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RD Garcia[a], PE Garcia[a] & M Reissig[a]

[a] INIBIOMA-CONICET, Bariloche, Rio Negro, Argentina

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RESEARCH ARTICLE

Sexual size dimorphism in calanoid copepods (Centropagidae) from Patagonia (Argentina)

RD Garcia, PE Garcia* and M Reissig

INIBIOMA-CONICET, Bariloche, Rio Negro, Argentina

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Calanoid copepods of the genus *Boeckella* and *Parabroteas* (*P. sarsi*) are dominant in zooplankton communities of Patagonian lakes and ponds. This study addresses the occurrence of sexual size dimorphism in calanoid copepods of the genus *Boeckella* and in the monospecific genus *Parabroteas* occurring in 12 lakes and ponds of Patagonia (Argentina). The morphometric analysis performed showed that in all the species studied the female is larger than the male, although the difference in size among sexes was found to be variable between species. Interestingly, all species showed significant intraspecific stability in their sexual size dimorphism despite potential differences in their environments regarding predation pressure, environmental stability (permanent or temporary waters) and altitude distribution of populations. Finally, we discuss the potential implications of sexual dimorphism in terms of resource use and vulnerability to predation among other environmental forces which may play a role in promoting larger female to male size.

Keywords: sexual size dimorphism; total length; *Parabroteas sarsi Boeckella*; calanoid copepods

Introduction

Some studies propose that sexual dimorphism evolves to reduce intraspecific competition for food (intersexual niche divergence or ecological sexual dimorphism) and that it is not associated directly with selection on reproductive traits (Ralls 1976; Slatkin 1984; Shine 1989; Andersson 1994). In several species, the selective processes producing sexual differences result in dimorphism of total body length (sexual size dimorphism [SSD]). SSD is a widespread phenomenon among different groups of animals (Fairbairn 1997; Blanckenhorn 2005). In particular, female-biased SSD (i.e. females larger than males) predominates among invertebrates (Teder & Tammaru 2005; Esperk et al. 2007). Planktonic copepods are not exceptional in this regard, with females usually being larger and their SSDs being related to certain environmental variables, such as salinity, temperature and ultraviolet radiation, among other factors (Bayly 1978; Gilbert & Williamson 1983; Maly 1983; Grad & Maly 1988; Maly & Maly 1999). The higher relative size of female copepods has been hypothesised to be due to the greater investment in reproduction and offspring in the female, particularly in the species that carry the eggs during their development (Gilbert & Williamson 1983). Large females are more fecund (Cole 1966; Corkett & McLaren 1969; Hopkins 1977; Maly 1983), but they may reach maturity slower than small females or males (Gilbert & Williamson 1983; Nishikawa & Maly 1996). Some females store most of the energy for reproduction during their development, so the adult final size represents the maximum potential resource base that can be put towards reproduction (Gilbert & Williamson 1983).

The male is the active partner and its primary role is geared towards the location and

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*Corresponding author. Email: blueameba@yahoo.com encounter of the female (Ohtsuka & Huys 2001). Thus the larger females may exhibit a greater mating success compared to smaller ones (Maly 1978). However, the fact that larger males also tend to exhibit greater mating success could minimise any positive selection of sexual dimorphism in copepods (Gilbert & Williamson 1983). Some authors found that low food availability can produce a reduction in the male length, which may enhance food availability for females (Maly 1978; Gilbert & Williamson 1983). According to Bayly (1978), the strongest dimorphism is found in species that occur exclusively in temporary waters where interspecific competition is likely to be low. In such conditions, a pronounced sexual dimorphism would enhance resource use by allowing access to an exceptionally wide range of particle sizes.

