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## Facultative lecithotrophy during larval development of the burrowing shrimp *Callinassa tyrrhena* (Decapoda: Callinassidae)

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**Abstract** Survival, developmental and consumption rate (*Artemia* nauplii ingested per day) as well as predation efficiency (ingested per available *Artemia* nauplii) were studied during the larval development of the shallow-water burrowing thalassinid *Callinassa tyrrhena* (Petagna, 1792), which exhibits an abbreviated type of development with only two zoeal stages and a megalopa. The larvae, hatched from berried females from S. Euboikos Bay (Aegean Sea, Greece), were reared at 10 temperature–food density combinations (19 and 24 °C; 0, 2, 4, 8 and 16 *Artemia* nauplii d<sup>-1</sup>). Enhanced starvation resistance was evident: 92 and 58% of starved zoeas I molted to zoea II, while metamorphosis to megalopa was achieved by 76 and 42% of the hatched zoeas at 19 and 24 °C, respectively. The duration of both zoeal stages was affected by temperature, food density and their interaction. Nevertheless, starvation showed different effects at the two temperatures: compared to the fed shrimp, the starved zoeae exhibited accelerated development at 19 °C (8.4 d) but delayed metamorphosis at 24 °C (5.9 d). On the other hand, both zoeal stages were able to consume food at an increased rate as food density and temperature increased. Predation efficiency also increased with temperature, but never exceeded 0.6. Facultative lecithotrophy, more pronounced during the first zoeal stage of *C. tyrrhena*, can be regarded as an adaptation of a species whose larvae can respond physiologically to the different temperature–food density combinations encountered in the wide geographical range of their natural habitat.

### Introduction

Food limitations have been studied in a variety of invertebrate larvae, as reviewed in Strathmann (1993) and Olson and Olson (1989). The latter authors were able to distinguish different trends in some animal groups: larval starvation is frequently important in crustaceans, occasionally important in molluscs and possibly important in echinoderms. Most of the research conducted on crustacean food limitations was actually focused on decapod larvae (Paul et al. 1979; Paul and Paul 1980; Anger and Dawirs 1981; Anger et al. 1981a, b; Paul and Nunes 1983; Anger 1987, 1991 and literature within; Wehrmann 1991) for which planktotrophic development is usually reported.

In some decapods, however, non-feeding larval stages have been observed during the transition from planktonic to benthic life; the megalopae of the pagurids *Clibanarius erythropus* and *Pagurus bernhardus*, and the pueruli of the spiny lobster *Panurilus cygnus* do not feed (Dawirs 1981, 1982; Harms 1992; Lemmens 1994a, b). Fully lecithotrophic development has been observed in the zoeae of the Australian terrestrial hermit crab *Coenobita variabilis*, the ocypodid crab *Uca subcylindrica* and the grapsid crab *Geosesarma perracae* (Soh 1969; Rabalais and Cameron 1983; Rabalais and Gore 1985; Harvey 1992), while an intermediate step towards nutritional independence, facultative lecithotrophy, characterises the larval development of *Sesarma reticulatum*, *Sesarma curacaoense*, *Metopaulias depressus* and *Armases miersii* (Staton and Sulkin 1991; Anger and Schuh 1992; Anger 1995a, b; Schuh and Diesel 1995).

In the oligotrophic environment of the eastern Mediterranean, food limitations for successful larval development could be a key factor in the maintenance of decapod populations. Because of the scarcity of food in these nutrient-poor coastal waters, the zoeae can encounter short or longer periods of insufficient feeding. No work exists on the food requirements of larval decapods in the region.

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Adult callianassids, on the other hand, are considered to play a significant role in shallow-water ecology because of their intensive burrowing activity. Bioturbation and its consequences have recently received increasing attention. However, studies on the biology of these important bioturbators and the factors influencing their life cycles are missing. The burrowing shrimp *Callianassa tyrrhena* has a wide northeastern Atlantic–Mediterranean distribution which extends from the English Channel to the coasts of Mauritania. Although it is considered the commonest callianassid in that region, its populations flourish mainly on low-energy sand flats of shallow or intertidal coasts (Thessalou-Legaki 1990; Dworschak 1992). Its larval development is of an advanced type, with only two zoeal stages and one megalopa (Thessalou-Legaki 1990). The hatching larvae are about 3 mm in total length, and no significant increment in length is shown when molting to zoea II and then to megalopa. Since Gurney's (1942) work, distinguishing two types of larval development in callianassids, the rearing of callianassid larvae hatched from berried females revealed a number of developmental patterns: six zoeal stages are present in *Callianassa petalura* and *Callianassa australiensis* (Konishi et al. 1990; Hailstone and Stephenson 1961), five in *Callianassa garthi*, *Callianassa uncinata*, *Callianassa filholi* and *Callianassa californiensis* (Devine 1966; McCrow 1972 in Johnson and Gonor 1982; Aste and Retamal 1983, 1984), three in *Callianassa major* (Pohl 1946; Rodrigues 1976), and finally two in *Callianassa kraussi*, *Callianassa louisianensis* (= *Lepidophthalmus louisianensis*), *Callianassa kewalramanii*, *Callichirus mirim* (= *Sergio mirim*) and *Lepidophthalmus sinuensis* (Forbes 1973; Sankolli and Shenoy 1975; Rodrigues 1979, 1984; Felder et al. 1986; Nantes et al. 1997). It seems, therefore, that advanced development is not unusual in callianassids, as was suggested by Forbes (1973) for *Callianassa kraussi*. Since advanced larval development is usually accompanied by an independence from external energy supply (see discussion in Anger 1995b), in this paper we investigate the extent of lecithotrophy in the larval development of *C. tyrrhena* using different temperature–food density combinations.

