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1 **Macroevolutionary Patterns of Sexual Size Dimorphism in Copepods**

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19 **Summary**

20 Major theories compete to explain the macroevolutionary trends observed in sexual
21 size dimorphism (SSD) in animals. Quantitative genetic theory suggests that the sex
22 under historically stronger directional selection will exhibit greater interspecific
23 variance in size, with covariation between allometric slopes (male to female size) and
24 the strength of SSD across clades. Rensch's Rule also suggests a correlation, but one
25 in which males are always the more size variant sex. Examining free-living pelagic
26 and parasitic Copepoda, we test these competing predictions. Females are commonly
27 the larger sex in copepod species. Comparing clades that vary by 4 orders of
28 magnitude in their degree of dimorphism, we show that isometry is widespread. As
29 such we find no support for either Rensch's Rule or for covariation between allometry
30 and SSD. Our results suggest that selection on both sexes has been equally important.
31 We next test the prediction that variation in the degree of SSD is related to the adult
32 sex ratio. As males become relatively less abundant it has been hypothesised that this
33 will lead to a reduction in both inter-male competition and male size. However, the
34 lack of such a correlation across diverse free-living pelagic families of copepods
35 provides no support for this hypothesis. By comparison, in sea-lice of the family
36 Caligidae there is some qualitative support of the hypothesis, males may suffer
37 elevated mortality when they leave the host and rove for sedentary females, and their
38 female-biased SSD is greater than in many free-living families. However, other
39 parasitic copepods which do not appear to have obvious differences in sex-based mate
40 searching risks also show similar or even more extreme SSD, therefore suggesting
41 other factors can drive the observed extremes.

42

43 **Key words:** Sexual size dimorphism, allometry, sex ratio, Copepoda

44

45 **1. Introduction**

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

61

62 Rensch's rule (RR) states that male body size varies more than female body size
63 among species [5, 6]. One prominent general hypothesis (i.e. evolutionary
64 mechanism) potentially generating RR is when, over evolutionary time, directional
65 (primarily sexual) selection for large male size is overall stronger than directional
66 (primarily fecundity) selection for large female size. The demonstration that females
67 are the more variant sex (or indeed that there is no difference in degree of variation,
68 i.e. isometry) in a range of taxa has led to the generality and utility of the rule being

69 questioned [7, 8]. As an alternative, quantitative genetic theory predicts that greater
70 interspecific variance in size occurs in the sex which has historically been under
71 stronger directional selection [8, 9]. Zeng's (1988) [9] model predicts that the sex
72 under more intense direct selection will be the more divergent phenotypically. It has
73 been suggested that because both sexual size dimorphism and allometry within a
74 single clade represent a history characterized by different intensities of selection on
75 male and female body size, allometric slopes may covary with the degree of SSD
76 across clades [8]. Female-biased SSD may evolve through negative directional
77 selection on male body size, or positive directional selection on female body size. A
78 positive correlation between allometric slopes and *SDI* among related clades would be
79 the expectation when direct selection on males is driving both (see fig. 1). Conversely,
80 a negative correlation between allometric slopes and *SDI* would be the expectation
81 when direct selection on females is driving both. Testing for covariation between
82 allometry and the degree of sexual dimorphism allows us to assess whether sex-
83 specific selection generates macroevolutionary patterns [see 8]. Indeed, a recent
84 analysis of amphibians has shown that females become the more size-variant sex
85 across species in a family as the magnitude of SSD in that family increases. The
86 suggestion being that selection on females drives both allometry and SSD in this case
87 [8]. Whether such covariation is widespread clearly needs further attention. Moreover,
88 there has been a general lack of testing of these patterns where there is a female-
89 biased SSD. As copepods commonly have such female-bias sizes (e.g. 10, 11, 12),
90 and demonstrate a huge range in the degree of SSD, they provide an excellent
91 opportunity to do this.

92

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

105

106 In order to test multiple theories based around predicting the causes of SSD and its
107 variation we need animal and plant groups in which extensive and accurate data on
108 body size exist, and in which body size, life history and behaviour are diverse. As we
109 will show, copepods provide an excellent test case and allow quantitative examination
110 of major SSD-based theory. The subclass Copepoda, which are members of the class
111 Maxillopoda, are crustaceans and possibly the most abundant animal group on earth
112 [14]. The striking variability in mate seeking behaviours (including sedentary and
113 roving types in some parasitic families) and sex ratios allows for quantitative and
114 qualitative tests of model predictions [1]. Male planktonic copepods often develop
115 faster [15] and mature at a smaller size than females [16]. Some copepod families
116 (within the Diaptomoidea) require repeat mating since they are unable to store sperm
117 and often have near equitable sex ratios [17, 18]. Others (many non-Diaptomoidea

118 families) are able to store sperm [19] and can produce multiple batches of eggs from a
119 single copulation event [14, 20]. Higher rewards from single mating events may lead
120 males to high mortality risk when mate searching. This has been used to explain the
121 greater adult male mortality and female-biased adult sex ratios in this latter group [15,
122 17]. Copepods present an opportunity to test Volrath and Parker's [1] model more
123 widely, if male-male competition were an important factor then large differences
124 observed across copepod families may be expected to drive variation in SSD.

125

126 While many advances in understanding the patterns in sex ratios and dynamics of
127 mate encounter have been made in pelagic copepods over the last few years [e.g. 15,
128 17], no attempt has been made to link such aspects to size dimorphism. We take the
129 opportunity to do this here. The main objectives of this paper are therefore to test the
130 following hypotheses:

- 131 1. Male body size varies more than female body size among species (Rensch's
132 rule).
- 133 2. Allometric slopes are >1 and covary positively with female-biased SSD across
134 related clades, indicating selection on male size has been more intense.
135 Conversely, allometric slopes are <1 and covary negatively with female-
136 biased SSD, indicating selection on female size as been more intense (both
137 predicted by quantitative genetic theory).
- 138 3. Female-biased SSD increases with increasing female-biased OSR (following
139 the model of Vollrath and Parker).

140

141 **2. Material and Methods**

142 *Copepod Data:*

143 In order to test various theories of sexual size dimorphism we compiled SSD data for
144 over 400 species from more than 40 families and several dominant orders within the
145 Copepoda. We included species with diverse life styles, including: pelagic free-living,
146 host associated (i.e. Sapphirinidae and Lubbockiidae) and fully parasitic forms (i.e.
147 Chondracanthidae, Monstrillidae and Caligidae). Chondracanthidae (order
148 Poecilostromatoida) consists of highly modified copepods which are parasitic on
149 many marine fishes; in some of these parasites the male may derive nourishment from
150 the female to which they are attached [11]. Males may attach to young immature
151 females at the second copepodite stage [21] and complete development on the female,
152 remaining attached until death. The Monstrillidae (order Monstrilloida) are poorly
153 described biologically and ecologically, but are parasites of marine benthic
154 invertebrates, especially on polychaetes and gastropods [22]. In Monstrilloida only the
155 1st nauplius and adult stages are free-swimming; the other larval stages are highly
156 modified internal parasites. The adults emerge from their hosts to reproduce [23] and
157 are incapable of feeding. Finally, the family Caligidae (order Siphonostomatoida)
158 commonly termed sea lice, are free-living until the copepodid stage, whereupon both
159 sexes settle as ectoparasites on fish hosts, and feed on their mucus, epidermal tissue,
160 and blood. The female's ability to store sperm reduces the need for repeat mating,
161 while in some species the adult males are known to leave the host and rove for mates
162 more readily than do the females [24, 25].

