

Dwarfs or giants? Sexual size dimorphism in Chondracanthidae (Poecilostomatoida, Copepoda)

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Summary

Sexual size dimorphism in the Chondracanthidae is very marked: whether it is a consequence of males being dwarfs or females becoming giants is investigated. Chondracanthid females are between two and 30 times larger than their conspecific males. Plotting contrasts in male size against female size and vice versa lead to opposing results, namely that the relationship between male and female size is allometric in the first instance and isometric in the second. Based on the results of an analysis of sexual size dimorphism against morphological distance, although not significant when phylogeny is controlled for, we argue that the relationship between males and females might be allometric, i.e. showing a trend towards increasing sexual size dimorphism. Both sexes show changes in size compared with free-living forms, indicating that changes in sexual size dimorphism are not limited to one sex. Chondracanthid females are probably selected for high fecundity leading to large body size, whereas males are probably selected for small size. If the male receives nutrients from the female, a small male is less drain on the female's resources, which leaves more energy that can be allocated into egg production. Our data suggest that chondracanthid males are dwarfs and that chondracanthid females are giants.

Keywords: sexual size dimorphism, copepods, Chondracanthidae, independent contrast

1. INTRODUCTION

Sexual dimorphism is defined as morphological differences between sexually mature males and females (Fairbairn 1997) and sexual size dimorphism (SSD) is a common phenomenon within sexually reproducing species, though its expression varies with males typically being larger than females in mammals and birds, while the opposite is the case for most other taxa.

Among the parasitic copepods a variety of different SSD strategies is found. Some species do not show any SSD in body length (which does not mean they cannot show SSD in other morphological traits e.g. maxilliped and antenna size). Examples include the sea louse *Caligus minimus* (Caligidae) and the harpacticoid *Tegastes cnidicus* (Tegastidae) (Kabata 1979; Humes 1981). However, most species show some degree of body length SSD.

Occasionally males are larger than their female counterpart, but in such cases they are only slightly larger (to a maximum of 1.25 times the body length of the female). Examples include both symbionts of invertebrates, such as *Monocheres cagarrensis* (Asterocheridae) on sponges (Johnsson & Bustamante 1997), and fish parasites such as *Caligus curtus* (Caligidae) (Kabata 1979). In the great majority of cases, SSD is female-biased and can be extreme. In fish parasites such as *Caligus zeii* (Caligidae) (Kabata 1979), and in symbionts of invertebrate hosts such as *Scottomyzon gibberum* (Asterocheridae) on echinoderms (Gotto 1993) and *Lichomolgus digitatus* (Lichomolgidae) on corals (Humes & Ho 1968) the females are about 1.25 times longer than males. However, more extreme cases of SSD are found in the fish parasite families Lernaeopodidae (e.g. *Clavellisa scombri*) and Sphyriidae (e.g. *Tripaphylus musteli*), where the postmetamorphic adult females are approximately 25 times larger than males (Kabata 1979, 1992). Females of fish parasite *Lernaeocera branchialis* (Pennellidae) are about 45 times larger than their males (Kabata 1992). The most extreme case of sexual size dimorphism involves *Gonophysema gullmarensis* in the ascidian, *Ascidella aspersa*,

which is cryptogonochoric, with the mature male reduced to little more than a testis, which is housed within a special receptacle in the female genital apparatus (Bresciani & Lützen 1960).

The proportional relationship between the mean values of the trait of two sexes is the most intuitive quantitative measure of SSD and is often expressed as the ratio of male:female body size. However, the use of ratios has been questioned and various other measures have been proposed. For example, the use of residuals from the regression of male against female values has been suggested (Ranta et al. 1994) and is probably the most widely used alternative. The lack of consensus in the literature whether to use ratios or residuals to measure SSD led Smith (1999) to look at the statistics behind the two approaches. It is evident that residuals cannot replace ratios and two equally appropriate ratio measures of SSD are recommended: one on a logarithmic scale ($\ln [F/M]$) (i.e. \ln (mean female length) - \ln (mean male length)), and one on a linear scale (the "two-step-ratio"). The property of both ratios is that they can also be used in comparative methods when correction for phylogenetic relationships among species in a data set is needed (Smith 1999).