## Materials and methods

Ovigerous females of *Callianassa tyrrhena* (Petagna, 1792), with ova close to hatching, were collected using a hand-operated pump similar to that of Manning (1975) in a small sand flat in South Euvoikos Bay (Greece; 37°55.4'N; 24°01.2'E) during the summer of 1991. They were transferred to the laboratory and maintained in a constant-temperature room of 19 °C. No sediment, food or aeration was provided to the females which were kept separately in plastic boxes (10 × 10 × 5 cm), skirted with black plastic. Sea water from the sampling site, paper-filtered, was changed every week.

After hatching, the larvae were transferred individually into small cylindrical wells, originally used for tissue culture (Costar, Data Packaging Corp., Cambridge, USA), with 1.6 ml paper-filtered natural sea water of 37 psu salinity. The vials were covered with black plastic in order to keep the larvae away from the water surface. Earlier experiments (Thessalou-Legaki 1990) have shown

that the larvae, due to their extreme positive phototaxis, can reach the water surface and be trapped with their prominent dorsal abdominal spine on the air–water interface, where they eventually die.

Five food densities (0, 2, 4, 8 and 16 newly hatched nauplii of *Artemia* per day) were used at two temperatures of the optimal range for zoeal survival (19 and 24 °C, in Thessalou-Legaki 1990) in constant-temperature rooms ( $\pm 0.5$  °C) with a 12 h light:12 h dark photoperiod. For each temperature–food combination 50 specimens were used.

During daily inspection, survival, molting and number of ingested nauplii were recorded. Food and medium were changed daily. During the whole experiment, each larva was provided with the same quantity of food. Animals in the process of molting during inspection were recorded as the next stage.

Data on the two zoeal stages and total zoeal development are generally used in the present study; data including the megalopa stage are used only with regards to survival over time. According to previous rearing experience (Thessalou-Legaki 1990), metamorphosis to megalopa is accompanied by a transition from planktonic to benthic mode of life. The megalopa can actively burrow in the sediment and become detritivorous. Since no sediment was provided in any phase of the present study, the megalopa food requirements were not taken into account.

Statistical treatment includes one- and two-way analysis of variance (ANOVA) with multiple comparisons of means (Tukey test) using the STATGRAPHICS programme. For principal components analysis (PCA), the programme STATISTICA was used in order to discriminate factors using mean duration, consumption rate, predation efficiency and percentage of successful molts (zoea I and II) or completed metamorphoses of hatched larvae (total zoeal development) as variables. The varimax rotation on raw data was applied to the factors. Mean substitution was used for the missing values in predation efficiency of the starved larvae.

