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ADVANCED LARVAL DEVELOPMENT OF *CALLIANASSA TYRRHENA* (DECAPODA: THALASSINIDEA) AND THE EFFECT OF ENVIRONMENTAL FACTORS

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ABSTRACT

The larval development of *Callianassa tyrrhena* was studied under laboratory conditions. Sixteen salinity-temperature combinations were used (14, 18, 22, 25°C and 40, 60, 80, 100% sea water of S = 37‰). Since only 2 zoeal stages and a megalopa were observed, the postembryonic development can be characterized as advanced. Morphological changes between stages are prominent, while size does not seem to increase. Salinity mainly affects successful molting to zoea II and metamorphosis, while temperature dominates the developmental rate. Low salinities and temperatures prohibit or do not favor larval development, but when these factors approximate natural conditions (S ≥ 80% sea water and T ≥ 18°C) metamorphosis is completed in a percentage equal to or greater than 70%. With increasing temperature, the zoeal duration is shortened drastically, but also the participation of the 2 zoeal stages in the total zoeal duration is equalized. The shortening of the larval duration up to 3.2 days (in 25°C and 100% sea water) is considered as advantageous for a species which, as adult, lives in a restricted habitat in the upper coastal zone.

The ghost shrimp *Callianassa tyrrhena* (Petagna) has an Eastern Atlantic–Mediterranean distribution. Its Atlantic range extends from the English Channel to the coasts of Mauritania (Saint Laurent and Bozic, 1976; Saint Laurent and Le Loeuff, 1979). In Greece it has been reported from many mainland and island coasts (see Thessalou-Legaki, 1986). Although it is considered the commonest callianassid of the Atlantic French coast and the European coast of the Mediterranean, its depth distribution is not clear because of the confusion of identifications in the past (Saint Laurent and Le Loeuff, 1979). Nevertheless, the majority of confirmed reports of the species and personal sampling suggest that the species lives in very shallow waters up to few meters (Saint Laurent and Manning, 1982; Picard, 1957; Saint Laurent and Bozic, 1976; Pastore, 1976; Garcia Raso, 1983; Manning, 1975).

The species forms dense populations on sand flats, descriptions of which are given in Ott *et al.* (1976) and Le Gall (1969). The impact of *C. tyrrhena* on redox potential and nutrient cycling of the sediment has been documented by Ott *et al.* (1976). The role of callianassids in shallow-water ecology has recently received increasing attention. Bioturbation and its consequences upon the sediment and its communities have been documented for callianassids (Aller and Dodge, 1974; Posey, 1986; Murphy, 1985; Suchanek, 1983; Dobbs and Guckert, 1988; Branch and Pringle, 1987). However, reproductive cycles and larval development of such species are largely unknown. Developmental series of known parentage have been described for *Callianassa garthi* Retamal (Aste and Retamal, 1983), *Callianassa uncinata* H. Milne Edwards (Aste and Retamal, 1984), *Callianassa kraussi* Stebbing (Forbes, 1973), *Callianassa kewalramanii* Sankolli (Sankolli and Shenoy, 1975), *Callichirus major* (Say) (Rodrigues, 1976), and *Callichirus mirim* (Rodrigues) (Rodrigues, 1979, 1984). There is also a considerable amount of information on callianassid larval forms from plankton material or hatching first stage larvae in the laboratory (Sandifer, 1973; Kurata, 1965; Williamson, 1967, 1970; Al Kholy and Firky-Mahmoud, 1967; Lebour, 1955; and Gurney, 1942, for earlier contributions). Larvae attributed to *C. tyrrhena* were first described by Cano (1891) from plankton material as *Callianassa subterranea* Leach. Caroli (1921) and Heegaard (1963) reported the hatching of the larvae in the laboratory but they did not give the total number of zoeal stages.

Callianassid larval ecology has not been adequately studied. Sandifer (1973) cited some environmental variables in plankton surveys. Salinity effects have been studied

Table 1. Main morphological characters and size (mean ± SD) of larval stages of *Callianassa tyrrhena*. TL = total length, CL = carapace length.

Stage	Thoracopods	Pleopods	Uropods	Size (mm) TL	Size (mm) CL	*N*
Zoea I	absent	absent	absent	2.93 ± 0.12	0.73 ± 0.03	8
Zoea II	present	present	absent	3.02 ± 0.02	0.71 ± 0.02	7
Megalopa	functional	functional	functional	2.52 ± 0.09	0.69 ± 0.02	4

in the larvae of *C. kraussi* (Forbes, 1978), and osmoregulatory adaptations are documented in *Callianassa louisianensis* Schmitt (Felder *et al.*, 1986).

