Freshwater Biology (2003) **48**, 432–439

Longevity of the freshwater anostracan *Streptocephalus mackini* (Crustacean: Anostraca) in relation to food (*Chlorella vulgaris*) concentration

ALEJANDRO ANAYA-SOTO*, S. S. S. SARMA† AND S. NANDINI‡

**College of Sciences and Humanities, Naucalpan, Calzada de los Remedios S/N, Col. Bosque de los Remedios, Municipio de Naucalpan de Juárez, Estado de México, Mexico*

†Laboratory of Aquatic Zoology (UMF), Division of Research and Postgraduate Studies, National Autonomous University of Mexico, Campus Iztacala, Los Reyes, Tlalnepantla, State of Mexico, Mexico

‡CyMA Project, Division of Research and Postgraduate Studies, National Autonomous University of Mexico, Campus Iztacala, Los Reyes, Tlalnepantla, State of Mexico, Mexico

SUMMARY

1. Temporary ponds are inhabited by a variety of invertebrates, of which anostracans are an important group. We studied the lifetables of male and female anostracan *Streptocephalus mackini* at 3 algal concentrations (0.5×10^6, 1.0×10^6 and 1.5×10^6 cells mL^{-1}).
2. Regardless of sex, *S. mackini* showed better survivorship at lower food levels. The longest average lifespan observed was 85 ± 2 days for males fed *Chlorella* at 0.5×10^6 cells mL^{-1}.
3. Both net reproductive rate and generation time decreased with increasing food level. The highest net reproductive rate was about 120 cysts per female. The longest generation time of about 40 days, observed at 0.5×10^6 cells mL^{-1}, was more than three times that at 1.5×10^6 cells mL^{-1}.
4. The rate of population increase (r) was nearly the same (0.31 ± 0.06) at high (1.5×10^6 cells mL^{-1}) and intermediate (1.0×10^6 cells mL^{-1}) food levels. The r-value at low food level (0.5×10^6 cells mL^{-1} of *Chlorella*) was 0.20 ± 0.01 per day.

Keywords: Algae, demography, food density, growth rate, life table

Introduction

Temporary ponds are inhabited by a variety of invertebrates, of which anostracans are an important group (Machado, Cristo & Da Fonseca, 1999). These waterbodies dry up in a cyclical manner so that overlapping generations of anostracans are usually absent (Brendonck, 1996). As fish predation is virtually non-existent in these temporary freshwater bodies, anostracans exhibit few defences exhibited by other branchiopods such as the development of spines and plasticity in body size among others (Dodson & Frey, 2001). The anostracans increase their population abundance rapidly through hatching of cysts and adults yield a large number of cysts to act as a seed bank for the next population cycle (Brendonck & Riddoch, 2000). This permits the population to utilise the existing resources rapidly which, in turn, results in food limitation, especially when inedible algae are present in the ponds (Kurmayer & Juettner, 1999). It is therefore of considerable interest to study differences in the demographic strategies of freshwater anostracans under various food concentrations.

A large body of data is available on the relation between food level and life history variables such as body size, age at first reproduction and rate of

---

Correspondence: S. S. S. Sarma, Laboratory of Aquatic Zoology (UMF), Division of Research and Postgraduate Studies, National Autonomous University of Mexico, Campus Iztacala, Avenue. de los Barrios s/n, Los Reyes, AP 314, CP 54090, Tlalnepantla, State of Mexico, Mexico. E-mail: sarma@servidor.unam.mx

population growth of small-sized crustaceans such as cladocerans (Dodson & Frey, 2001). Sexual reproduction in anostracans, which are exclusively non-parthenogenetic, is facilitated by the small size of the waterbodies where they are normally found. In these pools, there is a high rate of male–female encounters and the resultant cysts have a higher genetic variability relative to parthenogenetic reproduction, which may help ensure better adaptation to diverse and adverse environmental situations (Hildrew, 1985). The quantity of available food in temporary waterbodies is limited because of reduced photosynthesis as a result of high turbidity and limited nutrient availability (Hutchinson, 1967). Anostracans have high feeding rates and, thus, food limitation in these water bodies is common (Belk & Ballantyne, 1996). Cyst production is related to the quantity of available food in *Chirocephalus diaphanus* (Ali & Dumont, 1995). However, sensitivity to food concentration may vary among different taxa of branchiopods and there is some indication that lower algal levels actually yield better growth and reproductive performances in cladocerans (Nandini & Sarma, 2000). Thus it remains to be tested how different species of anostracans respond to given algal concentrations in terms of survival and reproduction, two of the most important components of life history characters.

The genus *Streptocephalus* is widely distributed with about 60 species world-wide. Mexico and the Southern United States have as many as 15 species of this genus (Maeda-Martínez *et al*., 1997). Many *Streptocephalus* species feed on microalgae from hatching until death. *S. mackini* is one of the common anostracans found in many temporary waterbodies in Mexico. This species can grow and reproduce on a diet of green algae. Although some information exists on cyst size and longevity of *S. mackini* (Castrejon-Ocampo, Soto-Arroyo & Soriano-Salazar, 1992), reproductive and survivorship patterns in relation to different food densities are unknown. The aim of the present work was to study the life table demography of *S. mackini* fed different densities of the edible green alga *Chlorella vulgaris*.

