Growth and Longevity of Exosphaeroma hylocoetes (Isopoda) Under Varying Conditions of Salinity and Temperature

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Growth and longevity of *Exosphaeroma hylocoetes* (Isopoda) under varying conditions of salinity and temperature

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The effect of temperature (15 and 25°C) and salinity (15 and 35 practical salinity units) combinations on the growth and longevity of the South African estuarine isopod *Exosphaeroma hylocoetes* was investigated and data analysed using the logistic growth model. No significant differences (P = 0.43 to 0.54) were obtained for the growth rates of male and female *E. hylocoetes* under the suite of temperature/salinity combinations. Among the variables considered, temperature was identified as the most important in influencing the growth rates of the isopod. Elevated temperatures promoted faster initial growth in both males and females. Salinity had no significant influence on the growth rates of males and females. Males (25.77 ± 3.40 weeks) lived significantly longer (P < 0.001) than females (21.52 ± 3.00 weeks), allowing males (8.08 ± 0.25 mm mean body length) to attain a significantly larger size than females (6.59 ± 0.25 mm) under experimental conditions. Females, however, attained sexual maturity (at 2.5 mm body length) 2–4 weeks earlier than males (5.5 mm in length). It is suggested that the faster growth rates at the higher temperature/salinity combinations allow the isopod to reach sexual maturity at an earlier stage than those at the lower combinations.

Key words: growth, longevity, estuarine isopod, temperature, salinity.

INTRODUCTION

Numerous studies have documented the importance of both temperature and salinity in influencing aquatic crustacean metabolic processes such as respiration and growth. For example, increased water temperatures have been shown to increase respiration rates in various species of shrimp (Chen & Nan 1993; Spanonopoulos-Hernándeza *et al.* 2005; Allan *et al.* 2006), and copepods (Isla & Perissinotto 2004). The response of invertebrates to changes in salinity is more complex, largely reflecting their evolutionary origins (Kinne 1966). For example, juvenile blue swimming crabs, *Portunus pelagicus,* displayed significantly faster growth and higher survival in response to increasing salinity (Romano & Zeng 2006). Additional factors that may influence the growth rates of crustaceans include photoperiod (Gambardella *et al.* 1997), food availability (Shuster & Guthrie 1999) and sex (Newman *et al.* 2007).

Most isopod growth studies have focused on terrestrial isopods using field-determined size frequency histograms, based on cephalothorax width or changes in mass, to establish a growth rate using the von Bertalanffy model (von Bertalanffy 1938; McQueen & Carnio 1974; Strong & Daborn 1979; Caseiro *et al.* 2000; Li 2002; Araujo & Bond-Buckup 2004; Meinhardt *et al.* 2007). The growth rates of isopods have, however, rarely been studied in the laboratory. Longevity has been examined mainly in terrestrial isopods, which appear to live longer than marine isopods, varying from 11 to 108 months (Achouri *et al.* 2003; Warburg 1993). In terrestrial isopods, females generally achieve a larger overall size, but grow at a slower rate and survive for longer than males (Araujo & Bond-Buckup 2004; Meinhardt *et al.* 2007). Females were thus able to produce more offspring as they had a larger body size permitting greater egg-bearing ability.

The estuarine isopod *Exosphaeroma hylocoetes* is widely distributed along the southeastern coastline of southern Africa (Kensley 1978). It is typically associated with submerged macrophytes in the littoral zones of the middle and upper reaches of estuaries, particularly temporarily open/closed estuaries (TOCEs) (Henninger *et al.* 2008). The isopod is primarily a detritivore feeding on particulate organic matter derived from a variety of sources including vegetation, zooplankton, nekton and microalgae attached to the submerged

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macrophytes (Henninger *et al.* 2009). *E. hylocoetes* is sexually dimorphic with males being significantly larger than females (Henninger *et al.* 2008). In the field males attained a maximum length of ≈12 mm, while females grew to ≈7.5 mm (Barnard 1940; Henninger *et al.* 2008). In the absence of experimental data, it is not known if the larger size attained by males is the result of elevated growth rates or extended longevity, or a combination of the two. Larger male body size has been linked to mate-guarding in marine isopods (Jormalainen 1998). The aim of this study, therefore, was to determine the growth rates of male and female *E. hylocoetes* under a combination of temperatures and salinities which are typically recorded in Eastern Cape estuaries (Henninger *et al.* 2008).