In inland waters from southern South America, the zooplankton is characterised by the frequent occurrence and/or dominance of copepods of the family Centropagidae (Soto & Zúñiga 1991; Modenutti et al. 1998; De los Ríos & Contreras 2005; Reissig et al. 2006; Adamowicz et al. 2010). This condition differs from that of lakes and ponds in the northern hemisphere, in which cladocerans and cyclopoid copepods codominate the zooplankton assemblages (Williamson 1984; Wong & Sprules 1985; Maier 1990). The genus *Boeckella* comprises 40 species distributed worldwide, of which 17 have been recorded in Argentina (Bayly 1992a; Menu-Marque & Zuñiga 1994; Adamowicz et al. 2007). *Parabroteas sarsi* is the largest centropagid copepod known and is found co-occurring with *Boeckella* in southern South America.

The Andean Patagonian region contains thousands of temporary and permanent ponds and lakes (Iriondo 1989). The zooplankton assemblages occurring in such ecosystems are dominated by endemic centropagids of the genus *Boeckella* (Modenutti et al. 1998; Menu-Marque et al. 2000; Marinone et al. 2006). They inhabit a remarkable diversity of habitats that range from small temporary pools to large and deep lakes coexisting with several invertebrate species as well as with endemic and introduced fishes.

In this study we address the occurrence of sexual dimorphism in nine centropagid species and describe the pattern of this trait. We discuss the potential relevance of sexual dimorphism in *Boeckella* spp. and *Parabroteas sarsi* as an adaptation to endure fluctuating environmental conditions, including resource limitation and predation, as well as other factors.

Methods

Study sites and sampling

The study was carried out in 12 Patagonian lakes and ponds, located between 38°58′–48°38′S and 70°22′–71°17′W (Table 1), sampled during different seasons from 2005 to 2010. Most of these lakes and ponds are shallow, with maximum depths less than 12 m (Table 1). Lake Rivadavia is a deep lake with a maximum depth of 147 m. Five of the studied ponds are temporary and fishless, whereas the other seven lakes and ponds are permanent (Fig. 1; Table 1). Lakes Rivadavia and Morenito, and Ocho Pond have fish, while the other set of lakes are fishless.

Conductance was measured with multiparameter probes. Zooplankton samples were collected with a 25 cm diameter plankton net of 55 µm mesh by horizontal tows at a central area of the ponds. The tows were pooled into one sample. In lakes Rivadavia and Morenito, zooplankton was collected with a 12 L Schindler-Patalas trap at different depths. The water from each depth was filtered through a 55 µm mesh net and pooled. All samples were preserved in 10% formalin. Copepods were separated from the samples under the microscope (Olympus SZ61 and Olympus SZ30). Adult copepods were identified to species level, following Bayly (1992b), and separated by sex. Two morphological parameters were measured on each individual from about 50–70 copepods per sex: the prosomal length (PL, from the anterior margin up to the end of the prosome) and the total length (TL, from the anterior margin of the prosome to the insertion of the caudal setae). In the case of the species from

Table 1 Characteristics of sampled lakes and ponds and distribution of *Boeckella* species.

								Centropagid species								
Lake	Location	Water regime	Z_{max} (m)	Presence of fish	Altitude (m.a.s.l)	Mean Conductivity (µS cm^{-1})	Area (km^2)	*B.brasiliensis*	*B.antiqua*	*B.michaelseni*	*B.brevicaudata*	*B.gracilis*	*B.gracilipes*	*B.meteoris*	*B.poppei*	*P.sarsi*
Jabón Pond	38°58′S, 70°22′W	P	4	No	1339	1555	1.2e-01		*							
Verde Pond I	39°00′S, 70°23′W	P	5	No	1282	NA	1.8e-01	*								
Los Juncos Pond	41°03′S, 71°00′W	T	1	No	907	345	7.0e-02		*							
Morenito Lake	41°03′S, 71°31′W	P	12	**Yes**	758	60	8.3e-01						*			
Fantasma Pond	41°05′S, 71°27′W	T	1.8	No	794	99.86	1.2e-02				*	*				*
Refugio Jesús Pond	41°07′S, 71°13′W	T	1	No	825	67.05	1.5e-02									*
Teleférico Pond	41°07′S, 71°22′W	T	1	No	816	183.74	2.6e-04					*				
Rivadavia Lake	42°34′S, 71°39′W	P	147	**Yes**	527	NA	2.2e + 01			*						*
Verde Pond II	42°43′S, 71°44′W	P	3	No	1525	28.96	3.5e-03						*			
Pto. San Julian Pond	48°24′S, 68°15′W	T	1	No	204	NA	1.2e-03							*		
Ocho Pond	48°29′S, 71°12′W	P	8.6	**Yes**	888	129.4	2.3e-01								*	
Oliva Pond	48°38′S, 71°17′W	P	1.5	No	958	4542	8.9e-02							*		

P, permanent water body; T, temporary or semi-temporary water body; Z_{max}, maximum depth; NA, not available.

