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COMBINED EFFECTS OF TEMPERATURE AND DIET ON GROWTH AND SURVIVAL OF YOUNG-OF-YEAR CRAYFISH: A COMPARISON BETWEEN INDIGENOUS AND INVASIVE SPECIES

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ABSTRACT

During a three-month rearing period we compared the (1) survival rate, (2) growth at moult, (3) number of moults, and (4) overall growth of the young of the year (YOY) of two crayfish species, the indigenous *Austropotamobius pallipes* and the nonindigenous *Procambarus clarkii*. One hundred twenty YOY of each species were reared in different test conditions, i.e., three temperatures (16°, 20°, and 24°C) combined with two different dietary regimes (either animal or detritus food items). The two species showed a number of similarities in their survival rate and growth format. First, in both species, animal proteins appeared fundamental for the YOY growth, because an exclusively vegetal diet significantly slowed growth rate. Thus, the YOY seemed to behave as obligate carnivores, and detritus appeared ineffective in sustaining growth. Then, an exclusively animal diet showed some deficiencies: exoskeleton appeared pale in its colour when the diet was composed of animal items only, possibly because carotenoids were lacking. Third, an increase in the temperature caused a decrease in both survival and growth rate, because it determined a reduction of the moult increment in both species. Differences between the two species were that the nonindigenous crayfish showed a significantly higher tolerance of elevated temperatures, and growth was significantly faster in *P. clarkii* than *A. pallipes*, being approximately double when the crayfish were reared with an animal diet. Together with other behavioural and ecological properties, these features make *P. clarkii* more competitive than *A. pallipes* in disturbed habitats and areas which are subject to man-induced modifications.

Despite the degree of interest in the culturing of both the white-clawed crayfish, *Austropotamobius pallipes* (Lereboullet, 1858)—for reintroduction and restocking purposes—and the red-swamp crayfish, *Procambarus clarkii* (Girard, 1858)—for its commercial value—little is known about the effect of diverse environmental parameters upon their survival and growth. The literature underlines the critical influence exercised by the water temperature. Although several reports described the relationships between survival or growth and temperature in juvenile crayfish (e.g., Firkins and Holdich, 1993; Austin, 1995; Jones and Romaine, 1995; Verhoef *et al.*, 1998), none examined the effects produced by the combination of different regimes of temperature and diet.

This study aims at providing an estimate of both the survival rate and growth of young of the year (YOY) of the two species in response to three temperatures combined with two different dietary regimes. The present work thus has the potential to give suggestions in order to maximise the culturing of these two species, and in particular may indicate the most appropriate conditions to rear the threatened *A.*

pallipes. Our second aim was to verify whether crayfish are less detritivores than commonly thought and whether juveniles require animal proteins as chief substances promoting their rapid growth, as suggested by Momot (1995).

Our main purpose was, however, to analyse those features associated with both the survival and the growth pattern that allow for a distinction in crayfish between *K*- and *r*-selected species, further justifying the success of *P. clarkii* over the invaded habitats. In fact, a fast growth has been considered one of the main properties making *P. clarkii* an invasive species, together with early maturity, high fecundity, and tolerance of varying degrees of environmental extremes (Lindqvist and Huner, 1999).

MATERIALS AND METHODS

Rearing experiments were conducted, using the following:

1. One hundred twenty YOY *A. pallipes* (1143 ± 30 mg mean weight; 15.68 ± 0.13 mm mean cephalothorax length), captured by hand from the stream Fosso di Farfereta (60 km from Florence, Italy). These crayfish were raised in the laboratory from July 30 to October 29, 1999.
2. One hundred twenty YOY *P. clarkii* (2393 ± 82 mg mean weight; 22.99 ± 0.30 mm mean cephalothorax

length), captured by hand from the marsh Padule di Fucecchio (50 km from Florence, Italy). These crayfish were raised in the laboratory from May 11 to August 10, 2000.

Collected specimens were defined as YOY according to the analysis of the two species' population structures in Gherardi *et al.*, 1997, 1999. As shown by field studies (Gherardi *et al.*, 1997, 1999), the period under study corresponds to that of maximum activity and growth.