Methods

The original stock of cysts of *Streptocephalus mackini* Moore was collected from a small temporary pond in Mexico City. The cysts hatched when maintained in reconstituted moderately hard water (Environmental Protection Agency (EPA) medium, Anonymous, 1985) under continuous aeration and diffused fluorescent illumination. This medium was prepared by dissolving 96 mg $NaHCO_3$, 60 mg $CaSO_4$, 60 mg $MgSO_4$ and 4 mg KCl in one litre of distilled water. A large number of nauplii were obtained 2–3 days following incubation. The nauplii were carefully transferred to a large glass aquarium (40 L) containing about 35 L of EPA medium with 0.5×10^6 cells mL^{-1} of the single-celled alga *Chlorella vulgaris*. The medium was replaced twice a week and fresh algal food was added every alternate day.

Chlorella vulgaris was mass cultured using Bold's basal medium (Borowitzka & Borowitzka, 1988). To feed individuals of the stock culture of *S. mackini* and for use in experiments, we harvested log phase algae, centrifuged at 800 *g* and resuspended in EPA medium. The stock algal density was estimated using a haemocytometer. From this we prepared the required volume of the test medium at three concentrations, namely 0.5×10^6, 1.0×10^6 and 1.5×10^6 cells mL^{-1}. In terms of carbon content these algal concentrations corresponded to 8.728, 5.819 and 2.909 $\mu g\ mL^{-1}$, respectively (Nandini & Sarma, 2002).

For life table demography experiments, we used 200 mL capacity transparent jars. Into each of the nine test jars (three algal concentrations × three replicates) containing 150 mL medium at the specified food level, we introduced a pair of immature *S. mackini* (male and female). As sexes cannot be differentiated in very young individuals, we first allowed them to grow for 1 week under similar test conditions and then they were used for the final experiments. All the test jars were maintained at 23 ± 1 °C with a photoperiod of 12 : 12 L : D. Following introduction of the test individuals, we collected daily data related to the survival of both males and females. The cysts from each test container were removed and counted, and eliminated every day. Surviving test individuals from each test container were transferred daily to fresh jars containing appropriate algal food levels. The experiments were discontinued when all test individuals of the original cohort had died.

Based on the data collected, we derived the following variables, separately for males and females: age-specific survivorship, age-specific reproduction, average lifespan, age-specific life expectancy, gross reproductive rate, net reproductive rate, generation time, stable age distribution and rate of population growth (*r*). The following formulae were used (Krebs, 1985; Pianka, 1988). A jackknife approach was used to correct the growth rates (Meyer *et al.*, 1986).

$$\text{Gross reproductive rate} = \sum_{o}^{\infty} m_x$$

$$\text{Net reproductive rate } R_o = \sum_{o}^{\infty} l_x m_x$$

$$\text{Generation time (T)} = \frac{\sum l_x m_x \cdot x}{R_0}$$

$$\text{Rate of population increase (r)} = \sum_{x=0}^{n} e^{-rx} l_x m_x = 1$$

$$\text{Stable age distribution } (C_x) = \frac{\lambda^{-x} l_x}{\sum_{i=0}^{\infty} \lambda^{-i} l_i}$$

Data were analysed statistically following Sokal & Rohlf (2000).

Results

The age-specific survivorship curves of female and male *Streptocephalus mackini* in relation to different densities of *Chlorella* are presented in Fig. 1. Regardless of sex, test individuals showed better survivorship at lower food levels. At 0.5 × 10^6 cells mL^{-1}, both male and female anostracans had nearly rectangular survivorship curves. These curves became steeper and fell sharply when the food supply was increased to 1.5 × 10^6 cells mL^{-1}. At lower food levels, males lived longer than females but the trends were reversed at increased algal levels. The longest average lifespan observed was 85 ± 2 days for males fed *Chlorella* at 0.5 × 10^6 cells mL^{-1}, while the highest food reduced the lifespan significantly ($P < 0.01$) to about 20 days (Fig. 2). The age-specific life expectancy curves showed trends similar to the survivorship curves but these trends were nearly the same for male and female *S. mackini* (Fig. 3).

Data on fecundity, measured as the number of cysts per female, showed increased peak cyst production in the latter part of the life cycle under lower food levels. However, when food levels were enhanced, peak cyst production was observed much earlier (Fig. 4). Data on the stable age distribution of female *S. mackini* indicated that the curves were stable after 40 days under 0.5 × 10^6 cells mL^{-1} while at higher food levels a shorter time was needed for stabilisation (Fig. 5). Results for net reproductive rate, rate of population increase and the generation time of female *S. mackini* in relation to different algal densities are shown in Fig. 6. Both net reproductive rate and the generation time decreased with increasing food level. The rate of population increase, however, was higher at the intermediate (1.0 × 10^6 cells mL^{-1}) food level. The highest net reproductive rate was about 120 cysts per female. The longest generation time, of about 40 days, observed at 0.5 × 10^6 cells mL^{-1}, was more than three times that at 1.5 × 10^6 cells mL^{-1}.

