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Macroevolutionary patterns of sexual size dimorphism in copepods

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Major theories compete to explain the macroevolutionary trends observed in sexual size dimorphism (SSD) in animals. Quantitative genetic theory suggests that the sex under historically stronger directional selection will exhibit greater interspecific variance in size, with covariation between allometric slopes (male to female size) and the strength of SSD across clades. Rensch's rule (RR) also suggests a correlation, but one in which males are always the more size variant sex. Examining free-living pelagic and parasitic Copepoda, we test these competing predictions. Females are commonly the larger sex in copepod species. Comparing clades that vary by four orders of magnitude in their degree of dimorphism, we show that isometry is widespread. As such we find no support for either RR or for covariation between allometry and SSD. Our results suggest that selection on both sexes has been equally important. We next test the prediction that variation in the degree of SSD is related to the adult sex ratio. As males become relatively less abundant, it has been hypothesized that this will lead to a reduction in both inter-male competition and male size. However, the lack of such a correlation across diverse free-living pelagic families of copepods provides no support for this hypothesis. By comparison, in sea lice of the family Caligidae, there is some qualitative support of the hypothesis, males may suffer elevated mortality when they leave the host and rove for sedentary females, and their female-biased SSD is greater than in many free-living families. However, other parasitic copepods which do not appear to have obvious differences in sex-based mate searching risks also show similar or even more extreme SSD, therefore suggesting other factors can drive the observed extremes.

1. Introduction

The different reproductive roles of males and females of a species act as strong sexual selection agents that can lead to dimorphism [1]. Dimorphic attributes can include behaviour, morphology and body size. Differences in body size, termed sexual size dimorphism (SSD), are commonly observed in the plant and animal kingdoms [2] and can be measured with a sexual dimorphic index (SDI). Female-biased SSD, where females are larger than the males, tends to predominate in ectothermic invertebrate and vertebrate species, whereas male-biased SSD is common in many birds and mammals [3,4]. Various rules and theories have been proposed to explain variation in SSD, both within and between species. Some of these focus on how the relative size ratio of the sexes of individual species change from small to large species within specific clades [5–9]; other theories focus on how the availability for mating and the mortality of the sexes impact the strength of mate competition and SSD [1]. Being able to test these various hypotheses and ultimately explain macroevolutionary patterns in SSD is important in resolving which models have predictive power, and what the ultimate drivers are.

Rensch's rule (RR) states that male body size varies more than female body size among species [5,6]. One prominent general hypothesis (i.e. evolutionary mechanism) potentially generating RR is when, over evolutionary time, directional (primarily sexual) selection for large male size is overall stronger than directional (primarily fecundity) selection for large female size. The demonstration that females are the more variant sex (or indeed that there is no

difference in degree of variation, i.e. isometry) in a range of taxa has led to the generality and utility of the rule being questioned [7,8]. As an alternative, quantitative genetic theory predicts that greater interspecific variance in size occurs in the sex that has historically been under stronger directional selection [8,9]. Zeng's [9] model predicts that the sex under more intense direct selection will be the more divergent phenotypically. It has been suggested that because both SSD and allometry within a single clade represent a history characterized by different intensities of selection on male and female body size, allometric slopes may covary with the degree of SSD across clades [8]. Female-biased SSD may evolve through negative directional selection on male body size or positive directional selection on female body size. A positive correlation between allometric slopes and SDI among related clades would be the expectation when direct selection on males is driving both (see figure 1). Conversely, a negative correlation between allometric slopes and SDI would be the expectation when direct selection on females is driving both. Testing for covariation between allometry and the degree of sexual dimorphism allows us to assess whether sex-specific selection generates macroevolutionary patterns [8]. Indeed, a recent analysis of amphibians has shown that females become the more size-variant sex across species in a family as the magnitude of SSD in that family increases. The suggestion being that selection on females drives both allometry and SSD in this case [8]. Whether such covariation is widespread clearly needs further attention. Moreover, there has been a general lack of testing of these patterns where there is a female-biased SSD. As copepods commonly have such female-bias sizes [10–12], and demonstrate a huge range in the degree of SSD, they provide an excellent opportunity to do this.

Vollrath & Parker [1] developed a model to explain multiple aspects of SSD which they tested against spiders. They argued that adult mortality may impact optimal size (age) at maturation; high mortality of the adult males leads to a female-biased operational sex ratio (OSR) and hence relaxation of male–male competition for mates. Conversely, a low male mortality results in intensified competition for females and a larger male size. OSR is the ratio of the number of fertilizable females to sexually active males at any one time [13]. Extremes can occur where females are sedentary and males rove, this being linked to the extreme dwarfing seen in male spiders, barnacles, angler fish *Ceratias* and the parasitic crab *Danalia curvata* [1]. These predictions do not relate to the allometry of SSD, but rather the degree of dimorphism being dependent upon mate finding behaviour and its impact upon mortality rate.