163

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

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

175

176 The taxonomic level at which patterns in SSD are examined has important
177 implications to the outcome [7, 8], hence we consider this carefully. In order to
178 examine allometry of SSD we divided species into clades. Such divisions were made
179 on a taxonomic basis, by family and order, as is common practice, but with additional
180 consideration of distinctive life styles and SSD for the latter. Hence, the orders
181 included were: Calanoida, Cyclopoida, Harpacticoida, Monstrilloida,
182 Siphonostomatoida, and Poecilostomatoida. In the final order we excluded the family
183 Chondracanthidae which has a radically different SSD from the other members (fig.
184 2). All our data are available on Dryad (doi:10.5061/dryad.1556p).

185

186 *Data treatment:*

187 To allow examination of allometry of sexual size dimorphism within a clade, \log_{10}
188 male lengths were regressed against \log_{10} female lengths (Table 1). Reduced Major
189 Axis (RMA) regressions [using software from reference source 28] were applied, and
190 slopes (β) and 95% confidence intervals (CI) determined. This regression model does
191 not infer a dependent and independent variable, and is most commonly applied in
192 such SSD analysis. Using OLS regressions produces slightly shallower slopes, but

193 does not alter our findings in any significant way. Regressions were only performed
194 on clades with 5 or more values, consequently allometries of 27 diverse families were
195 determined. Slopes were defined as departing from isometry (i.e. from a value of 1) if
196 the 95% CIs did not bound 1 (fig. 3 and table 1). We do not undertake phylogenetic
197 correction when determining slopes because appropriate data for many families
198 considered here are incomplete or uncertain. We note however, that where this had
199 been undertaken for sub-sets of the data presented here it did not significantly alter the
200 outcome [16].

201

202 Sexual Size Dimorphism was also quantified using the widely utilised *SDI* index of
203 [29], where:

$$204 \quad SDI = (\text{mass of larger sex} / \text{mass of smaller sex}) - 1 \quad (1.1)$$

205

206 This index has an advantage of providing symmetrical results around zero regardless
207 of which sex is larger [29]. We followed the convention that the index is given as a
208 positive value when females are the larger sex, and as negative value when males are
209 larger. *SDI* values were derived on each species and then averaged to obtain the clade
210 specific value. We derived mass as a proxy, simply from the cube of the compiled
211 lengths [see 30].

212

213 We wished to test whether sexual size dimorphism is influenced by the degree of
214 male-male competition in pelagic free-living copepods [1]. In order to do this we
215 assume that differences in sex ratio and reproductive strategy (sperm storage by
216 females) should reflect the relative degree of such competition: a male-biased
217 (operational) sex ratio and the ability to store sperm would both intensify the male-

218 male competition for females. We used the adult sex ratios as compiled by Hirst and
219 Kiørboe [18]. This extensive set of male to female adult field abundance ratios
220 includes both families within and outside of the Diaptomoidea (data presented in Fig
221 4a). The data set includes sex ratios from ~35 species with almost 4000 individual
222 measurements. In many cases animals were sampled with vertically towed nets
223 covering all or most of the depth range of the species. In some instances sampling was
224 over discrete depth ranges, but we do not consider this will produce important errors
225 given the degree of averaging. Of course, making an inference that adult sex ratios
226 reflect adult mortality is dependent upon the recruitment of the sexes into this stage,
227 specifically that these recruit equally, which when tested has been shown to occur [as
228 examined in 15]. We are therefore confident that the large variation observed in adult
229 sex ratios across families reflects gross differences in adult mortality rates. We
230 undertook a correlation between mean family *SDI* values and corresponding adult sex
231 ratios to test the prediction that male-male competition may determine SSD [1].

232

233 **3. Results**

234 In the vast majority of copepod families females are larger than their conspecific
235 males (figs 2 and 4). Mean *SDI* values in free-living families span a range from -0.15
236 to 1.27 (Table 1), which compared with the parasitic copepods is very narrow (figs. 3
237 and 4). Across all 27 families only 3 have negative *SDI* values (i.e. with larger males
238 on average), while no order level comparison shows a male size bias. The families
239 with negative *SDI* values are Heterorhabdidae, Sapphirinidae and Lubbockiidae.
240 While there are a diverse range of life-styles and feeding types in free-living
241 copepods, Sapphirinidae and Lubbockiidae are somewhat distinctive, having an

242 ecology strongly tied to living on the surface of salps. Heterorhabdidae include many
243 carnivorous species, but are free-living.

244

245 The fully parasitic copepods show striking sexual size dimorphism, varying markedly
246 from one another and from the many free-living families. The parasitic
247 Chondracanthidae has a mean *SDI* of 1833 (Table 1), while the mean is 4.49 for
248 Monstrillidae and 1.51 in Caligidae. Species within Chondracanthidae are massively
249 body size skewed, more so than any other copepod family, with females commonly
250 being >1,000 times larger in mass (as approximated from length herein) than
251 conspecific males (fig. 2c). The females of Chondracanthidae are larger on average
252 than those of the free-living species, whereas their males are smaller [13] (fig. 2). By
253 contrast, parasitic Monstrillidae and Caligidae both tend to have males and females
254 which are at the larger end of the range represented by free-living species.

255

256 Isometry in SSD is found in 22 of the 27 families examined. Only in the families
257 Arietellidae, Augaptilidae and Sapphirinidae are β values significantly greater than 1,
258 while in Calanidae and Oithonidae they are significantly less than 1. In 5 of the 6
259 orders β -values are statistically indistinguishable from isometry, including in the
260 Calanoida, Cyclopoida, Harpacticoida, Monstrilloida and Siphonostromatoida.

261 However, we should caution that the final two only include data from single families.

262 The only order to diverge from this is Poecilostomatoida, having positive allometry,
263 which is largely driven by Sapphirinidae that commonly have male-biased SSD (fig.
264 3). Mean β -values for all clades (including family and order) fall between ~0.8 and
265 1.4 (fig. 3), even though the index of size dimorphism (*SDI*) in these same groups
266 varies by over 1,000-fold.

267

268 Male to female adult sex ratios span a 7-fold range across the free-living species, with
269 mean values by family being from 0.16 to 1.10 (fig 4a). There are important
270 differences between the non-Diaptomoidea (and *Oncaea*) families versus those that
271 need to constantly re-mate, the Diaptomoidea. The latter have a more equitable sex
272 ratio. Regressing family-specific mean *SDI* values against their respective male to
273 female adult sex ratios we find no significant relationship ($r^2 = 0.03$, $n = 11$, $P >$
274 0.10). Furthermore, *SDI* values are not significantly different between the
275 Diaptomodea and the non-Diaptomoidea groups (Welch two sample t-test, $t = 0.0871$,
276 $df = 6.788$, $p\text{-value} = 0.933$), while male to female sex ratios do differ significantly
277 (Welch two sample t-test, $t = -5.478$, $df = 4.736$, $p\text{-value} = 0.003$). In conclusion, we
278 find no evidence that sex ratios (and therefore the inferred degree of male-male
279 competition) relates to SSD or gross reproductive behaviours (as defined broadly by
280 the Diaptomoidea vs. non-Diaptomoidea categories).