Prior to the experimentation, crayfish were acclimated to laboratory conditions for one week. Subsequently for each species, crayfish were randomly subdivided into six groups (20 animals each) and maintained separately in six aquaria (40 × 40 × 20 cm), each containing 25 L of well water (pH = 6.5, [Ca⁺⁺] = 98 mg/L). Water was totally replaced weekly. In each aquarium, water recirculated through a filter (generating a 360 L/h flow), this allowing catabolite filtering and oxygenation. Throughout the experiment, the photoperiod was 12L:12D. For each species, six groups of 20 crayfish were reared in six different conditions, i.e., three temperatures (16°, 20°, and 24°C) combined with two different dietary regimes. Temperature was maintained constant (±1°C) by heaters (25 W) or coolers (Teco RA 200). Crayfish were fed in excess on one of two different diets, one composed of plant detritus from the collection areas (hereafter referred to as detritus diet, DD) and one composed of earthworms (hereafter referred to as animal diet, AD). Individual crayfish were fed twice a week on about 3 g of detritus or 0.25 g of earthworms. Thus, in this experiment we compared two different food items, available in the habitat occupied by crayfish, which differed for quantity and quality of proteins (Ilhéu and Bernardo, 1995; Jones *et al.*, 1995).

In order to prevent cannibalism and to feed crayfish individually, in the experimental aquaria each of the 20 crayfish was housed in a separate glass container. The aperture of each container was closed using a net (mesh size: 2 mm), which guaranteed water passage through the glass containers and ensured that rearing conditions, and especially the temperature, were uniform within each treatment. The containers were numbered so that we were able to recognise each crayfish and follow its growth individually. Dead animals were removed; exuviae were always consumed by crayfish after ecdysis.

During the three-month rearing period, we recorded: survival, number of moults, weight, and cephalothorax length. Once per week each crayfish was weighed five times to the nearest 0.001 g, using an electronic balance (TRACK mod. BC150); maximum and minimum weight were discarded, and the average of the three other values was computed. Before weighing, each crayfish was gently dried to remove excess water by pressing it onto a piece of absorbent paper. The cephalothorax length was measured from the tip of rostrum to the posterior margin at the dorsal midline with a calliper (standard length, Fitzpatrick, 1977). Every day, animals were checked for moulting and mortality.

Weight and cephalothorax length increment per moult were always given as percentage of the initial or the premoult measurement (Hartnoll, 1982). Survival was analysed by comparing the percentage of animals survived until the end of the three-month rearing period in each treatment.

Statistical comparison amongst treatments was carried out using *G*-test in the case of survival, ANOVA in the other cases. Pairwise comparisons of means were performed using

Tukey's test. Curvilinear regression procedures were used to fit length-weight relationship. The level of significance under which the null hypothesis was rejected is $\alpha = 0.05$.

RESULTS

Survival

In both species, survival was higher when crayfish were fed on AD ($G = 12.018$, *d.f.* = 1, $P < 0.001$ for *A. pallipes* and $G = 7.722$, *d.f.* = 1, $P < 0.02$ for *P. clarkii*) and decreased with increasing temperature ($G = 39.315$, *d.f.* = 2, $P < 0.001$ for *A. pallipes* and $G = 8.742$, *d.f.* = 1, $P < 0.02$ for *P. clarkii*).

The effects of diet were not independent from those of temperature (Fig. 1). Only at elevated temperatures—when the survival was lower—DD determined a decreased survival with respect to the survival showed by crayfish fed on AD ($G = 6.150$, *d.f.* = 1, $P < 0.02$ and $G = 14.922$, *d.f.* = 1, $P < 0.001$ for *A. pallipes* reared at 20°C and 24°C respectively; $G = 8.023$, *d.f.* = 1, $P < 0.01$ for *P. clarkii* reared at 24°C). For instance, at 24°C, only 5% of *A. pallipes* raised with detritus diet survived, whereas with AD the survival rate was 60%.

The effect of elevated temperatures in reducing survival was stronger (already evident at 20°C) in the indigenous species and was accentuated when crayfish were fed on DD. This was evidenced when the two species were compared: in *P. clarkii*, survival was higher than in *A. pallipes* at 20° and 24°C ($G = 10.428$, *d.f.* = 1, $P < 0.01$ and $G = 19.744$, *d.f.* = 1, $P < 0.001$, respectively) when crayfish were fed on DD and only at 24°C when they were fed on AD ($G = 12.304$, *d.f.* = 1, $P < 0.001$).

The tolerance of elevated temperatures had a role in determining different survival of the two species during the three-month rearing period: at 16°C there was no difference in survival ($G = 0.001$, *d.f.* = 1, $P > 0.1$), whereas *P. clarkii* survival was higher at 20°C ($G = 12.023$, *d.f.* = 1, $P < 0.001$), and the difference was even more evident at 24°C ($G = 23.714$, *d.f.* = 1, $P < 0.001$).