In the frame of a more general study of the population biology of *C. tyrrhena,* the larval development and the effect of environmental factors were studied under laboratory conditions.

Materials and Methods

Ovigerous females were caught using a hand pump similar to that of Manning (1975) in a sand flat of a small temporary estuary in South Euboikos bay, Greece, in the summer of 1984. They were transferred to the laboratory and maintained in a constant temperature room with temperature similar to that of the habitat (22°C). They were put separately in plastic boxes 10 × 10 × 5 cm, skirted with black plastic, with sea water of the habitat. No sediment, food, or aeration was offered. The water was changed every week. One or two days before hatching, newly hatched nauplii of *Artemia* were added. The larvae hatched at night, usually on the same night.

For the salinity-temperature experiment, larvae from only one female were used in order to eliminate genetic and/or incubational variations. Sixteen salinity-temperature combinations were made, with temperatures 14, 18, 22, and 25°C and salinities 40, 60, 80, and 100% sea water of the habitat (14.8, 22.2, 29.6, and 37‰, respectively) in constant-temperature rooms (±0.5°C) and 12L:12D photoperiodism. Dilutions were made with distilled water. The sea water was previously filtered with filter paper. In each combination 30 larvae were used. They were put in groups of 5 in cylindrical vessels with 50 ml water and newly hatched nauplii of *Artemia* in excess. Food and medium were changed daily. The vessels were covered up to their medium height with black covers in order to keep the larvae away from the surface. Preliminary attempts at rearing the larvae had shown that they are extremely positively phototactic and many of them were found dead, trapped with their prominent abdominal spine on the water surface.

The larvae were checked daily and survival and molting were recorded. Larvae molting during observation were recorded to the next stage.

The carapace (CL) and total length (TL) of the larvae were measured on animals from a mass culture in 22°C with excess of food. Measurements were made under a stereomicroscope with a calibrated eyepiece from the eye socket to the posterior edge of the carapace (CL) or to the edge of the telson (TL).

Results

In the cultures, two zoeal stages and a megalopa were observed. The two zoeas are free-swimming, positively phototactic larvae. The megalopa can both swim by its pleopods and burrow when sediment is provided (Thessalou-Legaki, unpublished data).

The larval development of *C. tyrrhena* can be characterized according to Gore (1985) as an advanced type with great morphological changes between the stages as shown in Table 1. All thoracic legs as well as long biramous pleopods are present in zoea II. These appendages are functional in the megalopa where the uropods also appear. The megalopa is similar to the adult except that the pleopods of the first two abdominal somites are missing (they are present only in adult females) and the first pereiopods do not show prominent heterochely. Full morphological description of the larvae of *C. tyrrhena* is in preparation.

In spite of the great morphological differences, size does not actually increase at molting to zoea II and even shows a tendency to decrease in the megalopa (Table 1).

In Fig. 1, survival of zoea I (successful molting to zoea II) and total zoeal survival (successful molting to megalopa) are shown. The 40% sea water prohibits larval development, since no zoea I molted to zoea II. In 60% sea water the maximum survival to zoea II was observed at 22°C, while in greater salinities nearly all larvae survived to zoea II at all temperatures.

Metamorphosis was observed at all temperatures in 100% sea water, while in 80% sea water and 14°C no larva completed its zoeal development, although the larvae had all successfully passed to zoea II. In 60% sea water only a small percentage (13.33%) of

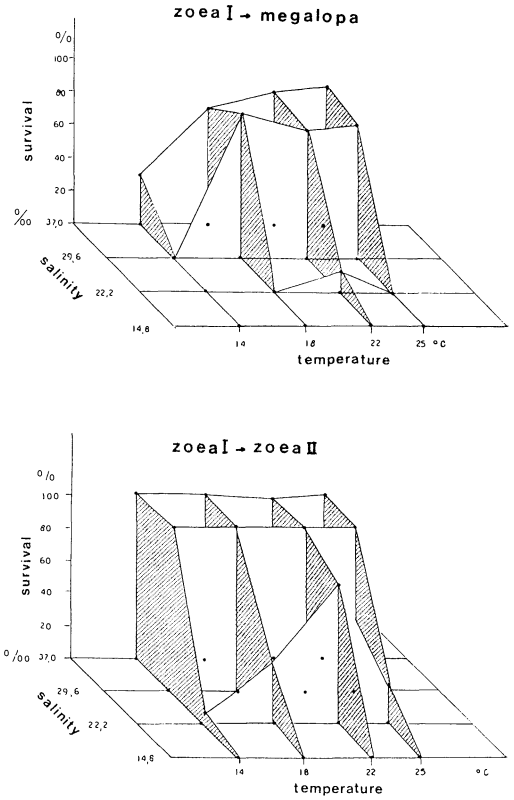

Fig. 1. Survival to metamorphosis and to zoea II of the larvae of *Callianassa tyrrhena* in 16 temperature–salinity combinations.

