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Reproductive strategies of *Moina* (Cladocera) in relation to their habitat

S. Nandini* and S.S.S. Sarma

Laboratory of Aquatic Zoology, Division of Investigation and Postgraduate Studies, UMF Building, National Autonomous University of Mexico, Campus Iztacala, AP 314, CP 54090, Tlalnepantla, State of Mexico, Mexico FAX: +52 55 5623 1256.

* Corresponding author: nandini@unam.mx

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ABSTRACT

Reproductive strategies of *Moina* (Cladocera) in relation to their habitat

Some *Moina* species are predominantly found in large ponds and lakes while others are restricted to temporary pools or estuaries. The life history strategies and resistance to starvation of different species of *Moina* depend on their habitat. We compared the demography and starvation resistance in three species of the genus: *Moina macrocopa* (isolated from a reservoir), *M.* cf. *micrura* (from a small lake) and *M.* cf. *wierzejskii* (from a temporary pool). Population growth of the three *Moina* species was followed for 15 days using *Chlorella vulgaris* at a density of 1 x 10^6 cells/ml. Daily the females, males and ephippia produced by each cladoceran species were enumerated and transferred to a fresh test medium. We also tested the differences in resistance to starvation of the adults and the neonates by comparing the days until all the unfed individuals had died. Population growth curves of *Moina macrocopa*, *M.* cf. *micrura* and *M.* cf. *wierzejskii* showed significantly different trends. *Moina macrocopa* had higher peak densities (5-6 ind/ml) and higher population growth rates (0.33 per day) than the other two species. However, *M.* cf. *wierzejskii* had higher production of both, males and ephippia (0.3-0.4 ind/ ml and 0.7-0.8 ind/ml, respectively) than the rest. Regardless of the species, neonates were less resistant to starvation than adults. We discuss here adaptations of the life history strategies of these taxa in relation to their habitat.

Key words: Crustacea, males, ephippia, reproduction, starvation

RESUMEN

Estrategias reproductivas de* Moina *(Cladócera) en relación con su hábitat

Algunas especies de Moina *se encuentran predominantemente en grandes estanques y lagos, mientras que otras están restringidas a estanques temporales o estuarios. Las estrategias de vida y la resistencia al hambre de diferentes especies de* Moina *dependen de su hábitat. Comparamos la demografía y la resistencia al hambre en tres especies del género:* Moina macrocopa *(de un embalse) y* M. *cf.* micrura *(aislado de un pequeño lago) y* M. *cf.* wierzejskii *(de un cuerpo de agua temporal). Se siguió el crecimiento poblacional de las tres especies de* Moina *durante 15 días utilizando* Chlorella vulgaris *a una densidad de 1 x* 10^6 *células/ml como alimento. Diariamente se enumeraron las hembras, machos y ephippia producidos por cada especie de cladócero y se transfirieron a un medio fresco. También probamos las diferencias en la resistencia a la inanición de los adultos y los recién nacidos al comparar los días hasta que todos los individuos sin alimento habían muerto. Las curvas de crecimiento poblacional de* Moina macrocopa*,* M. *cf.* micrura *y* M. *cf.* wierzejskii *mostraron tendencias claramente diferentes.* Moina macrocopa *tuvo mayores densidades máximas (5-6 ind./ml) y mayores tasas de crecimiento poblacional (0.33 por día) que las otras dos especies. Sin embargo,* M. *cf.* wierzejskii *tuvo una mayor producción de ambos, machos y ephippia, (0.3-0.4 ind/ml y 0.7-0.8 ind/ml, respectivamente) que al resto de las especies. Independientemente de la especie, los neonatos eran menos resistentes que los adultos. Discutimos aquí las adaptaciones de las estrategias de historia de vida de estos taxones con relación a su hábitat.*

Palabras clave: *Crustacea, machos, ephippia, reproducción, inanición*

INTRODUCTION

Cladocerans are found in diverse habitats ranging from permanent water bodies such as rivers, lakes and oceans to temporary water bodies such as rain pools and shallow ponds (Smirnov, 2017). Though predominantly parthenogenetic, when subject to stress, they produce males and ephippia. Switching from parthenogenesis to gametogenesis in cladocerans is induced by various factors including temperature, photoperiod, population density, and predator kairomones (Dodson & Frey, 2001). Ephippia, which are viable for several years, are extremely important in ensuring the survival of the population, especially in shallow pools subject to complete drying where the active egg bank is more than the inactive one (Cáceres & Hairston, 1998; Burge *et al.*, 2018).