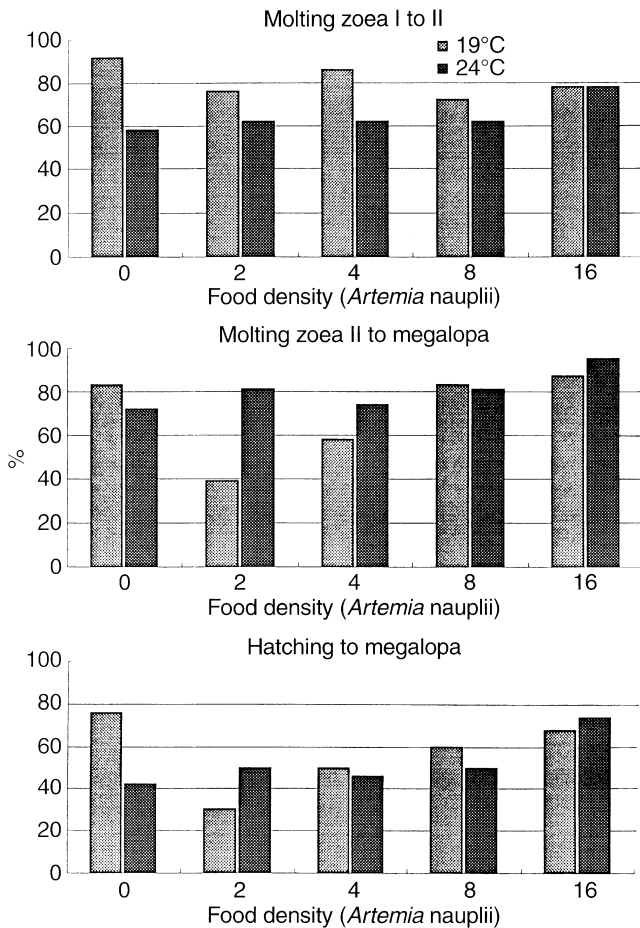
## Results

### Survival and molting success

Larval survival over time, not taking into account the developmental stage, showed a prolongation at the lower temperature of 19 °C (18 to 22 d) compared to that of 24 °C (11 to 15 d). Starvation did not dramatically affect the survival curve at either temperature; the larvae could live without food for as long as 19 and 11 d at 19 and 24 °C, respectively. At each food density, higher survival over time was exhibited at the lower temperature. When the larvae were starved or provided with small amounts of food (2 to 4 *Artemia* nauplii d<sup>-1</sup>), survival dropped most at the beginning of the experiment at 24 °C, and then ran parallel to that at 19 °C. On the contrary, the survival curves for the two temperatures diverged later in the two treatments at higher food densities (8 and 16 *Artemia* nauplii d<sup>-1</sup>).

Successful molting to the subsequent stage can provide a more realistic measure of successful larval development. The two contiguous moltings as well as the total zoeal development from hatching to megalopa are shown in Fig. 1. In general, metamorphosis was achieved by more than 30 and 40% of the hatched zoeas at 19 and 24 °C, respectively.

At the lower temperature of 19 °C, starvation resulted in the highest molting success of zoea I and of metamorphosis among all food densities tested, while



**Fig. 1** *Callinassa tyrrhena*. Successful molting to the next stage for zoea I and II, as well as completed metamorphosis (hatching to megalopa), at 19 and 24 °C and five food densities (0, 2, 4, 8 and 16 *Artemia* nauplii d<sup>-1</sup>)

starved zoeae II molted to megalopa almost as successfully as the well-fed specimens. When food was provided at 19 °C, the success of zoea II molting, as well as of that metamorphosis of the hatched zoeae, increased with food density.

At 24 °C, shrimp provided with the maximum food density exhibited the highest percentage of successful molts in two zoeal stages and of completed metamorphoses, while starved animals had the lowest.

**Table 1** *Callinassa tyrrhena*. Two-way ANOVA results (*F*-ratio and significance) of the effect of temperature and food density on the duration, consumption rate and predation efficiency of zoea I, zoea II and total zoeal development (hatching to metamorphosis). Data from individuals which completed each developmental stage are used; \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$

	Temperature	Food density	Interaction
Duration			
Zoea I	> 1000***	56.5***	49.0***
Zoea II	> 1000***	16.2***	62.1***
Total zoeal development	> 1000***	10.2***	99.8***
Consumption			
Zoea I	7.1***	228.4***	8.6***
Zoea II	64.2***	193.0***	6.6***
Total zoeal development	44.1***	313.6***	9.3***
Predation efficiency			
Zoea I	17.3***	11.3***	4.3**
Zoea II	43.5***	12.6***	2.7*
Total zoeal development	42.1***	13.6***	7.6***

## Duration of stages

Duration of zoea I and II, as well as that of total zoeal development, was highly affected by temperature, food density and their interaction (Table 1).

In general, the lower temperature resulted in longer duration (Fig. 2). When animals were provided with food, the 5 °C decrease of temperature at least doubled the time needed for completion of the stages, as well as that needed for total zoeal development. However, starvation made this temperature effect less prominent, especially in the development time for zoea I.

At each temperature, one-way ANOVA showed that food density affects the duration of each developmental stage, as well as that of the total zoeal development (Table 2). At 19 °C, multiple comparisons of the means proved that zoea I duration increased as food density increased from 2.4 d in starved specimens to 4.4 d in specimens provided with 16 *Artemia* nauplii d<sup>-1</sup>. At 24 °C the effect of food density, although statistically significant, was practically minimal, showing very similar mean zoea I duration values (range 1.8 to 2.0 d).

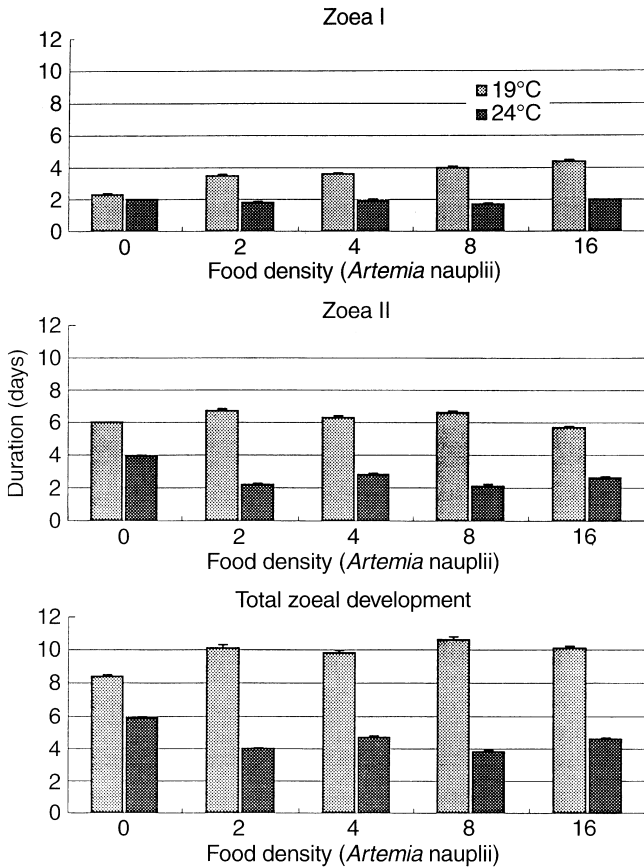
In zoea II, multiple comparisons revealed two cases of statistically different mean durations: among all the prey densities tested, the best-fed shrimp at 19 °C showed the shortest duration, while at 24 °C starved animals had the longest.