Evidence suggests that SSD reflects the adaptation of males and females to their different reproductive roles (Fairbairn 1997). SSD has often been interpreted as being controlled by sexual selection alone, while natural selection or ecological divergence has been claimed not to play an important part in its evolution. There are examples of adaptation of the sexes to different ecological niches, and ecological divergence should therefore not be overlooked as a possible factor although testing this hypothesis empirically is problematic (Shine 1989). Fairbairn (1997) argued that it is difficult to exclude the hypothesis that trophic dimorphism evolved as a consequence of pre-existing sexual dimorphism and concluded that niche divergence only plays a subsidiary role in the evolution of sexual dimorphism. Shine (1989) argued that sexual and natural selection can act at the same time in the same taxon and

that the ecological divergence hypothesis should not be rejected just because of difficulties in testing it.

Among sexually dimorphic invertebrates the female is usually larger than the male and it has been postulated since the time of Darwin, that large female size is typically driven by selection for high reproductive output as increases in female size have a greater positive impact on fitness than similar increases in males (Shine 1988, 1989). In parasites, a high reproductive output should be strongly favoured because of low probability of successful transmission, which is why female-biased size dimorphism in dioecious parasite taxa is expected (Poulin, 1996). Shine (1988) argued that this fecundity advantage model only applies to animals that are not energy-limited. Small male size, however, is more complicated to explain (Vollrath 1998). Often the reproductive success of male invertebrates is dependent on encounter rates with females and small, mobile males have been found to be favoured (Ghiselin 1974).

SSD is very marked in the copepod family Chondracanthidae. The size difference between sexes is variable, but females up to 30 times longer than their conspecific males have been recorded (e.g. *Medesicaste penetrans*) (Ho 1970) and chondracanthid males have often been referred to as dwarfs (e.g. Ho 1970; Kabata 1979; Rousset & Raibaut 1983). In Chondracanthidae, there is usually only one male per female, the former typically being found attached to the female genital region, gripping onto her nuptial organs with their antennae. It is speculated that the males of *Chondracanthus lophii* feed on secretions produced by the female in glands associated with the nuptial organs (Østergaard 2004; Østergaard & Boxshall in press). Vollrath (1998) defined a 'true' dwarf male as being on average 50% or less of the female size, and noted that this can be achieved by two different developmental mechanisms: 1) a reduction in the number of larval stages, or 2) a reduction in the time spent at each stage.

Alternatively, as Vollrath (1998) states, relatively small males may just be a consequence of natural selection for large females.

We address the following question: Are chondracanthid males true dwarfs, or are they only small relative to females that have become giants? We examine the distribution of body size on a genus-level phylogeny of Chondracanthidae to reveal whether there is any consistent pattern in the direction of body-size evolution in the sexes.

2. MATERIALS AND METHODS

Body size is defined as the length from anterior margin of the cephalosome to the posterior end of the urosome, excluding the caudal setae. Lengths of chondracanthids were taken from the literature (Østergaard 2003). Body lengths for 46 outgroup species (Taeniacanthidae and Bomolochidae) and for 493 species of free-living copepods (representing 213 genera from 71 families and 6 orders) were recorded (see electronic appendix for a full list of species and references on following URL: <http://www....>). Values used were either means based on measurements of several individuals, midpoints of ranges of variations, or measurements of holotypes when only those were available.

The analyses were performed on ln-transformed data. Fairbairn (1997) recommended using females as the independent variable, to facilitate comparison between studies, though Fairbairn & Preziosi (1994) had previously recommended the larger sex, in this case females, be used as the dependent variable. Here we present regressions of ln (female lengths) against ln (male length) and of ln (male length) against ln (female length) to test the strength of our data.

