey selectivity by *Clupea harengus* and *Mysis mixta*, with reference to prey escape reactions. Mar. Ecol. Prog. Ser. **216:** 191–200, doi:10.3354/meps216191

VOORDOUW, M. J., AND B. R. ANHOLT. 2002. Environmental sex determination in a splash pool copepod. Biol. J. Linn. Soc. **76:** 511–520, doi:10.1046/j.1095-8312.2002.00087.x

VUORINEN, I., M. RAJASILTA, AND J. SAIO. 1983. Selective predation and habitat shift in a copepod species—support for the predation hypothesis. Oecologia **59:** 62–64, doi:10.1007/BF00388073