281

282 4. Discussion

283 Allometry of Sexual Size Dimorphism

284 We begin by addressing our first two hypotheses (see Introduction), i.e., whether
285 copepods support Rensch's rule, and whether they demonstrate covariation between
286 the degree of sexual dimorphism and degree of allometry. In pelagic copepods
287 females of the species are commonly larger than the males (figs. 2 and 4). Across the
288 diverse copepod clades considered here β values indicate that isometry is almost
289 universal (fig. 3), hence we find little to support Rensch's rule. Previous studies on a
290 range of taxa have frequently found the degree of SSD to vary with body size. These
291 patterns have been reviewed for Mammalia, Aves, Reptilian, Amphibia, Arachnida

292 and Insecta [3]. In most instances these follow Rensch's rule, i.e. $\beta > 1$, and
293 exceptions to this only occurred when females were the larger sex. An extensive
294 comparison across birds found that Rensch's rule is commonly broken where female-
295 biased SSD occurs within a clade [7]. Recently, Blankenhorn et al. [31] evaluated the
296 evidence for Rensch's rule in a range of insect orders: the rule was found to apply
297 consistently to Diptera and Heteroptera, but not to any of the other insect groups
298 examined. This led them to conclude that the mechanisms causing the pattern are
299 unevenly distributed among taxa; our results further support this conclusion.

300

301 If Rensch's rule was general, and selection on males is the main driver of the
302 evolution of SSD, then allometric slopes should increase as the *SDI* increases across
303 clades. By contrast, if the evolution of size dimorphism were primarily driven by
304 selection on female size, then allometric slopes should decrease as the magnitude of
305 *SDI* increases (fig. 1, compare to fig. 3). As no significant relationships exist between
306 β and $\log_{10} SDI$ (the latter was logged to accommodate the skew) we find no support
307 for either of these predictions. The fact that relationships are commonly not
308 distinguishable from being isometric in many copepod clades suggests that selection
309 on each of the sexes may have been near equally important. Most previous empirical
310 assessments of allometry have focused on either vertebrates or invertebrates with
311 male-biased SSD (3, 6, 7, cf. 8) and in many of these studies the allometric slope
312 within clades often decreases as the magnitude of SSD increases (see fig. 2 of
313 reference [3]), this would tend to support selection on male size being a common
314 cause for the evolution of both positive allometry ($\beta > 1$) and male-biased SSD. By
315 contrast, analyses of clades that exhibit female-biased SSD indicate no clear patterns
316 to their allometry (no consistency in either female-divergent or male-divergent

317 allometry), indeed our analysis on copepods further reinforces this. Across related
318 clades when females are the larger sex, there is not strong evidence to support the
319 predictions of quantitative genetic theory [cf. 8].

320

321 **Life-History and SSD**

322 Kjørboe and Hirst's [32] model of size at maturation in free-living copepods shows
323 that high juvenile mortality favors early maturation at a smaller size, while late
324 maturation at a larger size becomes increasingly favored the steeper the increase in
325 reproductive output is with size. This prediction is consistent with classical life
326 history theory [33]. The balance between survival probability and reproductive
327 success determines the size and age at maturation. Vollrath and Parker [1] extended
328 such an argument by demonstrating that adult mortality may also impact optimal size
329 (age) at maturation; high mortality of the adult males leads to a female-biased
330 population, a relaxation of competition for females, and in turn this leads to earlier
331 maturation of males at a smaller size. Conversely, a low adult male mortality results
332 in intensified competition for females, in which circumstance larger male size is more
333 favorable. Importantly, rather than the numerical sex ratio being the relevant
334 parameter in these descriptions, it is the Operational Sex Ratio (OSR) [34]. The OSR
335 is the ratio of receptive females to ready-to-mate males, or the female/male sex ratio
336 corrected for 'time-outs', i.e., the fraction of time that each sex cannot mate because
337 they need to release one or several batches of eggs (females), or generate a new
338 spermatophore (males). In copepods the female time-outs are typically much longer
339 than male time-outs, and in some species the females need to be mated only once to
340 have sufficient sperm for the rest of their reproductive career. The question is

341 therefore whether inter-male competition for females is relevant or prevalent in
342 copepods, and hence whether the Vollerath and Parker model [1] applies.

343

344 *Free-living copepods*

345 The suggestion that OSR may account for SSD [1] appears unable to explain the
346 general lack of pattern in size dimorphism across the free-living copepod families, or
347 indeed the similarity in size ratios between Diaptomoidea and non-Diaptomodea (fig.
348 4). The sedentary vs roving dichotomy [1] is partly equivalent to ambush feeding
349 cyclopoid copepods, such as in the genus *Oithona*: in this example the female is an
350 ambush feeder and relatively non-motile, while the males spend ~1/3rd of their time
351 swimming at high speed in search for females [35]. As a result, the males have much
352 higher mortality, and adult sex ratios are strongly female-biased, typically with a male
353 to female ratio of 1:10 [15, 36]. However, timeout-ratios are strongly female-biased
354 because the females need to be mated only once, while the males can mate several
355 times per day, and OSR is likely less skewed than the sex ratio would suggest (fig. 4).
356 The other extreme can be represented by genera such as *Acartia*, in which males and
357 females have very similar mate finding behaviors [37] and mortalities, and adult sex
358 ratios near 1:1 (fig. 4); they may also have similar time-outs, because the males can
359 produce one to a small number of spermatophores each day, and females produce a
360 batch of eggs per day [38]. In *Acartia* male-male competition may potentially be
361 stronger and SSD would be predicted to be less skewed following Vollerath & Parker's
362 model [1], yet there are no obvious differences in the degree of SSD between *Acartia*
363 and *Oithona* (fig. 4). Our results therefore question the ability of their model [1] to
364 predict or explain patterns in SSD in copepods, and hence its generally universality.

365 Clearly more tests of this type across other taxa are needed to examine the degree to
366 which the predictions hold.

367

368 Another question is: how would male-male competition materialize in the pelagic
369 environment inhabited by free-living copepods? Combat competition is not an option
370 in copepods, but scramble competition is. Mate guarding by physically clasping the
371 female has been observed in a small number of copepod species [39], but is certainly
372 not widespread. Sperm competition may occur, but we have no direct evidence for
373 this as yet in the free-living pelagic species (although we note that there is evidence
374 for this in parasitic species). It is more likely that females become more or less choosy
375 depending on the availability of males, but importantly it is the absolute density of the
376 opposite sex rather than the relative densities that decides the intensity of choosiness
377 [40]. In the case of a low male density, when it is difficult for a female to find an
378 alternative mate, the female may mate indiscriminately. In several species large males
379 have a higher chance of fertilizing a female (and a larger female a higher chance of
380 being fertilized), and these differences are due to mate choice [37, 41, 42].