MATERIALS & METHODS

Collection and laboratory procedures

Exosphaeroma hylocoetes (Barnard, 1940) was collected from the temporarily open/closed Kasouga Estuary (33°39′11″S 26°44′01″E) located on the Eastern Cape coastline of southern Africa using a hand-held sweep net. After collection, the isopods were transported back to the laboratory before being maintained in constant environment (CE) rooms at the following salinity/temperature combinations: 15 practical salinity units (PSU)/15°C; 15/25°C; 35/15°C and 35 /25°C. All isopods were subjected to a light : dark phase of 12:12 hours. Recent studies indicated that the salinity of the Kasouga Estuary (a TOCE) ranged between 2 and 35, with a mean of 22.80 ± 8.90. The salinity only remained below 15 for two months of a 19-month study (Henninger *et al.* 2008). While water temperature fluctuated between an austral winter minimum of 12.5°C in July to a summer maximum of 26°C in February, with a mean temperature of 19.20 ± 4.42°C (Henninger *et al.* 2008). These conditions replicated the natural annual conditions experienced within the Kasouga Estuary (Henninger *et al.* 2008). The isopods, in aerated round polyethylene containers (diameter of ≈50 cm and a height of ≈12 cm), formed the brood stocks. Plastic hair curlers (in place of vegetation), were placed in the water to act as refugia for the brooding females. Densities of ≈1500 ind/m², equivalent to medium isopod densities in the Kasouga Estuary (Henninger *et al.* 2008), were maintained in the containers. The brood stocks were maintained for 18 months to ensure sufficient male and female isopod numbers. Initial trials, at

20°C and a salinity of 15, were conducted with 30 individuals as a feasibility study and to establish longevity. Individual juvenile *E. hylocoetes* ($n = 30$ to 50, as survival rates of the isopod varied, and only those individuals surviving ≥10 weeks were selected for the results section), produced by the brood stock, within the size range 1.5–2.0 mm (size of released mancas) were placed in 250 ml plastic containers of mesohaline (salinity 15) or 100 % seawater (salinity 35) and placed in CE rooms, (set at either 15 or 25°C). The containers were not aerated as it was considered that the small animals were not under O_2 stress in 250 ml water. Water was changed every seven days and the isopods fed *ad libitum* on commercially available dry fish food. The fish food had the following composition: min 40 % protein; 5 % fat; 5 % fibre and 12 % moisture.

All of the isopods were measured weekly, until their death, with the aid of a Wild M5A stereomicroscope (×120) fitted with an ocular micrometer. This entailed measurement, to the nearest 0.01 mm, along the mid-dorsal length from the anterior tip of the cephalon (in the case of *E. hylocoetes* this was the point of connection between the cephalon and the flagellae, or antenna one), to the posterior tip of the pleotelson (Barnard 1940). Growth rates were determined for at least 15 males and 15 females in each temperature/salinity combination. These results were used to determine the weekly growth rates, maximum length and longevity of the isopod.

Exosphaeroma hylocoetes can be sexed when ≥5 mm (total length), as male *E. hylocoetes* develop two pene situated anteriorly of the pleopods (Barnard 1940). Males also have a more pronounced triangular pleotelson with a definite inner ridge when viewed ventrally. This ridge is absent in females and they have a more rounded pleotelson (Barnard 1940).

Statistical analyses

Initial investigation of the plots of $\frac{dL}{dt}$ against $\bar{L}$ illustrated a quadratic relationship suggesting that growth in *E. hylocoetes* is logistic (Fig. 1). A quadratic model of the form

$$\frac{dL}{dt} = k\bar{L}\left(1 - \frac{\bar{L}}{L_\infty}\right) = k\bar{L} - \frac{a\bar{L}^2}{L_\infty},$$