In spite of the fact that there are more than 700 species of Cladocera (Smirnov, 2017), most of the ecological studies have focused on the family Daphniidae, particularly various species of the genus *Daphnia*. The family Moinidae has about 29 species worldwide of which seven are known from the Nearctic region (Forró *et al.*, 2008). Most species of *Moina* inhabit freshwater bodies around the world and are particularly abundant in the tropics and sub-tropics. While some are predominantly found in large ponds and lakes, others are restricted to temporary pools (Błędzki & Rybak, 2016). The life history strategies of species vary depending on the permanency of the habitat where they are found (Stearns, 1992).

In cyclical parthenogens including *Moina*, males are produced when the population reaches a critical density where there are sufficient females for random male-female encounters leading to the formation of ephippia (Winsor & Innes, 2002). Production of resting stages lowers the population growth rates of zooplankton (Brendonck *et al.*, 2017). However, species inhabiting temporary water bodies need to ensure the formation of resting stages and therefore should invest more in male and ephippial production than those that inhabit permanent waters (Dodson & Frey, 2010). Taxa living in temporary habitats with an uncertain supply of food resources should also be more resistant to starvation (Gross, 2012). Here, using three species of the same genus, *Moina*, we tested the hypothesis that species (*M.* cf. *wierzejskii*) isolated from temporary water bodies would invest earlier in male production than those (*Moina macrocopa* and *M.* cf. *micrura*) found in permanent ponds and lakes and would be more resistant to starvation.

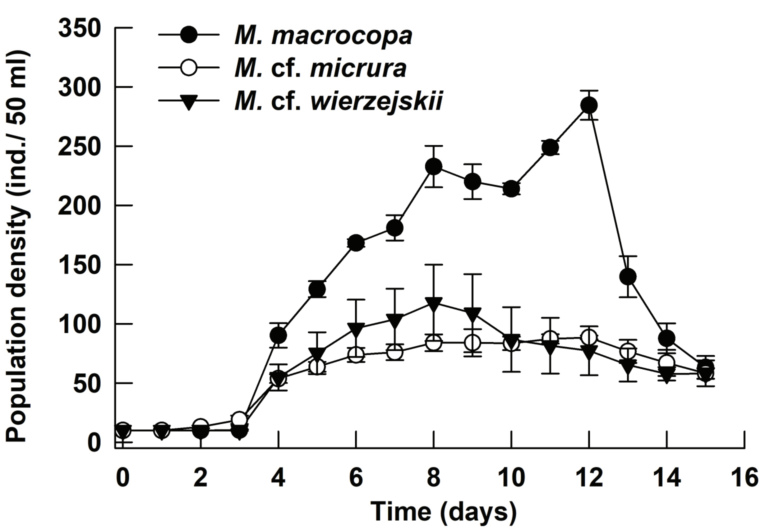

Figure 1. Population growth of *Moina* spp. in relation to culture time. Shown are the mean±standard error based on four replicates. *Crecimiento poblacional de* Moina *spp. en relación al tiempo. Se muestra la media ± error estándar basado en cuatro réplicas.*

MATERIAL AND METHODS

We isolated *Moina macrocopa americana* Goulden, 1968 from Lake Valsequillo (18° 55' 0" N and 98° 10' 0" W) in the State of Puebla, Mexico, *M.* cf. *micrura* Kurz, 1874 from Espejo de los Lirios Lake in the State of Mexico (19° 39' 2" N, Longitude: 99° 13' 19" W) and *M.* cf. *wierzejskii* Richard, 1895, from a shallow temporary water-body near Xochimilco Lake (19° 16' 30" N 99° 08' 20" W) in Mexico City. Clonal cultures for each cladoceran species were separately established using a single female on synthetic moderately hard water (EPA medium). We prepared the EPA medium by dissolving 96 mg $NaHCO_3$, 60 mg $CaSO_4$, 60 mg $MgSO_4$ and 4 mg KCl in one liter of distilled water (Weber, 1993). For food, we used *Chlorella vulgaris* at a density of 1 x 10^6 cells/ml. In terms of carbon, this was within the food level (4 mg/l C) recorded in eutrophic waters of Central Mexico (Enríquez García *et al.*, 2003). *Chlorella* was batch-cultured in 2L bottles using Bold's basal medium (Borowitzka & Borowitzka, 1988). Log phase alga was harvested by centrifuging at 2000 rpm for three minutes, then rinsed and re-suspended in a small quantity (10 ml) of distilled water. The concentrated alga was stored in a refrigerator (4 °C) until use. Algal density was estimated using a haemocytometer. The desired algal level (1 x 10^6 cells/ml) was obtained by diluting with EPA medium just before setting up the experiment.