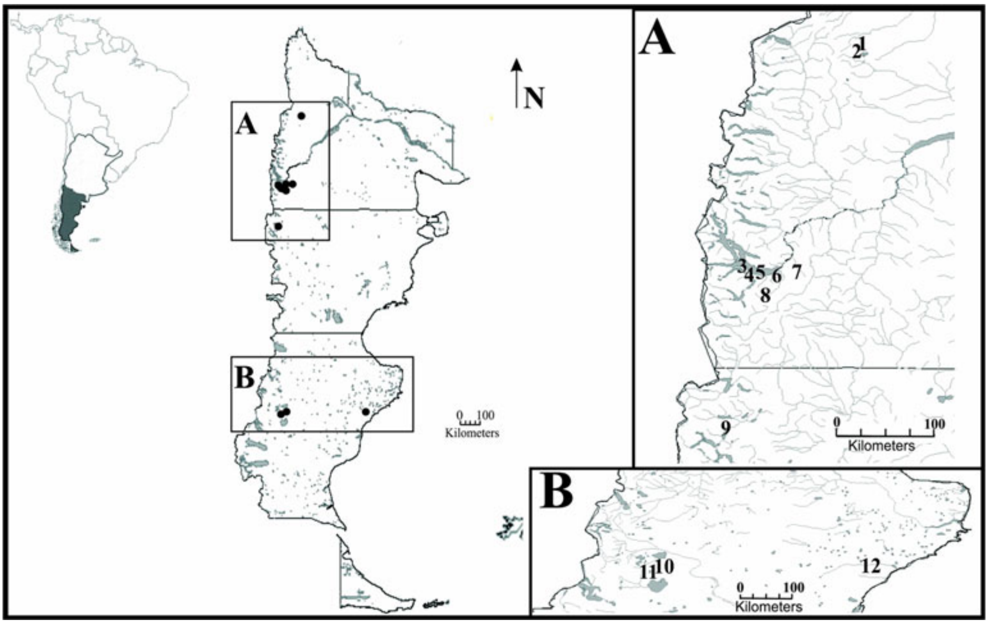

Figure 1 Map of the study area (Patagonia, Argentina) showing the sampled lakes and ponds. **1.** Verde I Pond. **2.** Jabón Pond. **3.** Lake Morenito. **4.** Fantasma Pond. **5.** Teleférico Pond. **6.** Refugio de Jesús Pond. **7.** Los Juncos Pond. **8.** Verde II Pond. **9.** Lake Rivadavia. **10.** Ocho Pond. **11.** Olivia Pond. **12.** Pto. San Julián Pond.

Lake Rivadavia, only TL was measured. In some cases, where abundance was low, the measurements were performed on at least 30 individuals per sex.

Data analysis

Mean lengths and standard deviations of morphometric parameters recorded in each sex were obtained for the different species studied. Pearson correlation was applied to assess the relationship between PL and TL of each population. Comparisons of means among sexes within each population and among populations were performed using the non-parametric Mann-Whitney test. The non-parametric Kruskal-Wallis test was applied to compare the somatic measurements of males and females when more than two populations of the same species were available (*P. sarsi*).

The SSD was calculated using the mean of lengths, as follow:

$$Sex\,Size\,Dimorphism(SSD)=\left(\frac{♀PL}{♂PL}+\frac{♀TL}{♂TL}\right)/2 \tag{1}$$

Where $♀PL$ = mean female prosomal length; $♂PL$ = mean male prosomal length; $♀TL$ = mean female total length; and $♂TL$ = mean male total length. In the case of copepods from Lake Rivadavia, the SSD was estimated with the total length ($♀TL/♂TL$). Linear regression was applied to assess the SSD in centropagids using log-transformed data.