the larvae molted to megalopa at 22°C. Zoea II thus showed a more restricted range of temperature-salinity combinations for successful molting.

Two-way ANOVA results (Table 2) show that survival of zoea I depends both on salinity and temperature as well as on their interaction. The same is true for successful metamorphosis (Table 2). If we consider the contribution of each of these effects on larval survival, using as an approximation the ratio of their sum of squares to the total sum of squares (Young, 1980), then salinity seems to contribute most in the total variability both in the zoeal I survival and the successful metamorphosis (Table 2).

Summing up, metamorphosis of *C. tyrrhena* occurred in eight out of the 16 combinations. Low salinities and temperatures prohibit or do not favor larval development. Under approximate natural conditions metamorphosis is completed in a percentage equal to or greater than 70%.

Larval survival with time, not considering stages, is shown in Fig. 2. A prolongation is evident as salinity increases. Zoeae in 40% sea water cannot live more than four days at any temperature and those in 60% sea water not more than nine days.

Molting rate (number of molts per day) is shown in Fig. 3. Temperature affects molting rate in two ways. With increasing temperature both the time between the two subsequent molting peaks and the time range of each molting are shortened. Therefore, molts occur faster and more simultaneously. The mean duration of zoea I and the total zoeal duration were calculated from those individuals that had molted to zoea II or to megalopa, respectively (Fig. 4). The two-way ANOVA (Table 3) shows that both temperature and salinity, as well as their interaction, affect the duration of zoea I,

Table 2. Two-way ANOVA results (with arcsine transformation) of zoea I and total zoeal survival of *Callianassa tyrrhena* in 16 temperature–salinity combinations; % = contribution of each source to the total variation, *** = $P < 0.001$.

Source of variation	SS	DF	MS	*F*	%
Zoea I survival					
Temperature	1,707.375	3	569.125	14.346***	2.0
Salinity	72,685.375	3	24,228.458	610.737***	86.9
Temperature–salinity	6,092.542	9	676.949	17.064***	7.3
Error	3,173.067	80	39.671		
Total	83,658.958	95	880.621		
Total zoeal survival					
Temperature	8,093.531	3	2,697.844	24.622***	12.7
Salinity	38,078.615	3	12,692.872	115.844***	59.8
Temperature–salinity	8,686.094	9	965.122	8.808***	13.7
Error	8,765.500	80	109.569		
Total	63,623.740	95	669.724		