In order to test multiple theories based around predicting the causes of SSD and its variation, we need animal and plant groups in which extensive and accurate data on body size exist, and in which body size, life history and behaviour are diverse. As we will show, copepods provide an excellent test case and allow quantitative examination of major SSD-based theory. The subclass Copepoda, which are members of the class Maxillopoda, are crustaceans and possibly the most abundant animal group on the Earth [14]. The striking variability in mate seeking behaviours (including sedentary and roving types in some parasitic families) and sex ratios allows for quantitative and qualitative tests of model predictions [1]. Male planktonic copepods often develop faster [15] and mature at a smaller size than females [16]. Some copepod families (within the Diaptomoidea) require repeat mating because they are unable to store sperm and often have near
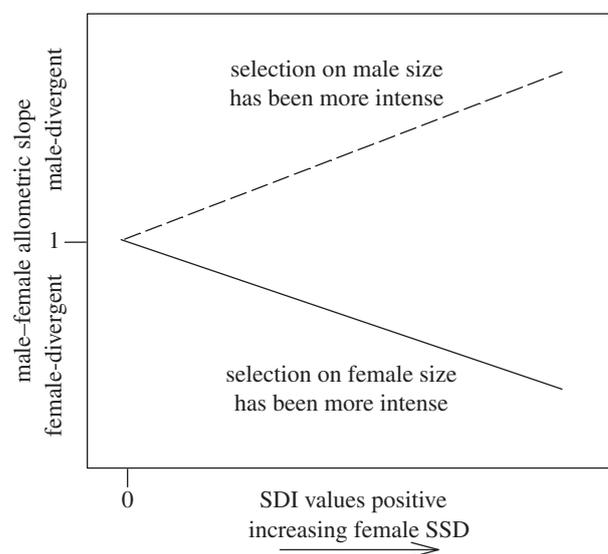

Figure 1. The covariation of allometric slopes (log male versus log female size) against the SDI, in this example the case of female-biased SDI is given. If RR is general and selection on males is a main driver of the evolution of SSD, then looking across related clades the allometric slopes will increase as the magnitude of SDI increases (denoted by dashed line). Alternatively, if the evolution of SSD is driven primarily by selection on female size then allometry will become female divergent (the allometric slope will decrease) as the magnitude of SDI increases (solid line) across clades. (Adapted from De Lisle & Rowe [8].)

equitable sex ratios [17,18]. Others (many non-Diaptomoidea families) are able to store sperm [19] and can produce multiple batches of eggs from a single copulation event [14,20]. Higher rewards from single mating events may lead males to high mortality risk when mate searching. This has been used to explain the greater adult male mortality and female-biased adult sex ratios in this latter group [15,17]. Copepods present an opportunity to test Vollrath and Parker's [1] model more widely, if male–male competition were an important factor then large differences observed across copepod families may be expected to drive variation in SSD.

While many advances in understanding the patterns in sex ratios and dynamics of mate encounter have been made in pelagic copepods over the last few years (e.g. [15,17]), no attempt has been made to link such aspects to size dimorphism. We take the opportunity to do this here. The main objectives of this paper are therefore to test the following hypotheses:

(1) Male body size varies more than female body size among species (RR).
(2) Allometric slopes are more than 1 and covary positively with female-biased SSD across related clades, indicating selection on male size has been more intense. Conversely, allometric slopes are less than 1 and covary negatively with female-biased SSD, indicating selection on female size as been more intense (both predicted by quantitative genetic theory).
(3) Female-biased SSD increases with increasing female-biased OSR (following the model of Vollrath and Parker).

2. Material and methods

(a) Copepod data
In order to test various theories of SSD, we compiled SSD data for over 400 species from more than 40 families and several
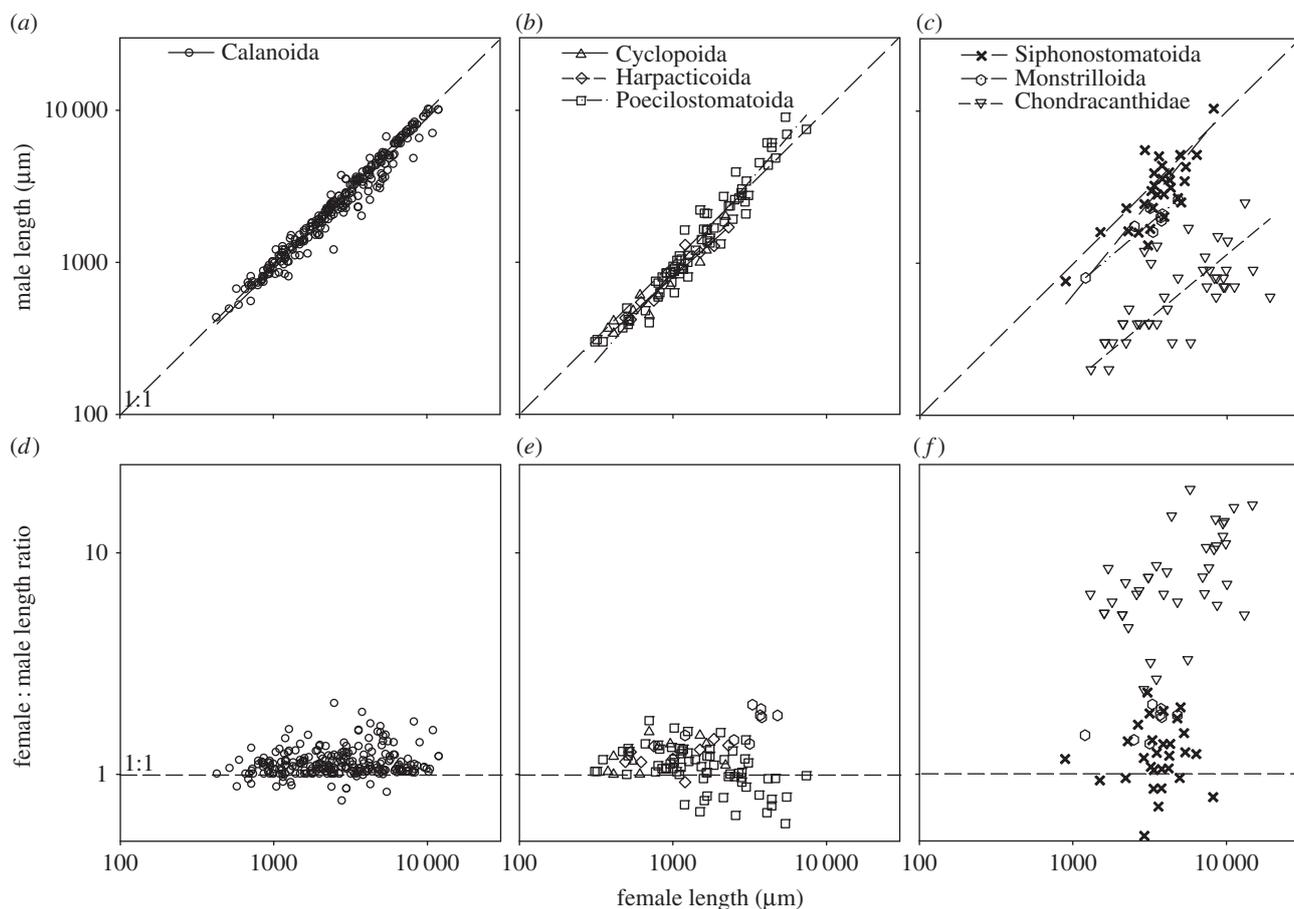
Figure 2. Pelagic copepod sizes (prosome or total lengths) in matched species-specific pairs. (a–c) Male versus female lengths, with RMA regressions through each identified clade: (a) Calanoida, (b) Cyclopoida, Harpacticoida and Poecilostomatoida (excluding Chondracanthidae), (c) Chondracanthidae, Monstrillidae and Caligidae. Data are available for only one family within these last two orders. (d–f) Female to male length ratios versus female length for the species from the respective panels above. Dashed lines indicate equal female to male lengths across all graphs.