By comparing the arrangement of mean duration values in ascending order (Table 2), it could be concluded that the effect of food density on the total zoeal duration resembles that of zoea I at 19 °C, and that of zoea II at 24 °C.

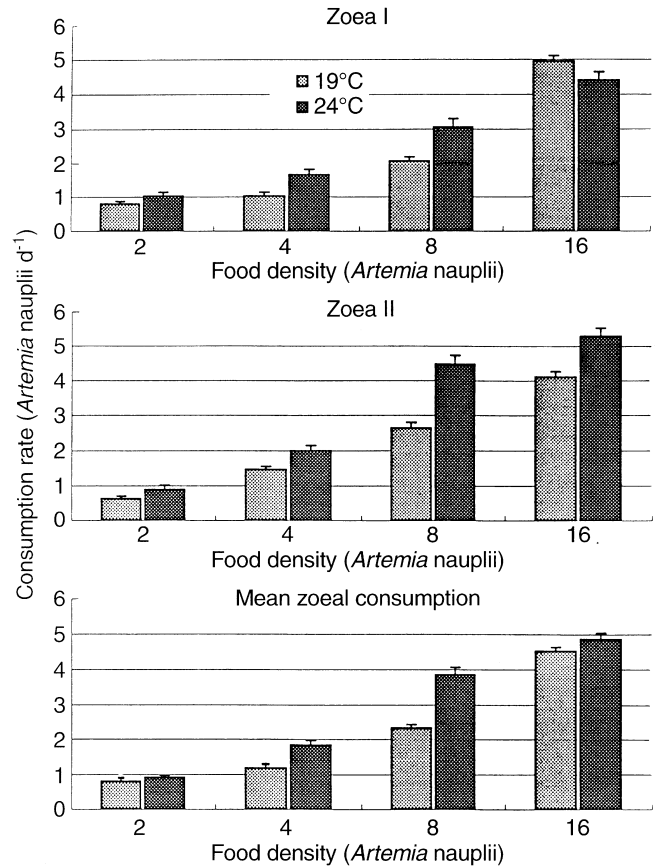
## Consumption rate and predation efficiency

Both zoeal stages could capture the nauplii of *Artemia* at a rate that is highly dependent on food availability and temperature, as well as their interaction (Table 1).

At both temperatures, larvae of both zoeal stages captured food at an increasing rate as food density increased (Fig. 3; Table 2). With the exception of zoea I fed on the maximum food density of 16 nauplii d<sup>-1</sup>, the higher temperature resulted in a significant increase of consumption rate of the food items available.



**Fig. 2** *Callianassa tyrrhena*. Duration (and SE) of zoea I and II, as well as that from hatching to megalopa, at 19 and 24 °C and five food densities (0, 2, 4, 8 and 16 *Artemia* nauplii d<sup>-1</sup>)



**Fig. 3** *Callianassa tyrrhena*. Consumption rate (and SE) of zoea I and II, and mean zoeal consumption rate, at 19 and 24 °C and four food densities (2, 4, 8 and 16 *Artemia* nauplii d<sup>-1</sup>)

It is worth mentioning that no depletion of food was observed at any temperature–food combination, as predation efficiency (ingested per available *Artemia* nauplii)