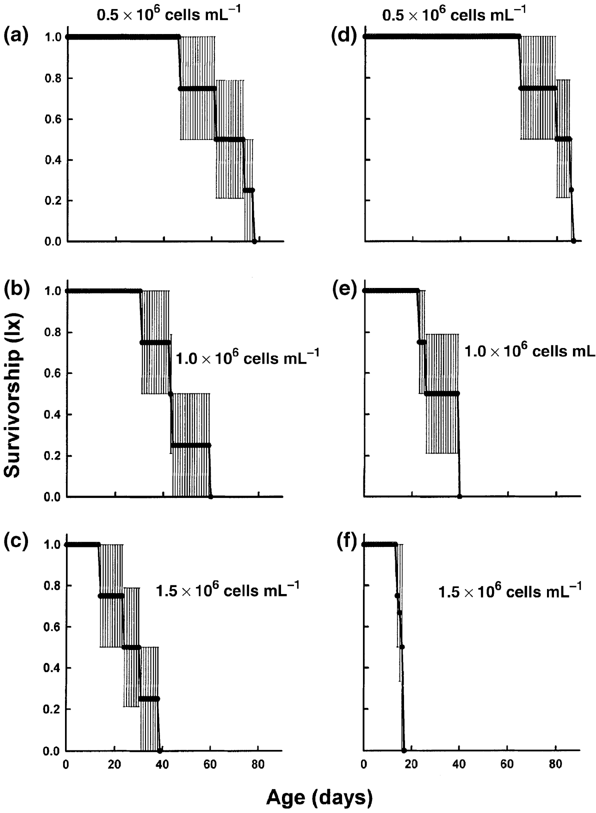

Fig. 1 Age-specific survivorship curves of *S. mackini* fed *Chlorella* at three densities. a to c represent data for females and d to f for males. Shown are the mean ±SE based on three replicate recordings.

Discussion

Demographic studies on various anostracans, including *Streptocephalus proboscideus* and *Chirocephalus diaphanus*, indicate the suitability of green algae such as *Chlorella* and *Scenedesmus* for their survival and growth (Ali, 1995; Sarma & Dierckens, 1999). How-

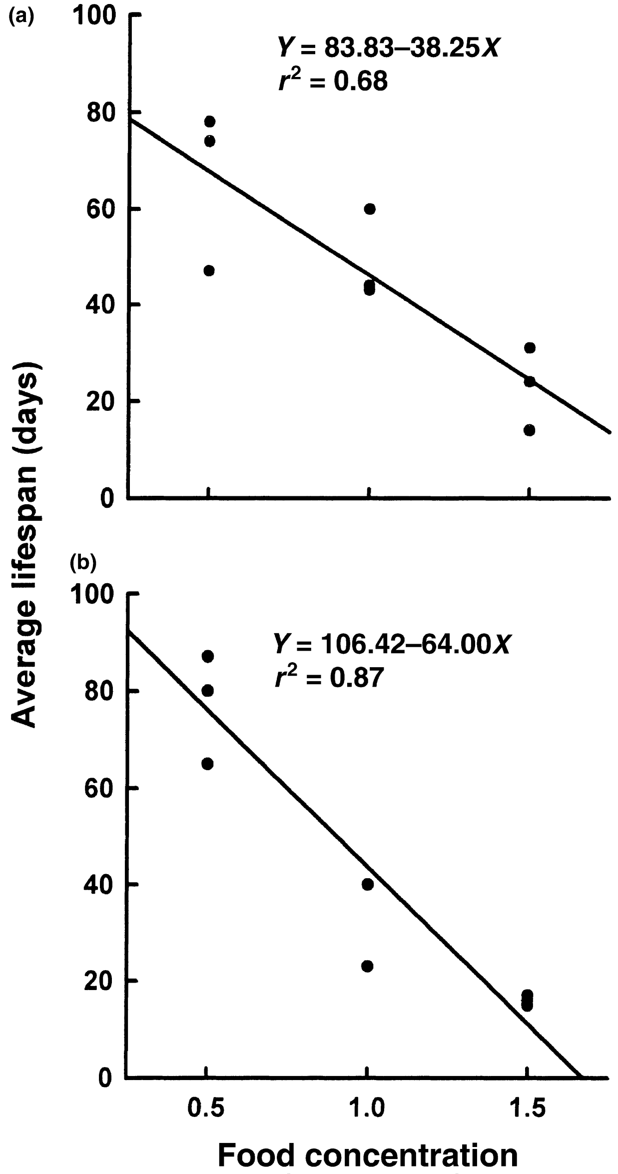

Fig. 2 Relationship between average lifespan and food density in male and female *S. mackini*. a: female, b: male. Data are plotted for each replicate.