where α is the instantaneous growth rate and L_∞ the asymptotic length, was subsequently fitted to each individual isopod's growth data using non-linear least squares regression. The resultant
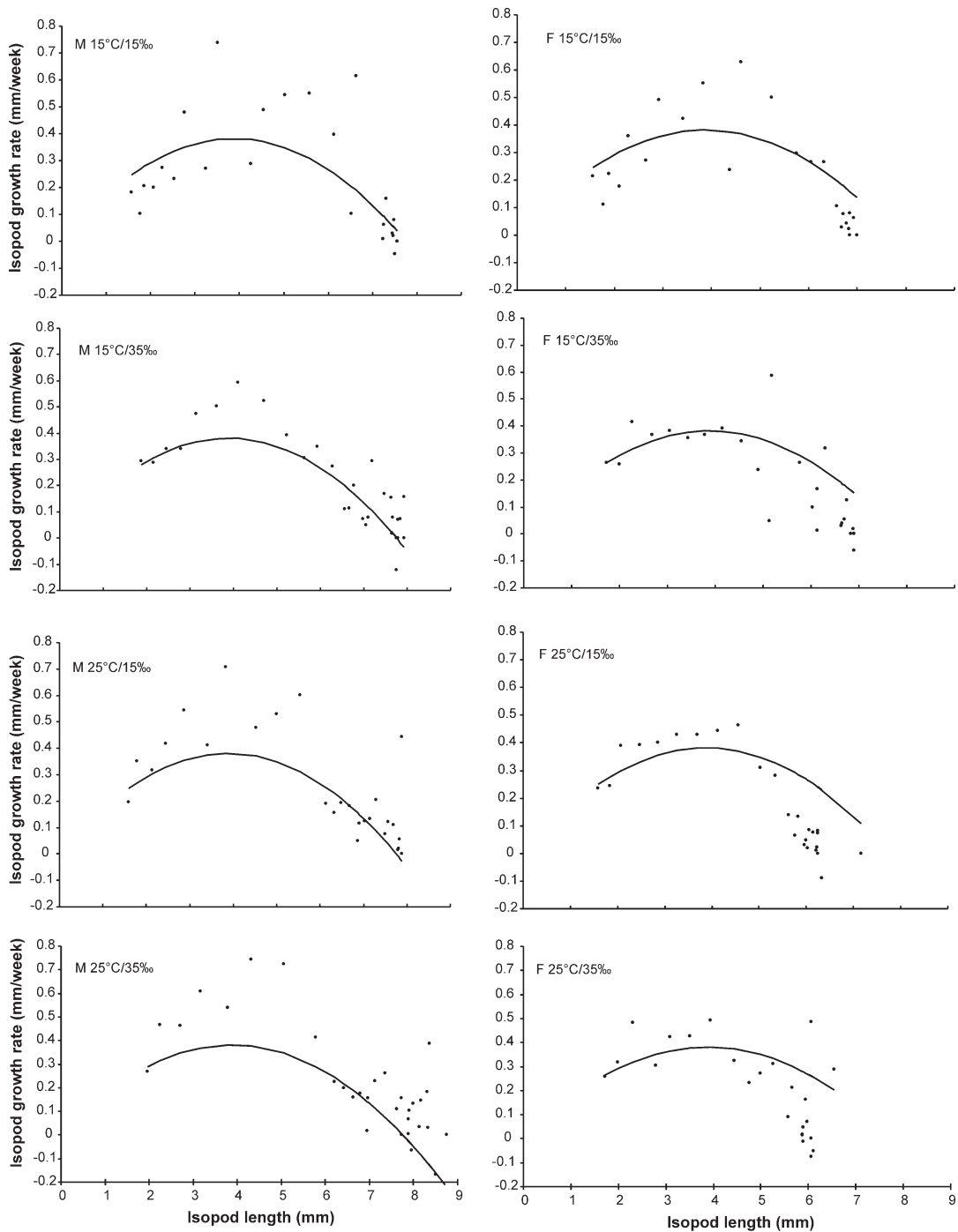
Fig. 1. Observed mean growth rates versus predicted growth rates of *Exosphaeroma hylocoetes* at combinations of temperatures (15 & 25°C) and salinities (15 & 35) based on plots of $\frac{dL}{dt}$ against $\bar{L}$. Dots represent observed values while curves represent predicted values. M = males; F = females.

133 individual parameter estimates of k and L_∞ were used as input in ANOVAs to determine if salinity, temperature and/or sex had an influence on either growth or asymptotic length rates of male and female *E. hylocoetes.* The data were log $(x + 1)$ transformed to ensure that the residuals were normally distributed. The analyses were carried out using Statistica 7 (StatSoft). Growth was further modelled using the logistic growth model of the form

$$\hat{L}_{it} = \frac{L_\infty}{1 + e^{-k(t_i - t_0)}} \ ,$$

where $\hat{L}_{it}$ is the model predicted length of isopod i at time t_i and t_0 the estimated age at zero length.

It was assumed that there was functional relation between each of the parameters and sex, temperature and salinity. Therefore, each of the growth parameters was modelled to include this functional relationship, such that:

$L_\infty = \beta_0 + \beta_1 \times \text{Sex} + \beta_2 \times \text{Temperature} + \beta_3 \times \text{Salinity}$

$k = \beta_4 + \beta_5 \times \text{Sex} \times \text{Temperature} + \beta_7 \times \text{Salinity}$

$t_0 = \beta_8 + \beta_9 \times \text{Sex} + \beta_{10} \times \text{Temperature} + \beta_{11} \times \text{Salinity}.$

Sex was included in the model as a dummy variable with females being assigned a 0 and males a 1. Two other parameters were included in the minimization routine: $\hat{\rho}$, the estimated autocorrelation between successive measurements, and $\hat{\sigma}$, the estimated model standard deviation. The autocorrelation coefficient was required as the data are repeated measures data. The parameter vector expressed as

$$\theta = \{\beta_0, \beta_1, ..., \beta_{11}; \sigma, \rho,\}$$

contained at most 14 parameters and was estimated by minimizing a negated normal log-likelihood of the form

$$\ln L = \sum_i \left[\ln \sigma + \frac{1}{2\sigma^2} \sum_j \left(\frac{\varepsilon_{ij} - \rho \varepsilon_{ij-1}}{\sqrt{1 - \rho^2}} \right)^2 \right] \ ,$$

where $\varepsilon_{ij} = L_{ij} - \hat{L}_{ij}$ is the jth residual for the ith isopod calculated, $\varepsilon_{i0} = 0$.

Likelihood ratio tests were conducted to assess whether individual parameters were statistically significant. The most parsimonious model was assessed using the AIC (Akaike's Information Criterion) statistic (Akaike 1974; Hurvich & Tsai 1989). Parameter variability was calculated using parametric bootstrapping with 250 bootstrap iterations.

T-tests were conducted to determine significant differences between male and female size, growth rates, survival and longevity at the different treatments. One-way ANOVAs were conducted to determine differences in the means between the treatments, and these were followed by Tukey HSD *post-hoc* tests to display significant differences and homogenous groups.