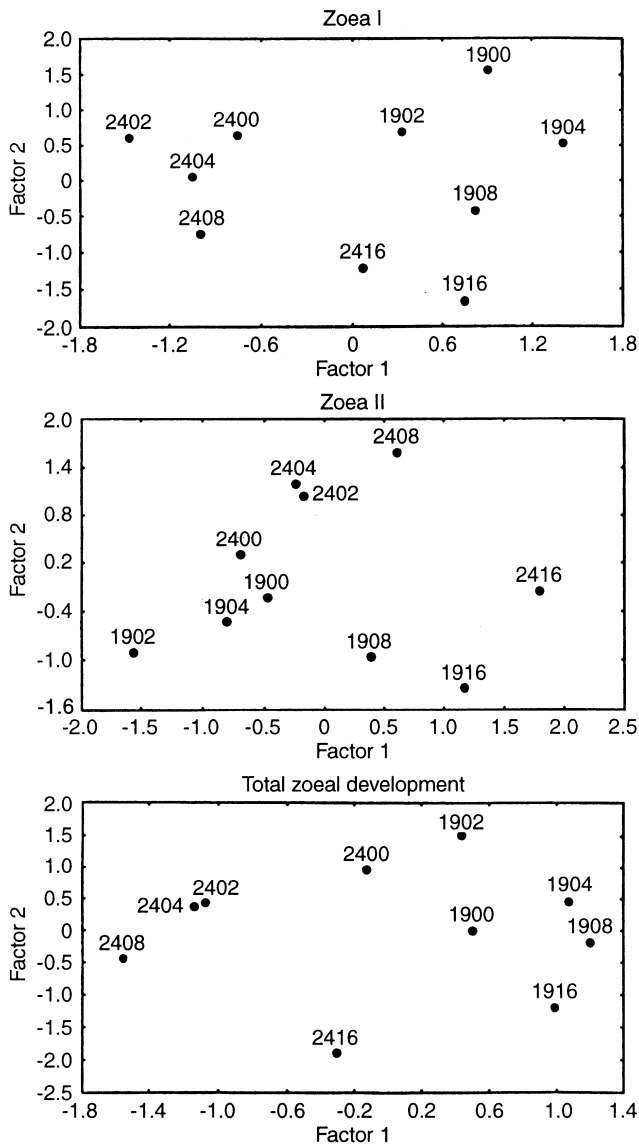
ranged from 0.26 to 0.56 (Fig. 4). The ability of the larvae to ingest food items is affected by both food density and temperature, as well as their interaction

**Table 2** *Callianassa tyrrhena*. One-way ANOVA results (*F*-ratio and multiple comparisons) of the effect of food density (2, 4, 8 and 16 *Artemia* nauplii d<sup>-1</sup>) on duration, consumption rate and predation efficiency of zoea I, zoea II and total zoeal development (hatching to metamorphosis) at the two rearing temperatures. Data

from animals which completed each developmental stage are used. In multiple comparisons the food densities are arranged in ascending order of means; horizontal lines indicate groups of equal means; \* *P* < 0.05, \*\* *P* < 0.01, \*\*\* *P* < 0.001

	19 °C		24 °C	
	<i>F</i> -ratio	Multiple comparisons	<i>F</i> -ratio	Multiple comparisons
Duration				
Zoea I	80.7***	0̄ 2̄ 4̄ 8̄ 16̄	3.9**	8̄ 2̄ 4̄ 0 16
Zoea II	23.9***	16̄ 0̄ 4̄ 8̄ 2	54.1***	8̄ 2̄ 16̄ 4̄ 0
Total zoeal development	46.7***	0̄ 4̄ 2̄ 16̄ 8	84.0***	8̄ 2̄ 16̄ 4̄ 0
Consumption				
Zoea I	260.5***	2̄ 4̄ 8̄ 16̄	56.5***	2̄ 4̄ 8̄ 16̄
Zoea II	103.9***	2̄ 4̄ 8̄ 16̄	99.5***	2̄ 4̄ 8̄ 16̄
Total zoeal development	296.5***	2̄ 4̄ 8̄ 16̄	120.9***	2̄ 4̄ 8̄ 16̄
Predation efficiency				
Zoea I	7.1***	4̄ 8̄ 16̄ 2	7.9***	16̄ 8̄ 4̄ 2
Zoea II	5.6**	16̄ 2̄ 8̄ 4	8.5***	16̄ 2̄ 4̄ 8
Total zoeal development	8.5***	16̄ 8̄ 4̄ 2	11.6***	16̄ 2̄ 4̄ 8





**Fig. 5** *Callianassa tyrrhena*. Plots of the factor scores for ten temperature–food density combinations from the principal components analysis for zoea I, zoea II and total zoeal development (hatching to metamorphosis). The first two numbers indicate temperature and the last, the food density

In the development of zoea II, the first factor was highly positively correlated with molting success and consumption rate, while the second one was positively correlated with predation efficiency and negatively with instar duration. In this zoeal stage no distinct groups of temperature–food density combinations were evident (Fig. 5). Nevertheless, the position of the temperature–food combinations suggests that the first factor represents developmental aspects affected by food density, while the second one reflects temperature effects.

Finally, in the total zoeal development (hatching to metamorphosis), the first factor of PCA was highly positively correlated with duration and negatively correlated with predation efficiency, while the second one was negatively correlated with both success in meta-

morphosis and consumption rate. It seems, therefore, that the first factor represents developmental aspects affected by temperature, while the second one reflects the effects of food density (Fig. 5).

In conclusion, in all three cases described above, larval duration and predation efficiency were correlated with the same factor which represents temperature effects, though in opposite positions. On the other hand, consumption rate was always represented in the other factor which represents food density. Finally, success in molting or in metamorphosis showed different relationships: in zoea I, it was situated close to duration, while in zoea II and in the total zoeal development, close to consumption (see factor loadings in Table 3).