dominant orders within the Copepoda. We included species with diverse lifestyles, including: pelagic free-living, host associated (i.e. Sapphirinidae and Lubbockiidae) and fully parasitic forms (i.e. Chondracanthidae, Monstrillidae and Caligidae). Chondracanthidae (order Poecilostromatoida) consists of highly modified copepods which are parasitic on many marine fishes; in some of these parasites the male may derive nourishment from the female to which they are attached [11]. Males may attach to young immature females at the second copepodite stage [21] and complete development on the female, remaining attached until death. The Monstrillidae (order Monstrilloida) are poorly described biologically and ecologically, but are parasites of marine benthic invertebrates, especially on polychaetes and gastropods [22]. In Monstrilloida, only the first nauplius and adult stages are free-swimming; the other larval stages are highly modified internal parasites. The adults emerge from their hosts to reproduce [23] and are incapable of feeding. Finally, the family Caligidae (order Siphonostomatoida) commonly termed sea lice are free-living until the copepodid stage, whereupon both sexes settle as ectoparasites on fish hosts, and feed on their mucus, epidermal tissue and blood. The female's ability to store sperm reduces the need for repeat mating, while in some species the adult males are known to leave the host and rove for mates more readily than do the females [24,25].

Species-specific prosome (body length excluding the urosome) or total lengths of adult male and female copepods were extracted from the published literature. We included values from either the upper size of a range or the mean, but always used the same for both sexes in a single species from a single reference. For Chondracanthidae, we used an extensive

compilation of body lengths [16]. At maturation, copepods do not continue to moult, although they can accumulate mass to some degree [26], any length change will be highly restricted. Some parasitic species are an exception to this as the adult female can continue to enlarge their body with an expandable exoskeleton. For such taxa, we use the reported sizes with no correction. All species identities were confirmed and ascribed to family and order using the World Registry of Marine Species [27].

The taxonomic level at which patterns in SSD are examined has important implications to the outcome [7,8], hence we consider this carefully. In order to examine allometry of SSD, we divided species into clades. Such divisions were made on a taxonomic basis, by family and order, as is common practice, but with additional consideration of distinctive lifestyles and SSD for the latter. Hence, the orders included were: Calanoida, Cyclopoida, Harpacticoida, Monstrilloida. Siphonostomatoida and Poecilostomatoida. In the final order, we excluded the family Chondracanthidae which has a radically different SSD from the other members (figure 2).

(b) Data treatment

To allow examination of allometry of SSD within a clade, $\log_{10}$ male lengths were regressed against $\log_{10}$ female lengths (table 1). Reduced major axis (RMA) regressions (using software from reference source [28]) were applied, and slopes (β) and 95% confidence intervals (CI) determined. This regression model does not infer a dependent and independent variable and is most commonly applied in such SSD analysis. Using OLS regressions produce

Table 1. Results from RMA regressions of log_{10} male versus log_{10} female size for Copepoda by order and family, where β is the slope, a the intercept and r the correlation coefficient. Analyses were only completed when $n \geq 5$. Rows in italic indicate that β differs significantly from 1 (hence is not isometric). Mean SDI values are also given for each clade. Where data are available for only one family within an order, this family is indicated in brackets. Poecilostomatoida excludes Chondracanthidae because of the extreme divergence of this family from the remaining species (see text for details). The orders Monstrilloida and Siphonostomatoida include single families here, which are identified within the brackets. In all cases regressions were highly significant ($p < 0.005$), except in the family Paracalanidae, in which p is significant at less than 0.02.