381

382 Evidence that reduced male-male competition can lead to stronger SSD [1], as
383 expected when adult sex ratio is female-biased, is weak or non-existing in free-living
384 pelagic copepods. However, size-dimorphism may simply arise when the advantage
385 of delayed maturation differs between genders [32]. In fact, there is no reason to
386 expect that the advantages of delayed maturation should be the same between the
387 sexes. In females, egg production may increase with size [32], and larger females
388 have a higher chance of being fertilized [38, 41]. These factors favor late maturation
389 and larger adult size, to the exact extent that it balances juvenile mortality. For males

390 we similarly know that larger males produce larger spermatophores and these contain
391 more spermatozoa [42]. Larger males also have a greater chance of fertilizing a
392 female [38, 41], which will act to select for later maturation in males to the extent that
393 this is balanced against juvenile mortality risk. Gamete production between males and
394 females appear to be very differently limited however. While females can produce
395 eggs at a daily rate equivalent to their own body mass [43, 44], males can produce
396 only a few spermatophores per day [45] each with rather few sperm cells [42].
397 Although such difference do not demonstrate differences in the relative advantage of
398 late maturation, they are suggestive of this.

399

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

407

408 *Parasitic Copepods*

409 Vollrath and Parker's explanation for dwarf males are in part supported by their
410 occurrence in a wide range of species where the female is relatively sedentary, while
411 the males rove and suffer higher mortality [1, 47]. In Caligidae, including the well-
412 known sea-lice, the males can mature somewhat earlier than females, but they settle at
413 a similar development stage [48]. Some species in this family have males which are
414 more mobile, and more likely than the females to disperse as adults in the absence of

415 the opposite sex [24, 25]. As Connors et al [25] point out, ‘Male fitness is therefore
416 dependent on access to mates, whereas female fitness is contingent on access to
417 resources for egg production. The resulting asymmetry in reproductive investment
418 likely underlies sex-specific benefits of dispersal as lice approach sexual maturity’.
419 ‘Roving’ behaviour, which includes leaving the host, may represent significant
420 mortality risk for the male (and this is dissimilar to that of the attached female) given
421 that being attached will afford protection from high levels of mortality which small
422 pelagic organisms typically suffer [18]. The markedly smaller size of males in the
423 parasitic Caligidae, and the observation that females are relatively sedentary while
424 males rove, qualitatively supports Volrath and Parker’s predictions. By contrast,
425 Chondracanthidae males may be dwarf parasites on the parasitic females [11], and
426 their size reduction given their likely sedentary nature may be driven more by their
427 direct coupling to the female rather than adult mortality. Through most of the life of
428 Monstrilloida (other than first nauplii and adults) the larvae are an internal parasite of
429 benthic organisms [22, 49]. We have no evidence of difference in risks between the
430 males and females of Monstrilloida and their *SDI* values are intermediate between the
431 two other parasitic families included here [see also 12, 50]. Therefore, while we find
432 that many parasitic taxa may display much larger females than males, we do not have
433 evidence that males always have a risky mate roving strategy. Differences in mortality
434 between the sexes in parasitic copepods are needed in future in order to explore this
435 issue more fully.

436

437 Dwarf males have been linked to reduced male-male competition [1]. Intriguingly,
438 precocious coupling and precopulatory mate guarding by the males of some Caligidae
439 [48, 51, 52] would rather suggest strong male-male competition. This is further

440 suggested by males having spermatophores which can block further mating by
441 females for some time [24, 53]. Mate guarding by males has been considered to be
442 more marked when there is a male-biased sex ratio, and hence high inter-male
443 competition [54, 55]. Many males of benthic and even parasitic harpacticoid copepods
444 also show some degree of mate guarding, and those which do often have strong
445 female-biased SSD, e.g. *Tisbe* [56]. There are therefore clear contradictions here.
446 Pelagic environments may be uncondusive to mate guarding in free-living copepods
447 because of increased predation risk from such a strategy [39], even when male
448 competition is strong. The degree to which mate-guarding may be associated with
449 dwarfing by males is in need of exploration both within the copepods and within other
450 groups of organisms too. To build and test quantitative models of SSD in future we
451 will need information on the role of body size in determining male fertility, and data
452 on the sex- and stage-dependent mortality across families with contrasting life-
453 histories.

454

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460

461 **Appendix**

462 Our data are available as an online appendix on Dryad (doi:10.5061/dryad.1556p).

463

464 **References**

- 465 1. Vollrath F, Parker G. 1992 Sexual dimorphism and distorted sex ratios in
466 spiders. *Nature* **360**, 156-159.
- 467 2. Darwin C. 1874 The descent of man and selection in relation to sex.
468 Humboldt, NY
- 469 3. Fairbairn DJ. 1997 Allometry for sexual size dimorphism: pattern and process
470 in the coevolution of body size in males and females. *Annu Rev Ecol Syst* **28**,
471 659-687.
- 472 4. Blanckenhorn WU, Dixon AFG, Fairbairn DJ, Foellmer MW, Gibert P, van
473 der Linde K, Meier R, Nylin S, Pitnick S, Schoff C, Signorelli M, Teder T,
474 Wiklund C. 2007 Proximate causes of Rensch's rule: does sexual size
475 dimorphism in Arthropods result from sex differences in development time?
476 *Am Nat* **169**, 245-257.
- 477 5. Rensch B. 1960 Evolution above the species level. Columbia University Press,
478 NY.
- 479 6. Abouheif E, Fairbairn DJ. 1997 A comparative analysis of allometry for
480 sexual size dimorphism: assessing Rensch's rule. *Am Nat* **149**, 540-562.
- 481 7. Webb TJ, Freckleton RP. 2007 Only half right: species with female-biased
482 sexual size dimorphism consistently break Rensch's Rule. *PLoS ONE* **2**, e897.
483 doi:10.1371/journal.pone.0000897
- 484 8. De Lisle SP, Rowe L. 2013 Evolution of allometry and sexual dimorphism
485 across higher taxa. *Am Nat* **182**, 630-639.
- 486 9. Zeng Z-B. 1988 Long-term correlated response, interpopulation covariation,
487 and interspecific allometry. *Evolution* **42**, 363-374.