RESULTS

Isopod size and growth rates

Males attained a larger size (mean body length, 8.08 ± 0.25 mm) than females (6.59 ± 0.25 mm) at all temperature and salinity combinations (Figs 2, 3 & 4). Male isopods consistently attained lengths greater than those predicted by the logistic growth model, while females, with the exception of those incubated at 15°C and a salinity of 15, did not attain the predicted lengths (Fig. 2). Initial growth occurred at a faster rate at the higher temperature (25°C) and salinity (35) combination in both males and females, but in both instances these individuals attained the lowest overall length (7.67 mm for males and 6.32 mm for females). They also reached their inflection points, on the curves, at five weeks. After an initial slower growth rate, reaching their inflection points at nine weeks (males) and six weeks (females), the isopods growing in the lowest temperature/salinity combination (15°C/15) attained the longest overall lengths of 8.03 mm (males) and 6.68 mm (females). Those exposed to the intermediate temperature/salinity combinations demonstrated intermediate growth rates, achieving total lengths midway between the two extreme conditions. Growth of male and female *E. hylocoetes* was not significantly affected by salinity, based on the LRT and ANOVA analyses ($P > 0.05$), and was therefore removed from the overall model (Table 1; Fig. 3).

Increased temperature, despite depressing the maximum attainable length, allowed the isopods to attain maturity earlier, two weeks for females and 6.5 weeks for males (at 25°C), than females (4 weeks) and males (11 weeks) at 15°C (Figs 3 & 4). There were no significant differences (ANOVA, $P = 0.432$ to 0.535) in growth rates between males and females under the various treatments (Fig. 5). Overall, ANOVA analyses revealed only significant temperature effects on the growth rates of *E. hylocoetes* ($P < 0.001$; $F_{1,128} = 18.419$). Salinity was shown to have no significant influence on the sex of the individuals' growth rates ($P = 0.415$; $F_{1,128} = 0.670$).
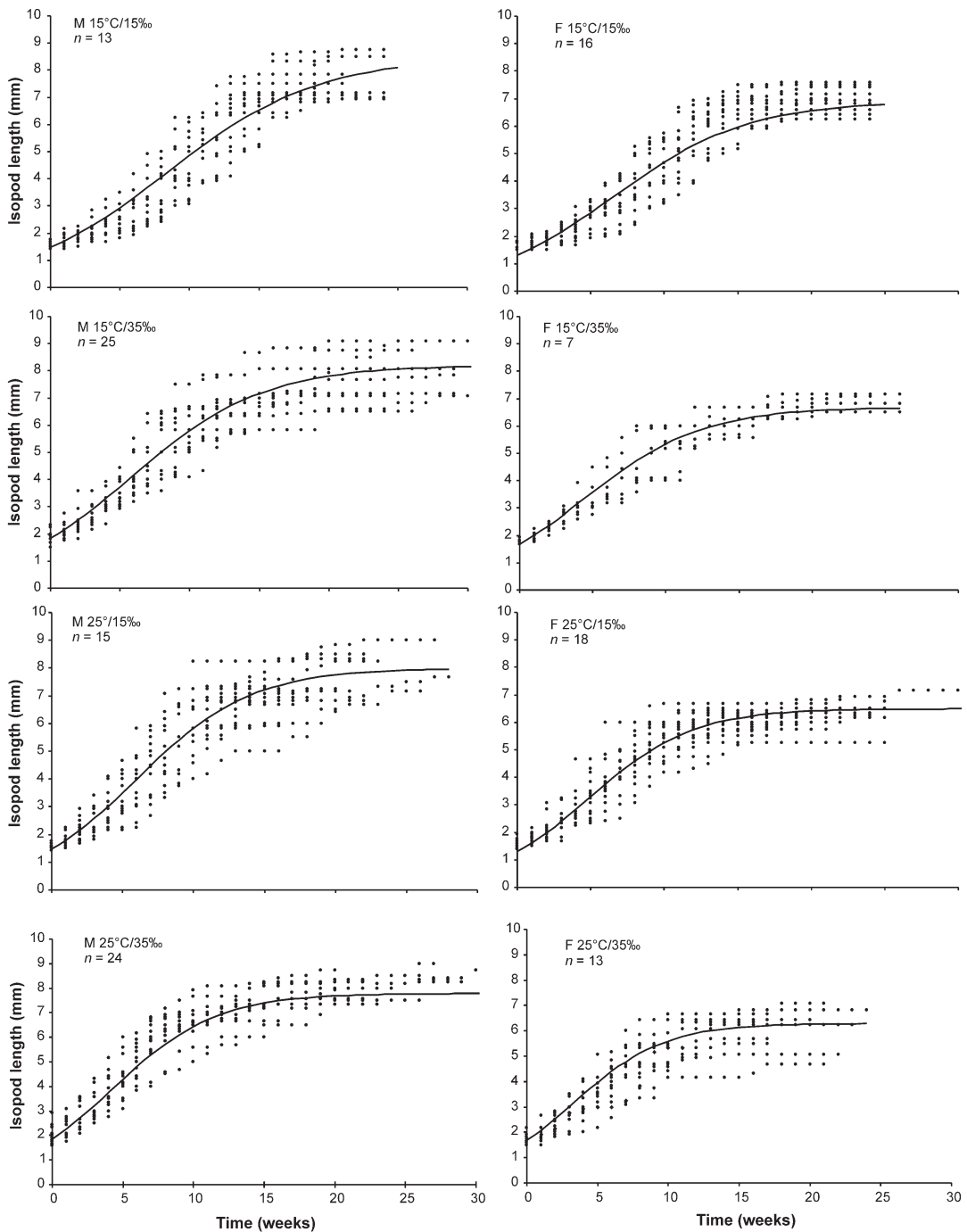
Fig. 2. Observed male (left) and female (right) growth of *Exosphaeroma hylocoetes* at combinations of two temperatures (15 & 25°C) and two salinities (15 & 35). The line indicates the predicted growth curve of isopods based on the predicted logistic growth model. M = males; F = females.
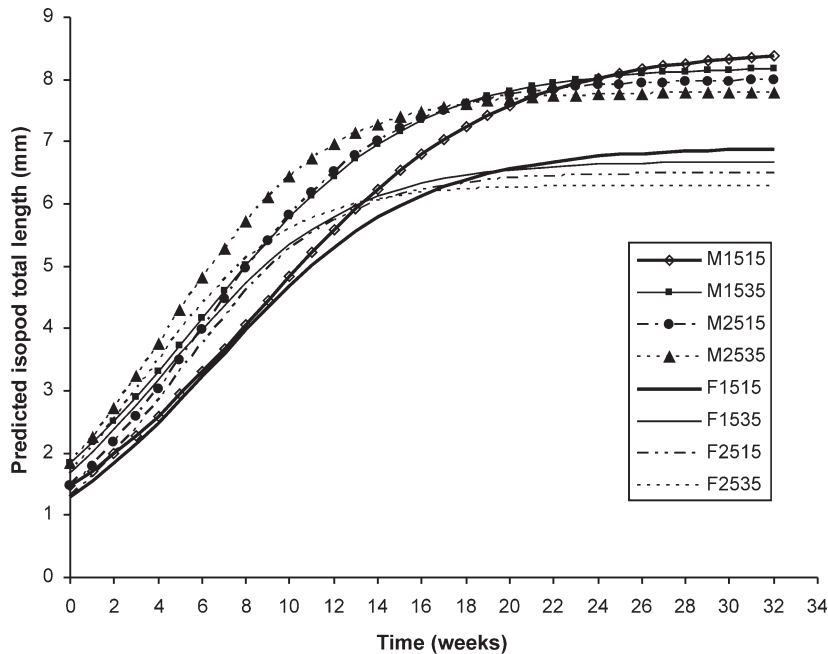
Fig. 3. Predicted male (M, lines with symbols) and female (F, lines without symbols) isopod length in combinations of two temperatures (15 & 25°C) and two salinities (15 & 35). Lines are the predicted logistic growth models. Output parameters of the model are shown in Table 1.