Results

The morphometric analysis performed in this study indicated that, except in *B. antiqua* and males of *P. sarsi* from Fantasma and Jesús ponds (Mann-Whitney test, $P > 0.05$; Kruskal-Wallis test, $P > 0.05$, respectively), the size of males and females of the remaining species showed inter-population variation (Mann-Whitney test, $P < 0.001$ in all cases). *Parabroteas sarsi*, the largest species, showed significant variation among populations, with the sizes of the copepods from Lake Rivadavia being significantly smaller than those from Fantasma and Jesús ponds (Fig. 2). *Boeckella brevicaudata* was the largest *Boeckella* studied, while *B. michalsenii* was the smallest species (Fig. 2). All the Patagonian species of Centropagidae analysed showed a female-biased dimorphism, with the females always being larger than the males (Figs. 2, 3). SSD varied strongly between species. The greatest relative size difference between females and males was found in *B. gracilis* and the smallest was recorded in *B. gracilipes* (SSD = 1.4 and c. 1,

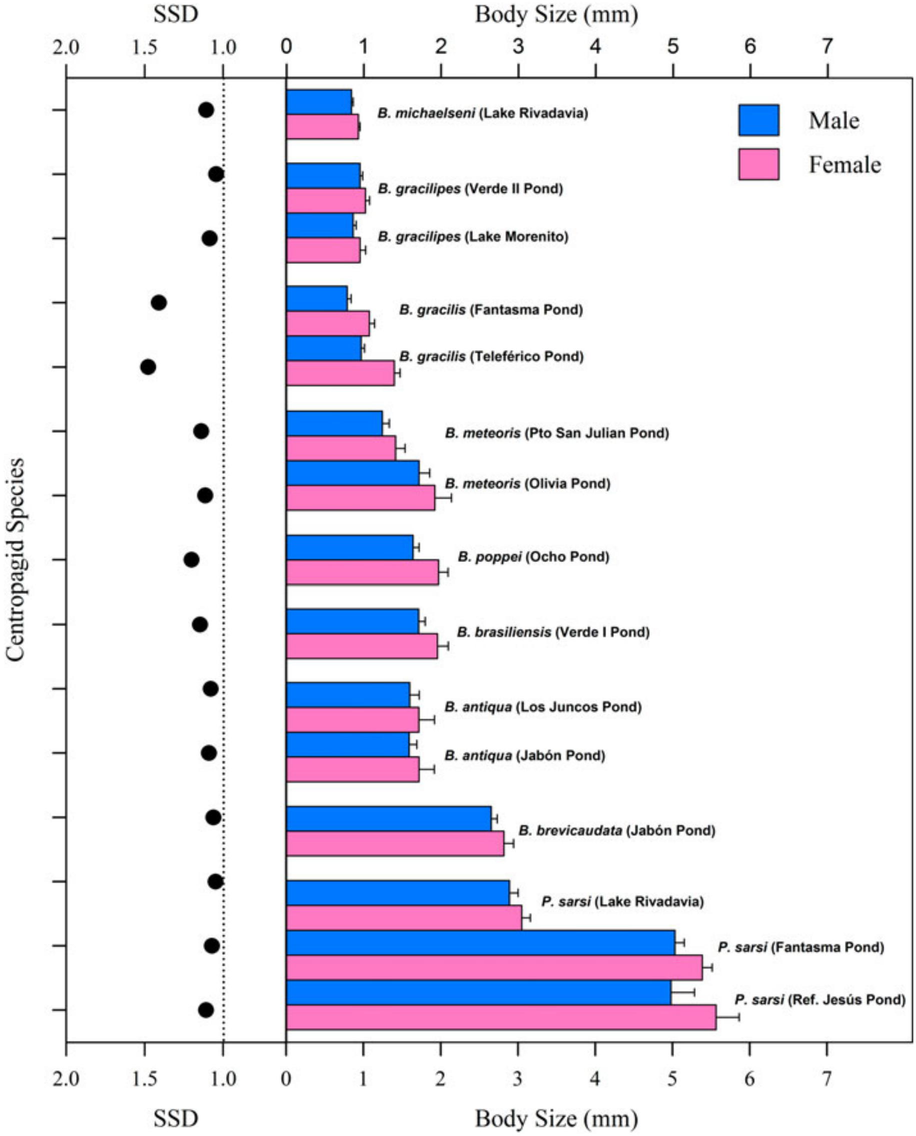

Figure 2 Mean body size (± SD) and sexual size dimorphism (SSD) of centropagid species from Patagonian lakes and ponds. Left panel: SSD – vertical dashed line indicates no SSD (size of males = size of females). Right panel: male and female body sizes of the different copepod species studied.

respectively; Fig. 2; Table 2). Larger species such as *P. sarsi* and *B. brevicaudata,* were found to be slightly dimorphic (SSD c. 1.06). The SSDs were relatively constant within species, despite there being intraspecific size differences among individuals from different environments (Fig. 2; Table 2). TL had a high positive correlation with PL (Pearson correlation, $R = 0.995$, $P < 0.001$, $n = 2251$) so the use of either measurement in *Boeckella* could be a helpful tool to describe their SSD.