- 488 10. Hirst AG, Sheader M, Williams JA. 1999 Annual pattern of calanoid copepod
489 abundance, prosome length and minor role in pelagic carbon flux in the Solent,
490 U.K. *Mar Ecol Prog Ser* **177**, 133-146.
- 491 11. Østergaard P, Boxshall GA. 2005 Giant females and dwarf males: a
492 comparative study of nuptial organs in female Chondracanthidae (Crustacea:
493 Copepoda). *Zool Anz* **243**, 65-74.
- 494 12. Poulin R. 1996 Sexual size dimorphism and transition to parasitism in
495 copepods. *Evolution* **50**, 2520-2523.
- 496 13. Emlen ST, Oring LW. 1977 Ecology, sexual selection, and the evolution of
497 mating systems. *Science* **197**, 215-223.
- 498 14. Ohtsuka S, Huys R. 2001 Sexual dimorphism in calanoid copepods:
499 Morphology and function. *Hydrobiol* **453/454**, 441-466.
- 500 15. Hirst AG, Bonnet D, Conway DVP, Kiørboe T. 2010 Does predation control
501 adult sex ratios and longevities in marine pelagic copepods? *Limnol Oceanogr*
502 **55**, 2193-2206
- 503 16. Østergaard P, Boxshall GA, Quicke DLJ. 2005 Dwarfs or giants? Sexual size
504 dimorphism in Chondracanthidae (Copepoda, Poecilostomatoida).
505 *Crustaceana* **78**, 397-408.
- 506 17. Kiørboe T. 2006 Sex, sex-ratios, and the dynamics of pelagic copepod
507 populations. *Oecologia* **148**, 40-50.
- 508 18. Hirst AG, Kiørboe T. 2002 Mortality of marine planktonic copepods: global
509 rates and patterns. *Mar Ecol Prog Ser* **230**, 195-209.
- 510 19. Barthélémy R-M, Cuoc C, Defaye D, Brunet M, Mazza J. 1998 Female genital
511 structures in Diaptomoidea (Copepoda Calanoida). *Phil Trans Roy Soc*
512 *London B* **353**, 721-736.

- 513 20. Marshall SM, Orr AP. 1952 On the biology of *Calanus finmarchicus*. VII.
514 Factors affecting egg production. *J Mar Biol Assoc UK* **30**, 527-547.
- 515 21. Heegaard P. 1947 Contribution to the phylogeny of the Arthropods.
516 Copepoda. *Spolia Zool Mus Haun* **8**, 1-236.
- 517 22. McAlice BJ, Jaeger GB. 1982 Seasonality of *Monstrilla helgolandica* Claus,
518 1863 (Copepoda, Monstrilloida) and the occurrence of the other monstrillids
519 in Maine. *J Crust Biol* **2**, 45-47.
- 520 23. Thompson PKM. 1973 Occurrence of *Cymbasoma longispinosus* (Copepoda:
521 Monstrilloida) from the Indian seas. *J Mar Biol Ass India* **15**, 616-620.
- 522 24. Hull MQ, Pike AW, Mordue AJ, Rae GH. 1998 Patterns of pair formation and
523 mating in an ectoparasitic caligid copepod *Lepeophtheirus salmonis* (Kroyer
524 1837): implications for its sensory and mating biology. *Philos Trans R Soc
525 Lond B Biol Sci* **353**, 753-764.
- 526 25. Connors BM, Lagasse C, Dill LM. 2011 What's love got to do with it?
527 Ontogenetic changes in drivers of dispersal in a marine ectoparasite.
528 *Behavioral Ecology*. doi:10.1093/beheco/arr024
- 529 26. Hirst AG, McKinnon AD. 2001 Does egg production represent adult female
530 copepod growth? A call to account for body weight changes. *Mar Ecol Prog
531 Ser* **223**, 179-199.
- 532 27. WoRMS Editorial Board. 2014 World Register of Marine Species. Available
533 from <http://www.marinespecies.org> at VLIZ. (Accessed 2014-03-11).
- 534 28. Bohonak AJ, van der Linde K 2004 RMA: software for Reduced Major Axis
535 regression, Java version. Available from
536 <http://www.kimvdlinde.com/professional/rma.html>.

- 537 29. Lovich JE, Gibbons JW. 1992 A review of techniques for quantifying sexual
538 size dimorphism. *Growth Dev Aging* **56**, 269-281.
- 539 30. Hirst AG. 2012 Intra-specific scaling of mass to length in pelagic animals:
540 ontogenetic shape change and its implications. *Limnol Oceanogr* **57**, 1579-
541 1590.
- 542 31. Blanckenhorn WU, Meier R, and Teder T. 2007 Rensch's rule in insects:
543 patterns among and within species. In: Sex, Size and Gender Roles
544 evolutionary studies of sexual size dimorphism. eds. Fairbairn DJ,
545 Blanckenhorn WU, Székely T. Oxford University Press, Oxford.
- 546 32. Kiørboe T, Hirst AG. 2008 Optimal development time in pelagic copepods. *Mar*
547 *Ecol Prog Ser* **367**, 15-22.
- 548 33. Stearns SC. 1992 The evolution of life histories. Oxford University Press,
549 Oxford.
- 550 34. Clutton-Brock TH, Vincent ACJ. 1991 Sexual selection and the potential
551 reproductive rates of males and females. *Nature* **351**, 58-60
- 552 35. Kiørboe T. 2007 Mate finding, mating, and population dynamics in a
553 planktonic copepod *Oithona davisae*: There are too few males. *Limnol*
554 *Oceanogr* **52**, 1511-1522.
- 555 36. Hirst AG, Ward P. 2008 Spring mortality of the cyclopoid copepod *Oithona*
556 *similis* in polar waters. *Mar Ecol Prog Ser* **372**, 169-180.
- 557 37. Bagøien E, Kiørboe T. 2005 Blind dating-mate finding in planktonic
558 copepods. III. Hydromechanical communication in *Acartia tonsa*. *Mar Ecol*
559 *Prog Ser* **300**, 129-133.

- 560 38. Ceballos S, Kiørboe T. 2010 First evidence of sexual selection by mate choice
561 in marine zooplankton. *Oecologia* **164**, 627-635. DOI 10.1007/s00442-010-
562 1755-5
- 563 39. Titelman J, Varpe Ø, Eliassen S, Fiksen Ø. 2007 Copepod mating: chance or
564 choice? *J Plankton Res* **29**, 1023-1030.
- 565 40. Kokko H, Monnagha P. 2001 Predicting the direction of sexual selection. *Ecol*
566 *Lett* **4**, 159-165.
- 567 41. Ceballos S Kiørboe T. 2011 Senescence and sexual selection in a pelagic
568 copepod. *PLoS ONE* **6**. e18870. doi:10.1371/journal.pone.0018870
- 569 42. Sichlau MH, Kiørboe T. 2011 Age- and size-dependent mating performance
570 and fertility in a pelagic copepod, *Temora longicornis*. *Mar Ecol Prog Ser*
571 **442**, 123-132.
- 572 43. Hirst AG, Bunker AJ. 2003 Growth in marine planktonic copepods: global
573 rates and patterns in relation to chlorophyll *a*, temperature, and body weight.
574 *Limnol Oceanogr* **48**, 1988-2010.
- 575 44. Bunker AJ, Hirst AG. 2004 Fecundity of marine planktonic copepods: global
576 rates and patterns in relation to chlorophyll *a*, temperature and body weight.
577 *Mar Ecol Prog Ser* **279**, 161-181.
- 578 45. Escaravage V, Soetaert K. 1993 Estimating secondary production for the
579 brackish Westerschelde copepod population *Eurytemora affinis* (Poppe)
580 combining experimental data and field observations. *Cah Biol mar* **34**, 201-
581 214.
- 582 46. Heron AC. 1973 A specialized predator-prey relationship between the
583 copepod *Sapphirina angusta* and the pelagic tunicate *Thalia democratica*.
584 *JMBA UK* **53**, 429-436.