taxa	n	SDI	β [95%CI range]	a	r
by order					
Calanoida	252	0.529	0.989 [0.965 – 1.013]	−0.007	0.98
Cyclopoida	11	1.034	0.909 [0.731 – 1.087]	0.176	0.97
Harpacticoida	9	0.931	0.948 [0.747 – 1.149]	0.069	0.97
Poecilostromatoida	*71*	*0.276*	*1.180 [1.114 – 1.246]*	*−0.598*	*0.97*
Siphonostomatoida (Caligidae)	29	1.511	1.230 [0.923 – 1.537]	−0.895	0.77
Monstrilloida (Monstrillidae)	8	4.487	0.851 [0.548 – 1.154]	0.287	0.93
by family					
Acartiidae	17	0.521	0.887 [0.527 – 1.247]	0.294	0.67
Aetideidae	19	0.201	1.204 [0.971 – 1.437]	−0.838	0.93
Arietellidae	*7*	*0.470*	*1.124 [1.054 – 1.194]*	*−0.485*	*1.00*
Augaptilidae	*24*	*0.927*	*1.359 [1.154 – 1.564]*	*−1.399*	*0.94*
Calanidae	*15*	*0.569*	*0.857 [0.765 – 0.949]*	*0.438*	*0.98*
Candaciidae	11	0.230	1.041 [0.814 – 1.268]	−0.167	0.96
Centropagidae	15	0.326	1.006 [0.931 – 1.081]	−0.059	0.99
Chondracanthidae	40	1833	0.837 [0.634 – 1.040]	−0.291	0.68
Clausocalanidae	9	0.370	0.982 [0.638 – 1.326]	0.019	0.92
Corycaeidae	18	0.634	0.931 [0.795 – 1.067]	0.152	0.96
Euchaetidae	12	0.597	0.891 [0.638 – 1.144]	0.358	0.92
Heterorhabdidae	12	−0.149	0.966 [0.819 – 1.113]	0.136	0.98
Lubbockiidae	13	−0.080	0.972 [0.586 – 1.358]	0.095	0.80
Lucicutiidae	14	0.212	1.022 [0.988 – 1.056]	−0.102	1.00
Metridinidae	13	0.485	1.138 [0.968 – 1.308]	−0.536	0.97
Oithonidae	*10*	*1.104*	*0.799 [0.622 – 0.976]*	*0.480*	*0.96*
Oncaeidae	19	1.271	0.890 [0.748 – 1.032]	0.207	0.95
Paracalanidae	7	0.347	0.792 [0.343 – 1.241]	0.573	0.87
Phaennidae	9	0.489	1.001 [0.807 – 1.195]	−0.050	0.98
Pontellidae	11	0.404	1.044 [0.868 – 1.220]	−0.198	0.97
Pseudocyclopiidae	6	0.061	0.987 [0.661 – 1.313]	0.031	0.97
Sapphirinidae	*21*	*−0.710*	*1.189 [1.031 – 1.347]*	*−0.602*	*0.96*
Scolecitrichidae	12	0.256	0.896 [0.788 – 1.004]	0.337	0.99
Stephidae	5	0.185	0.924 [0.667 – 1.181]	0.211	0.99
Temoridae	10	0.451	0.977 [0.611 – 1.343]	0.026	0.89

slightly shallower slopes, but do not alter our findings in any significant way. Regressions were only performed on clades with five or more values, consequently allometries of 27 diverse families were determined. Slopes were defined as departing from isometry (i.e. from a value of 1) if the 95% CIs did not bound 1 (figure 3 and table 1). We do not undertake phylogenetic correction when determining slopes because appropriate data for many families considered here are incomplete or uncertain. We note however, that where this had been undertaken for sub-sets of the data presented here it did not significantly alter the outcome [16].

SSD was also quantified using the widely used SDI of Lovich & Gibbons [29], where

$$SDI = \left(\frac{\text{mass of larger sex}}{\text{mass of smaller sex}} \right) - 1. \quad (2.1)$$