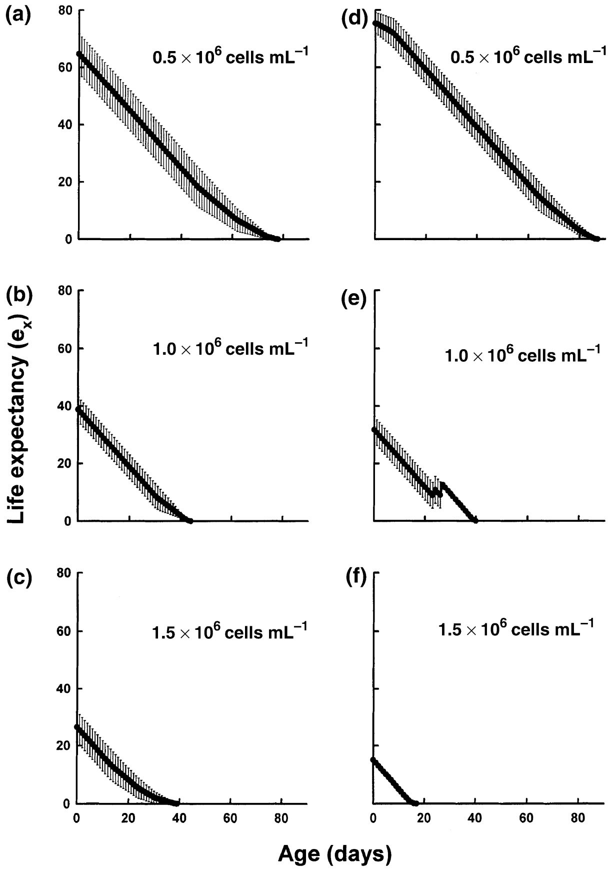

Fig. 3 Age-specific life expectancy curves of *C. mackini* under different levels of *Chlorella*. a to c represent data for females and d to f for males. Shown are mean ± SE based on 3 replicate recordings.

ever studies on food density-dependent effects on life history variables are scarce. In general, for many freshwater anostracans, females gather more algal food than males, possibly because of their larger size (Dierckens *et al.*, 1997). The negative influence of increased algal concentration on lifespan may be because of several factors. One factor is related to the reduced food intake at lower algal concentrations and the consequent lower metabolic rates which could promote longer lifespan of crustaceans such as *Daphnia* (MacArthur & Baillie, 1929; Dudycha, 2001). Additionally, at higher food concentrations most cladocerans spend much of their energy for cleaning the appendages from algal clogging which causes reduced food intake and increased respiratory loss (Dodson & Frey, 2001). In the present study, we did not quantify algal food consumed by test anostracans nor their respiration. However, the reduced lifespan of *S. mackini* with increasing algal concentration observed could be because of the above factors.

Depending on the source of test material, the lifespan of a given species of *Daphnia* may vary. For example, populations of *D. pulex-pulicaria* species complex from temporary ponds have reduced lifespans and earlier and steeper declines in fecundity patterns than those from permanent waterbodies because of genetic variation in life histories as a result