Discussion

In general, the size of males and females was found to be highly variable within species. In the case of *P. sarsi*, greater size difference was recorded among copepods from different lakes. Intraspecific plasticity in body size may be advantageous in the co-occurrence of centropagid species because it may prevent food niche overlap, thereby reducing competition for resources. However, other interactions, such as predation, may promote size divergence among separate populations. In the case of *P. sarsi*, the size difference found among the populations studied could be attributed to fish predation pressure. In Lake Rivadavia the predation pressure exerted by a fish assemblage composed of native and introduced species may explain the smaller relative size of *P. sarsi* as compared to the conspecifics present in the fishless system, Fanstasma Pond (Reissig et al. 2004). In other species, size differences could be attributed to differences in environmental conditions. For example, the body size of copepods has been shown to depend on temperature (Escribano & McLaren 1992; Van der Have & de Jong 1996; Atkinson & Sibly 1997; Hansen et al. 2010) and food conditions (Gilbert & Williamson 1983).

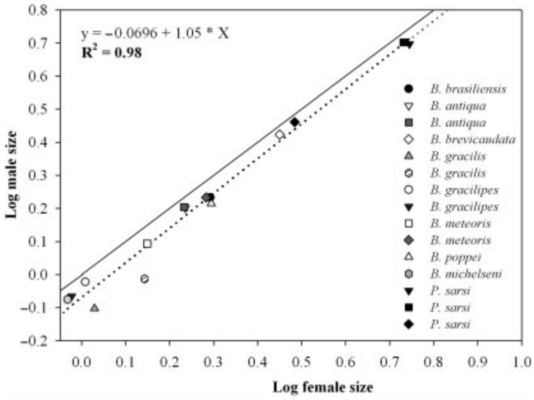

Figure 3 Relationship between the log female size and the log male size. Solid line represents no sexual size dimorphism (male size = female size). Dotted line below the diagonal represents female-biased size dimorphism in Patagonian centropagids.

Overall, the observed intraspecific size fluctuations recorded in *P. sarsi*, *B. antiqua, B. gracilis* and *B. meteoris* suggest that absolute body size, by itself, is of limited taxonomic value in centropagid copepods (Fig. 2).

