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Temperature-induced responses of a permanent-pond and a temporary-pond cyclopoid copepod: a link to habitat predictability?

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ABSTRACT

Temporary-pond species can be expected to use environmental cues to predict the onset of adverse conditions, while permanent-pond species may be insensitive to such cues. Temperature is such a potential cue in temporary waterbodies, as it fluctuates more widely with decreasing pond size than in deeper permanent ponds. We compared the temperature-induced response of a permanent-pond and a temporary-pond cyclopoid copepod focusing on juvenile development duration, diapause induction and survival during diapause. Non-linear regression analysis suggested a stronger effect of temperature on the duration of juvenile development in the temporary-pond species. This species also showed a higher and temperature-dependent variation in development duration (highest coefficient of variation 26%) compared with the permanent species, for which variation was lower and similar at all temperatures (maximal coefficient of variation 6%). Temperature significantly influenced the induction of diapause in the temporary-pond species, where the percentage of individuals entering diapause increased from 0% at 5°C and 10°C to 63% at 15°C and 91% at 20°C. In the permanent-pond species, diapause induction was independent of temperature and was induced in 100% of experimental specimens. This suggests an obligatory diapause in the permanent-pond species, a type of dormancy that has not been described previously for cyclopoid copepods. Survival during diapause in both species was higher when the diapausing copepodid stage was reached at lower temperatures. At higher temperatures, the temporary-pond species survived longer than the permanent-pond species. These results suggest different temperature optima of the two species. The strategy displayed by the permanent-pond species might be selected for in more stable habitats and may preclude the colonization of temporary ponds. Higher flexibility in life-history traits and the use of temperature as an environmental cue in the temporary-pond species could be favoured in unpredictable habitats.

Keywords: *Cyclops insignis*, *Cyclops strenuus*, developmental plasticity, diapause, ephemeral habitats, juvenile development.

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INTRODUCTION

Variable environments are often characterized by the absence of suitable habitat conditions during certain periods of the year. In aquatic environments, this is most obvious in temporary ponds that alternate between dry and wet phases, but there is evidence that permanent waterbodies also experience unfavourable periods due to food shortage or the presence of predators (Cáceres, 1997; Santer, 1998). Strategies used in response to the variability encountered in such ephemeral environments may differ according to their predictability. Life-history strategies in variable aquatic environments may include fast development (Williams, 1997), high reproductive effort (Wiggins *et al.*, 1980; Nix and Jenkins, 2000), migration to more suitable habitats among mobile organisms (Wiggins *et al.*, 1980; Williams, 1997) or timing of diapause (Cohen, 1970). In ponds with unpredictably variable hydroperiods, phenotypic plasticity may allow optimization of development and growth during favourable times (Wilbur, 1987; Newman, 1989), but this has not always been reported (Leips and Travis, 1994; Leips *et al.*, 2000). Risk-spreading is also viewed as an adaptation to unpredictably variable environments (for a review, see Hopper, 1999). If a sufficiently strong cue exists to indicate unfavourable changes in the environment, theory predicts selection for phenotypic plasticity, while a risk-spreading strategy should be favoured when such cues are absent (Hopper, 1999). Amphibians breeding in temporary ponds may display adaptive plastic responses to environmental cues, while permanent-pond species may be insensitive to them because they are not exposed to the selection pressures imposed by drying conditions (for a review, see Leips *et al.*, 2000).

Temperature has been suggested as a possible environmental cue indicating drying conditions in temporary waterbodies (Brown, 1979; Williams, 1997). Temperature is an important environmental factor in the shallow temporary waterbodies in which water temperature fluctuates more widely as water levels and pond area decrease. The life-history traits of temporary-pond species, especially development, can be linked to temperature (Wiggins *et al.*, 1980; Wilbur, 1987; Blaustein *et al.*, 1999). Temperature may shift the critical daylength for induction of diapause in cyclopoids (Watson and Smallman, 1971), which is often triggered by photoperiod (Einsle, 1964; Spindler, 1971). However, in two recent comparative studies between permanent-pond and temporary-pond species (treefrogs: Leips *et al.*, 2000; copepods: Piercey and Maly, 2000), temperature could not be confirmed as an environmental cue indicating drying conditions.