## Discussion

The present study demonstrates that the yolk reserves of the hatched larvae of *Callianassa tyrrhena* can support the development to megalopa. Nevertheless, both zoeal stages consumed the nauplii of *Artemia*, with an increasing rate as prey density increased. This tendency indicates that ingestion is mainly dependent on chance encounters. Predation efficiency also increases with temperature, as it increases mobility of both the predator and the prey, and thus the possibility of their encounters. Nevertheless, at the highest prey density of 16 nauplii  $d^{-1}$ , both zoeal stages exhibited a decrease in ingestion efficiency, which indicates that ingestion approached a condition of feeding saturation. The approach to a feeding saturation level is also supported by the fact that at that food density the effect of temperature on predation efficiency is minimum. The above-described feeding plasticity can be ascribed to facultative lecithotrophy. *Callianassa tyrrhena* and *Callianassa kraussi*, callianassids with advanced development, produce small numbers of large eggs (mean egg number 270 and 122  $female^{-1}$ ; maximum egg diameter 1.18 and 1.52 mm, respectively) (Forbes 1973; Thessalou-Legaki and Kiortsis 1997). The latter authors also report a high reproductive output in *Callianassa tyrrhena* which is about 20 and 35% of the dry and ash-free dry weight of the female, respectively.

The results of the present study provide evidence on the effect of starvation during larval development in the natural environment. *Callianassa tyrrhena* is a littoral species with a wide range of geographical distribution, from the English Channel to the eastern Mediterranean, and summer reproduction. The two temperatures used in the present study can be encountered by the larvae in the summer surface waters of these two distribution limits. At the lower temperature of 19 °C, commonly found at the northern limit, the period from hatching to metamorphosis of the starved larvae is shortened compared to that of the animals reared in any food density. The acceleration of larval development is mainly due to the shortened intermolt period of zoea I. At the same time, starved *C. tyrrhena* show higher success in meta-

morphosis in comparison to fed ones, especially those reared in low prey densities. It is suggested that, during possible starvation at this temperature, the yolk reserves can be mobilised so that morphological changes and molting can proceed. Anger (1995a) proposed this mechanism in order to explain the different developmental rates in *Armases miersii* larvae which hatched from broods with different endotrophic potentials. This specific to facultative lecithotrophy mechanism (Anger 1995b) changes the energy partitioning from growth (accumulation of additional energy reserves) to accelerated development (mobilisation of internal reserves) which results in rapid termination of the planktonic larval phase. The shortening of the planktonic phase could be important for the recruitment process of *C. tyrrhena*, since it may reduce predation and increase the possibility of remaining in inshore waters.

On the contrary, at the temperature of 24 °C, commonly found in the summer waters of the eastern Mediterranean, starvation delays development from hatching to megalopa, although the dominant effect of the increased temperature still keeps the developmental rate of starved animals at a higher level than that of the starved animals reared at 19 °C. This developmental delay is mainly due to zoea II. It is suggested that at this temperature most of the yolk reserves are channelled to increased metabolic demands. A similar retardation has been observed in *Rhithropanopeus harrisi* (Anger et al. 1981a), *Hyas araneus* (Anger and Dawirs 1981), *Homarus americanus* and two *Jasus* species (Abrunhosa and Kittaka 1997), and is considered a common response of the planktotrophic crustacean larvae (McConaughy 1985). It may be difficult at the moment to explain the selective advantage of facultative lecithotrophy in *Callinassa tyrrhena*, since no inter- or intraspecific comparison is feasible in the same family. It can be suggested, however, that its larvae exhibit a physiological flexibility that leads, under certain conditions, to lecithotrophy in the northern part of its geographical range or planktotrophy in the southern.

When food was provided, the duration of each zoeal stage, as well as of the total zoeal development, did not vary greatly with food availability, whereas it decreased significantly with temperature. During larval development, energy available from ingestion of external food and from yolk reserves should meet the energy requirements for standard metabolism, construction of new tissues and molting processes, as well as for capture, manipulation, ingestion and digestion of prey. It is suggested that complex relations exist among the above-mentioned energy components when nutritional flexibility exists. Anger (1991) reviews the bioenergetic aspects of decapod larvae and demonstrates the complexity of energy budgets during the molting cycles of larval decapods. Although no data exist on larval energy partitioning in callinassids, some assumptions can be made based on the present results. Higher metabolic demands of *Callinassa tyrrhena* larvae at higher temperatures can be met by increased consumption

(greater input of energy) and higher predation efficiency (lower loss of energy for prey capture). This response can be considered as favourable in the plankton-poor waters of the eastern Mediterranean, where *C. tyrrhena* can better exploit the available, even scarcer, food. At lower temperatures, food scarcity resulted in the lowest success from hatching to metamorphosis, which could indicate that the animals invest a relatively large amount of energy in food capture (decreased predation efficiency), which cannot be balanced by the energy gained.

Principal component analysis revealed that temperature and food density can represent the first two factors, which explain most of the variability found in larval development of *Callinassa tyrrhena*. With regard to molting success, different patterns were shown in the development of the two zoeal stages: in zoea I, temperature explains most of the variability and is negatively related to molting success, whereas temperature effects are less pronounced in the development of zoea II (lower percentage of total variance). In the latter stage, food availability becomes the principal component and reflects success in molting. Hence, the development of zoea I is mainly dependent on temperature, while that of zoea II is influenced by food availability. A similar decrease in the potential for endotrophic development during ontogeny has been demonstrated in the crab *Armases miersii*, which also exhibits advanced development and breeds in the highly variable environment of supratidal rock pools. In that species complete independence from food has been observed in zoea I, partial in zoea II, while zoea III is not able to cope with starvation (Anger 1995a).