The size differences between females and males were significant in all the species studied, with females being larger than the males. This constant pattern may indicate an adaptive advantage, perhaps reflecting that the production of offspring in the females demands a comparatively greater energy investment which is afforded by comparatively greater resource storage (Gilbert & Williamson 1983). In particular, *B. gracilipes* was found to be the least dimorphic species (SSD = 1.044), together with *B. michaelseni*, the smallest species in this study. Interestingly, the two larger centropagid species analysed, *P. sarsi* and *B. brevicaudata*, also had low SSDs. In contrast, the greatest dimorphism was recorded in *B. gracilis* (1.477), which typically inhabits highly temporally dynamic shallow lakes in Patagonia (Trochine et al. 2008; Adamowicz et al. 2010; De los Rios-Escalante et al. 2010). The remarkable dimorphism in *B. gracilis* could be related to reproduction. This species has been found to have long copulation periods, which may last for several days (Trochine et al. 2005; R.D. Garcia, pers. obs. 2010). In this case, it may be hypothesised that extended copulation periods could represent an energetic cost for the females, which could be attenuated by a size reduction in the male. Besides, Grad and Maly (1988) suggested that a pronounced SSD, such as observed in *Diaptomus*, may involve a cost

Table 2 Sexual size dimorphism and relationships between body lengths of centropagid species.

Species	Lakes/Ponds	Size diference between ♀ and ♂ TL	PL	Pearson correlation coefficient between TL and PL ♀	♂	SSD
B. brasiliensis	Verde Pond I	*	*	R = 0.883; *	R = 0.824; *	1.147
B. antiqua	Jabón Pond	*	*	R = 0.969; *	R = 0.904; *	1.090
	Los Juncos Pond	*	*	R = 0.985; *	R = 0.936; *	1.079
B. brevicaudata	Fantasma Pond	*	*	R = 0.820; *	R = 0.572; *	1.062
B. gracilis	Fantasma Pond	*	*	R = 0.779; *	R = 0.511; *	1.409
	Teleférico Pond	*	*	R = 0.835; *	R = 0.753; *	1.477
B. gracilipes	Verde Pond II	*	*	R = 0.748; *	R = 0.731; *	1.044
	Morenito Lake	*	*	R = 0.873; *	R = 0.781; *	1.085
B. meteoris	Pto. San JulianPond	*	*	R = 0.934; *	R = 0.911; *	1.139
	Oliva Pond	*	*	R = 0.960; *	R = 0.634; *	1.114
B. poppei	Ocho Pond	*	*	R = 0.865; *	R = 0.524; *	1.201
B. michaelseni	Rivadavia Lake	*	*	NA	NA	1.107
P. sarsi	R. Jesús Pond	*	*	R = 0.695; *	R = 0.879; *	1.109
	Fantasma Pond	*	*	R = 0.531; *	R = 0.538; *	1.071
	Lake Rivadavia	*	*	NA	NA	1.048

TL, total length; PL, prosomal length; NA, not available; *, $P < 0.05$; R, Pearson correlation coefficient; SSD, sexual size dimorphism.

because the small male would require more time to place the spermatophores properly in the female. If one sex carries the other one during courtship or mating, or if mating pairs remain attached for prolonged periods, the mating success of males may depend significantly on their relative size to their mates (Adams & Greenwood 1987; Fairbairn 1990, 1997; Lovich & Gibbons 1992).

This study shows that the SSDs of the centropagid species studied are variable, even though the most frequent values of SSD fall between 1.0 and 1.2. Bayly (1978) suggested that environmental seasonality could be a factor influencing SSD, showing that the SSDs were higher in temporary ponds than in permanent environments for several *Boeckella* species from New Zealand and Australia. This hypothesis seems not to apply in the case of the *Boeckella* studied here because most of the species can be found either in permanent or temporary environments (Reissig et al. 2006; this study). Perhaps the most difficult problem for testing the hypothesis outlined by Bayly (1978) is to determine which species are found exclusively in temporary or permanent waters, given the huge number of temporary and permanent environments in Patagonia and the tendency of *Boeckella* to occur in all of them. For example, we know through personal observations that *B. brevicaudata* and *B. antiqua* inhabit only temporary environments during winter, while the largest freshwater copepod, *P. sarsi* can be found in temporary ponds as well as in deep lakes (Vega 1999; Reissig et al. 2004, 2006; De los Ríos & Rivera 2008).