Number of Moults and Intermoult Period

There was no significant difference among temperatures in the number of moults (Fig. 2), but both species and diet had an effect ($P < 0.0001$) on it (Table 1). The unique significant interaction was the one between species and diet. When we considered separately these two factors, in both *A. pallipes* ($F = 35.398$; *d.f.* = 1,72; $P < 0.0001$) and *P. clarkii* ($F = 240.62$;

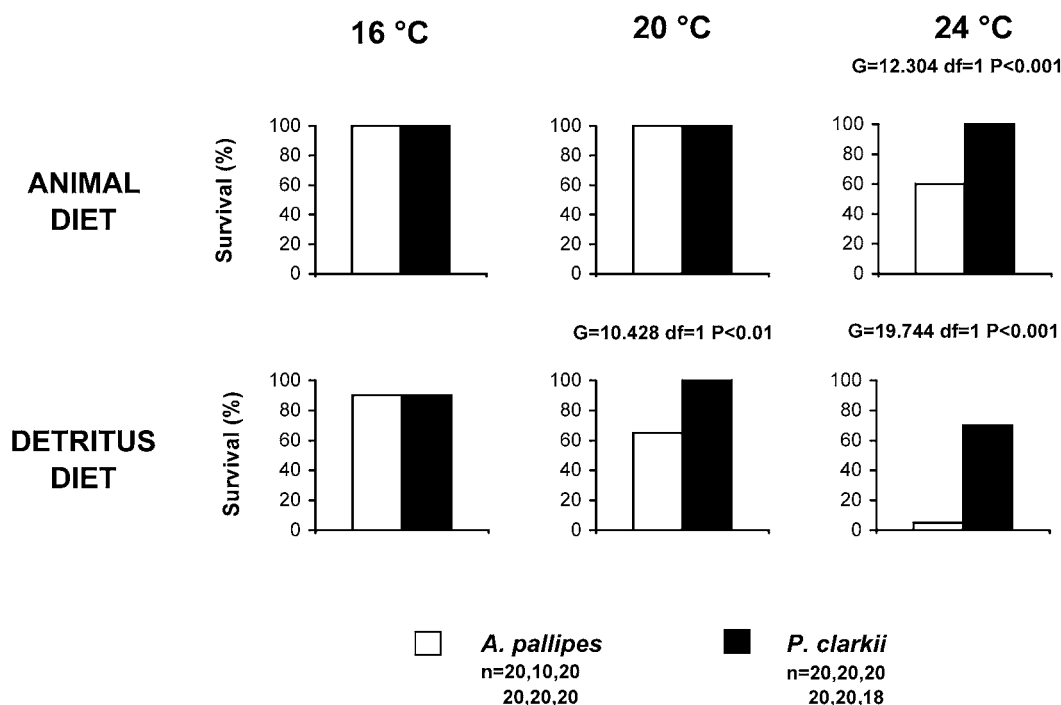


Fig. 1. Survival (%) of young of the year (YOY) *Austropotamobius pallipes* and *Procambarus clarkii* in response to three rearing temperatures combined with two different dietary regimes: earthworms (animal diet) and detritus (detritus diet).

$d.f. = 1,108$; $P < 0.01$), the number of moults was significantly higher with AD. Moreover, number of moults was significantly greater in *P. clarkii* than in *A. pallipes* ($F = 73.03$; $d.f. = 1,98$; $P < 0.01$) if crayfish were fed on AD, whereas there were no differences ($F = 1.38$; $d.f. = 1,82$; $P > 0.05$) if fed on DD.

Austropotamobius pallipes raised with AD moulted, on average, only one time during the three-month rearing period, whereas in *P. clarkii* moults were, on average, more than two. With DD, the average number of moults was less than one in both species.

The analysis of the duration of the intermoult period was done only on *P. clarkii* fed on AD (where the number of moults per individual was sufficient for the analysis). This was not influenced by temperature variation ($F = 2.16$; $d.f. = 2,51$; $P < 0.05$) (Fig. 3), being on average 41 days. In crayfish that moulted at least three times ($n = 17$), first intermoult period was 27 (± 1) days and second intermoult period was 34 (± 2) days.

Growth per Moults and Length-Weight Relationship

There was no significant difference between species in the length increment per moult (LI)

(Fig. 4a), but both temperature and diet had a significant effect (after a three-way ANOVA: $P < 0.0001$) (Table 2). A significant interaction between temperature and diet resulted, then we considered separately these two factors. With AD, an increase in temperature significantly determined a reduction in LI per moult ($F = 32.093$; $d.f. = 2,99$; $P < 0.0001$); Tukey's test showed that all pairs of temperature significantly differed. With DD, the temperature had no significant effects on this growth parameter ($F = 0.098$; $d.f. = 2,51$; $P > 0.05$). Diet determined significant differences at 16° and 20°C ($F = 28.412$; $d.f. = 1,59$; $P < 0.0001$ and $F = 17.947$; $d.f. = 1,50$; $P < 0.0001$, respectively), with AD inducing a higher weight gain, whereas there were no differences between diets at 24°C ($F = 0.435$; $d.f. = 1,41$; $P > 0.05$).