Diapause in copepods living in permanent waterbodies can be a strategy to avoid unfavourable periods caused by poor food conditions or increased predation (Hairston and Olds, 1984; Santer and Lampert, 1995). Together with the capability of a dormant stage to endure drought periods, a property found in many cyclopoid copepods (Frisch, 2002), diapause is also an important trait for survival in temporary ponds.

The two closely related cyclopoid copepods *Cyclops strenuus* (Fischer 1851) and *Cyclops insignis* (Claus 1857) present an excellent opportunity to compare life-history strategies with regard to habitat variability. The life histories of these two species were studied in permanent and temporary ponds in the Lower Oder Valley, Germany (Frisch, 2001). Both pond types were found to differ in their average temperatures, with temporary waterbodies reaching higher temperatures earlier in the year. The general life-cycle pattern of the two species is similar: in the study area, both species reproduce in winter and spring and spend diapause in the sediment in the fourth copepodid (C4) stage. However, the predominantly temporary-pond inhabitant (termed the temporary-pond species hereafter) *C. strenuus* is

bivoltine and enters diapause in May when water temperatures can reach up to 20°C. The predominantly permanent-pond inhabitant (termed the permanent-pond species hereafter) *C. insignis* is univoltine and enters diapause in March before the water temperature exceeds 10°C in spring. Here we focus on juvenile development duration up to the diapausing C4 stage, diapause induction and survival success during the diapause period in response to rearing temperature. The life cycle of cyclopoid copepods includes six naupliar stages, five copepodid stages and the adult stage. In diapausing species, the fourth copepodid stage (C4) is typically the dormant instar. Using laboratory experiments to compare the temperature-induced response of life-history traits of the permanent-pond species *C. insignis* and the temporary-pond species *C. strenuus*, we specifically addressed the following questions: Do the two cyclopoids respond differently to rearing temperatures with regard to the duration of juvenile development? What is the effect of temperature on diapause induction? Does the temperature at which species reach the diapausing C4 stage influence survival during the diapause period? We discuss the impact of temperature on the life histories of the two cyclopoid copepods with special emphasis on strategies in variable habitats with different degrees of predictability.

METHODS AND MATERIALS

Habitat description and life histories

The ponds from which both cyclopoid species were sampled are located in the floodplain of the Lower Oder Valley near the city of Schwedt (53°03′29″N, 14°17′14″E), Germany. The permanent pond Mariensee has a surface area of about 1500 m^2 and 1.8 m depth. Temporary ponds that are neighbouring Mariensee vary in size (10–40 m^2) and in depth (0.2–0.8 m). The hydroperiod duration of the temporary ponds depends on the water level of the main river and varies from year to year. They generally fill with water in November/December and dry up before June. Both pond types have similar water temperatures during the winter and spring months, but temporary waterbodies reach higher temperatures earlier in the year (Fig. 1).

The life history of *Cyclops strenuus* and *C. insignis* was studied in the ponds described above (Frisch, 2001). Although both species are not strictly excluded from either permanent

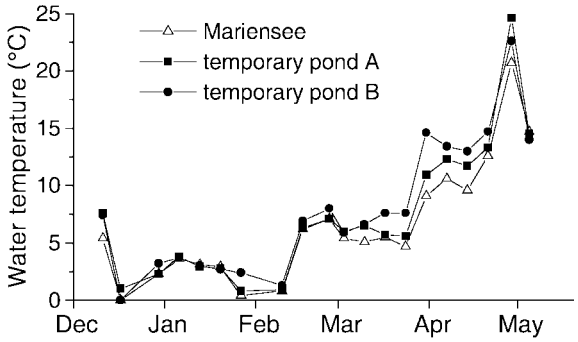

Fig. 1. Water temperatures of the water surface in a permanent pond (Mariensee) and two temporary ponds located in the floodplain of the Lower Oder Valley from December 1997 to May 1998.

or temporary ponds, populations showed a distinctive distribution across the study area. Although both pond types can become connected during the inundation period in winter and spring (Frisch, 2001), over 90% of *C. insignis* individuals were found in the permanent pond and about 80% of *C. strenuus* individuals in temporary ponds. Both species are present and reproduce during winter and spring. The temporary-pond species *C. strenuus* emerges from diapause in late autumn and produces two generations. The C4 stages of the second generation enter diapause in May and remain dormant in the sediment until the beginning of the aquatic period in autumn or winter. The diapausing C4 stages of the permanent-pond species *C. insignis* leave the sediment in late autumn. This species is univoltine and the C4 stages of the first generation enter diapause in March (Frisch, 2001).