Population growth experiments were conducted, separately for each *Moina* species, in 100 ml transparent jars containing 50 ml EPA medium and the chosen algal food density. Into each container, we introduced ten individuals of one of the three *Moina* species under a stereomicroscope using a Pasteur pipette. For each treatment, we set up four replicates. The test jars were maintained in a temperature controlled biological incubator set at 24±1 °C. The pH of the test medium was near neutral (7.2) and photoperiod in a 24 h cycle was set at 12h: 12h L: D. Following initiation of growth experiment, daily we counted the number of females, males and ephippia produced and returned them to fresh jars containing EPA medium with chosen algal food. The experiments

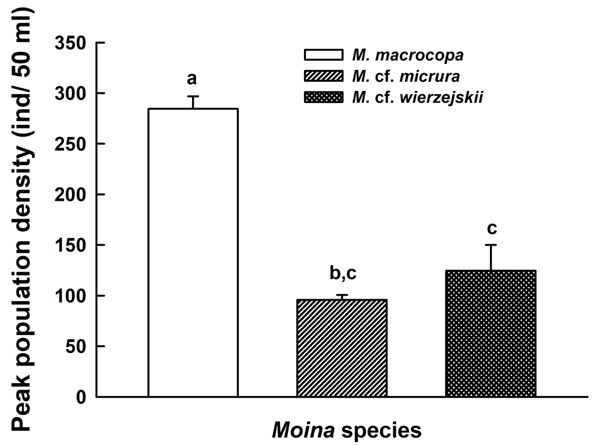

Figure 2. Peak population densities of *Moina* spp. cultured on *Chlorella vulgaris* at a density of 1 x 10^6 cells/ml). Shown are mean±standard error based on four replicates. Data bars carrying similar alphabets are not statistically significant ($p > 0.05$, Tukey test). *Las densidades máximas de población de* Moina *spp. cultivado en* Chlorella vulgaris *a una densidad de 1 x 10^6 células/ml. Se muestra la media ± error estándar en base a cuatro repeticiones. Las barras de datos con alfabetos similares no son estadísticamente significativas (*p *> 0.05, prueba de Tukey).*

were continued for 15 days by which time population densities of the three test species began to decline in each jar.

To test the differences in resistance to starvation of the adults and the neonates we placed ten adults and ten neonates of each species in different jars containing EPA medium but no food. Four replicates per treatment and per species were used. We counted the number of individuals alive in each jar daily and returned them to new jars containing fresh medium. Dead individuals, when present, were counted and discarded. The experiment lasted three days by which time most individuals were dead in each jar.

From the population growth data, we derived rate of population increase per day using the following exponential growth equation (Krebs, 1985): $r = (ln\ N_t - ln\ N_o)/t$, where: r = rate of population growth, N_o = initial population density, N_t = final population density, and t = time in days.

The differences in the rate of population increase and maximal population abundances of the tested species were analyzed using a one-way ANOVA and Tukey's test (Statistica version 5).

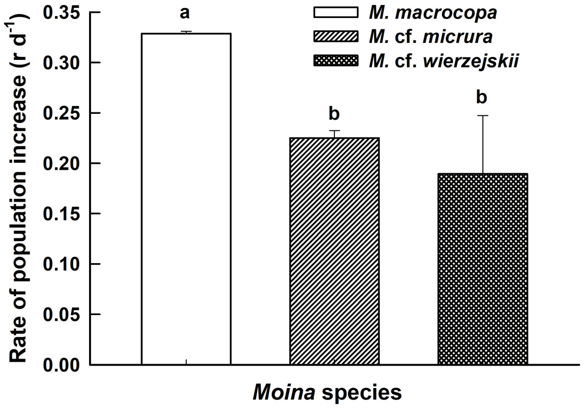

Figure 3. Rate of population per day (*r*) of *Moina* spp. cultured on *Chlorella vulgaris* at a density of 1 x 10^6 cells/ml. Shown are mean±standard error based on four replicates. Data bars carrying similar alphabets are not statistically significant ($p > 0.05$, Tukey test). *Tasa de crecimiento poblacional por día (r) de* Moina *spp. cultivado con* Chlorella vulgaris *a una densidad de 1 x 10^6 células/ml. Se muestra la media ± error estándar en base a cuatro repeticiones. Las barras de datos con alfabetos similares no son estadísticamente significativas (*p *> 0.05, prueba de Tukey).*