A second growth parameter we analysed is the weight increment (WI) per moult (Fig. 4b). Using a three-way ANOVA, a significant interaction among species, temperature, and diet was found ($F = 3.825$; $d.f. = 2$; $P = 0.024$), so that analysis was conducted separately for the two species using a two-way ANOVA. This statistical analysis showed that, considering *A. pallipes*, there is an interaction between diet and temperature ($F = 14.41$; $d.f. = 2,64$; $P < 0.01$).

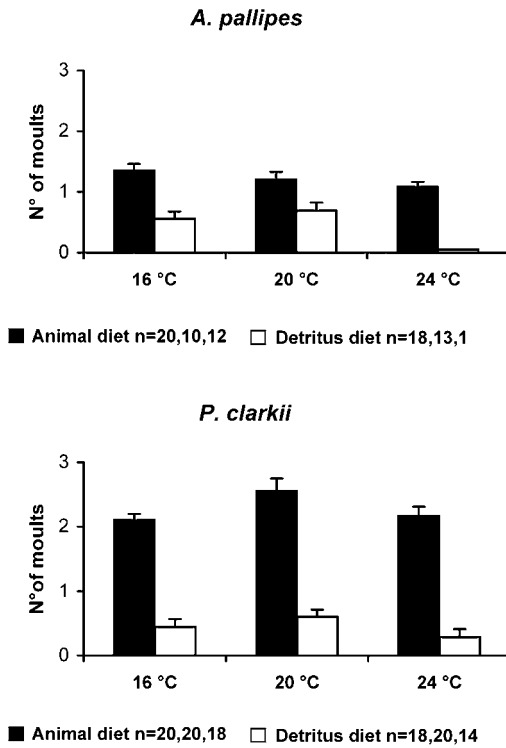


Fig. 2. Number of moults during a three-month rearing period for YOY *Austropotamobius pallipes* and *Procambarus clarkii* in response to three temperatures combined with two different dietary regimes. Average values and standard errors are shown. See text for statistical comparisons.

Austropotamobius pallipes fed on AD showed a reduction in its WI with an increase of temperature ($F = 56.21$; $d.f. = 2,41$; $P < 0.01$), and Tukey's test revealed significant differences for every pairwise comparison, whereas no differences were found for *A. pallipes* fed on DD ($F = 1.46$; $d.f. = 2,23$; $P > 0.05$). Considering the diet effect separately for each temperature, we determined that WI per moult was significantly higher with AD ($F = 75.82$; $d.f. = 1,30$; $P < 0.01$ and $F = 6.78$; $d.f. = 1,18$; $P < 0.05$ at 16°C and 20°C , respectively) but not at 24°C ($F = 2.74$; $d.f. = 1,16$; $P > 0.05$).

In the nonindigenous species *P. clarkii*, no significant interaction was shown between the two factors ($F = 1.61$; $d.f. = 2,80$; $P > 0.05$). The WI per moult was higher with AD ($F = 63.38$; $d.f. = 1,80$; $P < 0.01$) and varied with temperature ($F = 12.64$; $d.f. = 2,80$; $P < 0.01$). In particular, Tukey's test revealed that WI per moult at 16°C and 20°C was higher than at 24°C ($P < 0.05$).

In *P. clarkii*, weight increased faster through moults than in *A. pallipes* when the crayfish

Table 1. Results of a three-way ANOVA for the effect of species, temperature, and diet on the number of moults during the three-month rearing period.

Source	d.f.	F	P
Species	1	20.918	<0.0001
Temperature	2	2.913	0.0570
Species \times temperature	2	1.575	0.2100
Diet	1	121.549	<0.0001
Species \times diet	1	18.862	<0.0001
Temperature \times diet	2	0.327	0.7214
Species \times temperature \times diet	2	1.277	0.2815

were fed on AD ($F = 28.65$; $d.f. = 1,100$; $P < 0.01$) at all the temperatures analysed.

The cephalothorax length-weight relationship was the same, for each species, within each rearing condition. However, the relationship differed between the two species: *A. pallipes* had a greater body weight for a given length than *P. clarkii* (Fig. 5). In both species, the cephalothorax length-weight relationship fitted exponential growth functions.

Growth Model

Only in the case of *P. clarkii* fed on AD did a sufficient number of crayfish moult the minimum number of times (three) required for the analysis. Stepwise models for each temperature are provided by plotting the cumulative average moult increment against the cumulative average intermoult period (Fig. 6). The higher growth at lower temperature appeared because of a higher increment per moult, whereas the intermoult period was unaffected.