This index has an advantage of providing symmetrical results around zero regardless of which sex is larger [29]. We followed the convention that the index is given as a positive value when females are the larger sex, and as a negative value when males are larger. SDI values were derived on each species and then
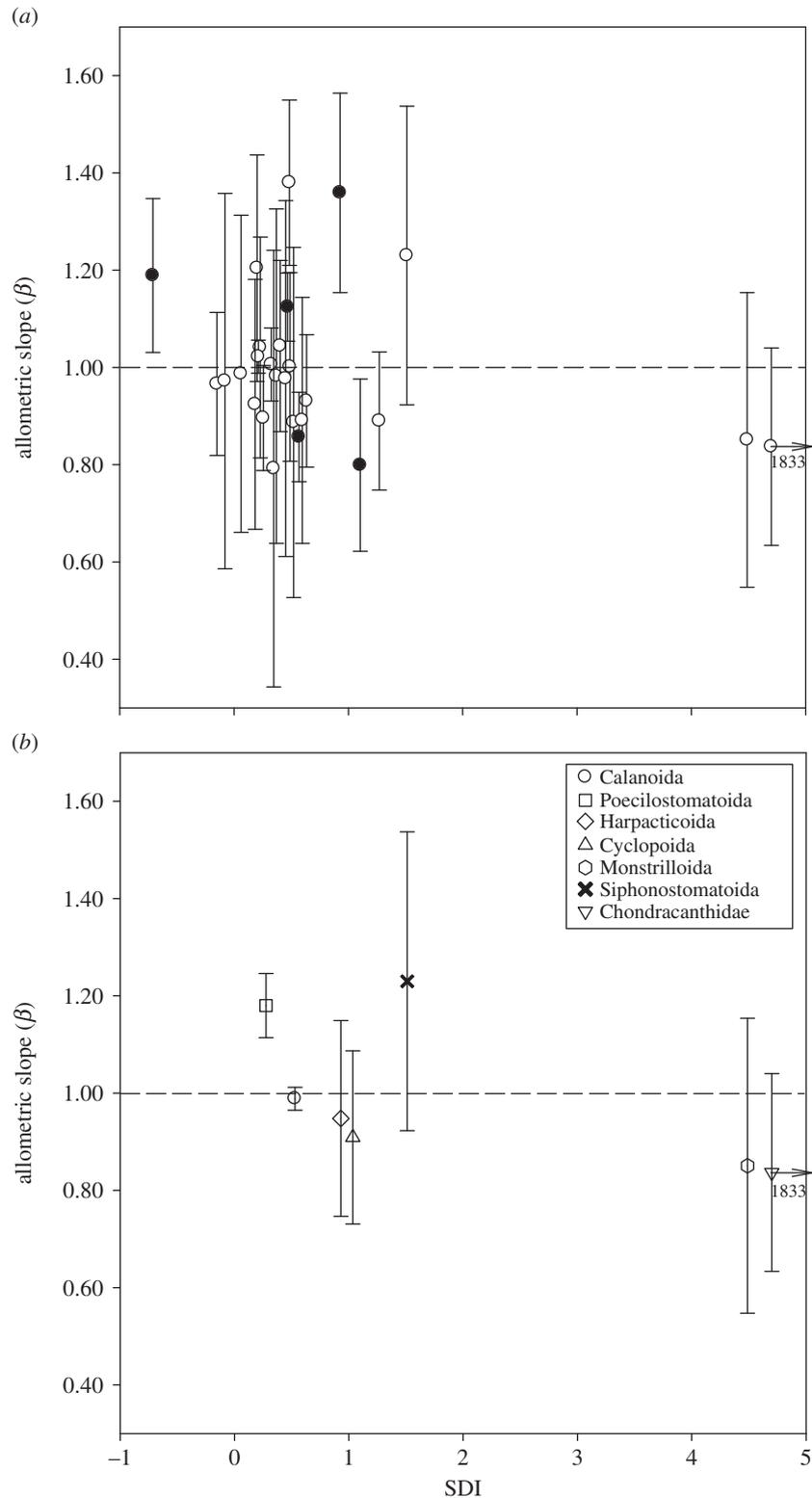
Figure 3. Allometric slopes (β) versus mean SDI by: (a) family and (b) order (also including Chondracanthidae for comparison). Dashed horizontal lines indicate isometry. Error bars represent 95% CIs of slope values. Filled symbols in panel (a) indicate a significant difference from isometry, whereas for open symbols there is no difference. Note that the very high SDI value for Chondracanthidae which falls off the scale is indicated.

averaged to obtain the clade-specific value. We derived mass as a proxy, simply from the cube of the compiled lengths [30].

We wished to test whether SSD is influenced by the degree of male–male competition in pelagic free-living copepods [1]. In order to do this, we assume that differences in sex ratio and reproductive strategy (sperm storage by females) should reflect the relative degree of such competition: a male-biased (operational) sex ratio and the ability to store sperm would both intensify the male–male competition for females. We used the adult sex ratios as compiled by Hirst & Kiørboe [18]. This extensive set of male