RESULTS

Population growth curves of *Moina macrocopa americana* (here after as *M. macrocopa*), *M.* cf. *micrura* and *M.* cf. *wierzejskii* (Fig. 1) showed that all the three species entered the exponential growth phase after day 3. However, *M. macrocopa* continued to grow until day 12, and after that, there was a steep fall in its abundances. On the other hand, both *M.* cf. *micrura* and *M.* cf. *wierzejskii* showed similar growth trends where after one week the populations began to decline. *Moina macrocopa* reached higher densities than the rest; *M.* cf. *micrura* had the least peak population abundance. The peak population abundances of the three *Moina* species ranged from 100 to 27 ind. 50 ml^{-1} and were significantly different ($p < 0.05$, One way ANOVA, Table 1). However, pairwise comparisons using post hoc tests showed that the peak population densities of *M.* cf. *micrura* and *M.* cf. *wierzejskii* were not significantly different ($p > 0.05$) (Fig. 2). The rate of

Table 1. Results of one-way ANOVA performed for peak population density, rate of population increase, total male density and total ephippial density among *Moina macrocopa*, *M.* cf. *micrura* and *M.* cf. *wierzejskii*. DF: Degrees of Freedom; SS: sum of square; MS: mean- square, F: Fisher´s ratio. *Resultados del ANOVA realizado para la densidad poblacional máxima, la tasa de crecimiento poblacional, la densidad total de los machos y la densidad de las ephippias total entre* Moina macrocopa*,* M. *cf.* micrura *y* M. *cf.* wierzejskii*. DF: Grados de libertad; SS: suma del cuadrado; MS: mean-square, F: Fisher's ratio.*

Source of Variation	DF	SS	MS	F	*p*
Peak population density					
Between groups	2	82 650	41 325	37.84	<0.001
Error	9	9828	1092		
Rate of pop. increase					
Between groups	2	0.042	0.021	4.63	<0.05
Error	9	0.041	0.004		
Male density					
Between groups	2	42 643	21 321	11.81	<0.01
Residual	9	16 247	1805		
Ephippial density					
Between groups	2	93 020	46 510	57.06	<0.001
Error	9	7336	815		

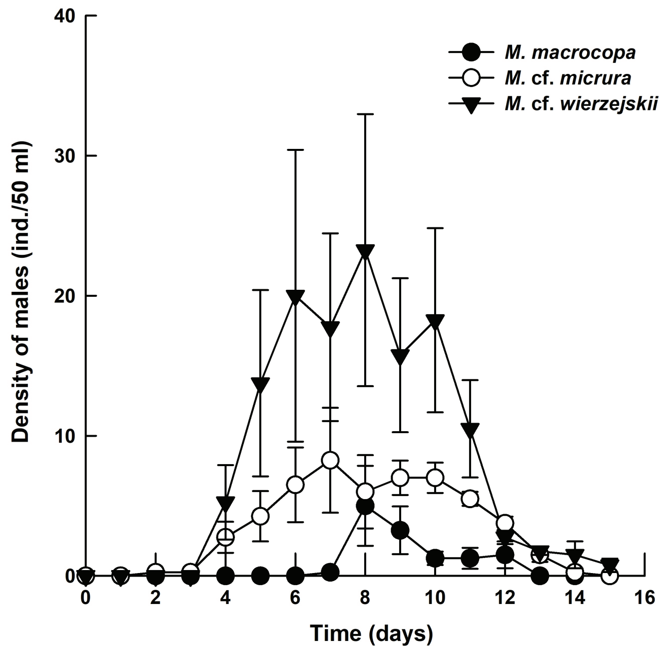

Figure 4. Dynamics of male production by *Moina* spp. in relation to culture period. Shown are the mean±standard error based on four replicates. *Dinámica de la producción de machos por* Moina *spp. en relación con el período de cultura. Se muestra la media ± error estándar en base a cuatro réplicas.*

population increase per day of the three *Moina* species varied from 0.19 to 0.33, with the highest for *M. macrocopa*. Statistically, the r values were significantly different among the three cladoceran species ($p < 0.001$, F test). However, pairwise comparisons showed that the r of *M.* cf. *micrura* was not significantly different from *M.* cf. *wierzejskii* ($p > 0.05$, Tukey test, Fig. 3).

