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

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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 predominately 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 name for this superfamily, Diaptomoidea (Boxshall 2004)). Included in the Diaptomoidea are the families Acartiidae, Canducidae, Centropagidae, Diaptomidae, Fossi-
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 (Kiorboe 2006). Other causes of a biased sex ratio might include environmental sex determination (ESD), wherein the environment alters the sex ratio (Irigoin 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 ~ 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
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 ($P_{\text{male}}$) in stage $i$ was determined as:

$$P_{\text{male}} = \frac{A_{\text{male}}}{A_{\text{male}} + A_{\text{female}}}$$

where $A_{\text{male}}$ and $A_{\text{female}}$ are the abundance of females and males, respectively. The proportion female ($P_{\text{female}}$) = 1 - $P_{\text{male}}$. 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 ($P_{\text{male, corrected}}$) is then

$$P_{\text{male, corrected}} = \frac{P_{\text{male}}/R_i}{(P_{\text{male}}/R_i) + P_{\text{female}}}$$

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 Hirsh and Kierboe (2002). The references they used were revisited, 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 measured (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. Kierboe 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 copepodes 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 age since molting to adulthood 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:

$$S = \frac{1}{1 + (t/T_{50})^2}$$

Where $T_{50}$ is age (days) to which 50% of the animals survive, and $\alpha$ 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 ($\beta_{\text{field}}$). Ideally, we would just

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**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.**

<table>
<thead>
<tr>
<th>Diaptomoeidae <em>Acartia</em> species (sex)</th>
<th>Equation</th>
<th>Incubation conditions</th>
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<tbody>
<tr>
<td></td>
<td>$z$ (SE)</td>
<td>$T_{50}$ (SE)</td>
</tr>
<tr>
<td><em>A. clausi</em> (male)</td>
<td>3.83(0.36)</td>
<td>11.19(0.29)</td>
</tr>
<tr>
<td><em>A. clausi</em> (female)</td>
<td>2.32(0.23)</td>
<td>10.14(0.43)</td>
</tr>
<tr>
<td><em>A. clausi</em> (male)</td>
<td>17.95(0.83)</td>
<td>6.32(0.02)</td>
</tr>
<tr>
<td><em>A. clausi</em> (female)</td>
<td>5.20(1.14)</td>
<td>6.62(0.33)</td>
</tr>
</tbody>
</table>
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 Diaptomoeida and non-Diaptomoeida broadly overlap and were merged. The mean male to female stage duration ratios are 0.75 in CIV ($\pm 0.095$, 95% CI) and 0.80 in CV ($\pm 0.084$, 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-
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 \( \sim 0.5 \) 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 *Oncaeae*) 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 Diaptomoidea 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
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-Diaplomoidea 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 copepodes 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 (1996b, 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).
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 (Kjørboe 2006; Ohman and Hsieh 2008). Unfortunately, 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
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),

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

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):

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

The resulting estimates of predation ($\beta_{pred}$) 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 mortality to make a major contribution to the total field mortality rates, accounting for $\geq 61\%$ in male and female Acartia, Pseudocalanus, and Oithona and in the females of Calanus; indeed, in most of these cases, predation accounts for $\geq 95\%$ 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 $\approx 36\%$, and in five of the seven cases, this value is $\geq 69\%$ (applying fed physiological longevities). In four of the six cases examined using starved physiological longevities, predation mortality was estimated to contribute $\geq 44\%$ of the field mortality.
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 ($b_{\text{field}}$, d$^{-1}$) of four copepod genera. These are combined according to Eqs. 4a and b to estimate predation mortality ($b_{\text{pred}}$, d$^{-1}$). The percentage that predation mortality contributes to the field mortality rate ($\beta_{\text{pred}} \% b_{\text{field}}$) 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 $b_{\text{field}}$. Physiological longevities and field mortality rates have been corrected to 15°C using $Q_{10}$ of 0.5 and 2.0, respectively (Hirst and Kiørboe 2002). Results are presented in Figs. 8 and 9.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>Condition</th>
<th>$P$ (d), mean ($\pm$95% CI)</th>
<th>$b_{\text{field}}$ (d$^{-1}$), mean ($\pm$95% CI)</th>
<th>$b_{\text{pred}}$ (d$^{-1}$), mean(range)</th>
<th>Mean $\beta_{\text{pred}} % b_{\text{field}}$</th>
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<td>4a</td>
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<td>Diaptomoidea</td>
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<td></td>
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<td></td>
</tr>
<tr>
<td><em>Acartia</em></td>
<td>Male</td>
<td>Fed</td>
<td>13.3(±2.3)</td>
<td>0.239(±0.049)</td>
<td>0.227(0.151–0.285)</td>
<td>95</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td></td>
<td>31.3(±4.7)</td>
<td>0.217(±0.042)</td>
<td>0.217(0.173–0.259)</td>
<td>100</td>
</tr>
<tr>
<td><em>Acartia</em></td>
<td>Male</td>
<td>Starved</td>
<td>8.9(—)</td>
<td>0.239(±0.049)</td>
<td>0.198</td>
<td>83</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td></td>
<td>8.3(±2.1)</td>
<td>0.217(±0.042)</td>
<td>0.159(0.027–0.237)</td>
<td></td>
</tr>
<tr>
<td>Non-diaptomoidea</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Calanus</em></td>
<td>Male</td>
<td>Fed</td>
<td>53.6(±22.1)</td>
<td>0.108(±0.005)</td>
<td>0.108(0.098–0.113)</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td></td>
<td>22.6(±12.8)</td>
<td>0.279(±0.076)</td>
<td>0.279(0.162–0.355)</td>
<td>100</td>
</tr>
<tr>
<td><em>Oithona</em></td>
<td>Male</td>
<td>Fed</td>
<td>35.7(±16.5)</td>
<td>0.044(±0.021)</td>
<td>0.027(0.077–0.063)</td>
<td>61</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td></td>
<td>11.7(±2.1)</td>
<td>0.744(±0.107)</td>
<td>0.744(0.668–0.820)</td>
<td>100</td>
</tr>
<tr>
<td><em>Pseudocalanus</em></td>
<td>Male</td>
<td>Fed</td>
<td>26.8(±3.3)</td>
<td>0.023(±0.007)</td>
<td>0.023(0.031–0.059)</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>Starved</td>
<td>16.6(±1.5)</td>
<td>0.108(±0.005)</td>
<td>0.079(0.064–0.091)</td>
<td>73</td>
</tr>
<tr>
<td><em>Oithona</em></td>
<td>Male</td>
<td>Starved</td>
<td>7.4(—)</td>
<td>0.079(±0.005)</td>
<td>0.228</td>
<td>82</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td></td>
<td>4.0(±2.7)</td>
<td>0.044(±0.021)</td>
<td>−0.712(−3.966–0.221)</td>
<td>0</td>
</tr>
<tr>
<td><em>Pseudocalanus</em></td>
<td>Male</td>
<td>Starved</td>
<td>14.6(±1.7)</td>
<td>0.023(±0.007)</td>
<td>−0.130(−0.203–0.079)</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td></td>
<td>—</td>
<td>0.023(±0.007)</td>
<td>−0.130(−0.203–0.079)</td>
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</tr>
</tbody>
</table>
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 (Vittasalo 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
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 Kiorboe 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; Kiorboe 2008).

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