- 585 47. Vollrath F. 1998 Dwarf males. *TREE* **13**, 159-163.
- 586 48. Costello MJ. 2006 Ecology of sea lice parasitic on farmed and wild fish.
587 *Trends in Parasitology* **22**, 475-483.
- 588 49. Oliveira Dias C. 1996 Monstrilloida (Copepoda) off the Brazilian coast.
589 *Hydrobiol* **324**, 253-256.
- 590 50. Poulin R. 1995 Clutch size and egg size in free-living and parasitic copepods:
591 A comparative analysis. *Evolution* **49**, 325-336.
- 592 51. Anstensrud M. 1992 Mate guarding and mate choice in two copepods,
593 *Lernaeocera branchialose* (L.) (Pennellidae) and *Lepeophtheirus pectoralis*
594 (Muller) (Caligidae), parasitic on Flounder. *J Crust Biol* **12**, 31-40.
- 595 52. Todd CD, Stevenson RJ, Reinard H, Ritchie MG. 2005 Polyandry in the
596 ectoparasite copepod *Lepeophtheirus salmonis* despite complex precopulatory
597 and postcopulatory mate-guarding. *Mar Ecol Prog Ser* **303**, 225-234.
- 598 53. Ritchie G, Mordue AJ, Pike AW, Rae GH. 1996 Observations on mating and
599 reproductive behaviour of *Lepeophtheirus salmonis*, Kroyer (Copepoda:
600 Caligidae). *J Exp Mar Biol Ecol* **201**, 285-298.
- 601 54. Grafen A, Ridley M. 1983 A model of mate guarding. *J Theor Biol* **102**: 549-
602 567.
- 603 55. Elwood RW, Dick JTA. 1990 The amorous *Gammarus*: the relationship
604 between precopula duration and size-assortative mating in *G. pulex*. *Anim*
605 *Behav* **39**, 828- 833.
- 606 56. Dürbaum J. 1995 Discovery of postcopulatory mate guarding in Copepoda
607 Harpacticoida (Crustacea). *Mar Biol* **123**, 81-88.
- 608

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

620

621

622 Taxa	n	<i>SDI</i>	β [95%CI range]	<i>a</i>	<i>r</i>
623 By Order:					
624 Calanoida	252	0.529	0.989 [0.965-1.013]	-0.007	0.98
625 Cyclopoida	11	1.034	0.909 [0.731-1.087]	0.176	0.97
626 Harpacticoida	9	0.931	0.948 [0.747-1.149]	0.069	0.97
627 Poecilostromatoida	71	0.276	1.180 [1.114-1.246]	-0.598	0.97
628 Siphonostomatoida (Caligidae)	29	1.511	1.230 [0.923-1.537]	-0.895	0.77
629 Monstrilloida (Monstrillidae)	8	4.487	0.851 [0.548-1.154]	0.287	0.93
630					
631 By Family:					
632 Acartiidae	17	0.521	0.887 [0.527-1.247]	0.294	0.67
633 Aetideidae	19	0.201	1.204 [0.971-1.437]	-0.838	0.93
634 Arietellidae	7	0.470	1.124 [1.054-1.194]	-0.485	1.00
635 Augaptilidae	24	0.927	1.359 [1.154-1.564]	-1.399	0.94
636 Calanidae	15	0.569	0.857 [0.765-0.949]	0.438	0.98
637 Candaciidae	11	0.230	1.041 [0.814-1.268]	-0.167	0.96
638 Centropagidae	15	0.326	1.006 [0.931-1.081]	-0.059	0.99
639 Chondracanthidae	40	1833	0.837 [0.634-1.040]	-0.291	0.68
640 Clausocalanidae	9	0.370	0.982 [0.638-1.326]	0.019	0.92

641	Corycaeidae	18	0.634	0.931 [0.795-1.067]	0.152	0.96
642	Euchaetidae	12	0.597	0.891 [0.638-1.144]	0.358	0.92
643	Heterorhabdidae	12	-0.149	0.966 [0.819-1.113]	0.136	0.98
644	Lubbockiidae	13	-0.080	0.972 [0.586-1.358]	0.095	0.80
645	Lucicutiidae	14	0.212	1.022 [0.988-1.056]	-0.102	1.00
646	Metridinidae	13	0.485	1.138 [0.968-1.308]	-0.536	0.97
647	Oithonidae	10	1.104	0.799 [0.622-0.976]	0.480	0.96
648	Oncaeidae	19	1.271	0.890 [0.748-1.032]	0.207	0.95
649	Paracalanidae	7	0.347	0.792 [0.343-1.241]	0.573	0.87
650	Phaennidae	9	0.489	1.001 [0.807-1.195]	-0.050	0.98
651	Pontellidae	11	0.404	1.044 [0.868-1.220]	-0.198	0.97
652	Pseudocyclopiidae	6	0.061	0.987 [0.661-1.313]	0.031	0.97
653	Sapphirinidae	21	-0.710	1.189 [1.031-1.347]	-0.602	0.96
654	Scolecitrichidae	12	0.256	0.896 [0.788-1.004]	0.337	0.99
655	Stephidae	5	0.185	0.924 [0.667-1.181]	0.211	0.99
656	Temoridae	10	0.451	0.977 [0.611-1.343]	0.026	0.89

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661 **Figures:**

662 **Figure 1.** The covariation of allometric slopes (log male versus log female size)
663 against the Sexual Dimorphic Index (*SDI*), in this example the case of female-biased
664 *SDI* is given. If Rensch's rule is general and selection on males is a main driver of the
665 evolution of SSD then looking across related clades the allometric slopes will increase
666 as the magnitude of *SDI* increases (denoted by dashed line). Alternatively, if the
667 evolution of SSD is driven primarily by selection on female size then allometry will
668 become female divergent (the allometric slope will decrease) as the magnitude of *SDI*
669 increases (solid line) across clades. Plot adapted from De Lisle and Rowe [8].

670

671 **Figure 2.** Pelagic copepod sizes (prosome or total lengths) in matched species-
672 specific pairs. Upper panels, male versus female lengths, with RMA regressions
673 through each identified clade: a. Calanoida, b. Cyclopoida, Harpacticoida, and
674 Poecilostomatoida (excluding Chondracanthidae), c. Chondracanthidae, Monstrillidae
675 and Caligidae. Data are available for only one family within these last two orders.
676 Plots d-f give female to male length ratios versus female length for the species from
677 the respective panels above. Dashed lines indicate equal female to male lengths (and
678 hence isometry) across all graphs.

679

680 **Figure 3.** Allometric slopes (β) versus mean *SDI* by: a. by family, and b. by order
681 (also including Chondracanthidae for comparison). Dashed horizontal lines indicates
682 isometry. Error bars represent 95% CIs of slope values. Filled symbols indicate a
683 significant difference from isometry, while for open symbols there is no difference.
684 Note that the very high *SDI* value for Chondracanthidae which falls off the scale is
685 indicated.

686

687 **Figure 4.** Sexual characteristics of marine copepods by family: a. Adult male to
688 female sex ratios, open circles give individual study means, filled circles family
689 means (data from Hirst and Kiørboe 2002). b. Adult female to male length ratios,
690 free-living families and associated families indicated. c. Adult female to male length
691 ratios in the parasitic families. Note scale change between panels b and c. Means
692 ($\pm 95\%$ CI) (in panels b and c) are only shown where $n \geq 3$. The symbols +, o and -
693 indicate whether female to male size ratios are significantly greater, less than, or not
694 significantly different from 1 respectively.

