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Is there a trade-off between fecundity and egg volume in the parasitic copepod *Lernanthropus cynoscicola*?

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Abstract Negative relationships between egg number and egg size are commonly seen in many animal taxa, supporting the idea that there is a trade-off between egg number and egg size resulting from the allocation of resources to either one or the other. In parasites, where availability of resources is presumably very high, there may be fewer energetic constraints acting on allocation strategies, and the trade-off may be weakened. We investigated the association between egg number and egg volume among females of the copepod *Lernanthropus cynoscicola* Timi and Etchegoin, 1996, parasitic on the fish *Cynoscion guatucupa* (Cuvier). Both egg number and egg volume were strongly correlated with female body size. After controlling for the effects of body size, we found absolutely no evidence of a trade-off, i.e. no negative relationship, between egg number and egg volume. For a given body length, females that produce many eggs do not tend to produce relatively small eggs, and vice versa. In contrast, under conditions in which resources are plentiful, large females produce large quantities of high-quality eggs, and have a marked fitness advantage over small females.

Introduction

Trade-offs between an organism's phenotypic traits play a central role in the evolution of life history strategies (Stearns 1989, 1992; Roff 2002). Trade-offs are expected because energy or other resources allocated to one function cannot simultaneously be used for different functions. The net result is a negative correlation between traits that compete for the same resources. One of the best documented trade-offs is the one that exists between the number of eggs produced by an animal and the size of those eggs: clearly, if most resources are invested in the production of many offspring, then there will only be limited resources available for each offspring. The resulting trade-off generates a negative relationship between relative egg size and egg number, i.e. a continuum of strategies from the production of many small eggs to the production of few large ones. This trade-off has been documented in a range of animal taxa (e.g. Elgar 1990; Guisande et al. 1996; Christians 2000; Kinnison et al. 2001; Brown 2003).

In principle, this trade-off should also apply to parasitic organisms. Limited information is available on the life history strategies of parasites (Poulin 1996, 1998), but the available data suggest that the trade-off may exist, at least at an interspecific level. For instance, there is a negative correlation between relative egg size and the number of eggs per clutch in parasitic copepods (Poulin 1995). At one end of the spectrum, copepods parasitic on sessile invertebrates produce few but relatively very large eggs, and at the other end copepods parasitic on highly mobile fish hosts can produce huge numbers of tiny eggs (Poulin 1995). However, whether or not there exists a trade-off between egg size and egg number within species of parasites remains to be determined. There are good reasons to suspect that parasites are not constrained by resource supply and that perhaps they may escape the trade-off at an intraspecific level. As emphasized previously (Price 1974; Jennings and Calow 1975; Calow 1983), parasites live attached to their food source, in a situation where all individuals have a resource supply that is practically infinite (at least when the parasites are small compared to their hosts, not too virulent, and occur at low abundance). Thus, high resource availability may allow parasites to allocate resources simultaneously to both egg number and egg

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size. In theory, trade-offs between egg size and egg number are obscured when the variation among individuals in resource acquisition is very high (van Noordwijk and de Jong 1986; Christians 2000; Brown 2003). In parasites, this variation is likely to be extremely small, and therefore all individuals are on equal footing. Thus, the high resource availability experienced by parasites should neutralize the trade-off between the number and size of eggs, while at the same time making the trade-off easy to detect if it exists.

Here, we examine reproductive strategies in the copepod *Lernanthropus cynoscicola* Timi and Etchegoin, 1996, a common parasite of the sciaenid fish *Cynoscion guatucupa* (Cuvier) from South American Atlantic waters (Timi and Etchegoin 1996; Timi 2003; Sabas and Luque 2003). The body size of this copepod species exhibits a high dependence on the body size of its host (J.T. Timi and A.L. Lanfranchi, unpublished data), and therefore a great variability in copepod size is observed when hosts of different sizes are sampled. This variability provides an interesting model to evaluate the existence of allocation "decisions" on how to apportion the resources invested in reproduction between egg size and egg number.

Our main objective is to determine whether there is a negative relationship between the number of eggs per clutch and the mean volume of these eggs among ovigerous female copepods. To our knowledge, this is the first investigation of intraspecific reproductive trade-offs in parasitic copepods.