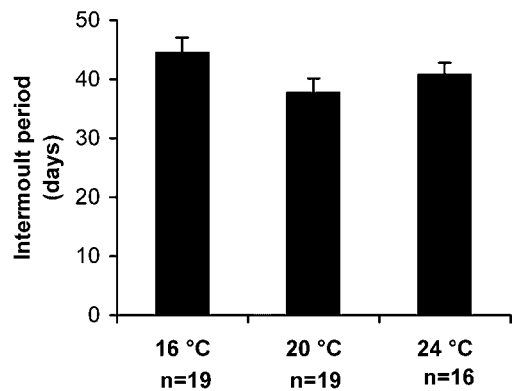
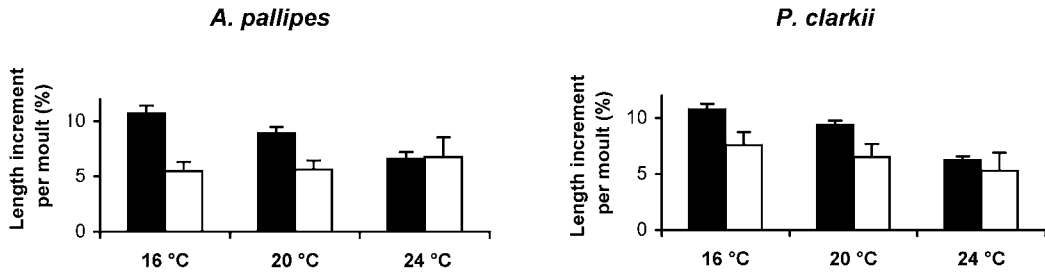


Fig. 3. Duration of the intermoult period of YOY *Procambarus clarkii* during a three-month rearing period at 16° , 20° , and 24°C . Only *P. clarkii* fed on the animal diet underwent a number of moult per individual sufficient to carry out analyses. Average values and standard errors are shown. See text for statistical comparisons.

a



b

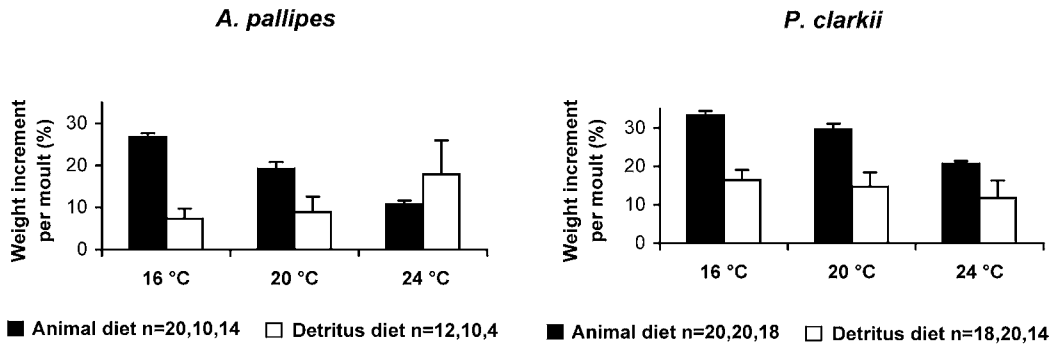


Fig. 4. Weight (a) and cephalothorax length (b) increment per moult—WI and LI—in percentage of premoult of YOY *Austropotamobius pallipes* and *Procambarus clarkii* in response to three rearing temperatures combined with two different dietary regimes. Average values and standard errors are shown. See text for statistical comparisons.

Overall Cephalothorax Length Increment and Weight Increment

The overall growth during the three-month rearing period was also considered, in order to compare the different growth potentials of the two species (Fig. 7). This analysis was conducted only on those animals that survived until the end of the rearing period; so, because of the high mortality of *A. pallipes* when reared at 24°C on DD, we analysed only data from the experiments conducted at 16° and 20°C. There was no significant difference between temperatures (16° and 20°C), but both species and diet had a significant effect (after a three-way ANOVA: $P < 0.0001$) on both the overall LI and WI (Tables 3, 4). There was no significant interaction, except that which occurred between species and diet. Considering separately these two factors, we determined that in both *A. pallipes* ($F = 86.750$; $d.f. = 1,59$; $P < 0.0001$ and $F = 41.943$; $d.f. = 1,72$; $P < 0.0001$ for WI and LI, respectively) and *P. clarkii* ($F = 97.048$; $d.f. = 1,76$; $P < 0.0001$ and $F = 103.441$; $d.f. = 1,108$; $P < 0.0001$ for WI and LI, respectively)

the overall growth was significantly higher with AD. Moreover, growth in *P. clarkii* was significantly greater than in *A. pallipes* with both diets, considering the overall WI ($F = 39.044$; $d.f. = 1,68$; $P < 0.0001$ and $F = 8.582$; $d.f. = 1,67$; $P = 0.005$ with AD and DD, respectively), but only with AD, considering LI ($F = 29.582$; $d.f. = 1,98$; $P < 0.0001$ and $F = 3.648$; $d.f. = 1,82$; $P = 0.0596$ with AD and DD, respectively).