Survival rates and longevity

The initial trials at 20°C and a salinity of 15 indicated that males lived significantly longer than females ($P < 0.001$), with males averaging 25.77 ± 3.40 weeks and females, 21.52 ± 3.00 weeks. Two males lived for 35 weeks, while one female achieved a maximum lifespan of 30 weeks (T.O. Henninger, unpubl. data).

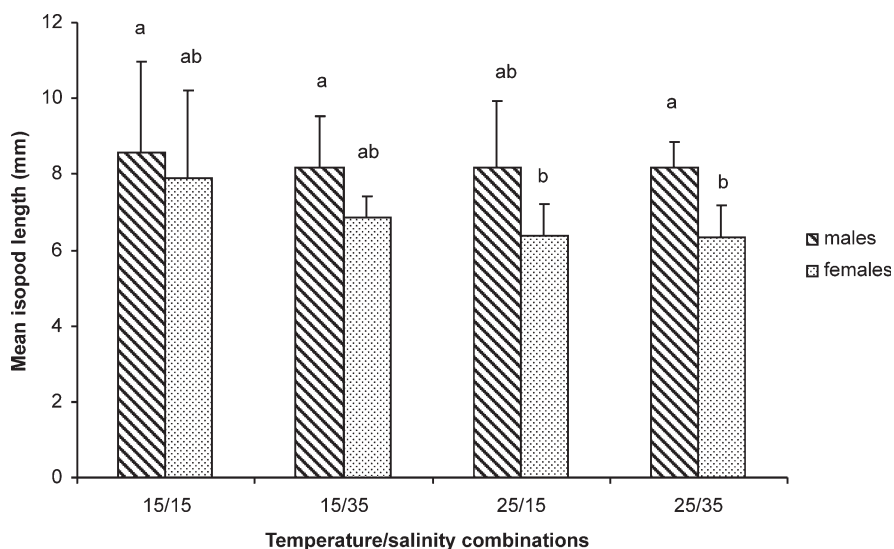During this study males reached a maximum length of 11.17 mm (mean length = 8.00 ±