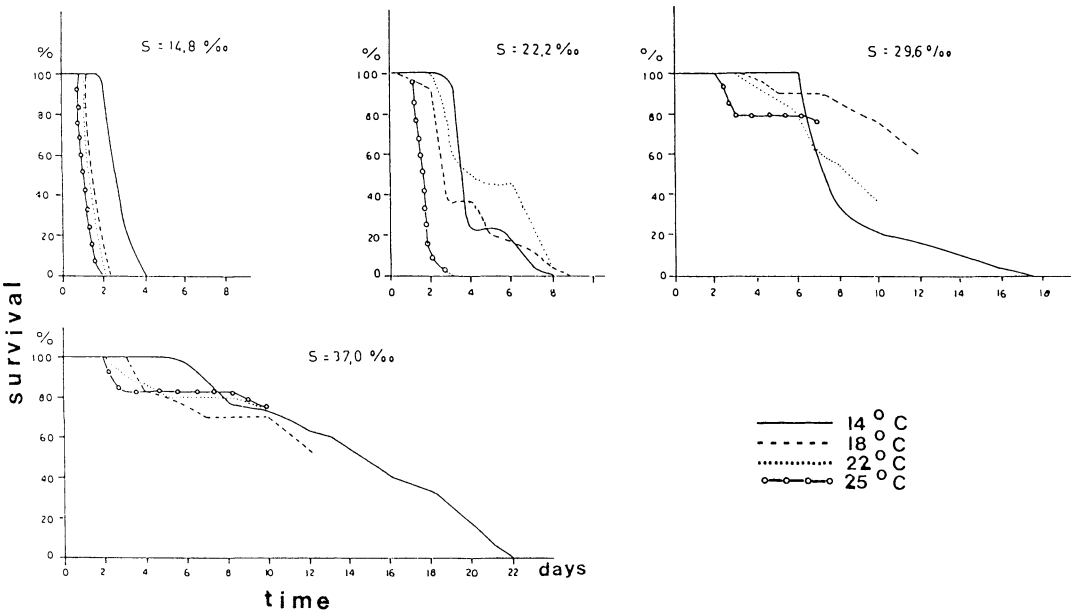

Fig. 2. Larval survival of *Callianassan tyrrhena* with time in 16 temperature–salinity combinations.

whereas in the total zoeal duration only the effect of temperature is significant (Table 3).

For 100% sea water the regression of total zoeal duration (TZD) upon temperature (Fig. 5) is:

$$\log TZD = 3.505 - 2.234 \log(T - 3.4)$$
$$r = -0.996.$$

The increase of temperature not only shortens drastically (slope = −2.234) larval duration, but also equalizes the participation of each stage in the total zoeal duration (Table 4). At low temperatures, zoea II lasts about 79% of the time to metamorphosis, while with increasing temperature its duration is greatly decreased, so that at 25°C

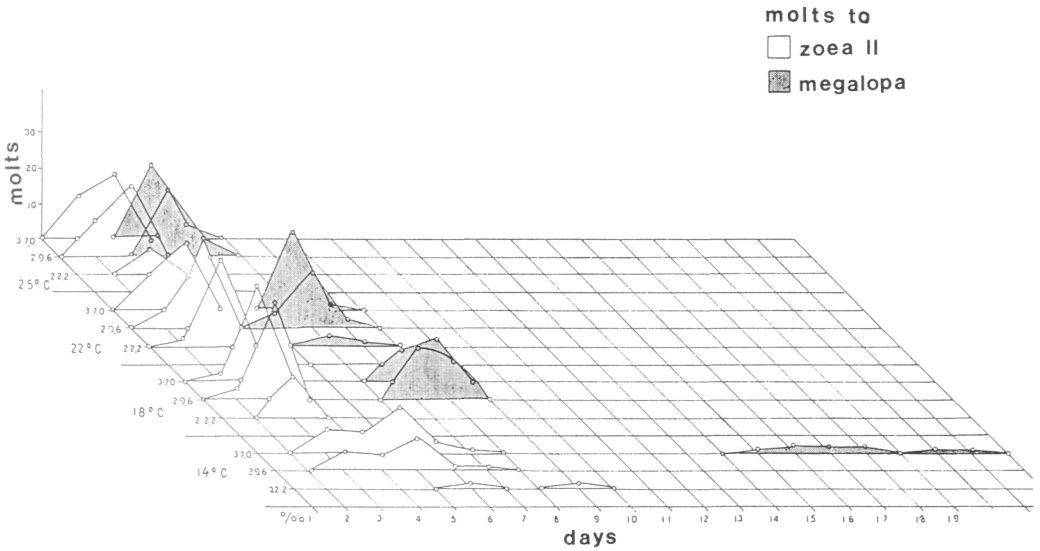

Fig. 3. Molting rate (number of molts per day) during zoeal development of *Callianassa tyrrhena* in 16 temperature–salinity combinations.