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## References

- Abrunhosa FA, Kittaka J (1997) Effect of starvation on the first larvae of *Homarus americanus* (Decapoda, Nephropidae) and phyllosomas of *Jasus verreauxi* and *J. edwardsii* (Decapoda, Palinuridae). *Bull mar Sci* 61: 73–80
- Anger K (1987) The D<sub>0</sub> threshold: a critical point in the larval development of decapod crustaceans. *J exp mar Biol Ecol* 108: 15–30
- Anger K (1991) Developmental changes in the bioenergetics of decapod larvae. *Mem Qd Mus* 31: 289–308
- Anger K (1995a) Developmental biology of *Armases miersii* (Grapsidae), a crab breeding in supratidal rock pools. I. Facultative lecithotrophy of larval stages. *Mar Ecol Prog Ser* 117: 75–81
- Anger K (1995b) Starvation resistance in larvae of a semiterrestrial crab, *Sesarma curacaoense* (Decapoda: Grapsidae). *J exp mar Biol Ecol* 187: 161–174
- Anger K, Dawirs RR (1981) Influence of starvation on the larval development of *Hyas araneus* (Decapoda, Majidae). *Helgoländer Meeresunters* 34: 287–311
- Anger K, Dawirs RR, Anger V, Costlow JD (1981a) Effects of early starvation periods on zoeal development of brachyuran crabs. *Biol Bull mar biol Lab, Woods Hole* 161: 199–212