Fig. 4. Mean length (+S.D.) of male (M) and female (F) *Exosphaeroma hylocoetes* at temperatures of 15°C and 25°C and at a salinities of 15 and 35. Different letters above columns indicate significant differences (*post-hoc* LSD test on homogeneous groups).
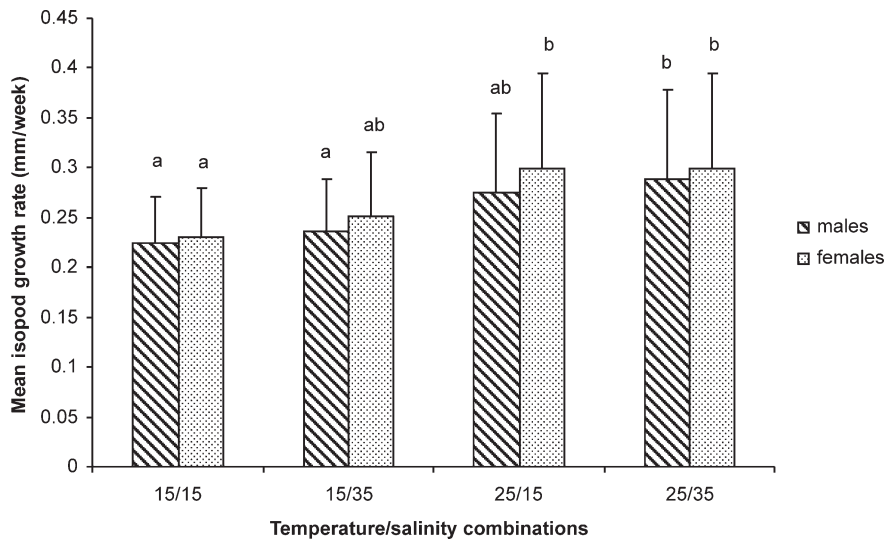
Fig. 5. Growth rates (+S.D.) of male (M) and female (F) *Exosphaeroma hylocoetes* at temperatures of 15°C and 25°C and at a salinities of 15 and 35. Different letters above columns indicate significant differences (*post-hoc* LSD test on homogeneous groups).

0.86 mm) and females 7.92 mm (mean length = 6.32 ± 0.59 mm; Fig. 4). Longevity contributed to males achieving a significantly larger size than females during the experiments. At a salinity of 15

Table 1. Logistic growth model maximum likelihood estimates (MLE), their coefficients of variation (CV) and 95% confidence intervals (CI). The model fit is summarised with the negated log-likehood value (–lnL), number of estimated parameters (*p*) and Akaike Information Criterion (AIC) statistic. The model fitted was $\hat{L}_{it} = \dfrac{L_{\infty}}{1 + e^{-k(t_i - t_0)}}$, where $L_{\infty} = \beta_0 + \beta_1 \times \text{Sex} + \beta_2 \times$ Temperature, $k = \beta_3 + \beta_4 \times \text{Sex} + \beta_5 \times$ Temperature and $t_0 = \beta_6 + \beta_7 \times \text{Sex} + \beta_8 \times$ Temperature $+ \beta_9 \times$ Salinity.

	MLE	CV (%)	CI
β_0	7.41	1.76	(7.17; 7.67)
β_1	1.32	3.83	(1.21; 1.41)
β_2	−0.04	15.10	(−0.05; −0.03)
β_3	0.15	9.21	(0.13; 0.18)
β_4	−0.01	44.07	(−0.03; 0.00)
β_5	0.00	14.14	(0.00; 0.01)
β_6	10.64	2.69	(10.14; 11.22)
β_7	0.90	11.79	(0.70; 1.12)
β_6	−0.18	5.98	(−0.20; −0.16)
β_9	−0.08	4.60	(−0.09; −0.08)
ρ	0.60	11.73	(0.52; 0.56)
σ	0.57	6.50	(−0.46; −0.41)
−lnL	−48.41		
p	12		
AIC	−72.81		

and a temperature of 15°C, male (mean 22.82 ± 1.47 weeks) and female (mean 23.27 ± 1.28 weeks) *E. hylocoetes* showed no significant difference in their life expectancy ($P = 0.415$; $t = 0.829$, d.f. = 24), whereas at 25°C, males (mean 27.73 ± 3.069 weeks) lived significantly longer (P <0.001; $t = 5.615$, d.f. = 21) than the females (mean 20.58 ± 3.03 weeks; Fig. 6). When comparing males incubated at 15°C with those incubated at 25°C, at the same salinity, the males at 25°C lived significantly longer ($P < 0.001$; $t = 4.784$, d.f. = 20) than the males at the lower temperature (Fig. 6). Females incubated at 15°C, however, lived significantly longer than those females at 25°C at the same salinity ($P = 0.005$; $t = 3.113$, d.f. = 25).

At a salinity of 35, males lived significantly longer than females at both 15°C and 25°C, (P <0.001; $t = 4.738$, d.f. = 18 and P <0.001; $t = 3.987$, d.f. = 15; Fig. 6). However, when comparing males at 15°C (mean 26.42 ± 2.91 weeks) with those at 25°C (mean 26.67 ± 3.93 weeks) there was no significant difference in life expectancy ($P = 0.880$; $t = 0.153$, d.f. = 16). Similarly, females at 15°C (mean 21.00 ± 1.69 weeks) and 25°C (19.00 ± 3.72 weeks) did not show any significant difference in their longevity ($P = 0.176$; $t = 1.412$, d.f. = 17; Fig. 6).