To consider the effect of a wider range of temperatures (16–24°C), further analyses were conducted on *A. pallipes* fed on AD, in which the survival rate was higher (60%) at 24°C. A one-way ANOVA showed a significant effect of temperature on both WI and LI ($F = 12.52$; $d.f. = 2,39$; $P < 0.01$ and $F = 5.92$; $d.f. = 2,39$; $P < 0.01$). Tukey's test revealed significant differences for pairwise comparisons between 16° and 24°C only (the growth was lower at elevated temperature).

To analyse the effect of temperature on overall WI and LI of *P. clarkii*, we carried out a two-way ANOVA, including in the analysis

Table 2. Results of a three-way ANOVA for the effect of species, temperature, and diet on the cephalothorax length increment (LI) per moult.

Source	df.	F	P
Species	1	0.415	0.5203
Temperature	2	7.390	0.0009
Species \times temperature	2	1.421	0.2448
Diet	1	26.634	<0.0001
Species \times diet	1	0.161	0.6887
Temperature \times diet	2	4.573	0.0119
Species \times temperature \times diet	2	0.773	0.4635

three temperatures and two diets, because the survival of this species was sufficiently high in every rearing condition. No significant interaction was found ($F = 3.56$; $d.f. = 2, 104$; $P > 0.05$ and $F = 2.4$; $d.f. = 2, 104$; $P > 0.05$ for WI and LI, respectively). Both WI and LI significantly differed among temperatures ($F = 6.09$; $d.f. = 2, 104$; $P < 0.01$ and $F = 3.36$; $d.f. = 2, 104$; $P < 0.05$) and Tukey's test revealed significant differences for every pairwise comparison ($P < 0.05$) except between 16° and 20°C. At these temperatures, growth was higher than at 24°C. Moreover, as already shown, growth was higher with AD ($F = 133.64$; $d.f. = 1, 104$; $P < 0.01$ and $F = 120.63$; $d.f. = 1, 104$; $P < 0.01$).

DISCUSSION

Survival

A comparison between the two species analysed in the present study showed that temperature has a different importance in determining their survival. It is not surprising that *P. clarkii*, a "warm water" species native to northeastern Mexico and the south-central USA, tolerates elevated temperatures better than *A. pallipes*,

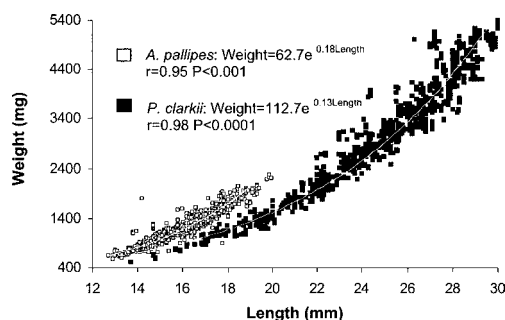


Fig. 5. Relationship between weight and cephalothorax length of YOY *Austropotamobius pallipes* and *Procambarus clarkii* obtained by plotting the weight against the length recorded at each measurement. Data of all rearing conditions were summed because the relationship did not vary among temperature-diet combinations. The curves fit exponential growth functions.

P. clarkii's growth model

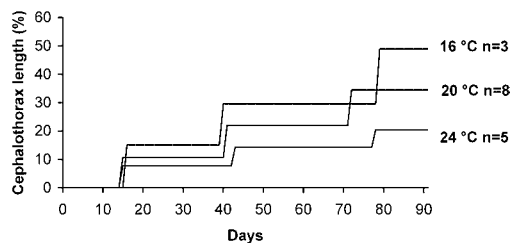


Fig. 6. Stepwise growth model of YOY *Procambarus clarkii* fed on the animal diet and reared at three temperatures, cumulative average moult increment is plotted against cumulative average intermoult period.

native to medium latitudes and occurring in fast-moving water. Just this greater tolerance of elevated temperatures confers to *P. clarkii* an adaptive advantage and facilitates its diffusion and replacement of the native species, because of the increase in temperature of the inner waters of Europe (caused by: deforestation, reduction of flow of many water courses, and thermal pollution).

Moreover, a diet rich of animal proteins seems to increase crayfish survival at elevated temperatures. This might be due to the higher assimilation rate (Withledge and Rabeni, 1997) that guarantees crayfish can better face an increased metabolic activity. The inability of crustaceans to control their body temperature seems to suggest that their metabolic rate varies directly with a change in the ambient temperature (Vernberg, 1982).