- Anger K, Dawirs RR, Anger V, Goy JW, Costlow JD (1981b) Starvation resistance in first stage zoeae of brachyuran crabs in relation to temperature. *J Crustacean Biol* 1: 518–525
- Anger K, Schuh M (1992) Bioenergetics of abbreviated larval development in the bromeliad crab, *Metopaulias depressus* (Decapoda: Grapsidae). *Comp Biochem Physiol* 103A: 507–518
- Aste A, Retamal MA (1983) Desarrollo larval de *Callianassa garthi* Retamal, 1975 bajo condiciones de laboratorio. *Cienc tecnol Mar* 7: 5–26
- Aste A, Retamal MA (1984) Desarrollo larval de *Callianassa uncinata* H. Milne Edwards, 1837 (Decapoda, Callianassidae) bajo condiciones de laboratorio. *Gayana, Chile* 48: 41–56
- Dawirs RR (1981) Elemental composition (C, N, H) in the development of *Pagurus bernhardus* (Decapoda: Paguridae) megalopa. *Mar Biol* 64: 117–123
- Dawirs RR (1982) Methodological aspects of rearing decapod larvae, *Pagurus bernhardus* (Paguridae) and *Carcinus maenas* (Portunidae). *Helgoländer Meeresunters* 35: 439–464
- Devine CE (1966) Ecology of *Callianassa filholi* Milne Edwards, 1878 (Crustacea, Thalassinidea). *Trans R Soc NZ, Zoology* 8: 93–110
- Dworschak PC (1992) The Thalassinidea in the Museum of Natural History, Vienna; with some remarks on the biology of the species. *Annln naturhist Mus Wien (Ser B)* 93: 189–238
- Felder JM, Felder DL, Hand SC (1986) Ontogeny of osmoregulation in the estuarine ghost shrimp *Callianassa jamaicense* var. *louisianensis* Schmitt (Decapoda, Thalassinidea). *J exp mar Biol Ecol* 99: 91–105
- Forbes AT (1973) An unusual abbreviated larval life in the estuarine burrowing prawn *Callianassa kraussi* (Crustacea, Decapoda, Thalassinidea). *Mar Biol* 22: 361–365
- Gurney R (1942) Larvae of decapod Crustacea. Ray Society, London
- Hailstone TS, Stephenson W (1961) The biology of *Callianassa (Trypaea) australiensis* Dana, 1852 (Crustacea, Thalassinidea). *Pap Qd Univ* 1: 259–285
- Harms J (1992) Larval development and delayed metamorphosis in the hermit crab *Clibanarius erythropus* (Latreille) (Crustacea, Diogenidae). *J exp mar Biol Ecol* 156: 151–160
- Harvey AW (1992) Abbreviated larval development in the Australian terrestrial hermit crab *Coenobita variabilis* McCulloch (Anomura: Coenobitidae). *J Crustacean Biol* 12: 196–209
- Johnson GE, Gonor JJ (1982) The tidal exchange of *Callianassa californiensis* (Crustacea, Decapoda) larvae between the ocean and the Salmon River estuary, Oregon. *Estuar cstl Shelf Sci* 14: 501–516
- Konishi K, Quintana RR, Fukuda Y (1990) A complete description of larval stages of the ghost shrimp *Callianassa petahura* Stimpson (Crustacea: Decapoda: Callianassidae) under laboratory conditions. *Bull natn Res Inst Aquaculture, Nansei, Japan* 17: 27–49
- Lemmens JWTJ (1994a) The Western rock lobster *Panulirus cygnus* (George, 1962) (Decapoda: Palinuridae): the effect of temperature and developmental stage on energy requirements of pueruli. *J exp mar Biol Ecol* 180: 221–234
- Lemmens JWTJ (1994b) Biochemical evidence for absence of feeding in puerulus larvae of the Western rock lobster *Panulirus cygnus* (Decapoda: Palinuridae). *Mar Biol* 118: 383–391
- Manning RB (1975) Two methods for collecting decapods in shallow water. *Crustaceana* 29: 317–319
- McConaughy JR (1985) Nutrition and larval growth. In: Wenner AM (ed) *Crustacean issues 2. Larval growth*. AA Balkema, Rotterdam, The Netherlands, pp 127–154
- McCrow LT (1972) The ghost shrimp *Callianassa californiensis*, in Yaquina Bay, Oregon. M.Sc. thesis, Oregon State University, Corvallis, pp 1–56
- Nantes SF, Felder DL, Lemaitre R (1997) Comparative larval development in two species of the burrowing ghost shrimp genus *Lepidophthalmus* (Decapoda: Callianassidae). *J Crustacean Biol* 17: 497–519
- Olson RR, Olson MH (1989) Food limitation of planktotrophic marine invertebrate larvae: does it control recruitment success? *A Rev Ecol Syst* 20: 225–247
- Paul AJ, Nunes P (1983) Temperature modification of respiratory metabolism and caloric intake of *Pandalus borealis* (kroyer) first zoeae. *J exp mar Biol Ecol* 66: 163–168
- Paul AJ, Paul JM (1980) The effect of early starvation on later feeding success of king crab zoeae. *J exp mar Biol Ecol* 44: 247–251
- Paul AJ, Paul JM, Shoemaker PA, Feder HM (1979) Prey concentrations and feeding response in laboratory-reared stage-one zoeae of king crab, snow crab and pink shrimp. *Trans Am Fish Soc* 108: 440–443
- Pohl ME (1946) Ecological observations on *Callianassa major* Say at Beaufort, North Carolina. *Ecology* 27: 71–80
- Rabalais NN, Cameron JN (1983) Abbreviated development of *Uca subcylindrica* (Stimpson, 1859) (Crustacea, Decapoda, Ocypodidae) reared in the laboratory. *J Crustacean Biol* 3: 519–541
- Rabalais NN, Gore RH (1985) Abbreviated development in decapods. In: Wenner AM (ed) *Crustacean issues. 2. Larval growth*. AA Balkema, Rotterdam, The Netherlands, pp 67–126
- Rodrigues SdeA (1976) Sobre a reproducao, embriologia e desenvolvimento larval de *Callinectes major* Say, 1818 (Crustacea, Decapoda, Thalassinidea). *Bolm Zool, Univ S Paulo* 1: 85–104
- Rodrigues SdeA (1979) Desenvolvimento larval de *Callinectes mirim* (Rodrigues, 1971) obtido em laboratorio (Crustacea, Decapoda, Callianassidae). *Anais Acad bras Cienc* 51: 571–572
- Rodrigues SdeA (1984) Desenvolvimento pos-embrionario de *Callinectes mirim* (Rodrigues, 1971) obtido em condicoes artificiais (Crustacea, Decapoda, Thalassinidea). *Bolm Zool, Univ S Paulo* 8: 239–256
- Sankolli KN, Shenoy S (1975) Larval development of mud shrimp *Callianassa (Callinectes) kewalramanii* Sankolli, in the laboratory (Crustacea, Decapoda). *Bull Dep mar Sci, Univ Cochín* 7: 705–720
- Schuh M, Diesel R (1995) Effects of salinity and starvation on the larval development of *Sesarma curacaoense* De Man, 1892, a mangrove crab with abbreviated development (Decapoda: Grapsidae). *J Crustacean Biol* 15: 645–654
- Soh CL (1969) Abbreviated development of non-marine crab *Sesarma (Geosesarma) perracae* (Brachyura; Grapsidae) from Singapore. *J Zool, Lond* 158: 357–370
- Staton JL, Sulkin SD (1991) Nutritional requirements and starvation resistance in larvae of the brachyuran crabs *Sesarma cinereum* (Bosc) and *S. reticulatum* (Say). *J exp mar Biol Ecol* 152: 271–284
- Strathmann RR (1993) Hypotheses on the origins of marine larvae. *A Rev Ecol Syst* 24: 89–117
- Thessalou-Legaki M (1990) Advanced larval development of *Callianassa tyrrhena* (Decapoda: Thalassinidea) and the effect of environmental factors. *J Crustacean Biol* 10: 659–666
- Thessalou-Legaki M, Kiortsis V (1997) Estimation of the reproductive output of the burrowing shrimp *Callianassa tyrrhena*: a comparison of three different biometrical approaches. *Mar Biol* 127: 435–442
- Wehrtmann IS (1991) How important are starvation periods in early larval development for survival of *Crangon septemspinosa* larvae? *Mar Ecol Prog Ser* 73: 183–190