Juvenile development

Adult females of *Cyclops strenuus* and *C. insignis* were collected in January 1999 from a flooded area that connected Mariensee with the temporary waterbodies described above. The eggsacs were removed from gravid females and each placed into 100-ml screw cap glass jars filled with food solution (see below). The eggs developed under experimental conditions in temperature- and light-controlled chambers (5, 10, 15, 20°C and 8 : 16 h light : dark) and were checked daily until they hatched. Most eggs from one eggsac hatched on the same day. Eggs that had not hatched on that day were removed and the number of nauplii was reduced to 30–40 individuals per jar.

The juveniles were raised at four different temperatures (5, 10, 15, 20°C) using a short-day photoperiod (8 : 16 h light : dark), which resembles spring conditions in the field when both species are abundant and reproduce. They were fed a mixture of cryptomonad strains at a constant carbon concentration of 1 mg $C \cdot l^{-1}$. In the first 7 weeks of the experiment, a 1 : 1 mixture of *Cryptomonas* A (mean length 11.4 μm, mean width 6.7 μm; all means computed from 100 single measurements) and *Cryptomonas* sp. (mean length 18.6 μm, mean width 11.9 μm) was used. After that period, the *Cryptomonas* sp. culture declined and was replaced by the similarly sized *Cryptomonas erosa* (mean length 18.2 μm, mean width 12.1 μm). Algae were cultured with WC medium (Guillard and Lorenzen, 1972) in frequently diluted batch cultures in tubes or Erlenmeyer flasks. The food suspension was prepared and changed daily. For its preparation, the carbon content of the algal cultures was measured as described in Hansen and Santer (1995) and diluted with WC medium to a final concentration of 1 mg $C \cdot l^{-1}$ for all treatments. This solution was placed in the experimental vials and adjusted to the respective experimental temperatures before transferring animals to the new medium. For the experiments, three replicates were run for each temperature tested. The numbers of developmental stages were checked daily at 20°C and every other day at 5, 10 and 15°C.

For the assessment of post-embryonic development duration, we followed Hansen and Santer (1995). A developmental stage was defined as being reached when 50% of the population had moulted to that stage. The development of nauplii was recorded as the sum of all naupliar stages (N1–N6), whereas for copepodid stages stage-specific development times were recorded. Development times were calculated using Landry's (1983) method of least-square regression, prior to which percentages were arcsine square root transformed to meet the assumptions of the regression model (Sokal and Rohlf, 1969).

Specimens entering diapause in both cyclopoids were identified by the accumulation of oil droplets in the body cavity and by cessation of feeding as evidenced by consistently

empty guts. Diapausing animals were primarily resting on the bottom of the culture vials and mostly only moved when disturbed. The combination of all of these characteristics are typical signs of cyclopoid diapause (Watson and Smallman, 1971; Elgmork and Nilssen, 1978).

Survival during diapause

Diapausing C4 stages of *Cyclops insignis* were taken from the experiment on juvenile development described above (for numbers and rearing temperatures, see Table 1). The C4 stages of *C. strenuus* came from permanent cultures reared at 5, 10, 15 and 20°C. These cultures were followed up from the experiments on development duration and contained animals from the first and second generations. Although temperature was kept constant, the cultures received natural light, which changed to long-day photoperiod (16 : 8 h light : dark) during the culturing period. All specimens of both species chosen for the experiment showed the typical signs of cyclopoid copepod diapause as described above. For both species, survival during diapause was tested under terrestrial conditions to ensure comparability of data. Although *C. insignis* usually does not experience drying of its habitat, it is able to survive during diapause in terrestrial conditions for several months, similar to *C. strenuus* (Frisch, 2001). Terrestrial conditions were achieved by keeping animals on moistened plaster of Paris, thus avoiding immersion in water (see Frisch, 2002, for details). After placement on the plaster surface, live specimens showed occasional movement of the guts and a moist body surface. Dead animals were distinguished by desiccated cuticle and rapid fungi infection.