In order to correct data for phylogenetic non-independence, the same ln (lengths) were then used to calculate independent contrasts according to the methods described by Felsenstein (1985) and Pagel (1992) using the *ape* library (Analysis of Phylogenetics and

Evolution) for the computer program "R version 1.8.1" (R Development Core Team, 2003). The chondracanthid phylogeny used was the MFU tree from Østergaard et al. (2003: Fig 8a) which is a completely resolved tree giving a total of 40 independent contrasts. As branch lengths in the phylogeny were not known the lengths of all branches were set to 2. Relationships among contrasts were assessed using correlations and regressions forced through the origin.

The relationship between male and female size is isometric when every change in female size is accompanied by a change in male size in the same direction and of an equal magnitude (i.e. the slope is 1.0). A coefficient significantly different from 1.0 indicates that the degree of SSD changes allometrically (Fairbairn & Preziosi 1994; Fairbairn 1997).

SSD was calculated as $\ln(F/M)$ i.e. with the larger sex as the numerator as recommended by Smith (1999). These SSD values were arbitrarily divided into 6 intervals (scored 0-5), $0 = < 0.99$, $1 = 1.00-1.49$, $2 = 1.50-1.99$, $3 = 2.00-2.49$, $4 = 2.50-2.99$, and $5 = >3.00$. The character was then mapped onto the phylogeny using MacClade 3.0 (Maddison & Maddison, 1992).

Male size, female size and SSD for each genus were compared with the morphological distance of that taxon from the outgroup. The outgroup node was defined as zero and morphological distance was calculated as the number of character changes taking place from that node through all ingroup nodes to each individual taxon.

3. RESULTS

The frequency distributions of body size for free-living copepods and for chondracanthids (Fig. 1) suggest that on average chondracanthid females are larger than free-living ones, whereas their males are smaller. The mean body length of free-living males is 1.58 mm ($n = 469$ species) which is significantly larger than that of chondracanthid males whose mean

length is 0.72 mm (t -test: $p = 0.0016$). In contrast, the mean body length for free-living females of 2.03 mm ($n = 493$ species) is significantly shorter than the 5.90 mm of chondracanthid females (t -test: $p < 0.0001$).

The mean female:male size ratio for the Chondracanthidae is 9.0:1.0. Some chondracanthid females are only two to four times larger than the males (e.g. *Juanettia*, *Pharodes*, *Rhynchochondria*, *Hoia* and *Lagochondria*) but most are five to 15 times larger (e.g. *Blias*, *Auchenochondria*, *Strabax*, and *Andreina*) (see Appendix A). The most extreme ratio is *Medesicaste*, where mean body length of the female is 19.1 mm and the male is 0.6 mm, i.e. 30 times larger. In contrast, the mean female:male size ratio for free-living copepods is 1.1:1.0 and for the outgroup used here 1.8:1.0. In the free-living copepods, the outgroup and the Chondracanthidae, males are smaller than females, but in Chondracanthidae SSD is more pronounced than in the outgroup and free-living forms.

Male size and female size for Chondracanthidae were strongly correlated, however, the slope (0.574) of the linear regression of \ln (male length) on \ln (female length) was significantly different from 1.0 ($p < 0.0001$) (Fig. 2a). The slope for the phylogenetic contrasts (0.555) is also significantly less than 1.0 ($p < 0.0001$) (Fig. 2b). These regressions indicate an allometric relationship between male and female size, which increases with body size. In contrast, the slope (0.805) of the linear regression of \ln (female length) on \ln (male length) was not significantly different from 1.0 ($p = 0.1810$) (Fig. 3a). Using phylogenetic contrasts also gives a slope (0.8558) which is not significantly different from 1.0 ($p = 0.3541$) (Fig. 3b). This suggests that SSD is isometric, i.e. the proportional difference in male and female size did not change as body size increased. SSD appeared to remain constant relative to body size across genera.

Plots of \ln (female length) as a function of morphological distance as well as female size contrasts as function of morphological distance showed a positive but not significant

correlation ($p = 0.9189$ and $p = 0.6744$ respectively). Similar plots of male size showed a negative correlation with distance which was not significant ($p = 0.3701$ and $p = 0.5898$).