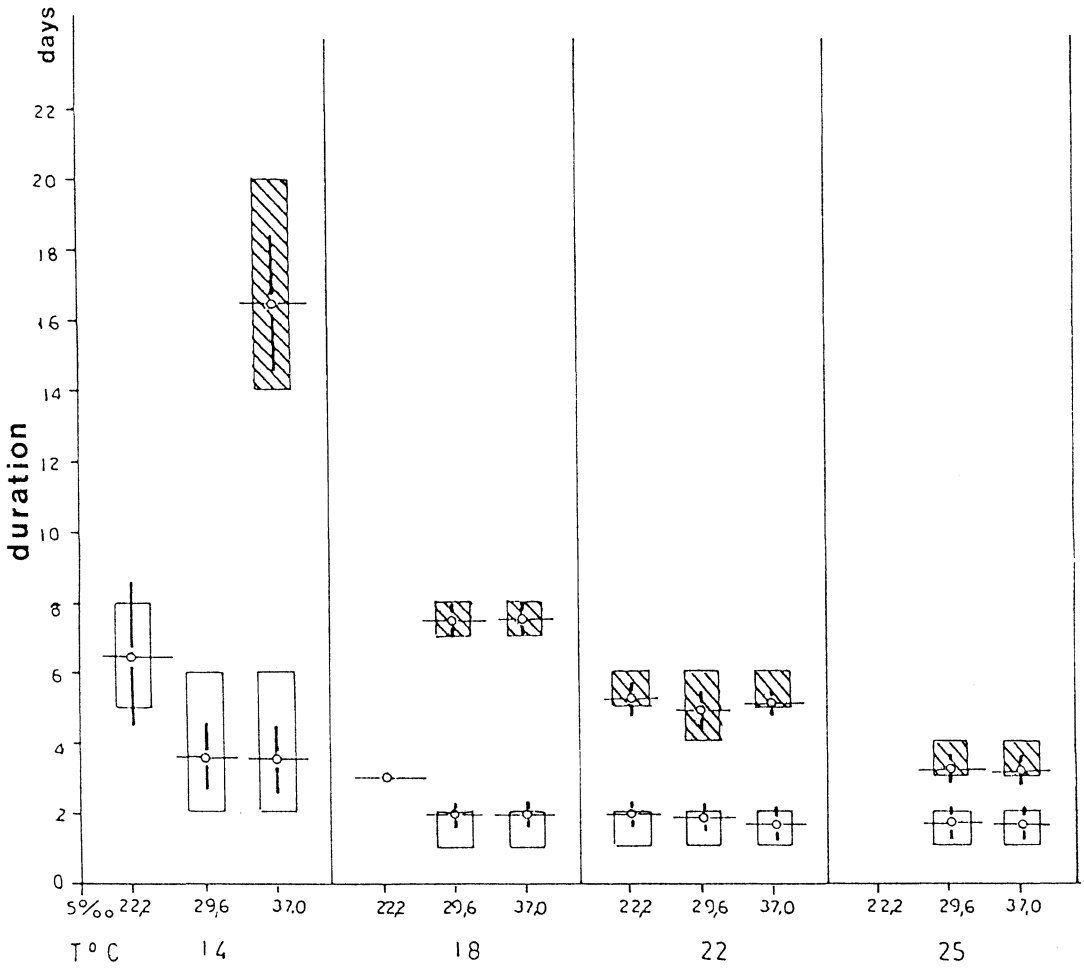

Fig. 4. Mean duration (in days) of zoea I and total zoeal development of *Callianassa tyrrhena*. -O- = mean values, vertical lines = ±SD, bars = range. Hatched bars = zoeae I and II, open bars = zoea I.

the two stages have equal contribution to the total zoeal duration.

Discussion

Two types of larval development of *Callianassa* Leach have been determined by Gurney (1937, 1938, 1942). *Callianassa tyrrhena* conforms, according to the present study, to Gurney's type II as having two zoeal stages with a broad, convex telson with many spines, while callianassids of type I develop through five zoeal stages and possess a telson with 7+1+7 spines. Nevertheless, not all of the published descriptions conform to the above types. Aste and Retamal (1983) describe the larval development of *C. garthi,* which bears a telson characteristic of type II although it has five zoeal stages. Sandifer (1973) reported that Biffar observed four stages in a species of *Callianassa* of type II. With our present knowledge of callianassid larval development, we can not conclude whether these cases are exceptional in the general scheme of Gurney or whether there is actually a continuous variation of larval development between these two extreme types.

Cano's (1891) description of three zoeal stages, instead of two of the present study, may be due to the origin of the material from the plankton. Although Thiriot (1974) and Bourdillon-Casanova (1960) reported larvae of *C. tyrrhena* from plankton material, they did not specify the stages. They may have been led to such an identification by the fact that *C. tyrrhena* was the name given to the only type II species of the region described until then.

Table 3. Two-way ANOVA results (with log(x + 1) transformation) of zoea I and total zoeal duration of *Callianassa tyrrhena* in temperature–salinity combinations where completion of zoea I and metamorphosis were observed. *** = $P < 0.001$. NS = not significant.