At a temperature of 15°C, males at a salinity of 35 (mean 26.42 ± 2.91 weeks) did not live significantly longer ($P = 0.880$; $t = 0.153$, d.f. = 16) than those males exposed to a salinity of 15 (22.82 ± 1.47 weeks). Similarly, at temperature of 25°C,
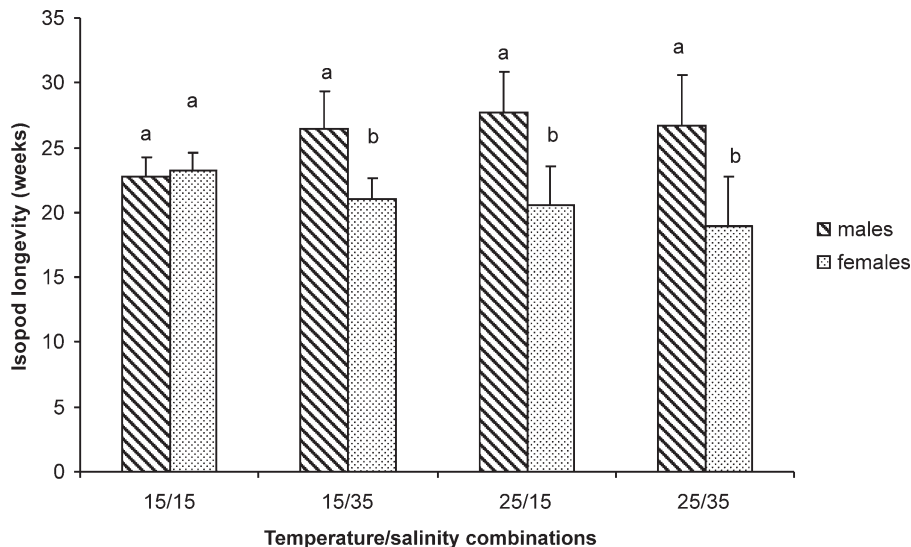
Fig. 6. Male (M) and female (F) *Exosphaeroma hylocoetes* longevity (mean weeks survived ± S.D.) at temperatures of 15°C and 25°C, salinities of 15 and 35. Different letters above columns indicate significant differences (*post-hoc* LSD test on homogeneous groups).

males exposed to a salinity of 15 (mean = 27.73 ± 3.10 weeks) did not live significantly longer ($P = 0.546$; $t = 0.618$, d.f. = 15) than males exposed to a salinity of 35 (mean 26.67 ± 3.93 weeks; Fig. 6). At a temperature of 15°C female *E. hylocoetes* at a salinity of 15 (mean 23.26 ± 1.28 weeks) did live significantly longer ($P = 0.002$; $t = 3.621$, d.f. = 21) than females exposed to a salinity of 35 (mean 21.00 ± 1.69 weeks). By contrast, at 25°C females exposed to a salinity of 15 (mean 20.58 ± 3.03 weeks) did not live significantly longer ($P = 0.273$; $t = 1.125$, d.f. = 21) than females incubated at a salinity of 35 (mean 19.00 ± 3.72 weeks; Fig. 6).

DISCUSSION

Results of this study indicated that male *Exosphaeroma hylocoetes* attained a significantly larger size than females under all salinity and temperature combinations. This pattern is consistent with field studies, which have shown that *E. hylocoetes* demonstrates strong sexual dimorphism (Henninger *et al.* 2008). However, the individuals at the lower temperature/salinity combination attained an overall longer size than those individuals incubated at the higher temperature/salinity, in agreement with the Gulf of California isopod, *Paracerceis sculpta* (Shuster & Guthrie 1999) and for other crustaceans (Steele & Steele 1991; McKenny 1994; McKenny & Celestial 1995). This may support the reproductive drain hypothesis (Koch & Weiser 1983; Pauly 1984; Thorpe 1987), indicating faster

growth at the higher temperature/salinity, allowing the isopods to put more effort into reproduction while penalising longer overall growth.

In agreement with several other studies on marine crustaceans (McKenny 1994; McKenny & Celestial 1995), both male and female *E. hylocoetes* grew significantly faster at the temperature/salinity combination of 25°C/35 than those individuals incubated at the low temperature/salinity combination (15°C/15). The influence of temperature and salinity on the growth rates of crustaceans is highly variable and appears to be species-specific, reflecting amongst others ontogeny and specific habitat requirements (Zein-Eldin & Aldrich 1965; Staples & Heales 1991; Steele & Steele 1991; Kondzela & Shirley 1993; McKenny & Celestial 1995). For example, the growth of the juvenile amphipod *Gammarus lawrencianus* was greatest at intermediate salinities, reflecting the normal conditions in the estuaries where the animals are commonly found (Steele & Steele 1991). Similarly, the tropical estuarine mysid *Mysidopsis bahia* demonstrated age-dependent interactions with temperature and salinity. Mysid growth rates were retarded by both a low temperature–low salinity interaction, and a high temperature–low salinity interaction. Maximum sizes were achieved at high temperature–high salinity combinations (McKenny & Celestial 1995). Kinne (1964) postulated that changes in osmotic concentration could influence not only metabolic rates, but also meta-

Table 2. Longevity of selected terrestrial, estuarine and marine isopod species.