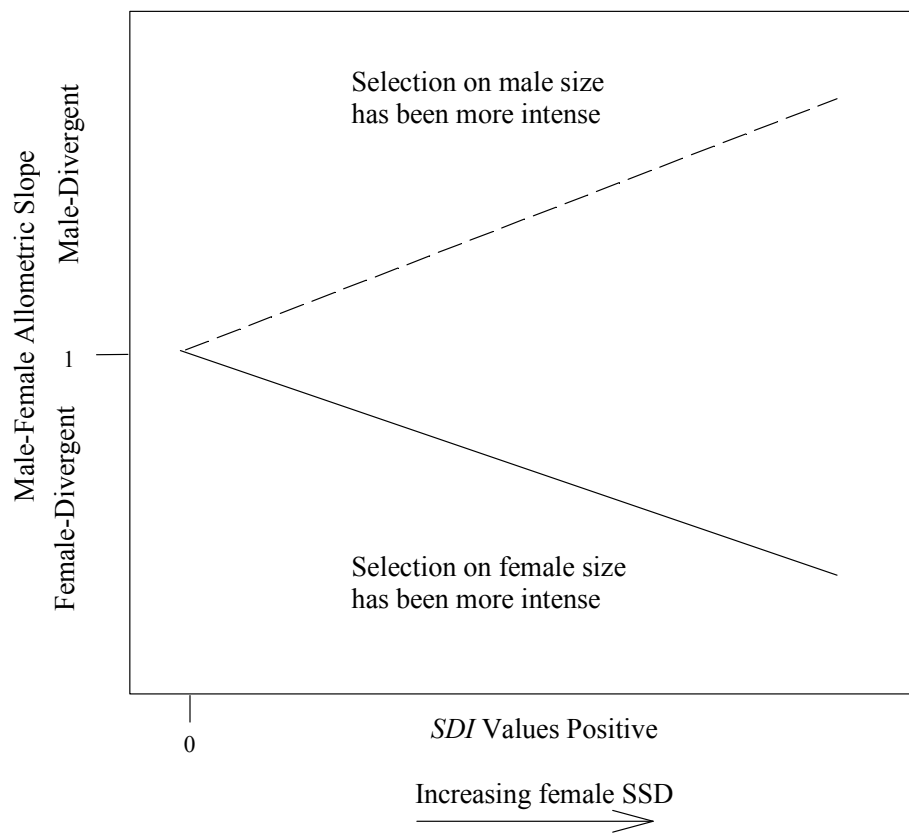
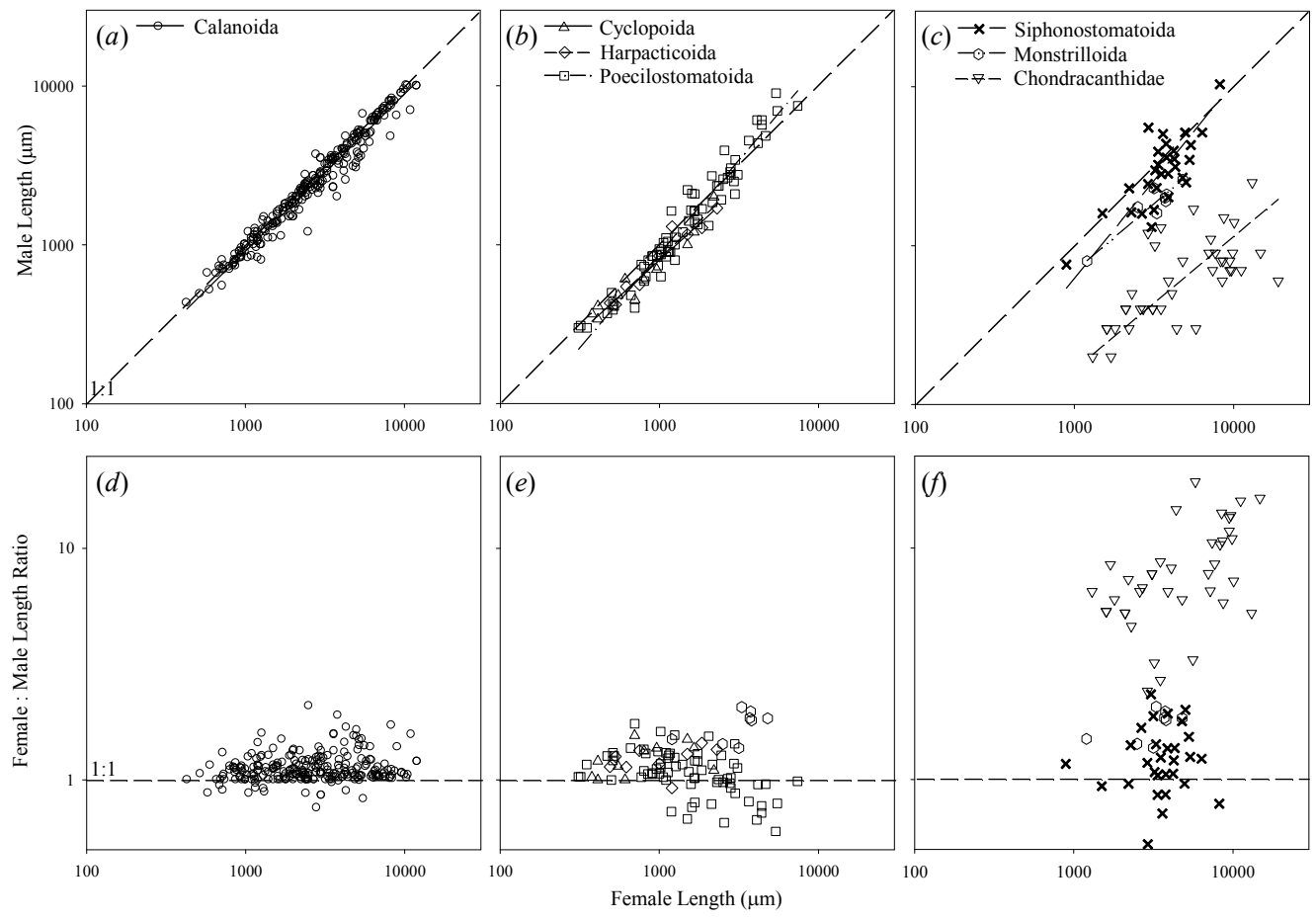
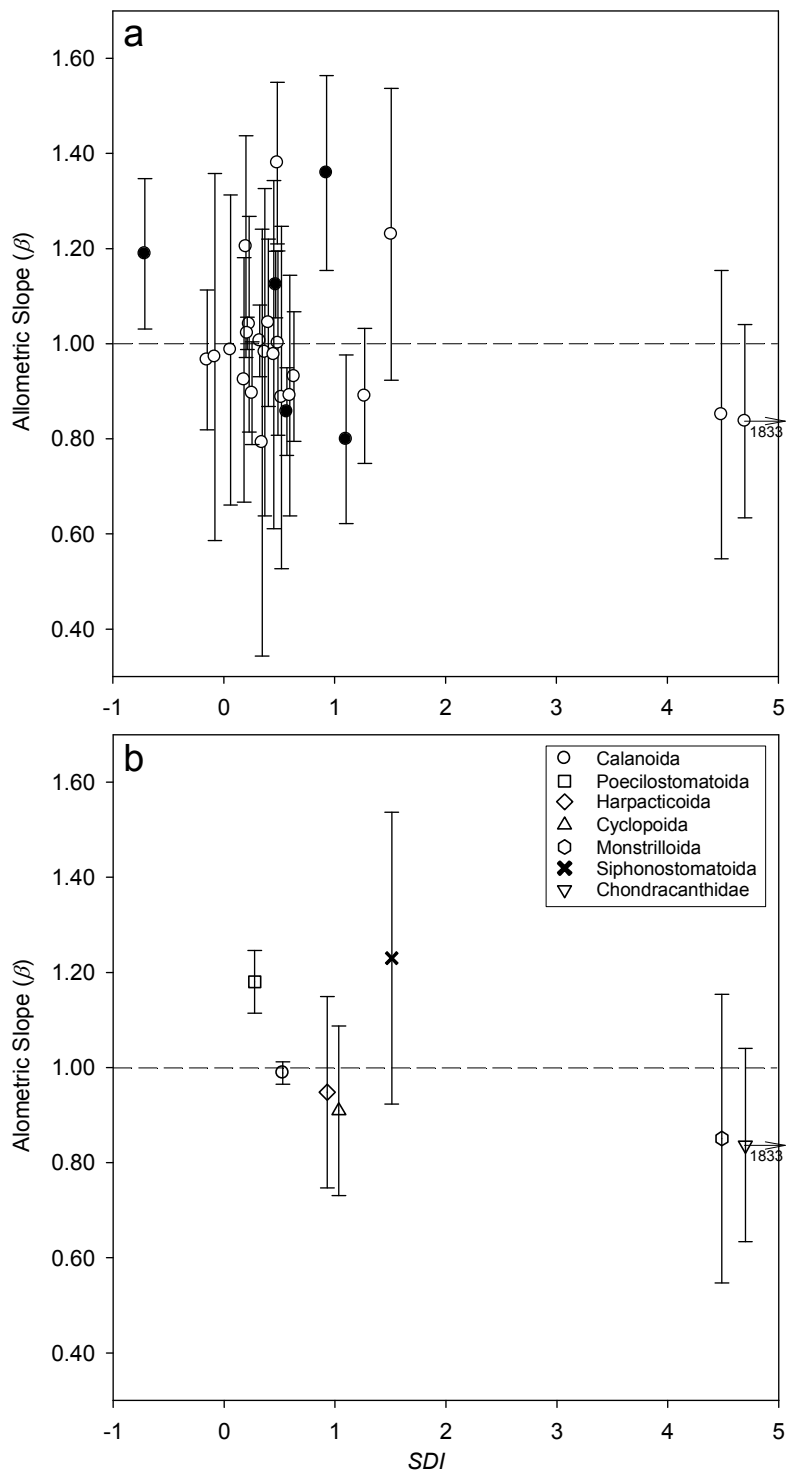