Growth: Effect of the Diet

The animal diet induced a faster growth in the juveniles of both species than a detritus-based diet. This result supports Momot's statements (1995) that crayfish juveniles are obligate, even if not exclusive, carnivores and that detritus may, at the best, provide some energy for maintenance but may be quite incapable of sustaining growth.

The importance of an animal diet for growth in *P. clarkii* has been stressed by Huner and Meyers (1979), who indicated as optimal for growth of this species a level of animal protein of 15–20%. Similarly, Tsvetnenko *et al.* (1995) determined that the maximum growth rate of *Cherax tenuimanus* was reached when crayfish were fed on food items containing 20% and 30% protein. Huner and Meyers (1984) showed growth response being proportional to the amount of protein in the diet. The present study

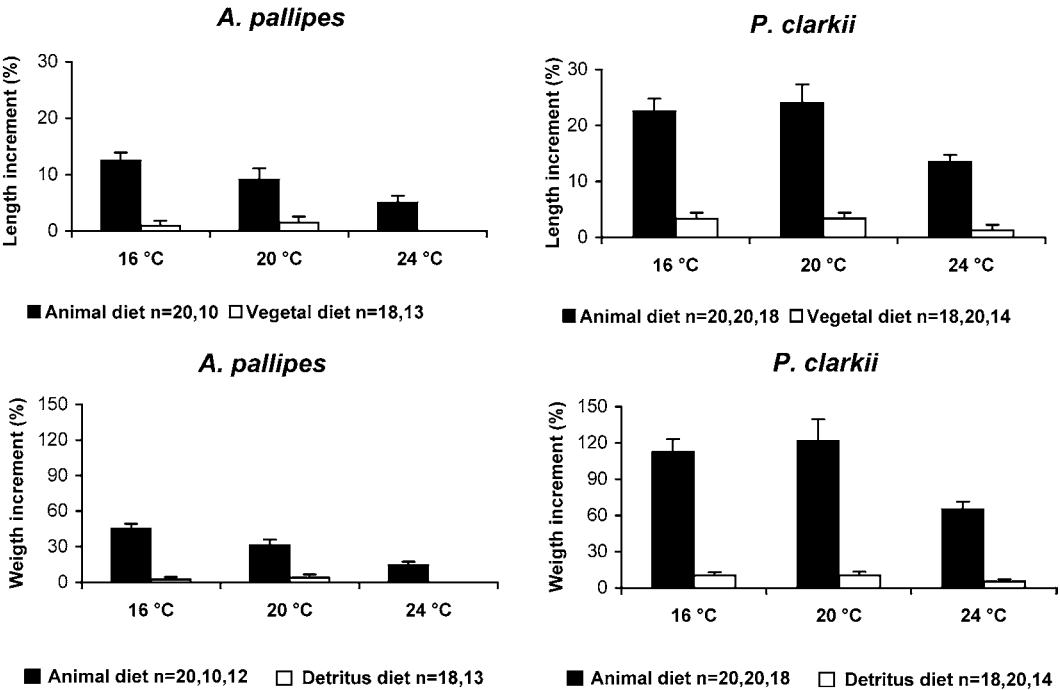


Fig. 7. *Procambarus clarkii* and *Austropotamobius pallipes* overall growth (estimated through the weight and cephalothorax length increment per moult in percentage of the initial measurements) during the three-month rearing period. Average values and standard errors are shown for the two species in each rearing condition (temperature–diet combination). See text for statistical comparisons.

demonstrated that detritus (and eventually its potential epibionts), which is recognised as the main food item of the adults' diet in most crayfish species (e.g., in *Cherax tenuimanus* (O'Brien, 1995) and in *Procambarus clarkii* (Gutiérrez-Yurrita *et al.*, 1998, Ilhéu and Bernardo, 1993) cannot sustain growth of the juveniles. These need animal proteins for their development, and, being necessarily more predators than detritivores, may occupy a different ecological niche from the adults.

However, an exclusively animal diet also shows some deficiencies, even if not irreversible. At the end of the rearing period with the

animal diet, crayfish of both species assumed an abnormal colour, extremely pale and sometimes bluish, whereas crayfish fed on detritus maintained a normal colour. This phenomenon can be due to the lack of carotenoids that are contained in vegetal items. A similar effect was shown by Tsvetnenko *et al.* (1995) in *Cherax tenuimanus* and by Huner and Meyers (1984) in *P. clarkii* fed on formulated diets of varied protein content; in those cases, this effect disappeared if β -carotene or a source of carotenoid were added to the food items. Crayfish are dependent on exogenous sources of carotenoids for the production of their natural

Table 3. Results of a three-way ANOVA for the effect of species, temperature, and diet on the overall weight increment (WI) during the three-month rearing period.