Species	Life span (months)	Source
Terrestrial		
Porcellionides pruinosus	11–14	Achouri *et al.* 2003
Hemilepistus reaumuri	12	Warburg 1993
Atlantoscia floridana	♂ = 18; ♀ = 28	Araujo & Bond-Buckup 2004
Balloniscus glaber	♂ = 28; ♀ = 36	Meinhardt *et al.*, 2007
Trichoniscus pygmaeus	24	Sutton *et al.* 1984
Philoscia muscorum	27	Sutton *et al.* 1984
Porcellio scaber	36	Sutton *et al.* 1984
Armadillidium vulgare	42	Sutton *et al.* 1984
Armadillo officinalis	108	Warburg 1993
Marine		
Dynoides daguilarensis	7–12	Li 2002
Excirolana braziliensis	19–31.5	Cardoso & Defeo 2004
Eurydice pulchra	24	Fish 1970
Cirolana harfordi	24	Johnson 1976
Elaphognathia cornigera	36	Tanaka 2003
Estuarine		
Exosphaeroma hylocoetes	♂ = 6.5–8.5 ♀ = 5.5–7.5	Present study

bolic efficiency. Temperatures and salinities beyond those to which the animal is normally acclimatized could induce stress on those animals and alter their respiration and growth rates.

Results of the growth studies indicated that there were no significant differences in the growth rates of male and female *E. hylocoetes* under the range of temperature and salinity combinations ($P > 0.05$; Fig. 5). The observed pattern is in contrast to a number of other studies which have demonstrated that growth rates of female crustaceans generally exceed those of the males. For example, females of the kelp forest mysid *Holmesimysis costata* grew at a mean rate of 41 μm compared to the 35 μm/day for males (Turpen *et al.* 1994). The elevated growth rates observed for the females were related to the increased brood carrying ability of larger sized females. Similar patterns have also been reported for the prawn *Palaemon xiphias* and the freshwater shrimp *Exopalaemon modestus* (Guerao *et al.* 1994; Oh *et al.* 2002). Berglund (1981) theorized that a reduced male energy investment in growth could lead to a reduced risk of predation.

Longevity in crustaceans, including shrimps and prawns, have been shown to be strongly influenced by temperature (Guerao *et al.* 1994; Oh *et al.* 2002). Isopods having a wide latitudinal range show variations in longevity, with an increase in longevity generally associated with colder water temperatures (Table 2). The results of the longevity

experiments obtained here are in the lower range reported for other estuarine and marine isopods of similar size (Table 2). For example, *Excirolana braziliensis* lives for 19 months at a latitude of 20° south, stretching to 31.5 months at 40° South (Cardoso & Defeo 2004). Similarly, the sponge-dwelling gnathiid isopod *Elaphognathia cornigera* lives for more than 36 months (Tanaka 2003). The reduced life expectancy of *E. hylocoetes* compared to other studies can likely be related to the fact that it occurs in warm-temperate waters. Interestingly, it appears that terrestrial isopods appear to live longer than their marine counterparts (Table 2).

Results of growth trials indicated that longevity of male *E. hylocoetes* was significantly longer than those of the females at the different combinations of temperature and salinity. The extended life expectancy of the males allowed them to attain a significantly larger size than the females ($P < 0.05$). Larger male size in *E. hylocoetes* is related to mate guarding, as it is also found in many other crustaceans, including isopods (Jormalainen 1998) and crabs (Kobayashi 2002). Polymorphism, with regard to male body size, has been described in some isopods, in which three distinct male morph types coexist (Shuster 1987; Shuster & Wade 1991), and in freshwater prawns (Ra'anan & Sagi 1985). Larger males, as in *E. hylocoetes,* are thought to have an advantage in male–male conflicts, whereas smaller males could attain maturity faster or engage

in alternative mating behaviours, e.g. female mimicry, searching for females located further away from large males, or by sneak mating (Kobayashi 2002). Smaller female *E. hylocoetes* may be a result of not feeding during the brooding period when the size of the gut is reduced, as well as greater energy being placed in brooding the off-spring (Shuster 1995).

In conclusion, this is the first study to present the findings of a laboratory-based study which examined the growth of *E. hylocoetes* under a suite of environmental conditions. There were no significant differences between the growth rates of males and females at all combinations of temperature and salinity. Males achieved an overall larger size than the females, as males lived longer than females which allowed them to attain a significantly larger size. Growth in *E. hylocoetes* occurred at a faster rate at the higher temperature (25°C) than at 15°C (at a salinity of 15), coinciding with summer conditions commonly found in TOCEs along the southeastern sea board of southern Africa. The smaller female *E. hylocoetes,* however, attained sexual maturity at a faster rate (smaller overall length) than males.

ACKNOWLEDGEMENTS

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