When mapping SSD, $\ln(F/M)$, on the tree there are apparent trends in size change (Fig. 4a). The basal genera generally have a smaller female to male size ratio compared to the more derived genera, with the largest proportional differences between the sexes in the more distal taxa. This is supported by a plot of SSD as function of morphological distance which showed a positive correlation (slope = 0.0044) (Fig. 4b). The slope is significantly different from zero ($p = 0.0002$) indicating that SSD is positively correlated with the degree of morphological divergence from the outgroup, which supports the findings of Fig. 4a. A similar positive correlation (slope = 0.0062) was found with phylogenetic contrasts although it is not significant ($p = 0.2406$) (Fig. 4c).

4. DISCUSSION

Locating a host is crucial and is the greatest challenge in a parasite' s life cycle. A common strategy to meet this challenge is to increase probability of encounters with potential hosts by increasing reproductive output. The more difficult the host is to locate the more fecund the parasite (Gotto 1962). Further, it has been suggested that the challenge for fish parasites is greater than for invertebrate parasites, as fish may be more difficult to infect than invertebrates, the latter also tending to be less mobile or even sessile (Gotto 1962). Other things being equal, a high fecundity will be strongly favoured by selection, resulting in large females. Space and food are often not limiting, so many parasites evolve large body size, especially in females. Female gigantism is not only common in parasitic copepods but also among parasitic nematodes (Kirchner et al. 1980) and other crustaceans, e.g. Rhizocephala (Raibaut & Trilles 1993). However, alternative strategies are also known in Crustacea. Poulin (1995a) and Poulin & Hamilton (1995) found that switching from free-living to parasitic

strategies in both isopods and amphipods resulted in decrease in female body size, independently of the type of hosts colonised. Parasitic isopods and amphipods thus appear to have evolved towards higher fecundity without evolving towards larger body sizes after diverging from free-living ancestors (Poulin 1995a).

In parasitic copepods there is a general trend towards SSD in which females are significantly longer than males (Poulin 1996) and this is more pronounced in the Chondracanthidae than in close relatives, such as the Taeniacanthidae and Bomolochidae.

Whether the relationship between male and female size is isometric or allometric is equivocal. Following the recommendations of Fairbairn (1997) would lead to the conclusion that the relationship between males and females is allometric. However, placing the female as the dependent variable as recommended by Fairbairn & Preziosi (1994), would lead to the conclusion that the relationship between the sexes is isometric. Fairbairn (1997) advocated placing females on the x-axis in order to make standardize presentation and facilitate comparison of data from different studies. In theory, there should be no difference in results whichever way the data are presented. The difference observed here is likely due to relatively noisy nature of our data, which is probably not that uncommon. It is clear that if such noisy data is analysed only one way, false conclusions might arise.

Although not significant and not supported by analysis of phylogenetic contrasts, our data suggest that in chondracanthids the relationship is allometric. Poulin (1996) generalised for all copepods parasitic on fish that: "The pressures from life of parasitism on fish have not been felt equally by males and females: females have been selected for high fecundity, males for their ability to inseminate females. This has typically led to small, mobile males capable of exploring the surface of the host in search of the large permanently attached females... with male size under weak selection the degree of SSD may be determined to a large extent by female size itself" (Poulin 1996: pg. 2522). In contrast, we found that changes in body size

were not limited to female Chondracanthidae, males also showed changes (Fig. 1). It appears that both sexes are driving the SSD and that SSD is related to degree of morphological divergence. In a female-biased dimorphism, an increasing SSD with increasing female size, (called hyperallometry by Fairbairn & Presiozi (1994)), may indicate an increasing degree of specialization to a parasitic mode of life, which we saw when comparing SSD to morphological distance (Fig. 4).