Source	df.	F	P
Species	1	43.749	<0.0001
Temperature	1	0.004	0.9510
Species \times temperature	1	0.588	0.4446
Diet	1	114.835	<0.0001
Species \times diet	1	30.419	<0.0001
Temperature \times diet	1	0.036	0.8497
Species \times temperature \times diet	1	0.716	0.3990

Table 4. Results of a three-way ANOVA for the effect of species, temperature, and diet on the overall cephalothorax length increment (LI) during the three-month rearing period.

Source	df.	F	P
Species	1	28.467	<0.0001
Temperature	1	0.152	0.6975
Species \times temperature	1	0.356	0.5521
Diet	1	110.628	<0.0001
Species \times diet	1	14.382	0.0002
Temperature \times diet	1	0.347	0.5570
Species \times temperature \times diet	1	0.564	0.4540

pigmentation (Dall and Moriarty, 1983; Goddard, 1988). A correct crayfish pigmentation can also be ensured with a diet containing a crustacean meal (Jones *et al.*, 1996), thus combining high animal protein with sources of carotenoids. Colour is an important factor to take into account in aquaculture, especially when the objectives of rearing are either reintroduction or restocking of a threatened species, such as *A. pallipes*, because pale crayfish are less cryptic in the environment.

In both species, the observed number of moults was below that expected (Lowery, 1988). Conditions could have been suboptimal for growth even with the AD. Moreover, physical confinement of crayfish in individual compartments has been shown to inhibit crayfish moulting and growth (Goyer and Avault, 1978).

Growth: Effect of Temperature

Our results that growth in *A. pallipes* diminished progressively from 16° to 24°C contrast, in part, with those obtained by Firkins and Holdich (1993), who showed that growth was greater at 20° and 25°C than at 15° and 28°C. Therefore, in the population used in this study, the range of optimal temperatures would seem shifted towards lower values. However, different rearing conditions or different dietary regimes might explain the observed differences.

Hartnoll (1982) reported various examples of crustaceans in which an increase in temperature shortened the intermoult period and decreased the increments per moult. Therefore, higher temperature may determine faster growth if higher moult frequency compensates for reduced increment per moult. As an example, Verhoef *et al.* (1998) showed in recently hatched juveniles of *Cherax destructor* that a shorter intermoult period, in spite of a reduced moult increment, caused a higher growth rate at 25° and 28°C when compared to 22°C.

In the present study, a higher temperature failed to increase the number of moults in both species and affected their moult increment only. This contrasts with what reported by Hartnoll (1982) and Verhoef *et al.* (1998) and with the conviction that just the ambient temperature is the main factor restricting growth to the summer period. Other factors could control the duration of the intermoult period, including photoperiod (Hartnoll, 1982). Ackefors *et al.* (1995) found a lengthening of intermoult period during winter months in *Astacus astacus* juveniles reared in the laboratory under constant "summer" tem-

perature conditions. This result suggests the existence of an endogenous rhythm in freshwater crustaceans of temperate zones.

In both species, growth rate diminished with an increase in temperature because moult increment was reduced and the intermoult period remained unchanged. The depression of moult increment with an increase in temperature agrees with that reported by Hartnoll (1982) for crustaceans. For this author, this effect may be related to the abbreviation of the intermoult period at higher temperatures, which perhaps allows for the accumulation of only limited reserves for the increase in size. The higher respiration rate at increased temperature may also contribute to this effect (Hartnoll, 1982). In this study, the intermoult period did not change with the temperature; therefore, differences in the moult increment (and, consequently, in the overall growth) could be due to an increased metabolic activity caused by elevated temperatures (Vernberg, 1982).

Growth of the two species, estimated as both the weight increment and the cephalothorax length increment per moult, decreased with an increase in temperature. Such a decrease might be the result of an increased metabolic consumption that nearly equalled the caloric intake. Little energy was left for growth, despite the animals being fed to excess.

Growth: Comparison Between *Austropotamobius pallipes* and *Procambarus clarkii*

Besides the higher tolerance of elevated temperatures (see the Survival section), in *P. clarkii* growth was much faster (approximately double with an animal diet) than in *A. pallipes*. This is one trait in the life history of *r*-selected species (MacArthur and Wilson, 1967; Adams, 1980), which are adapted to unpredictable environments, exhibit rapid growth rate and short life spans, and are able to take maximum advantage of abundant resources. Together with other behavioural and ecological properties, faster growth make *P. clarkii* more competitive than *A. pallipes* in disturbed habitats and other areas that are subject to man-induced modifications, thus making *P. clarkii* a successful invasive species.

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