Materials and methods

A total of 856 specimens of striped weakfish, *C. guatucupa*, obtained from commercial catches at Mar del Plata Port (38°08′S 57°32′W), from July 1992 to March 2004, were examined for parasitic copepods. Gill arches were excised, placed in a Petri dish and examined using a stereoscopic microscope. Copepods were counted, fixed and stored following standard procedures.

A total of 54 female copepods carrying at least one intact egg string were selected, and their total length (excluding legs) and the length of one egg sac were measured under a stereoscopic microscope. When both egg sacs were present, either the left or right string was randomly selected for measurement. The number of eggs per egg sac was determined and ten eggs from the middle section of each egg string were measured (diameter and height, for volume calculation, as each egg is shaped like a thick disc) under a light microscope. All copepods were pooled in a single sample following their removal from the fish as part of an earlier study, and thus unfortunately no information on the host of each individual parasite was available.

Our analyses are based on measurements from a single egg string only per female. Therefore, the values we present are "per egg string" and not "per female". We present them in this way to avoid any error associated with extrapolating to both egg strings, though the numbers of eggs are roughly the same in each egg string on the same female. We obtained total reproductive effort, defined as the total volume of eggs produced in a string, by multiplying egg number and mean egg volume. Both egg numbers and values of total reproductive effort were $\log_{10}$-transformed to meet the assumptions of normality. Relationships between variables were evaluated using Pearson's correlation coefficients. To control for significant effects of female body length on either egg number or mean egg volume, we used the residuals of the linear regression between these two variables and female body length as relative measures, i.e. measures corrected for body length.

Results

The mean (±SE) body length of the 54 female copepods included in this study was 3.16±0.10 mm (range 2.15–4.68). The length of the egg sac was longer on average than the body length (4.55±0.36 mm, range 1.76–12.87). The number of eggs per string ranged from 28 to 323 (105.8±9.1), and the mean egg volume ranged from 0.00074 to 0.00181 mm^3 (0.00117±0.00003). This means that some females were producing eggs that were more than twice as big as those of other females. The total reproductive effort ranged from 0.026 to 0.524 mm^3 (0.132±0.015).

Female body length correlated strongly and positively with egg number ($r=0.860$, $n=54$, $P<0.001$), mean egg volume ($r=0.657$, $n=54$, $P<0.001$), and total reproductive effort ($r=0.888$, $n=54$, $P<0.001$). Body length explained 74%, 43% and 79%, respectively, of the variance in these measures of reproduction (Fig. 1).

Without any correction for female body length, egg number and mean egg volume were positively correlated ($r=0.541$, $n=54$, $P=0.001$). However, when using the residuals of these variables regressed against body length instead, we found no relationship at all between relative egg number and relative mean egg volume ($r=-0.061$, $n=54$, $P=0.662$). In other words, for a given body length, females that produce many eggs do not tend to produce relatively small eggs, and vice versa (Fig. 2).

Discussion

Trade-offs between phenotypic traits, in particular negative relationships between egg number and egg size, are characteristic features of most animals (e.g. Stearns 1989, 1992; Elgar 1990; Guisande et al. 1996; Christians 2000; Kinnison et al. 2001; Brown 2003). The present results, however, clearly show that despite the high variability in body size, there is no association between egg number and egg volume in the parasitic copepod *L. cynoscicola*, once the effects of body size are taken into account. This result supports the idea that high resource availability may overcome any conflicts in