Dynamics of male production by the three species of *Moina* is shown in Fig. 4. In general, we found a higher number of males in *M.* cf. *wierzejskii* as compared to the other two *Moina* species. The differences in the total male production as well as the peak abundances of males were statistically significant ($p < 0.01$, one way ANOVA, Table 1) (Fig. 5). Few ephippia were produced by *M. macrocopa*, while for *M.* cf. *micrura* and *M.* cf. *wierzejskii* the mean total of ephippial density was 100 and 215 numbers per jar, respectively (Fig. 6).

Regardless of the species, neonates of *Moina* are less resistant than adults (Fig. 7). Both neonates and adults of the three tested species did not survive beyond four days of starvation. How-

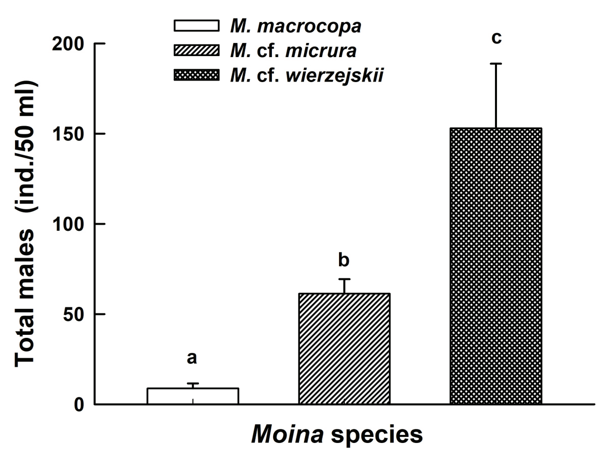

Figure 5. Total males produced by different *Moina* spp. cultured on *Chlorella vulgaris* at a density of 1 x 10^6 cells/ml. Shown are the mean±standard error based on four replicates. Data bars carrying dissimilar alphabets are statistically significant ($p < 0.05$, Tukey test). *Machos totales producidos por diferentes* Moina *spp. cultivado en* Chlorella vulgaris *a una densidad de 1 x 10^6 células/ml. Se muestra la media ± error estándar en base a cuatro réplicas. Las barras de datos que llevan alfabetos diferentes son estadísticamente significativas (*p < 0.05*, prueba de Tukey).*

ever, adults of *M.* cf. *wierzejskii* showed better survival until the third day than *M. macrocopa* and *M.* cf. *micrura*.

DISCUSSION

Reproductive characteristics of cladocerans, including *Moina*, are considered from population growth rates, age, size at first reproduction and clutch size (Stearns, 1992). Although essential, these cannot adequately explain adaptation to harsh environmental conditions. For example, when conditions are not favourable, most cladocerans switch to male, followed by, ephippia production (Alekseev & Lampert, 2001). When ponds and other temporary waterbodies dry up, the only surviving forms of cladocerans are the ephippia (Gerhard *et al.*, 2017). *Moina* spp. are adapted to living in both temporary and permanent waters. In seasonally drying ponds or, ponds, which experience a high degree of environmental changes such as temperature and food levels, *Moina* cf. *wierzejskii* is common (Goulden, 1968). On the other hand, species like *M. macrocopa* and *M.* cf. *micrura* occur in ponds and lakes which do not dry completely (Bledzki & Rybak, 2016). Therefore, their reproductive and survival characteristics reflect their adaptations to the conditions in which they naturally occur.

It is believed that cladoceran genera such as *Daphnia* and *Moina* reproduce parthenogenetically when conditions are favourable, and males and ephippia appear only when conditions are not favourable (Dodson & Frey, 2010). In the present study, this was also the case for *M. macrocopa* and *M.* cf. *micrura*. However, for *Moina* cf. *wierzejskii*, both male and ephippia production started within a week even when the conditions were favourable which has an adaptive advantage for this species (Zadereev, 2003). When the conditions are unpredictable, a greater investment in parthenogenetic reproduction alone does not ensure the survival of the species (Jiménez & Zoppi de Roa, 1987). If a species invests a portion of its assimilated energy into the production of males when the resources are