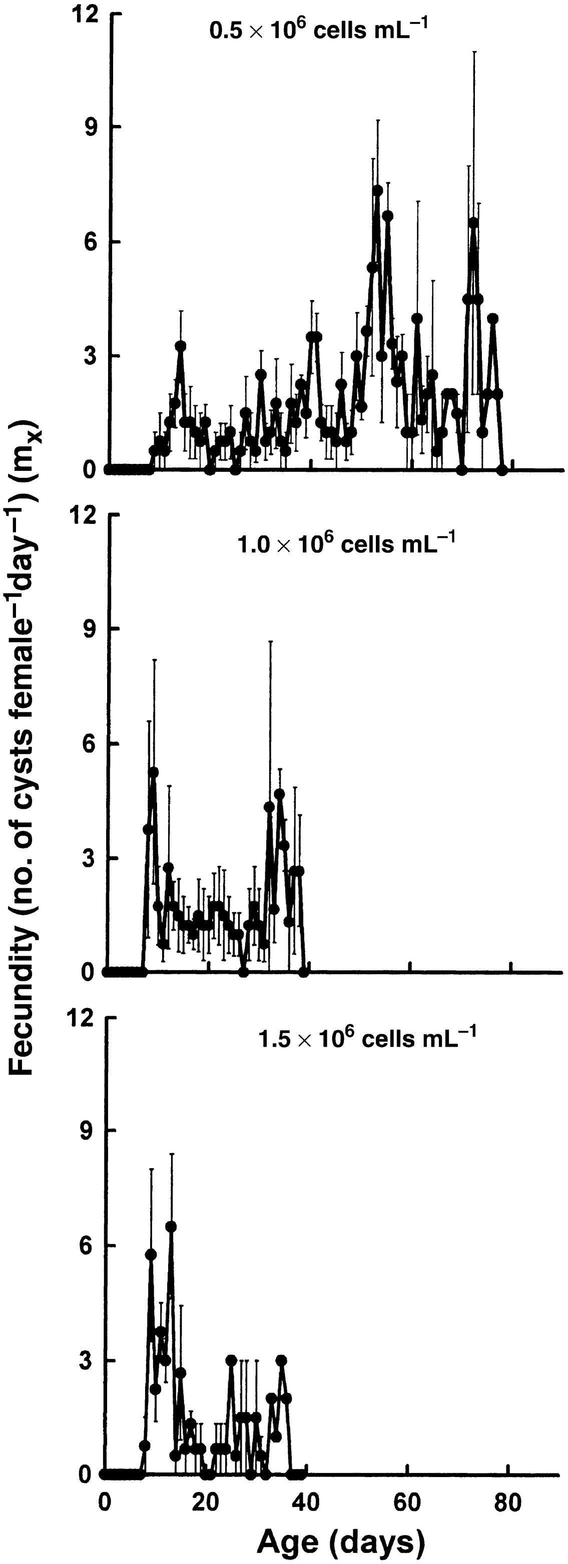

Fig. 4 Fecundity curves of female *S. mackini* fed *Chlorella* at 3 different levels. Shown are the mean ± SE based on three replicate recordings.

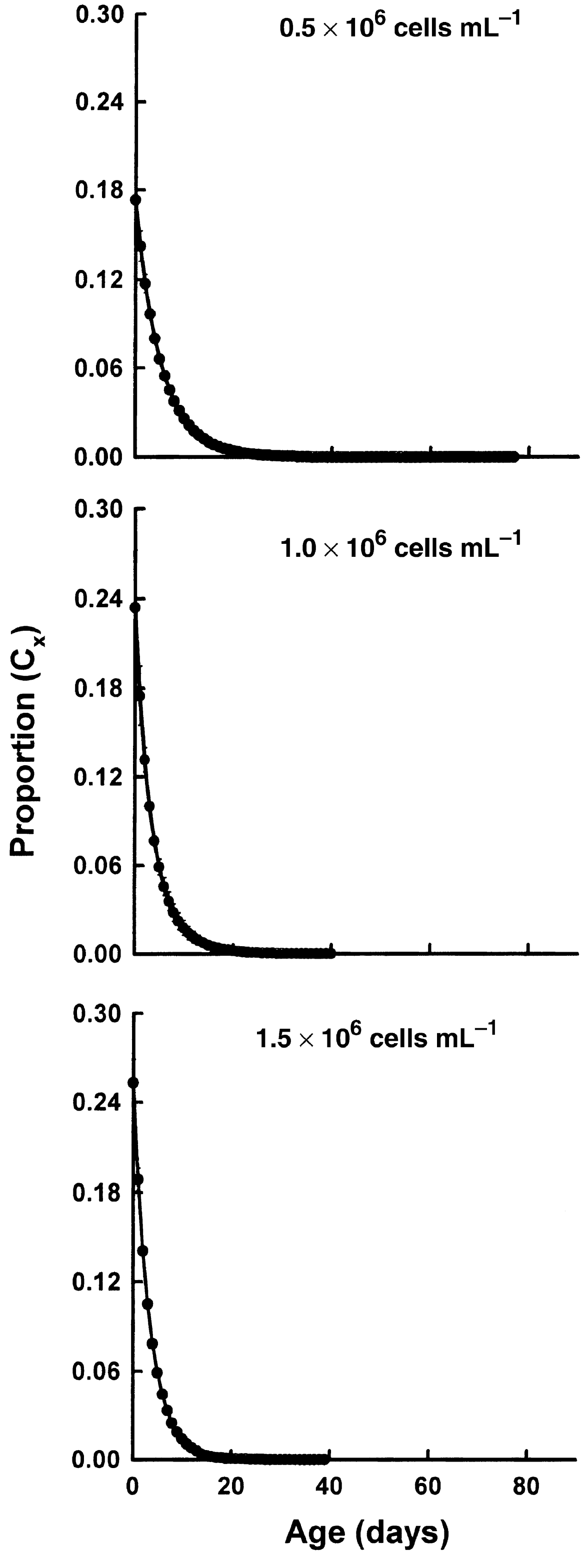

Fig. 5 Stable age distribution curves of female *S. mackini* fed *Chlorella* at different densities.