Statistical analysis

The results for juvenile development duration were analysed with a three-way analysis of variance (ANOVA) (independent variables: temperature, species and developmental stage), followed by Tukey HSD (honest significance difference) *post-hoc* tests. Analyses were carried out with StatSoft Statistica 5.1. The temperature-dependent duration of juvenile development (N1 to C4) of both species was fitted separately by non-linear regression analysis using the equation $y = (\text{top} - \text{bottom}) \times e^{-k \times x} + \text{bottom}$. An *F*-test was used to determine whether the models obtained differed statistically between species.

Table 1. Number of C4 copepodids of *Cyclops strenuus* and *C. insignis* used for survival analysis during diapause

Temperature	*Cyclops strenuus*	*Cyclops insignis*
5°C	9 (4)	12 (1)
10°C	10 (2)	10 (1)
15°C	12 (6)	10 (1)
20°C	12 (4)	7 (1)

Note: Number of individuals is given for the different temperatures at which copepodids reached the diapause stage. Initial mortality is indicated in parentheses and specifies the number of individuals that had died in the first 4 days of the experiment.

To compare intraspecific survival rates during diapause, the non-parametric Cox-Mantel test (StatSoft Statistica Version 5.1, Survival Analysis) was used. Survival rates containing censored data can be compared with this test – for example, if some individuals were still alive at the end of the experiment.

RESULTS

Juvenile development duration and diapause induction

Three-way ANOVA was performed to examine the main effects of temperature, developmental stage and species, and their interactions (summarized in Table 2). All three significantly influenced juvenile development duration. The development of both species was shorter at higher temperatures and increased from the first to the fourth copepodid stage. Naupliar development was longest because it included all six naupliar stages, and therefore does not allow direct comparison with the separately considered copepodid stages. The permanent-pond species *Cyclops insignis* developed faster than the temporary-pond species *C. strenuus*.

Juvenile development duration (naupliar stages, C1, C2 and C3) was significantly different between species and temperatures (ANOVA, two-way interaction of temperature and species; Table 2). Temperature-dependent development duration of nauplii, C1, C2 and C3 stages combined was fitted by non-linear regression analysis (Fig. 2). The curves obtained for each species differed significantly ($F_{3,18} = 8.24$, $P < 0.01$). A steeper decline for *C. strenuus* suggested a stronger effect of temperature on the development duration of this species when compared with *C. insignis* primarily at high temperatures.

The three-way interaction between species, developmental stage and temperature was significant (Table 2). A Tukey HSD *post-hoc* test indicated that interspecific development duration differed between naupliar stages at 5°C ($P < 0.01$), with *C. insignis* nauplii developing faster than *C. strenuus* nauplii. As with naupliar development, copepodid development of *C. strenuus* tended to be shorter at higher temperatures (Fig. 3). Due to specimens entering diapause, the development duration of the C4 stages of *C. strenuus* was retarded at 15 and 20°C (Fig. 4a). Of the *C. strenuus* specimens reaching the C4 stage,

Table 2. Summary of all effects (three-way ANOVA) on development duration of *Cyclops strenuus* and *C. insignis*

	d.f. effect	MS effect	d.f. error	*F*	*P*
Developmental stage*	3	822.17	64	265.09	<0.001
Species	1	62.58	64	20.18	<0.001
Temperature	3	458.35	64	147.78	<0.001
Developmental stage × species	3	4.63	64	1.49	0.2250
Developmental stage × temperature	9	98.36	64	31.71	<0.001
Species × temperature	3	10.06	64	3.24	0.032
Developmental stage × species × temperature	9	15.00	64	4.84	<0.001

* Developmental stage (N1–N6, C1, C2, C3).