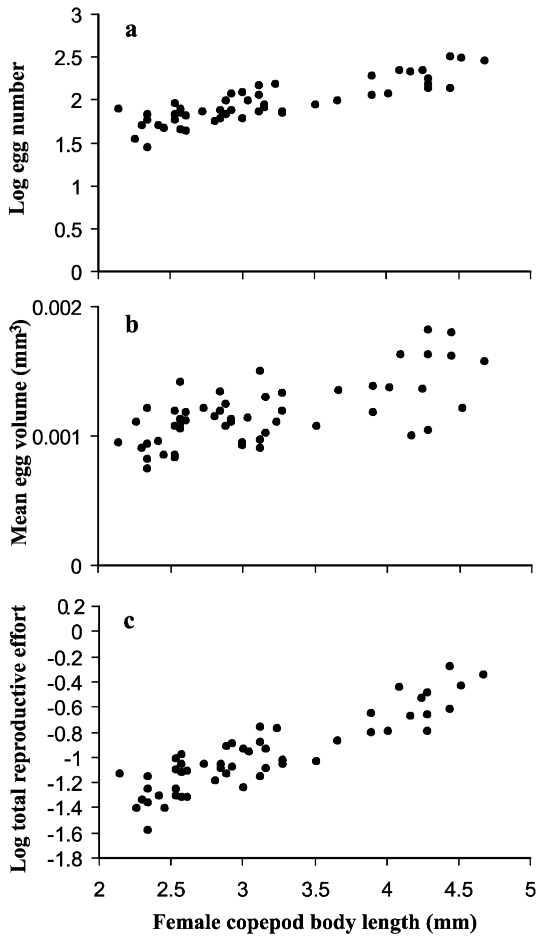

Fig. 1 Relationship between body length and: **a** log-transformed egg number, **b** mean egg volume, and **c** log-transformed total reproductive effort among 54 ovigerous females of the parasitic copepod *Lernanthropus cynoscicola*

resource allocation between the number and size of offspring in parasites. In contrast to other animal taxa, individual female *L. cynoscicola* appear capable of investing simultaneously in both number and size of eggs.

Because the copepods were pooled following their collection and no information is available on the characteristics of their fish host, it is possible that other variables may have influenced the reproductive strategies of the females in our sample. For instance, perhaps the size of the fish host and the number of other copepods attached to it are capable of affecting the allocation of energy between the number and size of eggs. However, this appears very unlikely for two reasons. First, the size of the host and how many other copepods it harbours are unlikely to affect resource availability for any given female copepod, because of the huge difference in size between the host and the parasite and the fact that infection levels are always very low. For instance, mean abundance and mean intensity of *L. cynoscicola* were 0.08 ± 0.37 and 1.31 ± 1.36, respectively in fish samples from Argentina and Uruguay (Timi 2003) and 0.39 ± 1.4 and 3.2 ± 3.0 respectively in Brazil (Sabas and Luque 2003). The size of the host and its infection level are also poor predictors of the transmission probability that free-swimming copepod juveniles will experience, and there is no reason to expect that females are adapted to adjust their reproductive investments in response to these cues. Second, most of the variance in all measures of reproductive investment is explained by female body length (see Fig. 1). This is thus by far the most important determinant of both egg number and egg volume, and other variables can only play minor roles. The only way in which host characteristics affect copepod reproduction is indirectly, as the size of female *L. cynoscicola* depends on host size (J.T. Timi and A.L. Lanfranchi unpublished data).

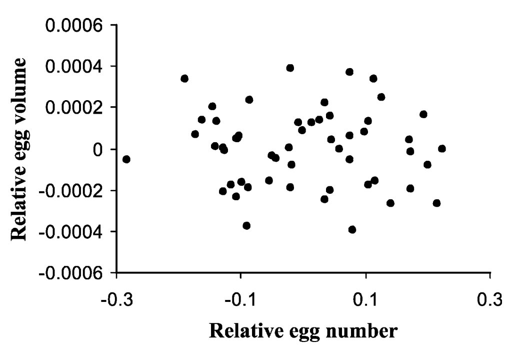

Fig. 2 Relationship between relative mean egg volume and relative egg number among 54 ovigerous females of the parasitic copepod *L. cynoscicola*. The data for both variables are residuals of linear regressions against female body length, and are thus corrected for body size

Size related egg production has some interesting implications. If a female copepod achieves a larger size, it will not only produce more eggs per clutch, but it will also produce larger eggs. Larger eggs generally result in larger offspring with greater survivorship, in both vertebrates (e.g., Ware 1975; Sinnervo 1990) and free-living copepods (Cooney and Gehrs 1980; Guisande et al. 1996). If this also applies to parasitic copepods, it would mean that larger eggs would produce larger offspring with a greater probability of reaching and infecting a fish host. Therefore, if adult copepods kept growing as adults, the quality of offspring produced by a female copepod would probably increase during its lifetime as it increases in body size. However, *L. cynoscicola* is probably like other copepods and thus it most likely stops moulting and growing when it attains its adult stage (Kabata 1981). If it is iteroparous like other copepods (Hairston and Bohonak 1998), it would thus have the same body size for all its reproductive events. Hence, the adult copepod population consists of females of various sizes, with the larger females not only producing a greater quantity of offspring, but also offspring of better quality. Body size and fitness are apparently very strongly linked in this species.

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