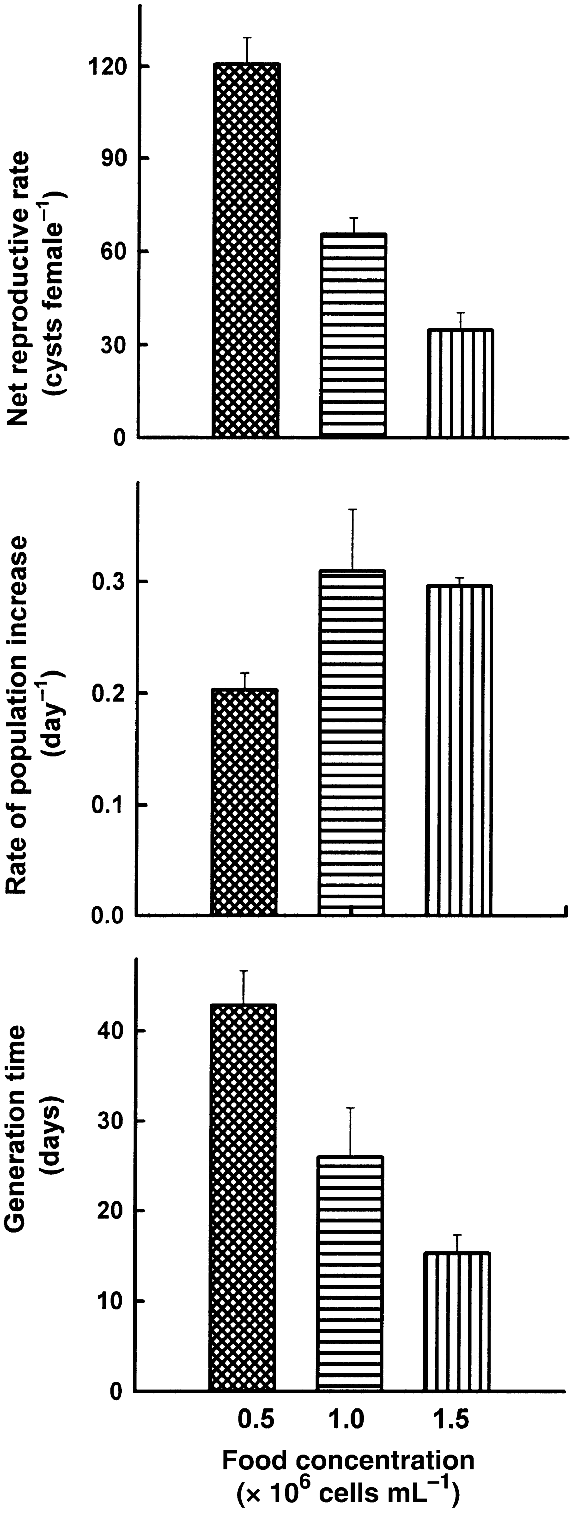

Fig. 6 Selected life history variables of *S. mackini* fed *Chlorella* at different densities. Shown are mean ± SE based on 3 replicate recordings.

of temporal environmental changes under field conditions (Dudycha & Tessier, 1999). Freshwater anostracans including *Streptocephalus* are restricted to temporary waterbodies and are never found in large and permanent lakes as they are highly vulnerable to fish predation and, cysts, without an obligatory period of drying, fail to hatch (Bohonak & Whiteman, 1999). Therefore the comparison of life history traits of *Streptocephalus* taxa from temporary versus permanent waterbodies may never arise.

Large branchiopods generally have longer lifespans than smaller ones, such as cladocerans which may live only a few weeks. The shortest lifespans are normally found in the genus *Moina* while longer lifespans of up to 2 months or more can be found in the genera *Simocephalus* and *Daphnia* (Nandini, 2000). In the present study, *Streptocephalus mackini* had an average lifespan of 20–90 days depending on food density. Earlier work on *S. mackini* indicates that this species could live as long as 90 days (Castrejon-Ocampo & Soriano-Salazar, 1990) and our present data support this observation. The fecundity of *S. mackini* observed in this study is low compared with some other members of the genus. For example, *S. proboscideus* had a lifetime fecundity of more than 400 cysts, while we found a gross reproductive rate of about 100 cysts per female. One possible reason for this low fecundity could be the lack of fertilisation by the male. In *Streptocephalus*, unlike *Artemia*, copulation by the male is often not evident and lasts only for a short period of time (Dodson & Frey, 2001). Moreover, for effective fertilization, the number of males per female might need to be higher than the 1 : 1 ratio we used (Ali, 1995). We also found several unfertilised cysts. It has been documented that if females are not fertilised, the oocytes are either resorbed or simply released into the medium (reviewed in Murugan *et al.*, 1996). From our results, it was evident that a certain number of unfertilised oocytes of *S. mackini* was released into the medium. However, we cannot rule out the possibility of simultaneous occurrence of oosorption and release of unfertilised oocytes.

The inverse relation between generation time and food level observed in this study has also been reported for small branchiopods (Cladocera) such as *Alona*, which showed longer generation times at lower food levels (Nandini & Sarma, 2000). The rate of population increase of a species is of considerable interest, particularly from the point of view of its role