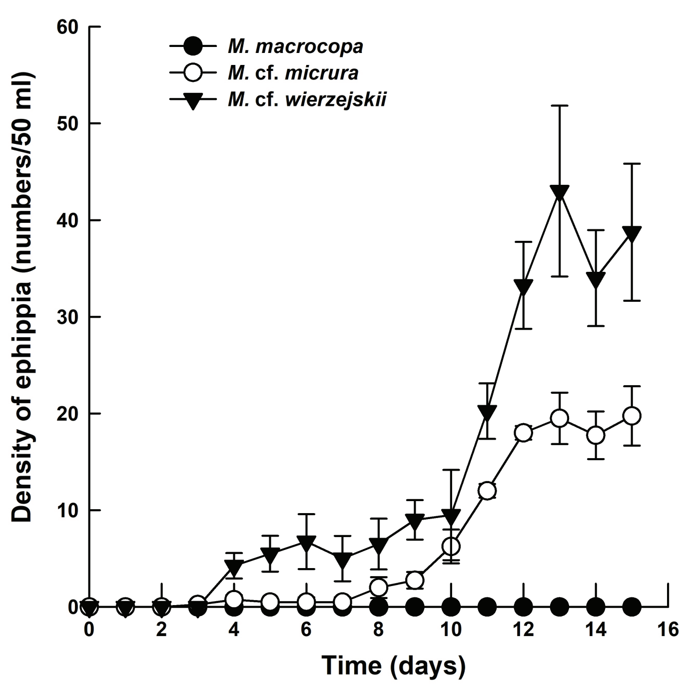

Figure 6. Dynamics of ephippial production by *Moina* spp. in relation to culture period. Shown are the mean±standard error based on four replicates. *Dinámica de la producción de ephippial por* Moina *spp. en relación con el período de cultura. Se muestra la media ± error estándar en base a cuatro réplicas.*

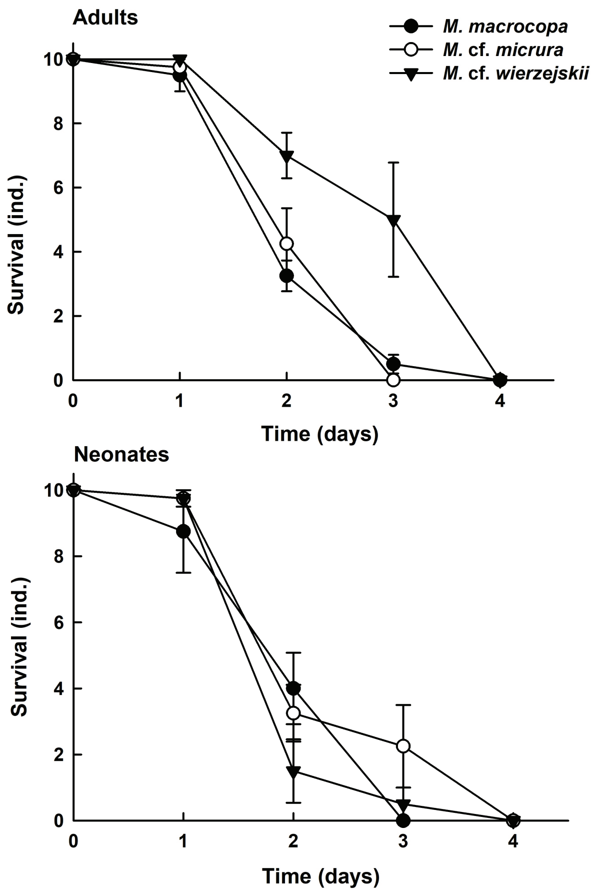

Figure 7. Resistance to starvation by *Moina* spp. adults and neonates. Shown are the mean±standard error based on four replicates. *Resistencia al hambre por* Moina *spp. adultos y recién nacidos. Se muestra la media ± error estándar en base a cuatro réplicas.*

