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REPLY COMMENT

Female-biased sex ratios in marine pelagic copepods: Response to Hirst et al. (2013)

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ABSTRACT: Hirst et al. (2013; Mar Ecol Prog Ser 489:297–298) suggest that Gusmão et al. (2013; Mar Ecol Prog Ser 482:279–298) misinterpreted the findings of Hirst et al. (2010; Limnol Oceanogr 55:2193–2206). They restate that the major factors determining sex ratio in pelagic copepods act upon the adult stage, but they place less emphasis on the idea that predation on male copepods is a likely determinant, and highlight the role of physiological longevity. Here we reconsider the data and confirm our position that at present there is limited evidence to support the theory of male-skewed predation. However, we agree that sex determination is governed by a combination of factors, with the relative emphasis being the main point of contention between the 2 parties.

KEY WORDS: Predation · Sex ratio skew · Physiological longevity · Sex change · Environmental sex determination · Intersexuality

Correct citation

Hirst et al. (2013) argue that our addition to a quote from Hirst et al. (2010) substantively changed the meaning of their text. Our insertion was a logical extension of 2 conclusions in Hirst et al. (2010): that 'adult sex ratio skew in pelagic copepods is primarily due to differential mortality of the sexes in the adult stage and not in juveniles' (Hirst et al. 2010, p. 2193) and that 'predation on the adults is a major contributor to field mortality' (Hirst et al. 2010, p. 2203).

Hirst et al. (2010) stated explicitly that their findings on male-specific predation apply to the genera *Pseudocalanus* and *Oithona*. However, a reader is given the impression that this is likely to apply to other species as well: 'We need such data to unequivocally show that the males are indeed consumed at greater rates than the females' (p. 2204). Consequently, Hirst et al. (2010) has been cited as evidence that predation is the main control of sex ratios in pelagic copepods (e.g. Heuschele & Kiørboe 2012, Lasley-Rasher & Yen 2012, Heuschele et al. 2013). Moreover, the statement in Hirst et al. (2013, p. 297) that 'predation being important does not infer a bias towards one sex or the other' is at odds with the conclusions in Hirst et al. (2010, p. 2193) and the hypothesis advanced previously (Kiørboe 2006).

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Skewed sex ratios

Hirst et al. (2013) suggest that we derive much of our analysis from genera that do not have female-skewed sex ratios (Table 3 in Gusmão et al. 2013). We have used all available information, as there are data on sex-based differences in predation for only 12 of 330 genera of pelagic copepods (Razouls et al. 2013). We agree that studies focused on heavily female-biased families are required to clarify the determinants of adult sex ratios. Nevertheless, our analyses of predator selection and sexual bias are valid for the following reasons:

- The evidence in Gusmão et al. (2013) for *Pseudocalanus* and *Oithona* does not support the hypothesis that male-biased predation is responsible for skewed sex ratios. Species of both genera fit the description of optimal test organisms, as suggested by Hirst et al. (2013).
- Analyses of predation and sex ratios in Gusmão et al. (2013) are focused on copepod species having female-skewed sex ratios (p. 287), and state in which cases the hypothesis of predator-determined sex ratio skew is either valid or not (p. 288).
- The generalization that copepod families such as Acartidae, Temoridae, Centropagidae and Oncaeidae do not show consistent and strong female-biased sex ratios (Hirst et al. 2013) is debatable. Using quasi-weekly seasonal data from the White Sea from 1965 to 1970, Gusmão et al. (2013, Fig. 4) show that, similarly to other copepods, sex ratios in *Acartia longiremis* and *Oncaea borealis* are mostly female-biased. Therefore, the relationship between predator selection and sexual bias can be tested in these species.

Study of predation effects

Our review of sex skew and its potential causes in *Oithona* and *Pseudocalanus* (Gusmão et al. 2013) does not support the hypothesis of male-selective predation for the following reasons: (1) planktonic predators show strong preference towards females of both *Pseudocalanus* and *Oithona*, contradicting male-specific predation (Table 3 in Gusmão et al. 2013); (2) comprehensive data on predators and sex ratios from the English Channel and the White Sea indicate that sex ratios in *Pseudocalanus* and *Oithona* are not correlated with predator abundance *in situ* (see Figs. 1 & 2 in Gusmão et al. 2013); (3) in the absence of predation, sex ratios are extremely female-biased in *Oithona* and vary considerably in *Pseudocalanus* (Table 4 in Gusmão et al. 2013); (4) in the absence of differential mortality and in a food-satiated and predator-free environment, temperature affects adult sex ratios in *Pseudocalanus* (Lee et al. 2003).