Source of variation	SS	DF	MS	*F*
Zoea I duration				
Temperature	2.432	3	0.811	138.958***
Salinity	0.220	2	0.110	18.840***
Temperature–salinity	0.116	6	0.019	3.322***
Error	1.593	273	0.006	
Total	4.178	284	0.015	
Total zoeal duration				
Temperature	4.065	3	1.355	1,207.579***
Salinity	0.002	2	0.001	0.742 NS
Temperature–salinity	0.002	2	0.001	0.705 NS
Error	0.166	148	0.001	
Total	4.311	155	0.028	

As far as we know, there are no published data on the combined effect of temperature and salinity on callianassid larval development. Forbes (1973) reported that the successful development of *C. kraussi* from the egg through to the postlarval stages requires salinities greater than 20‰.

Although there must be many other factors affecting larval survival (see Sastry, 1983), some conclusions may be made from the present study. Larval development of *C. tyrrhena* is most successful in salinities equal to or greater than 29‰ and in temperatures equal to or greater than 18°C. Although upper limits of these factors were not included in the present study, metamorphosis of *C. tyrrhena* seems to be favored in marine waters of the summer months of low latitudes. In South Euboikos bay summer temperatures are about 24°C and salinity about 37‰ (Siokou-Frangou *et al.*, 1984). At the collection site, temperatures up to 29°C have been observed in the midday hours of the summer months.

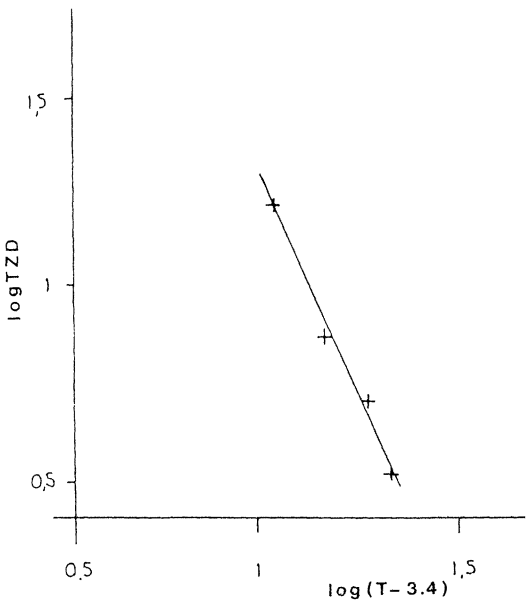

Fig. 5. Relation of the total zoeal duration of *Callianassa tyrrhena* with temperature (S = 37‰).

Although salinity seems to play the major role in the survival to metamorphosis, temperature has the sole effect on developmental rate. A shortening of the total zoeal development up to 3.2 days in 25°C, a temperature that larvae actually encounter in nature, is advantageous for a species living in the upper coastal zone or on sand flats, since the possibilities of recruitment of the megalopae to the parent population are increased. Although there are no data on larval dispersal and return to the parent habitat, I suggest that some kind of transportation to the waters of the South Euboikos bay and a return must take place. Tidal flushing of larvae and development in coast-

Table 4. Mean duration (in days) of zoeae I and II of *Callianassa tyrrhena* and their participation in total zoeal development (%). S = 37‰.

Temperature °C	Zoea I		Zoea II	
	Duration	%	Duration	%
14	3.5	21.1	13.1	78.9
18	1.9	25.0	5.7	75.0
22	1.7	33.0	3.4	66.7
25	1.6	50.0	1.6	50.0

al waters is documented for *Callianassa californiensis* Dana (Johnson and Gonor, 1982).

Larvae of Gurney's type II that are considered to belong to *C. tyrrhena* have been found in the summer months (from May to October) in western Mediterranean coastal plankton (Bourdillon-Casanova, 1960; Thiriot, 1974). The latter author also reported the presence of these larvae in the English Channel for a shorter period, from August to October. One may suggest, in combination with our results, that favorable temperatures for advanced larval development exist for a wider period in the Mediterranean than in the English Channel. In addition, we have to consider that the period of larval presence in the plankton of an area has to do with the reproductive and hatching period of a species rather than with the actual larval duration, unless hatching and larval moltings are more or less synchronous for all the individuals.

The fact that the duration of zoea I is affected by temperature, salinity, and their interaction, while total zoeal duration is affected only by temperature, is not surprising, since the low salinity of 60% dilution of 37‰ sea water, which is the main cause of retardation of the development of zoea I, does not allow most of the zoeae II to metamorphose. In higher salinities, zoeae II are very sensitive to temperature increase. In normal sea water (100%) the temperature increase shortens mainly the duration of zoea II and balances the contribution of the two stages in the total larval duration with a parallel increase of success in metamorphosis.

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