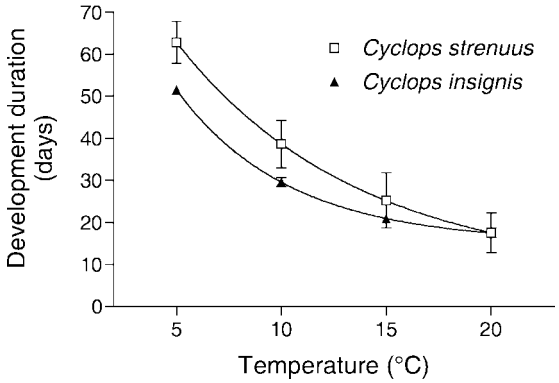

Fig. 2. Non-linear regression analysis for temperature-dependent juvenile development (nauplii, C1, C2 and C3 combined) of *C. strenuus* and *C. insignis*. The regression curves are described by the equations $y = 97.973 \times e^{-0.1158 \times x} + 7.93$ for *Cyclops strenuus* ($R^2 = 0.936$) and $y = 91.7 \times e^{-0.1859 \times x} + 15.3$ for *Cyclops insignis* ($R^2 = 0.997$). Bars indicate the standard deviation of three replicates.

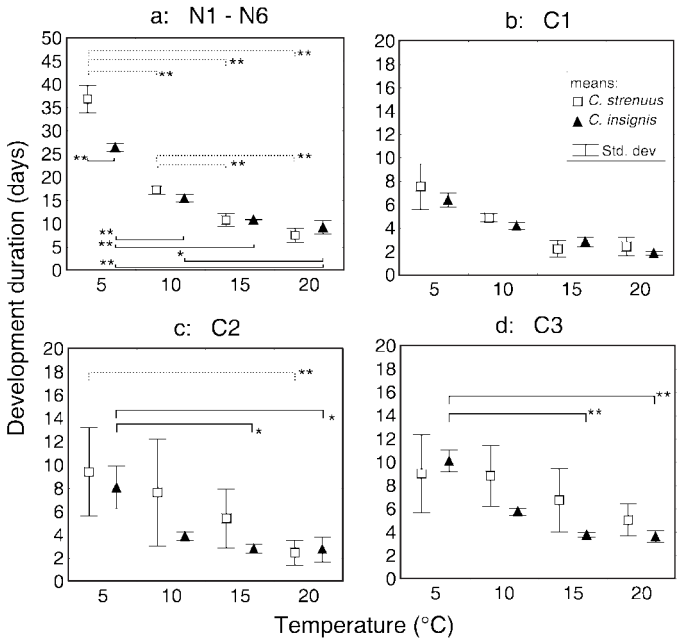

Fig. 3. Juvenile development duration of *C. insignis* and *C. strenuus* at four temperatures. Means and standard deviation from three replicates are indicated (see key in b). $*P < 0.05$; $**P < 0.01$. (a) Total duration of naupliar stages N1–N6. (b–d) Duration of copepodid stages C1, C2, C3. Note different scale of time axis for nauplii.

a maximum of 63% at 15°C and of 91% at 20°C did not moult to the C5 stage for at least 3 weeks (see Fig. 5a for means and extremes). These specimens entered diapause, indicated by reduced swimming activity and cessation of feeding. Animals that did moult to the C5 stage developed to adults within 6–9 days (Fig. 4b). In *C. insignis*, significant differences

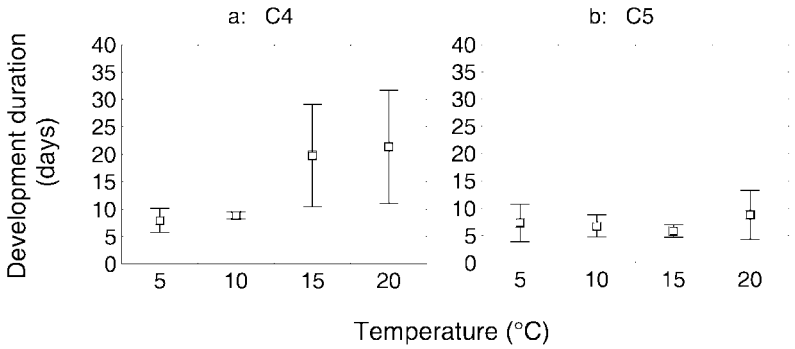

Fig. 4. Development duration (C4 and C5 stages) of *C. strenuus* at four temperatures. Means and standard deviation of three replicates are indicated (see key in Fig. 3b). (a) Duration of C4 stage. (b) Duration of C5 stage.