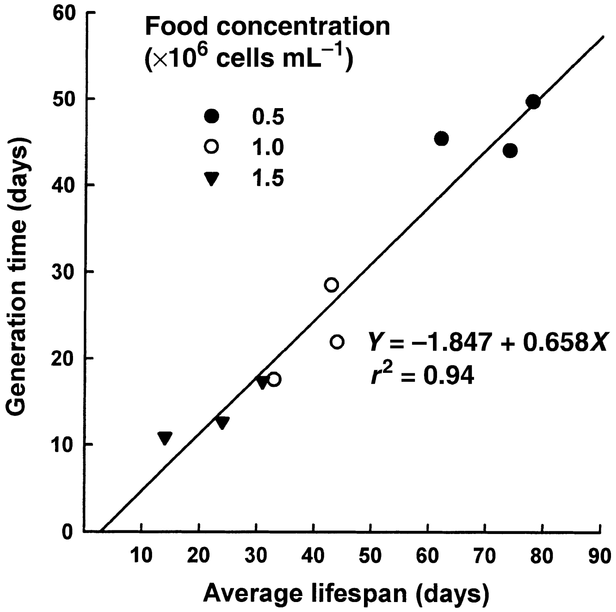

Fig. 7 Relationship between lifespan and generation time of *S. mackini*. Data are plotted for each replicate at three algal food concentrations.

in community dynamics. In general, most branchiopods have population growth rates in the range of 0.01–1.00 (Dodson & Frey, 2001). In the present study, *r*-values were in the range of 0.20–0.35, depending on food level. The rate of population increase is a variable that is sensitive to food, temperature and many other environmental factors (Krebs, 1985). In the present study, although the average lifespan and generation time decreased with increasing algal food density, the rate of population increase was optimal at intermediate food levels of (1.0×10^6 cells mL^{-1}). King (1982) found a relation between generation time and mean lifespan. He suggested that for iteroparous organisms, lifespan should be twice the generation time. In the present study too there existed a direct relation between lifespan and generation time (Fig. 7) and the ratio between them was close to two. In many other iteroparous zooplankton (e.g. rotifers), this ratio can vary from 1.4 to 2.3 (reviewed in Sarma & Rao, 1991). King (1982) also suggested that survival of females of a parthenogenetic species beyond the median lifespan had no role in contributing towards population growth. However, freshwater anostracans reproduce sexually and until the end of their lifespan. In addition, there is little or no postreproductive period (Ali, Sarma & Dumont, 1999) and therefore they can add to net reproductive rate throughout their lifespan. This is evident in the present study too, where the female *S. mackini* continued to reproduce until death.

The use of cysts for deriving population growth rates in fairy shrimps is different from that used for cladocerans. In anostracans, cysts are treated as potential offspring, although 100% hatching following an obligatory diapause is not documented (Ali, 1995). In cladocerans, however, the population growth rates also include the egg developmental time (Dodson & Frey, 2001). If low hatching of anostracan cysts occurs, this could reduce population growth rates. In this work we did not measure the hatching success of cysts; instead we considered them as potential offspring.

In conclusion, our results suggest that lower algal food levels extended the lifespan of *S. mackini*. At 1.0×10^6 cells mL^{-1} of *Chlorella*, higher population growth rates were recorded. The effect of algal concentrations, lower than those used here, on both survival and reproduction of *Streptocephalus* could probably give a better insight into the food influence on lifespans.

Acknowledgments

S. S. S. Sarma acknowledges PAPIIT IN204101 for support. Alejadro Maeda-Martínez confirmed the identification of the test species. We thank G. Murugan for revising a previous draft of the manuscript and Javier Arias-Velázquez for bibliographic help. SN thanks SNI – 20520 for financial support.

References

Ali A.J. (1995) *Aspects of biology of the freshwater fairy shrimp Streptocephalus Proboscideus (Crustacea: Anostraca).* PhD Thesis. University of Ghent, Ghent, Belgium.

Ali A.J. & Dumont H.J. (1995) Larviculture of the fairy shrimp, *Streptocephalus proboscideus* (Crustacea: Anostraca): effect of food concentration and physical and chemical properties of the culture medium. *Hydrobiologia*, **298**, 159–165.

Ali A.J., Sarma S.S.S. & Dumont H.J. (1999) Cyst production in the fairy shrimp *Streptocephalus proboscideus* (Anostraca) in relation to algal and loricated rotifer diet. *Crustaceana*, **72**, 517–530.

Anonymous (1985) *Methods of measuring the acute toxicity of effluents to freshwater and marine organisms.* US Environment Protection Agency, EPA/600/4–85/013.

Belk D. & Ballantyne R. (1996) Filamentous algae an additional food for the predatory anostracan *Branchinecta gigas*. *Journal of Crusacean Biology*, **16**, 552–555.

Bohonak A.J. & Whiteman H.H. (1999) Dispersal of the fairy shrimp *Branchinecta coloradensis* (Anostraca): effects of hydroperiod and salamanders. *Limnology and Oceanography*, **44**, 487–493.

Borowitzka M.A. & Borowitzka L.J. (1988) *Micro-Algal Biotechnology*. Cambridge University Press, London.

Brendonck L. (1996) Diapause, quiescence, hatching requirements: what we can learn from large freshwater branchiopods (Crustacea: Branchiopoda: Anostraca, Notostraca, Conchostraca). *Hydrobiologia*, **320**, 85–97.

Brendonck L. & Riddoch B.J. (2000) Egg bank dynamics in anostracan desert rock pool populations (Crustacea: Branchiopoda). *Archiv für Hydrobiologie*, **148**, 71–84.