We infer that selection for high fecundity in Chondracanthid females has resulted in a trend towards larger body size. Poulin (1995b) found that fecundity increases in copepods that become parasitic on fish and that it is positively correlated with female size. Conversely, Chondracanthid males are probably selected for small body size. Dwarf males commonly eat less than females but maximize their reproductive output by living in intimate association with the female (Shine 1988). Ghiselin (1974) observed that dwarf males are often found when the female parasite is sedentary and Vollrath (1998) concluded that when males derive nourishment from the female, the optimum strategy would be to commit resources into sperm production, reducing investment in basic metabolism, leading to small size. He argued that dwarfism could even be favoured in male-male competition, if large male size is too costly. Chondracanthid males conform to Vollrath's (1998) definition of a dwarf male, being less than half as long as conspecific females. This is partly due to dwarfing (males were smaller than in free-living copepods) but also due to selection for large females (which are larger than in free-living copepods). Small body size could benefit the male by reducing feeding requirements and since the male probably derives nourishment from the female (see Øtergaard & Boxshall submitted), a small male is a lesser drain on resources. This allows the female to put highest possible amount of resources into egg production, which will lead to increased reproductive success; beneficial to both individuals. It appears that the strategy

exhibited by the Chondracanthidae combines dwarf males with giant females, but this needs further study.

ACKNOWLEDGEMENTS

We thank David Orme (Imperial College, London) for helping with the independent contrasts analysis.

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FIGURE CAPTIONS

Figure 1. Length-frequency distributions of copepods included in the analysis. White arrows indicate median and black arrows indicate mean length. (a) Male Chondracanthidae, median = 0.64; mean = 0.72; $n = 40$. (b) Free-living males, median = 0.97; mean = 1.58; $n = 469$. (c) Female Chondracanthidae, median = 4.61; mean = 6.00; $n = 40$. (d) Free-living females, median = 1.20; mean = 2.03; $n = 493$.

Figure 2. Relationship between male and female body length. (a) Ln (male length) plotted versus Ln (female length). (Regression: $y = 0.574x - 1.396$; $p < 0.0001$). (b) Phylogenetically independent contrast in male length on contrast in female length. (Regression: $y = 0.555x$; $p < 0.0001$). Slopes in (a) and (b) are not significantly different ($p = 0.9155$) from each other. They are both significantly different from 1 ($p < 0.0001$).

Figure 3. Relationship between female and male body length. (a) Ln (female length) plotted versus Ln (male length). (Regression: $y = 0.805x + 1.9593$; $p < 0.01$). (b) Phylogenetically independent contrast in female length on contrast in male length. (Regression: $y = 0.856x$; $p < 0.001$). Slopes in (a) and (b) are not significantly different ($p = 0.8433$) from each other and they are not significantly different from 1 ($p = 0.1810$ and $p = 0.3541$ respectively).

Figure 4. Relationship between sexual size dimorphism (SSD) and morphological distance.

(a) SSD mapped as size ratio ($\ln(F/M)$) on the Chondracanthidae tree. (b) SSD plotted versus morphological distance. (Regression: $y = 0.004x + 1.1706$; $p = 0.0003$). (c)

Phylogenetically independent contrast in sexual size dimorphism plotted versus contrast in morphological distance. (Regression: $y = 0.006x$; $p = 0.2409$). Slopes in (b) and (c) are not significantly different ($p = 0.8657$) from each other. They are both significantly different from zero ($p < 0.0002$).

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Sexual size dimorphism in Chondracanthidae