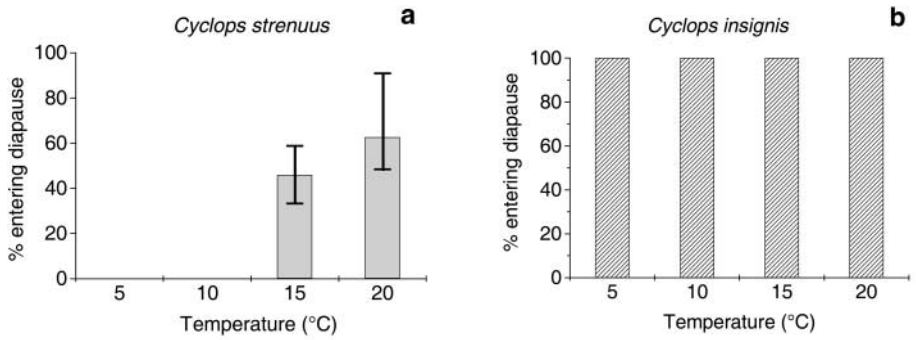

Fig. 5. Percentages of individuals of *Cyclops strenuus* (a) and *Cyclops insignis* (b) entering diapause at four different temperatures. Means (columns) and range (error bars) of three replicates are indicated.

in development duration were found in most developmental stages studied but not between all temperatures tested (Fig. 3). Naupliar, as well as copepodid, stages developed faster at higher temperatures, although these differences were not always significant between the higher temperatures. *Cyclops insignis* entered diapause in the C4 stage at all temperatures tested (Fig. 5b). None of the experimental animals developed to the C5 stage during the experiment. Instead, moulting took place about 6 months later.

Variation in development duration (nauplii to C4) of *C. strenuus* was dependent on temperature. The coefficient of variation increased markedly from 8% at 5°C to 26% at 15°C and 20°C. In *C. insignis*, variation within development duration remained relatively low at all temperatures (coefficient of variation between 1% at 5°C and 6% at 20°C).

Survival during diapause

During the first 4 days of the experiment, we observed mortality in both species (Table 1). Mechanical stress caused by placing animals on the plaster surface most likely led to injuries in the smaller and less robust *C. strenuus* and thus to a higher mortality in this species. To

ensure comparability of the data, we disregarded mortality during the first 4 days for statistical analysis among the groups reared at different temperatures. The following results therefore represent percentages of the number of individuals still alive after 4 days.

Survival of *C. strenuus* was lowest in specimens that had reached the C4 stage at 20°C (Fig. 6a). All individuals of this group had died after 126 days of the experiment. Fifty per cent of the C4 copepodids that had been reared at 10 and 15°C and 40% of the group reared at 5°C survived the experimental terrestrial conditions until the end of the experiment (160 days). The C4 stages of *C. insignis* reared at the three higher temperatures (10, 15 and 20°C) showed only slight differences among the groups (Fig. 6b). All individuals reared at 15 and 20°C died before the 76th day of the experiment. Only one individual of the 10°C group survived as long as 90 days. In contrast, specimens that had reached the C4 stage at 5°C survived longest. More than 60% of this group survived until the end of the experiment (95 days).

Survival analysis of *C. strenuus* showed a significantly higher survival rate of the groups reared at 5, 10 and 15°C than at 20°C (Table 3). In *C. insignis*, the group reared at 5°C survived significantly longer than the groups reared at higher temperatures.