not limiting or when the conditions are not yet harsh enough, then viable ephippial numbers are guaranteed which would ensure population buildup when favourable conditions return. On the other hand, since both *M. macrocopa* and *M.* cf. *micrura* are adapted to nearly predictable environmental conditions, production of males is not desirable since the production of males and ephippia results in lower population growth rates (Sommer *et al.*, 2016). It thus seems that *M.* cf. *wierzejskii* invests its energy in early male and ephippial production to ensure a seed bank even when the conditions are appropriate for parthenogenetic reproduction. This species, often found in small, shallow, rain-fed pools, is also capable of reaching critical densities earlier which could result in successful male-female encounters and ephippia production (Carvalho & Hughes, 1983). High male-producing clones become extinct faster in daphniids (Innes & Singleton, 2000); we also observed this here when *M.* cf. *wierzejskii* began to decline earlier other *Moina* species tested. However, by producing the ephippia earlier, this species ensures its survival in unpredictable or temporary environments (Hairston & Cáceres, 1996). Delaying sexual reproduction influences fitness differentially, depending on the habitat. In permanent waters, investment in parthenogenesis will ensure more individuals and a higher success at sexual reproduction due to more male-female encounters. In temporary habitats, however, delaying sexual reproduction will lower the fitness since the habitat may disappear (Burke & Bonduriansky, 2018).

Resistance to starvation is yet another essential characteristic of populations living under unpredictable or highly fluctuating environmental conditions. In general, longer the period of resistance to starvation, higher is the possibility of utilizing a future food source (Kirk, 2012). The fact that *M.* cf. *wierzejskii* showed higher survival of the population than the other two species implies its adaptation to unpredictable environmental conditions where daily food availability is not guaranteed.

Moina macrocopa has higher lifespan and population growth rates as compared to *M.* cf. *wierzejskii* (Nandini & Sarma, 2006). Here too we show that *M. macrocopa* had higher growth rates than *M.* cf. *wierzejskii*. Previous studies indicate that the threshold food concentration of cladocerans is inversely or curvilinearly related to their body size (Gliwicz 1990; Nandini & Sarma, 2006). *Moina macrocopa* has a higher threshold food concentration than *Daphnia laevis* (Nandini & Sarma, 2003), probably because it is not as efficient as *Daphnia* in filtering food as a result of the density of setules on the thoracopods (Monakov, 2003; Smirnov, 2017). It is possible that competition between the three species would result in *Moina macrocopa* displacing the other two taxa. However, we rarely found all three species coexisting in the same habitat.

CONCLUSIONS

Our study thus showed that though the three *Moina* species were cultured under similar conditions, they differed in their population growth characteristics, male and ephippial production suiting the habitats to which they are adapted. These differences in life history strategies explain their physical separation from each other too.

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REFERENCES

ALEKSEEV, V. & W. LAMPERT. 2001. Maternal control of resting-egg production in *Daphnia*. *Nature*, 414: 899-901. DOI: 10.1038/414899a

BLEDZKI, L. A. & J. I. RYBAK. 2016. *Freshwater crustacean zooplankton of Europe: Cladocera & Copepoda (Calanoida, Cyclopoida). Key to species identification, with notes on ecology, distribution, methods and introduction to data analysis*. Springer, New York.

BOROWITZKA, M. A. & L. J. BOROWITZKA. 1988. *Micro-algal biotechnology*. Cambridge University Press, London

BRENDONCK, L., T. PINCEEL & R. ORTELLS. 2017. Dormancy and dispersal as mediators of zooplankton population and community dynamics along a hydrological disturbance gradient in inland temporary pools. *Hydrobiologia*, 796:201–222. DOI: 10.1007/s10750-016-3006-1

BURGE, D. R. L., M. B. EDLUND & D. FRISCH. 2018. Paleolimnology and resurrection ecology: The future of reconstructing the past. *Evolutionary Applications*, 11(1): 42–59. DOI: 10.1111/eva.12556

BURKE, N. W. & R. BONDURIANSKY. 2018. The fitness effects of delayed switching to sex in a facultatively asexual insect. *Ecology and Evolution,* 8(5): 2698–2711. DOI: 10.1002/ece3.3895

CARVALHO, G. R. & R. N. HUGHES. 1983. The effect of food availability, female culture-density and photoperiod on ephippia production in *Daphnia magna* Straus (Crustacea: Cladocera). *Freshwater Biology*, 13(1): 37–46. DOI: 10.1111/j.1365-2427.1983.tb00655.x

CÁCERES, C. E. & N. G. HAIRSTON JR. 1998. Benthic-pelagic coupling in planktonic crustaceans: The role of the benthos. *Ergebnisse der Limnologie*, 52: 163–174.

DODSON, S. I. & D. G. FREY. 2001 *Cladocera and other Branchiopoda. In: Ecology and classification of North American freshwater invertebrates*. J. H. Thorp & A. P. Covich (ed.): 850-914. Academic Press. San Diego, USA.