to female adult field abundance ratios includes both families within and outside of the Diaptomoidea (data presented in figure 4a). The dataset includes sex ratios from approximately 35 species with almost 4000 individual measurements. In many cases, animals were sampled with vertically towed nets covering all or most of the depth range of the species. In some instances, sampling was over discrete depth ranges, but we do not consider this will produce important errors given the degree of averaging. Of course, making an inference that adult sex ratios reflect adult mortality is dependent upon the recruitment of the sexes into
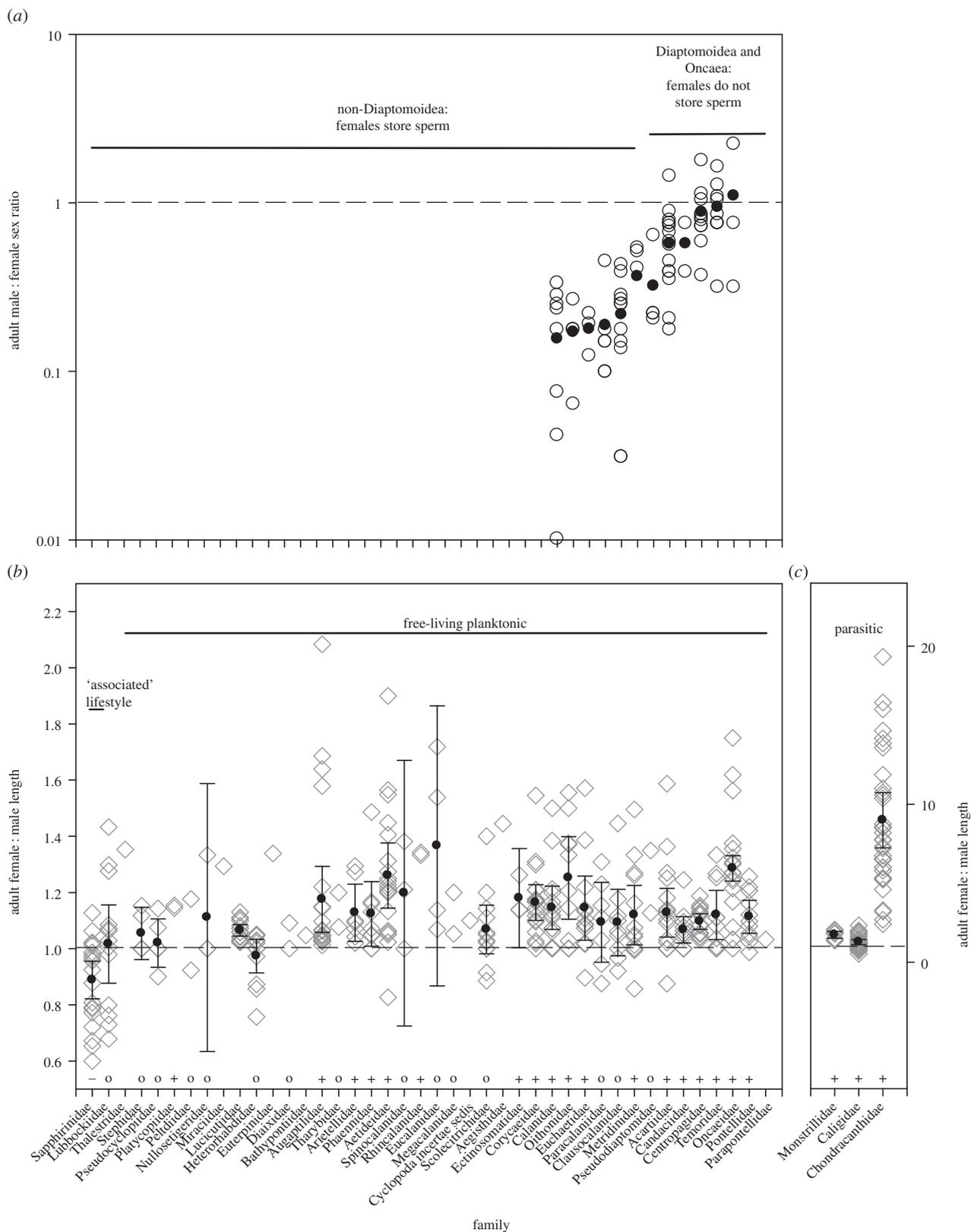
Figure 4. Sexual characteristics of marine copepods by family: (*a*) adult male to female sex ratios, open circles give individual study means, and filled circles family means (adapted from Hirst & Kiørboe [18]). (*b*) Adult female to male length ratios, free-living families and associated families indicated. (*c*) Adult female to male length ratios in the parasitic families. Note scale change between panels (*b*) and (*c*). Means ($\pm$ 95% CI) (in (*b,c*)) are only shown, where $n \geq 3$. The symbols $+$, $-$ and o indicate whether female to male size ratios are significantly greater, less than or not significantly different from 1, respectively.

this stage, specifically that these recruit equally, which when tested has been shown to occur (as examined in [15]). We are therefore confident that the large variation observed in adult sex ratios across families reflects gross differences in adult mortality rates. We undertook a correlation between mean family SDI values and corresponding adult sex ratios to test the prediction that male–male competition may determine SSD [1].

3. Results

In the vast majority of copepod families, females are larger than their conspecific males (figures 2 and 4). Mean SDI values in free-living families span a range from −0.15 to 1.27 (table 1), which compared with the parasitic copepods is very narrow (figures 3 and 4). Across all 27 families, only three have

negative SDI values (i.e. with larger males on average), while no order level comparison shows a male size bias. The families with negative SDI values are Heterorhabdidae, Sapphirinidae and Lubbockiidae. While there are a diverse range of lifestyles and feeding types in free-living copepods, Sapphirinidae and Lubbockiidae are somewhat distinctive, having an ecology strongly tied to living on the surface of salps. Heterorhabdidae include many carnivorous species but are free-living.

The fully parasitic copepods show striking SSD, varying markedly from one another and from the many free-living families. The parasitic Chondracanthidae has a mean SDI of 1833 (table 1), while the mean is 4.49 for Monstrillidae and 1.51 in Caligidae. Species within Chondracanthidae are massively body size skewed, more so than any other copepod family, with females commonly being more than 1000 times larger in mass (as approximated from length herein) than conspecific males (figure 2c). The females of Chondracanthidae are larger on average than those of the free-living species, whereas their males are smaller [13] (figure 2). By contrast, parasitic Monstrillidae and Caligidae both tend to have males and females which are at the larger end of the range represented by free-living species.

Isometry in SSD is found in 22 of the 27 families examined. Only in the families Arietellidae, Augaptilidae and Sapphirinidae are β-values significantly greater than 1, whereas in Calanidae and Oithonidae they are significantly less than 1. In five of the six orders, β-values are statistically indistinguishable from isometry, including in the Calanoida, Cyclopoida, Harpacticoida, Monstrilloida and Siphonostromatoida. However, we should caution that the final two only include data from single families. The only order to diverge from this is Poecilostomatoida, having positive allometry, which is largely driven by Sapphirinidae that commonly have male-biased SSD (figure 3). Mean β-values for all clades (including family and order) fall between approximately 0.8 and 1.4 (figure 3), even though the SDI in these same groups varies by over 1000-fold.