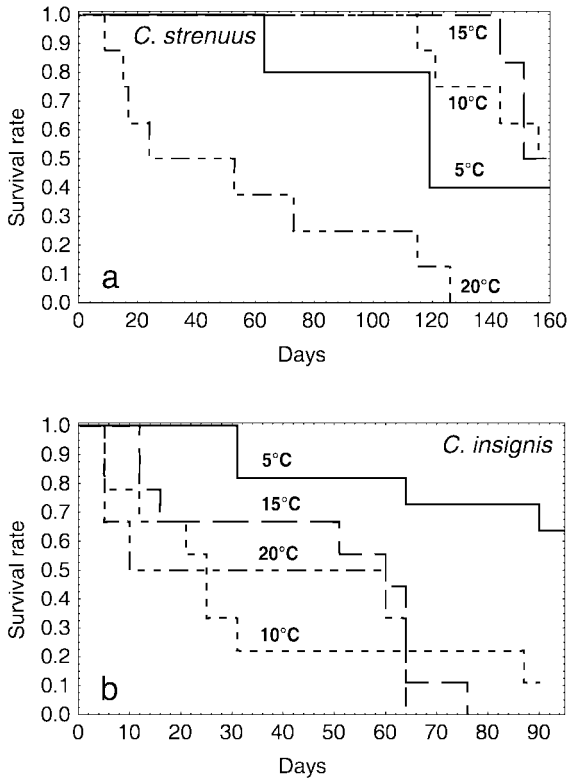

Fig. 6. Survival rate at 20°C and contact water of C4 stages of *Cyclops strenuus* (a) and *Cyclops insignis* (b) that had reached the C4 stage at different temperatures (indicated in the figure). The data were corrected for initial mortality during the first 4 days of the experiment (see text for explanation). Note different scale of time axes.

Table 3. Results of the Cox-Mantel test (*P*-values) on survival rate in terrestrial conditions of C4 copepodids (*C. strenuus* and *C. insignis*) reared at different temperatures

		5°C	10°C	15°C	20°C
C. strenuus	5°C	–	0.507	0.399	0.026
	10°C		–	0.835	0.001
	15°C			–	0.001
C. insignis	5°C	–	0.002	0.002	0.002
	10°C		–	0.877	0.734
	15°C			–	0.349

Note: Before analysis, the survival data were corrected for initial mortality (see Table 1 for explanation).

DISCUSSION

Juvenile development and induction of diapause

Both species were able to decrease the juvenile period preceding diapause at the higher temperatures, but non-linear regression analysis suggests a stronger influence of temperature on juvenile development duration in *Cyclops strenuus* (Fig. 2). The coefficients of variation obtained for both species at all temperatures studied indicate a higher variance of within-temperature development duration in the temporary-pond species. This observation suggests environmental or genetic variance, both of which are adaptive for life in unpredictable habitats (Bull, 1987; Seger and Brockmann, 1987; Newman, 1988).

For *C. strenuus*, our results indicate faster development at higher temperatures only for nauplii and copepodid stages C1–C3. Maier (1990) reported a delay in development of fourth copepodids of *C. strenuus* at 25°C. In our study, we found that this species already entered diapause at 15°C, suggesting that temperature is used as a cue for the induction of diapause. Diapause in cyclopoids can be induced by photoperiod alone (Spindler, 1971) or a combination of either photoperiod and temperature (Watson and Smallman, 1971) or photoperiod and poor food conditions (Hansen and Hairston, 1998). It is unlikely that food was limited in our experiments. The mortality of nauplii measured during our experiment on temperature-dependent development tended to decrease with higher temperatures (Frisch, 2001), suggesting sufficient food availability. Most specimens of *C. strenuus* resumed development after several weeks of the temperature experiment, suggesting that its extended diapause observed in the field (Frisch, 2001) might be cued by other factors (e.g. photoperiod) in addition to temperature.