Hirst et al. (2013) suggest that our title contradicts results from some of the predator preference data referred to in our review (namely Ohman 1986, Saito & Kiørboe 2001). There is weak evidence in Ohman (1986), Álvarez-Cadena (1993) and Saito & Kiørboe (2001) for male-skewed predation on copepods by *Sagitta* spp., and the evidence in Saito & Kiørboe (2001) is for *Paracalanus parvus*, which belongs to a family for which Hirst et al. (2010) did not find predation mortality to be the dominant cause of sex skew (Gusmão et al. 2013, p. 287). Our title agrees with data shown in Ohman (1986): in 12 of 17 predator–prey pairs, predators show preference for female copepods, and all predators prefer females of both *Oithona* spp. and *Pseudocalanus* spp.

Intersex individuals, which are indicative of sex change, have been observed in *Pseudocalanus* spp. (Cattley 1948, see Gusmão & McKinnon 2009). Further, species of the family Paracalanidae have sex ratios consistently and strongly skewed towards females and have environmental sex determination in the later copepodite, not in the adults (dismissed by both Hirst et al. 2010, 2013).

Common ground

We agree that it is premature to exclude predation as a driver of skewed sex ratios in copepods. Whilst we did not ourselves find evidence of male-selective predation, we stated that 'the existence of a relationship between copepod sex ratios and predation may still exist in other environments or in special conditions' and 'In a group such as the copepods, where species show extremely diverse life strategies, it is unrealistic to assume that a single process will control sex ratios in all species' (Gusmão et al. 2013, p. 295). Drivers of sex ratio may include physiological longevity, environmental factors, sex change, and endosymbionts, as well as predation.

Interestingly, much of the difference in perspective emerging from our respective studies may be due to differences in the relative importance of a suite of determining factors in contrasting environments. Accordingly, Gusmão et al. (2013) concluded with a multi-disciplinary strategy for research on sex determination in pelagic copepods, and identified some of the many unanswered questions for which new studies are required.

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LITERATURE CITED

Álvarez-Cadena JN (1993) Feeding of the chaetognath *Sagitta elegans* Verrill. Estuar Coast Shelf Sci 36: 195–206

Cattley JG (1948) Sex reversal in copepods. Nature 161:937

Gusmão LFM, McKinnon AD (2009) Sex ratios, intersexuality and sex change in copepods. J Plankton Res 31:1101–1117

Gusmão LFM, McKinnon AD, Richardson AJ (2013) No evidence of predation causing female-biased sex ratios in marine pelagic copepods. Mar Ecol Prog Ser 482:279–298

Heuschele J, Kiørboe T (2012) The smell of virgins: mating status of females affects male swimming behaviour in *Oithona davisae.* J Plankton Res 34:929–935

Heuschele J, Eliassen S, Kiørboe T (2013) Optimal mate choice patterns in pelagic copepods. Oecologia 172: 399–408

Hirst AG, Bonnet D, Conway DVP, Kiørboe T (2010) Does predation control adult sex ratios and longevities in marine pelagic copepods? Limnol Oceanogr 55:2193–2206

Hirst AG, Bonnet D, Conway DVP, Kiørboe T (2013) Female-biased sex ratios in marine pelagic copepods: Comment on Gusmão et al. (2013). Mar Ecol Prog Ser 489:297–298

Kiørboe T (2006) Sex, sex-ratios, and the dynamics of pelagic copepod populations. Oecologia 148:40–50

Lasley-Rasher RS, Yen J (2012) Predation risk suppresses mating success and offspring production in the coastal marine copepod, *Eurytemora herdmani.* Limnol Oceanogr 57:433–440

Lee HW, Ban S, Ikeda T, Matsuishi T (2003) Effect of temperature on development, growth and reproduction in the marine copepod *Pseudocalanus newmani* at satiating food condition. J Plankton Res 25:261–271

Ohman MD (1986) Predator-limited population growth of the copepod *Pseudocalanus* sp. J Plankton Res 8:673–713

Razouls C, de Bovée F, Kouwenberg J, Desreumaux N (2013) Diversity and geographic distribution of marine planktonic copepods. Available at: http://copepodes.obs-banyuls.fr/en (accessed August 5, 2013)

Saito H, Kiørboe T (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

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