Male to female adult sex ratios span a sevenfold range across the free-living species, with mean values by family being from 0.16 to 1.10 (figure 4a). There are important differences between the non-Diaptomoidea (and *Oncaea*) families versus those that need to constantly re-mate, the Diaptomoidea. The latter have a more equitable sex ratio. Regressing family-specific mean SDI values against their respective male to female adult sex ratios, we find no significant relationship ($r^2 = 0.03$, $n = 11$, $p > 0.10$). Furthermore, SDI values are not significantly different between the Diaptomodea and the non-Diaptomoidea groups (Welch two sample t-test, $t = 0.0871$, d.f. = 6.788, p-value = 0.933), while male to female sex ratios do differ significantly (Welch two sample t-test, $t = -5.478$, d.f. = 4.736, p-value = 0.003). In conclusion, we find no evidence that sex ratios (and therefore the inferred degree of male–male competition) relates to SSD or gross reproductive behaviours (as defined broadly by the Diaptomoidea versus non-Diaptomoidea categories).

4. Discussion

(a) Allometry of sexual size dimorphism

We begin by addressing our first two hypotheses (see Introduction), i.e. whether copepods support RR, and whether they demonstrate covariation between the degree of sexual dimorphism and degree of allometry. In pelagic copepods, females of the species are commonly larger than the males (figures 2 and 4). Across the diverse copepod clades considered here, β-values indicate that isometry is almost universal (figure 3), hence we find little to support RR. Previous studies on a range of taxa have frequently found the degree of SSD to vary with body size. These patterns have been reviewed for Mammalia, Aves, Reptilian, Amphibia, Arachnida and Insecta [3]. In most instances, these follow RR, i.e. $\beta > 1$, and exceptions to this only occurred when females were the larger sex. An extensive comparison across birds found that RR is commonly broken where female-biased SSD occurs within a clade [7]. Recently, Blanckenhorn *et al.* [31] evaluated the evidence for RR in a range of insect orders: the rule was found to apply consistently to Diptera and Heteroptera, but not to any of the other insect groups examined. This led them to conclude that the mechanisms causing the pattern are unevenly distributed among taxa; our results further support this conclusion.

If RR was general, and selection on males is the main driver of the evolution of SSD, then allometric slopes should increase as the SDI increases across clades. By contrast, if the evolution of size dimorphism were primarily driven by selection on female size, then allometric slopes should decrease as the magnitude of SDI increases (figure 1, compare to figure 3). As no significant relationships exist between β and $\log_{10}$ SDI (the latter was logged to accommodate the skew), we find no support for either of these predictions. The fact that relationships are commonly not distinguishable from being isometric in many copepod clades suggests that selection on each of the sexes may have been near equally important. Most previous empirical assessments of allometry have focused on either vertebrates or invertebrates with male-biased SSD ([3,6,7], cf. 8]) and in many of these studies the allometric slope within clades often decreases as the magnitude of SSD increases (see fig. 2 of Fairbairn [3]), this would tend to support selection on male size being a common cause for the evolution of both positive allometry ($\beta > 1$) and male-biased SSD. By contrast, analyses of clades that exhibit female-biased SSD indicate no clear patterns to their allometry (no consistency in either female-divergent or male-divergent allometry), indeed our analysis on copepods further reinforces this. Across related clades when females are the larger sex, there is not strong evidence to support the predictions of quantitative genetic theory (cf. [8]).

(b) Life history and sexual size dimorphism

Kiørboe & Hirst's [32] model of size at maturation in free-living copepods shows that high juvenile mortality favours early maturation at a smaller size, while late maturation at a larger size becomes increasingly favoured the steeper the increase in reproductive output is with size. This prediction is consistent with classical life-history theory [33]. The balance between survival probability and reproductive success determines the size and age at maturation. Vollrath & Parker [1] extended such an argument by demonstrating that adult mortality may also impact optimal size (age) at maturation; high mortality of the adult males leads to a female-biased population, a relaxation of competition for females, and in turn this leads to earlier maturation of males at a smaller size. Conversely, a low adult male mortality results in intensified competition for females, in which circumstance larger male size is more favourable. Importantly, rather than the numerical

sex ratio being the relevant parameter in these descriptions, it is the OSR [34]. The OSR is the ratio of receptive females to ready-to-mate males, or the female/male sex ratio corrected for 'time-outs', i.e. the fraction of time that each sex cannot mate because they need to release one or several batches of eggs (females) or generate a new spermatophore (males). In copepods, the female time-outs are typically much longer than male time-outs, and in some species the females need to be mated only once to have sufficient sperm for the rest of their reproductive career. The question is therefore whether inter-male competition for females is relevant or prevalent in copepods, and hence whether the Vollrath & Parker model [1] applies.

(i) Free-living copepods

The suggestion that OSR may account for SSD [1] appears unable to explain the general lack of pattern in size dimorphism across the free-living copepod families, or indeed the similarity in size ratios between Diaptomoidea and non-Diaptomodea (figure 4). The sedentary versus roving dichotomy [1] is partly equivalent to ambush feeding cyclopoid copepods, such as in the genus *Oithona*: in this example, the female is an ambush feeder and relatively non-motile, whereas the males spend approximately one-third of their time swimming at high speed in search for females [35]. As a result, the males have much higher mortality, and adult sex ratios are strongly female-biased, typically with a male to female ratio of 1 : 10 [15,36]. However, time-out ratios are strongly female-biased because the females need to be mated only once, whereas the males can mate several times per day, and OSR is likely less skewed than the sex ratio would suggest (figure 4). The other extreme can be represented by genera such as *Acartia*, in which males and females have very similar mate finding behaviours [37] and mortalities, and adult sex ratios near 1 : 1 (figure 4); they may also have similar time-outs, because the males can produce one to a small number of spermatophores each day, and females produce a batch of eggs per day [38]. In *Acartia*, male–male competition may potentially be stronger and SSD would be predicted to be less skewed following Vollrath & Parker's model [1], yet there are no obvious differences in the degree of SSD between *Acartia* and *Oithona* (figure 4). Our results therefore question the ability of their model [1] to predict or explain patterns in SSD in copepods, and hence its generally universality. Clearly more tests of this type across other taxa are needed to examine the degree to which the predictions hold.