Ours are the first data on development duration of the permanent-pond species *C. insignis*. Between 5 and 20°C, the C1–C3 stages of this species developed over about the same time span as *C. strenuus*, whereas at 5°C nauplii developed significantly faster in *C. insignis*. Frisch (2001) found naupliar mortality of *C. strenuus* to be significantly higher than that of *C. insignis* at 5°C. Egg production of *C. insignis* is limited to lower temperatures in the field, while in *C. strenuus* it increases at higher temperatures in the field (Frisch, 2001). All of these observations indicate a higher temperature optimum for development and

reproduction in the temporary-pond species *C. strenuus*, and might also explain the interspecific difference in development duration of the naupliar stages. As expected, diapause induction in the permanent-pond species *C. insignis* cannot be considered a response to temperature. Diapause induction in this species is likely to be induced by internal factors independent of temperature. Such an obligate diapause has been described for insects and other arthropods (Müller, 1992; Wohltmann, 2001), but to our knowledge has not previously been reported for cyclopoid copepods. A laboratory artefact is unlikely, since the same pattern was observed in the field, where the species is univoltine with the first generation entering diapause in the C4 stage (Frisch, 2001).

Survival during diapause

The temperature at which the cyclopoids reached the diapausing stage clearly influenced survival of the C4 stages during diapause in both species. For *C. strenuus*, groups reared at 5, 10 and 15°C survived significantly longer than at 20°C. In contrast, the temperature limit for significantly longer survival of *C. insignis* was already observed at 5°C. While these findings show that both species are able to undergo an extended dormancy period at 20°C after induction of diapause within the range of rearing temperatures tested, they support a higher temperature optimum for *C. strenuus*, complementing observations for development duration and juvenile mortality (this study; Frisch, 2001). A possible cause for lower vitality during diapause might be a reduced amount of available storage lipids in copepodids raised at higher temperatures. Wierzbicka and Kedzierski (1970) described decreasing amounts of lipid during the diapause phase. Diapausing copepodids show an increased metabolic rate at higher temperatures without termination of diapause (Krylov *et al.*, 1996). We observed smaller and fewer oil droplets in specimens reared at higher temperatures, especially in *C. insignis* (personal observation). Considering the relatively high experimental temperature of 20°C in our study, it is likely that storage lipids were used. Although the numbers of specimens used in each replicate of the survival analysis were low, we are convinced that our results represent a valid trend that was observed over a range of temperatures.

Ephemeral versus permanent habitats

In unpredictable environments, life-history traits often show considerable plasticity, thereby spreading the risk of reproductive failure within a given population (Sasaki and Ellner, 1995; Simovich and Hathaway, 1997; Blaustein *et al.*, 1999; Leips *et al.*, 2000). Strategies are selected for that allow the organism to escape from unfavourable conditions in space (migration) or in time (diapause) (Wiggins *et al.*, 1980; Williams, 1997). However, diapause is also frequent in permanent-pond species, implying that permanent waterbodies also experience unfavourable periods for a given organism (Cáceres, 1997; Santer, 1998). In the present study, a similar life-cycle pattern with the expression of summer diapause in both cyclopoids suggests that conditions in both pond types become unfavourable during the summer months. Life-history trait responses to temperature, especially with regard to diapause induction, differ between the two cyclopoid species, which might suggest differing predictability of the habitats. The portion of diapausing individuals increased with temperature, which indicates the use of temperature as an environmental cue to predict harsh (drying) conditions in habitats with unpredictable hydroperiods. This cued response is suggestive of phenotypic plasticity, which could enable *C. strenuus* to produce two

generations when lower temperatures allow for further development, which is hindered in turn by acceleration of temperature. The experimental design, however, cannot determine whether the effect on the diapause trait and the observed variance in development duration is caused by genetic polymorphisms or phenotypic plasticity. Although the underlying mechanisms are different, both are favoured in variable environments. The diapause strategy of *C. strenuus* clearly cannot be regarded as bet-hedging *sensu* Seger and Brockmann (1987) and Philippi and Seger (1989), because this strategy requires independence from environmental cues (Hopper, 1999).

The strategy displayed by the permanent-pond species (low variance in juvenile development duration, obligatory diapause with a resulting univoltine life cycle) might be selected for in more stable environments, where the onset of unfavourable conditions is relatively predictable. Increased predation pressure by fish in spring has been demonstrated as such a predictable factor leading to exact timing of diapause (Hairston and Olds, 1984). It is likely that predation is an important factor also in the pond inhabited by *C. insignis*, where juvenile fish were frequent (personal observation). A limited ability to survive extended terrestrial periods during diapause (Frisch, 2001) might preclude this species from colonizing temporary habitats.

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