Figure 1

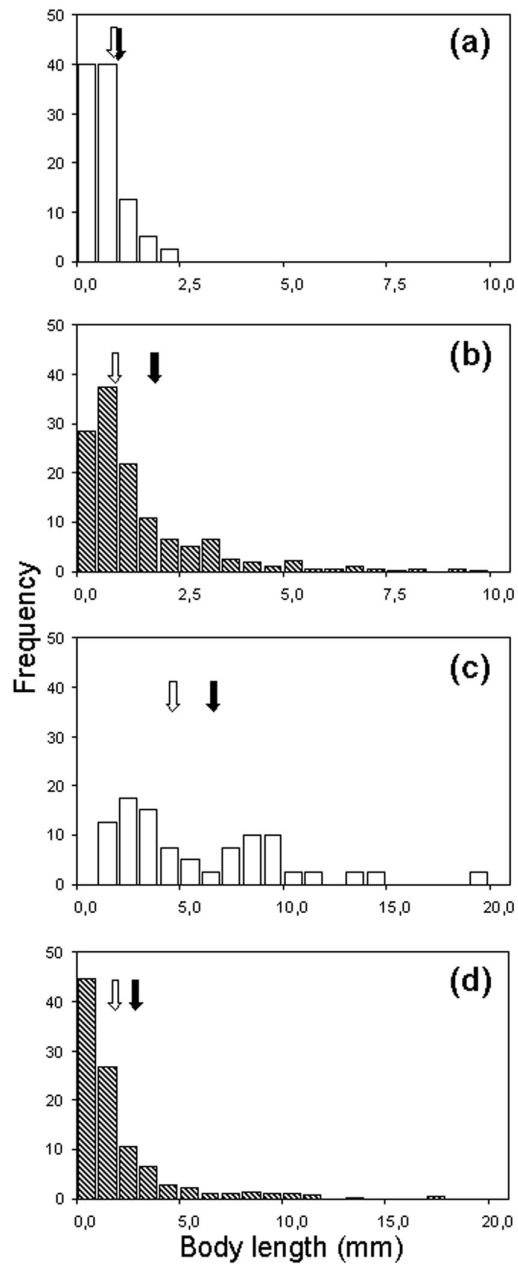


Figure 2

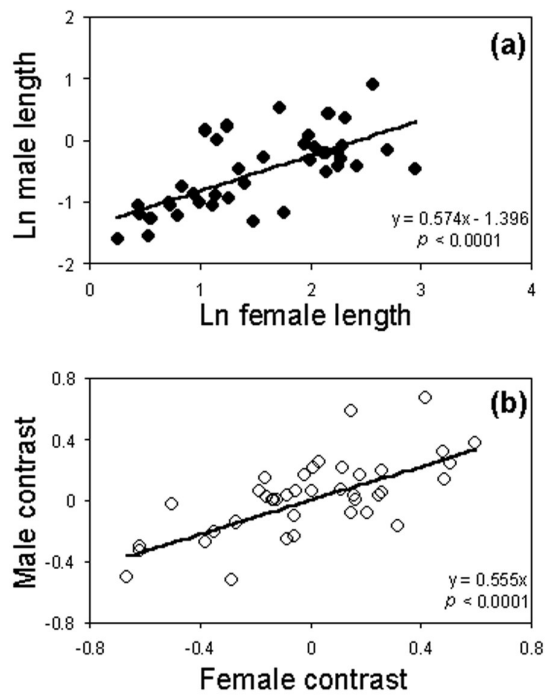


Figure 3

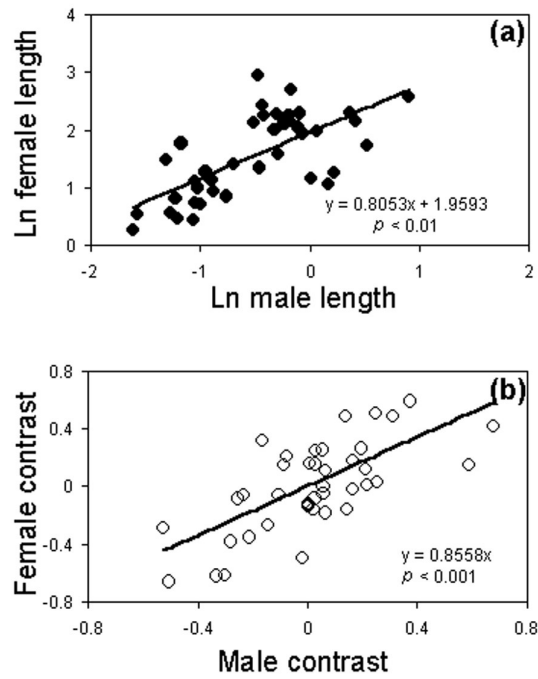


Figure 4