Another question is: how would male–male competition materialize in the pelagic environment inhabited by free-living copepods? Combat competition is not an option in copepods, but scramble competition is. Mate guarding by physically clasping the female has been observed in a small number of copepod species [39] but is certainly not widespread. Sperm competition may occur, but we have no direct evidence for this as yet in the free-living pelagic species (although we note that there is evidence for this in parasitic species). It is more likely that females become more or less choosy depending on the availability of males, but importantly it is the absolute density of the opposite sex rather than the relative densities that decides the intensity of choosiness [40]. In the case of a low male density, when it is difficult for a female to find an alternative mate, the female may mate indiscriminately. In several species, large males have a higher

chance of fertilizing a female (and a larger female a higher chance of being fertilized), and these differences are due to mate choice [37,41,42].

Evidence that reduced male–male competition can lead to stronger SSD [1], as expected when adult sex ratio is female-biased, is weak or non-existent in free-living pelagic copepods. However, size dimorphism may simply arise when the advantage of delayed maturation differs between genders [32]. In fact, there is no reason to expect that the advantages of delayed maturation should be the same between the sexes. In females, egg production may increases with size [32], and larger females have a higher chance of being fertilized [38,41]. These factors favour late maturation and larger adult size, to the exact extent that it balances juvenile mortality. For males, we similarly know that larger males produce larger spermatophores and these contain more spermatozoa [42]. Larger males also have a greater chance of fertilizing a female [38,41], which will act to select for later maturation in males to the extent that this is balanced against juvenile mortality risk. Gamete production between males and females appear to be very differently limited however. While females can produce eggs at a daily rate equivalent to their own body mass [43,44], males can produce only a few spermatophores per day [45] each with rather few sperm cells [42]. Although such differences do not demonstrate differences in the relative advantage of late maturation, they are suggestive of this.

The Sapphirinidae, Lubbokiidae and Heterorhabdidae are the only families in which males are on average larger than the females. Sapphirinidae and Lubbockiidae are commonly associated with feeding on pelagic invertebrate hosts such as salps [46]. Given the aberrant nature of SDI in these three families (table 1), a better understanding of differences in the life history of their sexes may be illuminating with respect to understanding drivers of SSD and the strong differences to free-living copepods.

(ii) Parasitic copepods

Vollrath and Parker's explanation for dwarf males are in part supported by their occurrence in a wide range of species where the female is relatively sedentary, while the males rove and suffer higher mortality [1,47]. In Caligidae, including the well-known sea lice, the males can mature somewhat earlier than females, but they settle at a similar development stage [48]. Some species in this family have males that are more mobile, and more likely than the females to disperse as adults in the absence of the opposite sex [24,25]. As Connors *et al.* [25, p. 591] point out, 'Male fitness is therefore dependent on access to mates, whereas female fitness is contingent on access to resources for egg production. The resulting asymmetry in reproductive investment likely underlies sex-specific benefits of dispersal as lice approach sexual maturity'. 'Roving' behaviour, which includes leaving the host, may represent significant mortality risk for the male (and this is dissimilar to that of the attached female) given that being attached will afford protection from high levels of mortality which small pelagic organisms typically suffer [18]. The markedly smaller size of males in the parasitic Calaigidae, and the observation that females are relatively sedentary while males rove, qualitatively supports Volrath and Parker's predictions. By contrast, Chondracanthidae males may be dwarf parasites on the parasitic females [11], and their size reduction given their likely sedentary nature may be driven more by their direct coupling

to the female rather than adult mortality. Through most of the life of Monstrilloida (other than first nauplii and adults), the larvae are an internal parasite of benthic organisms [22,49]. We have no evidence of difference in risks between the males and females of Monstrilloida and their SDI values are intermediate between the two other parasitic families included here (see also [12,50]). Therefore, while we find that many parasitic taxa may display much larger females than males, we do not have evidence that males always have a risky mate roving strategy. Differences in mortality between the sexes in parasitic copepods are needed in future in order to explore this issue more fully.

Dwarf males have been linked to reduced male–male competition [1]. Intriguingly, precocious coupling and precopulatory mate guarding by the males of some Caligidae [48,51,52] would rather suggest strong male–male competition. This is further suggested by males having spermatophores which can block further mating by females for some time [24,53]. Mate guarding by males has been considered to be more marked when there is a male-biased sex ratio, and hence high inter-male competition [54,55]. Many males of benthic and even parasitic harpacticoid copepods also show some degree of

mate guarding, and those that do often have strong female-biased SSD (e.g. *Tisbe* [56]). There are therefore clear contradictions here. Pelagic environments may not be conducive to mate guarding in free-living copepods because of increased predation risk from such a strategy [39], even when male competition is strong. The degree to which mate guarding may be associated with dwarfing by males is in need of exploration both within the copepods and within other groups of organisms too. To build and test quantitative models of SSD in future, we will need information on the role of body size in determining male fertility, and data on the sex- and stage-dependent mortality across families with contrasting life histories.

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