ENRÍQUEZ-GARCÍA, C. E., S. NANDINI & S. S. S. SARMA. 2003. Food type effects on the population growth patterns of littoral rotifers and cladocerans. *Acta hydrochimica et hydrobiologica*, 31(2): 120-133. DOI: 10.1002/aheh.200300480

FORRÓ, L., N. M. KOROVCHINSKY, A. A. KOTOV & A. PETRUSEK. 2008. Global diversity of cladocerans (Cladocera; Crustacea) in freshwater. *Hydrobiologia*, 595: 177–184. DOI: 10.1007/s10750-007-9013-5

GERHARD, M., C. IGLESIAS, J. M. CLEMENTE, G. GOYENOLA, M. MEERHOFF, J. P. PACHECO, F. TEIXEIRA DE MELLO & N. MAZZEO. 2017. What can resting egg banks tell about cladoceran diversity in a shallow subtropical lake? *Hydrobiologia* 798: 75–86. DOI: 10.1007/s10750-016-2654-5

GOULDEN, C. E. 1968. The systematics and evolution of the Moinidae. *Transactions of American Philosophical Society*, 58(6): 1-101.

GROSS, J. B. 2012. *Cave Evolution*. In: *Enclyclopedia of Life Sciences*. eLS. John Wiley & Sons Ltd, Chichester. DOI: 10.1002/9780470015902.a0023628

HAIRSTON, N. G. & C. E. CÁCERES. 1996. Distribution of crustacean diapause: micro-and macroevolutionary pattern and process. *Hydrobiologia*, 320: 27–44. DOI: 10.1007/BF00016802

INNES D. J. & D. R. SINGLETON. 2000. Variation in allocation to sexual and asexual reproduction among clones of cyclically parthenogenetic *Daphnia pulex* (Crustacea: Cladocera). *Biological Journal of the Linnean Society*, 71:

771–787. DOI: 10.1111/j.1095-8312.2000.tb01290.x

JIMÉNEZ, B. & E. ZOPPI DE ROA. 1987. Reproductive variations of cladocerans in grasslands periodically flooded for irrigation in Mantecal, Venezuela. *Hydrobiologia*, 145: 293-298. DOI: 10.1007/978-94-009-4039-0_32

KIRK, K. L. 2012. *Starvation in rotifers: Physiology in an ecological context*. In: M. D. McCue (ed.). *Comparative Physiology of Fasting, Starvation, and Food Limitation*. Springer, Berlin. 25-35 pp. DOI: 10.1007/978-3-642-29056-5_3

KREBS, C. J., 1985. *Ecology; the experimental analysis of distribution and abundance*. 3rd edn. Harper & Row, New York.

NANDINI, S. & S. S. S. SARMA. 2003. Population growth of some genera of cladocerans (Cladocera) in relation to algal food (*Chlorella vulgaris*) levels. *Hydrobiologia*, 491: 211-219.

NANDINI, S. & S. S. S. SARMA. 2006. Ratio of neonate to adult size explains life history characteristics in cladoceran zooplankton. *Acta hydrochimica et hydrobiologica*, 34: 474-479.

SMIRNOV, N. N. 2017. *Physiology of the Cladocera*. Second Edition, Academic Press / Elsevier, London.

SOMMER, S., R. PISCIA, M. MANCA, D. FONTANETO & A. OZGUL. 2016. Demographic cost and mechanisms of adaptation to environmental stress in resurrected *Daphnia*. *Journal of Limnology*, 75(s2): 30-35. DOI: 10.4081/jlimnol.2016.1292

STEARNS, S. C. 1992. The evolution of life histories. Oxford University Press, New York.

WEBER, C. I. 1993. Methods for measuring the acute toxicity of effluents and receiving waters to freshwater and marine organisms. 4th ed. United States Environmental Protection Agency, Cincinnati, Ohio, EPA/600/4-90/027F, xv + 293 pp.

WINSOR, G. L. & D. J. INNES. 2002. Sexual reproduction in *Daphnia pulex* (Curstacea: Cladocera): observations on male mating behaviour and avoidance of inbreeding. *Freshwater Biology*, 47: 441-450. DOI: 10.1046/j.1365-2427.2002.00817.x

ZADEREEV, Y. S. 2003. Maternal effects, conspecific chemical cues, and switching from parthenogenesis to gametogenesis in the cladoceran *Moina macrocopa*. *Aquatic Ecology*, 37(3): 251–255. DOI: 10.1023/A:1025850417717

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