Interestingly, the SSDs were relatively constant within species of centropagids (Fig. 2) despite size differences between populations, such as observed in populations from shallow fishless ponds or lakes with complex fish assemblages. The intraspecific stability in SSD observed could indicate genetic rather than ecological control of SSDs, as was suggested previously by Bayly (1978). Further, Jersabek et al. (2007) postulated that populations of *Arctodiaptomus alpinus* from fishless alpine lakes exhibit higher SSD (c. 1.4) than those of lowland species (c. 1.2). Among centropagid species *B. gracilipes* inhabits a wide environmental gradient from deep piedmont lakes to high altitude ponds (Menu-Marque et al. 2000). Remarkably *B. gracilipes* was the least dimorphic species recorded in this study (SSD = 1.044), contrasting with the findings of Jersabek et al. (2007) in diaptomid copepods. Centropagids seem to bear low to null intraspecific differences in SSD among populations in contrasting environments. In this way, the SSD may qualify as a more suitable morphometric variable for taxonomic purposes than body size, because of its intraspecific stability.

In crustaceans, body size is a major factor determining the potential egg mass (Jensen 1958; McLaren 1965; Dagg 1976). Particularly in copepods, larger females tend to have larger clutches (Smyly 1968; Maly 1973) which may represent an advantageous reproductive trait. Nevertheless, environmental variables, such as temperature and food availability, also play an important role in determining egg production potential (Dagg 1978; Jamieson & Burns 1988). Furthermore, predation pressure may influence the body size of co-existing potential prey, perhaps favouring larger females that can produce and carry more eggs, but not so large so as to increase their vulnerability to predation (Hall et al. 1976; DeFrenza et al. 1986). In contrast, predation may be influenced by the degree of dimorphism, as it may be adaptive for both males and females to achieve a size that minimises the loss by predation. Also, predation may threaten reproductive success through the differential removal of one sex, as may be the case when the males become small enough to fall within the feeding range of a planktonic predator (Dodson 1974) or when the females become large enough to be eaten by a nektonic predator (insect or fish; Bayly 1978). Only a few studies have analysed the susceptibilities of male and female copepods to predators but, ultimately, the outcome of sex-dependent predation appears to be related to the assemblage of predators occurring in nature (Maly 1970; Gerritsen 1978; Cooper & Goldman 1980; Trochine et al. 2005).

In southern Argentina, the zooplankton assemblages are characterised by the dominance of endemic calanoid copepods of different species, which have a central ecological role in pelagic food webs of large and deep lakes as well as in shallow ponds (Menu-Marque et al. 2000; Hansson & Tranvik 2003; Reissig et al. 2004, 2006; Trochine et al. 2008; Lancelotti et al. 2009). Most boeckellids have a tendency to exploit larger food items towards adulthood. Small species of *Boeckella*, such as *B. gracilipes*, *B. gracilis* and *B. michaelseni*, feed on phytoplankton and small ciliates while larger species, such as *B. brevicaudata* and *B. antiqua*, appear to be able also to access larger food items. In contrast, *P. sarsi* shifts its diet, being herbivorous in naupliar stages, omnivorous in early copepodid stages and carnivorous from copepodite IV to adulthood. Food niche differences have been reported between species of *Boeckella* and among developmental stages of *P. sarsi*; however, as far as we know, there is no evidence of food niche divergence among sexes based on their size difference. Due to the ecological relevance of centropagid copepods in lake foodwebs of Antarctic, Patagonian and Andean lakes, it could be hypothesised that SSD could increase complexity in pelagic food webs if size differences between sexes are sufficiently large to segregate food niches according to sex. Furthermore, there is a lack of information regarding SSDs in these copepods in relation to predation pressure by invertebrates or fish, such that females and males of similar size would have similar vulnerability to predation while females larger than males would imply differences in vulnerability depending on the predator type and selectivity. In this context, our results show a first record of the presence of dimorphic pairs within centropagid species, which may increase the complexity of interactions within their habitats. Further investigations are needed to determine the ecological implications of the observed patterns of dimorphism in Patagonian systems.

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