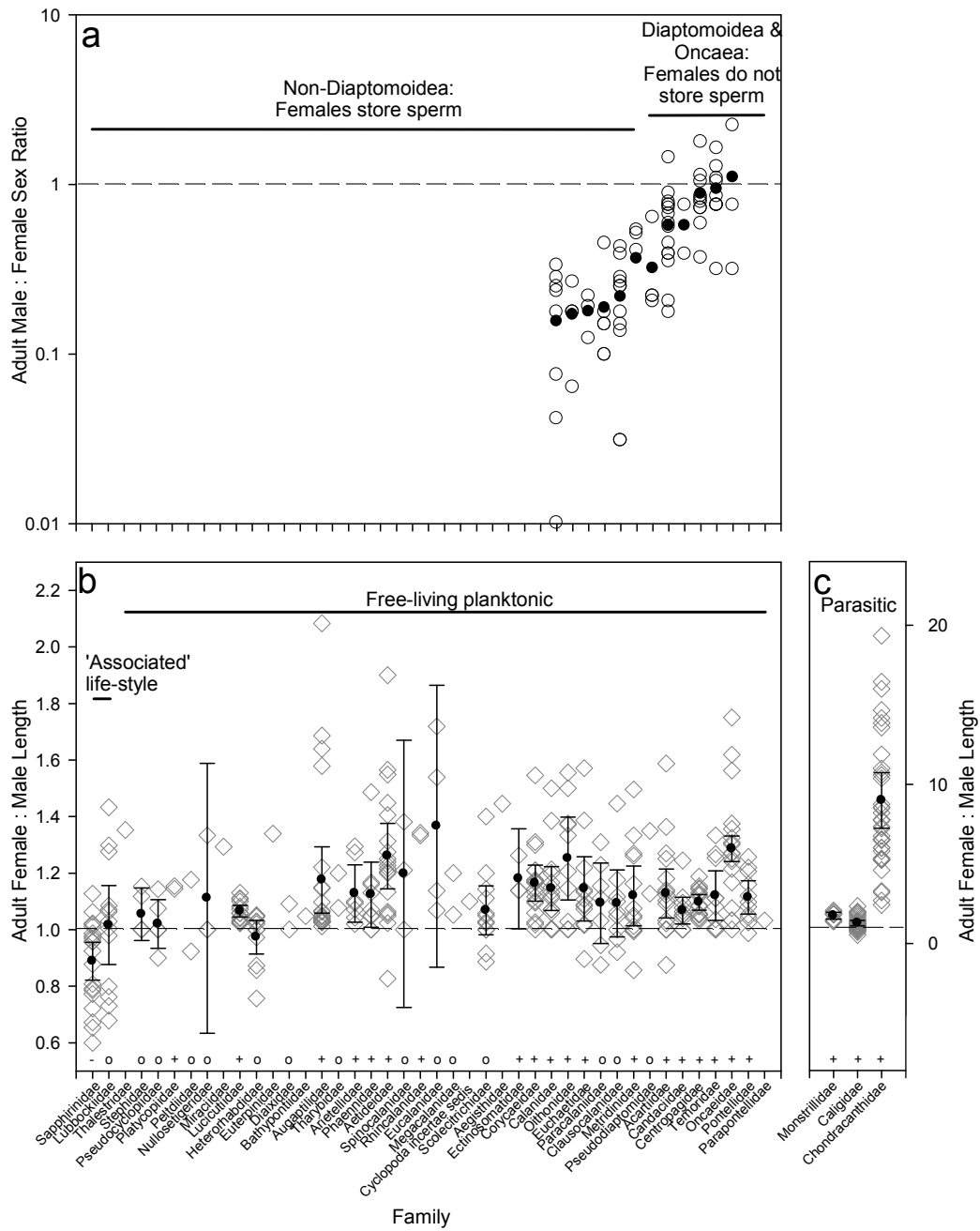
Figure 1



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Figure 4