Castrejon-Ocampo L. & Soriano-Salazar M. (1990) Características del desarrollo del camarón duende: *Streptocephalus mackini* en el embalse Chalcatzingo, Morelos, México. *Universidad: Ciencia Y Tecnología*, **1**, 27–32.

Castrejon-Ocampo L., Soto-Arroyo E. & Soriano-Salazar M. (1992) Calidad de los quistes de *Streptocephalus mackini* (Crustacea: Anostraca). *Universidad: Ciencia Y Tecnología*, **2**, 113–119.

Dierckens K.R., Beladjal L., Vandenberghe J., Swings J. & Mertens J. (1997) Filter-feeding shrimps (Anostraca) grazing on bacteria. *Journal of Crustacean Biology*, **17**, 264–268.

Dodson S.I. & Frey D.G. (2001) Cladocera and other Branchiopoda. In: *Ecology and Classification of North American Freshwater Invertebrates* (Eds J.H. Thorpe & A.P. Covich), pp. 723–786. Academic Press, New York.

Dudycha J.L. (2001) The senescence of *Daphnia* from risky and safe habitats. *Ecology Letters*, **4**, 102–105.

Dudycha J.L. & Tessier A.J. (1999) Natural genetic variation of life span, reproduction, and juvenile growth in *Daphnia*. *Evolution*, **53**, 1744–1756.

Hildrew A.G. (1985) A quantitative study of the life history of a fairy shrimp (Branchiopoda: Anostraca) in relation to the temporary nature of its habitat, a Kenyan rainpool. *Journal of Animal Ecology*, **54**, 99–110.

Hutchinson G.E. (1967) *A Treatise on Limnology*. **Vol. 2**. *Introduction to the Lake Biology and the Limnoplankton*. John Wiley & Sons, New York.

King C.E. (1982) The evolution of lifespan. In: *Proceedings in Life Sciences: Evolution and Genetics of Life Histories* (Eds H. Dingle & J.P. Hegmann), pp. 121–138. Springer-Verlag, New York.

Krebs C.J. (1985) *Ecology. The Experimental Analysis of Distribution and Abundance*, 3rd edn. Harper & Row, New York.

Kurmayer R. & Juettner F. (1999) Strategies for the co-existence of zooplankton with the toxic cyanobacterium *Planktothrix rubescens*. Lake Zurich. *Journal of Plankton Research*, **21**, 659–683.

MacArthur J.H. & Baillie W.H.T. (1929) Metabolic activity and duration of life. II. Metabolic rates and their relation to longevity in *Daphnia magna*. *Journal of Experimental Zoology*, **53**, 243–267.

Machado M., Cristo M. & Da Fonseca L.C. (1999) Non-cladoceran branchiopod crustaceans from southwest Portugal. I. Occurrence notes. *Crustaceana*, **72**, 591–602.

Maeda-Martínez A.M., Belk D., Obregon-Barboza H. & Dumont H.J. (1997) Large branchiopod assemblages common to Mexico and the United States. *Hydrobiologia*, **359**, 45–62.

Meyer J.S., Ingresol C.G., McDonald L.L. & Boyce M.S. (1986) Estimating uncertainity in population growth rates: Jackknife vs bootstrap techniques. *Ecology*, **67**, 1156–1166.

Murugan G., Maeda-Martínez A.M., Criel G. & Dumont H.J. (1996) Unfertilized oocytes in streptocephalids: resorbed or released? *Journal of Crustacean Biology*, **16**, 54–60.

Nandini S. (2000) Responses of rotifers and cladocerans to *Microcystis aeruginosa* (Cyanophyceae): a demographic study. *Aquatic Ecology*, **34**, 227–242.

Nandini S. & Sarma S.S.S. (2000) Lifetable demography of four cladoceran species in relation to algal food (*Chlorella vulgaris*) density. *Hydrobiologia*, **435**, 117–126.

Nandini S. & Sarma S.S.S. (2002) Population growth of some genera of cladocerans (Cladocera) in relation to algal (*Chlorella vulgaris*) food levels. *Hydrobiologia*, in press.

Pianka E.R. (1988) *Evolutionary Ecology*. Harper & Row, New York, 3rd edn.

Sarma S.S.S. & Dierckens K.R. (1999) A comparison of the feeding rates of *Streptocephalus Torvicornis* and *Chirocephalus diaphanus* (Crustacea: Anostraca) on rotifers. *Advances in fish and wildlife ecology and biology*. (Ed. B. L. Kaul), **Vol. 2** pp., pp. 78–82. Daya Publishing House, Tri Nagar, Delhi, India.

Sarma S.S.S. & Rao T.R. (1991) The combined effects of food and temperature on the life history parameters of *Brachionus patulus* Müller (Rotifera). *International Revue Gesamten Hydrobiologie*, **76**, 225–239.

Sokal R.R. & Rohlf F.J. (2000) *Biometry*. W.H. Freeman, San Francisco.

(Manuscript accepted 17 September 2002)