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Estimation of the reproductive output of the burrowing shrimp *Callianassa tyrrhena*: a comparison of three different biometrical approaches

Abstract Reproductive output, as the percentage of the mother weight devoted to egg production, was estimated for the burrowing shrimp *Callianassa tyrrhena* in wet, dry and ash-free dry weight. Three biometrical approaches were used. First, the relationship between the egg mass and the mother weight was determined. A second approach was to estimate the weight loss of the female caused by oviposition. Similar results were obtained from these methods for dry and ash-free dry weight (about 20 and 35%, respectively), but not for the wet weight estimation. The third approach, based on the weight loss of the ovary, did not reveal a constant value for reproductive output throughout the female size range, although it was found that the ovary loses a constant percentage of its weight during oviposition. This discrepancy is due to the fact that the ovary weight shows positive allometry to the weight of the female body. The comparison of the three methods offers insight into the biological events that are related to ovary maturation and oviposition. It is suggested that molting just before oviposition and its inhibition during the yolk accumulation in the ovary play dominant roles in the expression of the reproductive output in the different approaches used.

Introduction

Reproductive effort (RE) has been defined as the fraction of the total available energy which is used in reproduction (Tinkle and Hadley 1975; Clarke 1987). This includes energy for collecting extra food, for territorial or mating behaviour, and the energy for carrying and caring for a brood of eggs. Thus RE is difficult to measure in practice, and the term reproductive output (RO) has been introduced which approximates RE. RO is expressed as the biomass of the reproductive products per unit biomass of the female (Pianka 1972).

Decapod crustacean reproductive output is considered one of the most determinant factors of their life history pattern. Interspecific comparisons of reproductive output have provided much of the basis for theoretical considerations of life history tactics; insight into life strategies and the verification of theories have been based upon it (Clarke 1979, 1987; Hines 1982; King and Butler 1985).

On the other hand, intraspecific variations of the reproductive output have been considered as prominent decapod population characteristics. They have been used in defining stock units in species which support fisheries (Morizur et al. 1981), in detecting population variability in relation to habitat variations (Thessalou-Legaki 1992), and in studying the reproductive biology of the species (Somerton and Meyers 1983).

Many ways of measuring reproductive output have been proposed. Most of the studies use allometric regression equations which relate reproductive output to the body size. The brood is measured by weight (wet, dry and occasionally ash-free dry weight), volume or number of eggs. Other variables such as the egg size or the gonadosomatic index are often used. In some cases, the ratio of the mean values of the above variables over a size range of females is presented. Although the variables are well-determined and the comparisons well-documented in each paper, there is great uncertainty when comparisons of different components of the reproductive output are attempted.

In the present paper biometric relationships have been used in order to compare estimations of the reproductive output of *Callianassa tyrrhena*. These different approaches and expressions of weight (wet, dry and

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ash-free dry weight) provided insight into the underlying biological events which are related to the reproductive process. First, the relationship between the reproductive output and the size of the mother was determined. A second approach, not applied in decapods until now, was the determination of the reproductive output based on weight loss in the mother caused by oviposition. A serious constraint to the latter estimation is the fact that a large number of oocytes remain in the ovaries of *C. tyrrhena* after oviposition and are later absorbed (Thessalou-Legaki 1987). Thus, the third approach in the present paper was the estimation of reproductive output based on the loss of ovary weight due to oviposition.

The reproductive output of this burrowing shrimp was investigated as part of a comparative study of the reproductive strategies of the poorly known thalassinids. *Callianassa tyrrhena* lives in very shallow waters, from the intertidal to a few meters depth, forming dense populations on protected sand flats of the Mediterranean coasts (Ott et al. 1976; Thessalou-Legaki 1986; Dworschak 1992). The impact of *C. tyrrhena* on redox potential and nutrient cycling of the sediment has been documented by Ott et al. (1976). The advanced type of larval development of *C. tyrrhena* and the effect of salinity, temperature and food variations on the zoeal development have been described in Thessalou-Legaki (1990) and Thessalou-Legaki et al. (1993). The larval phase of the species consists of only two free-swimming zoeal stages and a megalopa which exhibits an ability both in swimming and burrowing in the sediment.

Materials and methods

Sampling site

Sand shrimps were collected from Vraona Bay situated in S. Euboikos Bay on the east coast of Greece. The bay is a sand flat not deeper than 30 cm, with a surface area of about 0.26 km². The outer part is sparsely covered by the phanerogam *Cymodocea nodosa* while in the inner part, where a small river intermittently flows, the more euryoecous seagrass *Zostera noltii* exists. Parts of the bay can be exposed during spring tides which have a range of 18 to 65 cm in S. Euboikos Bay.

Sampling and treatment of the material

The shrimps that were used in the present study were collected at the beginning of the reproductive period of 1985 (29 March, 3 May, 30 May and 14 June). A box corer similar to that described by Conan (1978) for the sampling of *Emerita analoga* was used. The corer was pushed into the sediment with a handle and closed underneath by a moving plate, providing an undisturbed sediment cube of 25 cm edge. Only newly berried females or females with gravid ovaries were taken into account. Just prior to oviposition the gravid ovaries are composed of three to four series of bright orange oocytes which can be seen through the transparent exoskeleton of the abdomen. Newly extruded eggs have the same colour, and the embryo is not yet visible under the stereomicroscope. The shrimps were placed individually in plastic vessels with sea water. In the laboratory the samples were frozen at −20 °C.

They were then thawed in groups and treated as follows: the eggs were removed from the pleopods and numbered. Using a stereomicroscope and a calibrated eyepiece the carapace length (CL) of the shrimps was measured to the nearest 0.01 mm, in the dorsal median line, from the eye socket (rostrum excluded) to the rear edge of the carapace. Shrimps and egg masses were then rinsed with distilled water. After absorption of excess water, they were weighed (WW) and dried in porcelain cups (60 °C, 24 h) for dry weight (DW). Ash-free dry weight (AFDW) was measured after combusting the samples at 550 °C for 3.5 h. All weights were measured with an accuracy of 0.1 mg. Wet weights were rounded to the nearest milligram. For the ovarian regressions, data from samples taken at the beginning of the 1983 reproductive period (March to May) were used. They were collected from the same locality using a hand-operated pump, kept for 1 d in 4% formaldehyde in sea water and then processed as above. After determining the wet weight of the female bodies, the ovaries were dissected and weighed. In ovigerous females the eggs were previously removed. Dry weight of ovaries was determined as above; to estimate dry weight of the whole female body, the CL–DW equations were used. In consideration of a possible loss of weight due to formaldehyde fixation, the data were not pooled with those of the other two methods. The comparison of the three methods is justified as each method was applied to similarly treated material and the final estimates of the reproductive output are expressed as ratios.

Statistical analysis

To study the biometric relations the allometric model ($Y = aX^b$) with the $\log_{10}$ transformation was used in order to meet or approach a normal distribution. Regressions were tested for isometry using a Student's *t*-test. Regression lines were compared using ANCOVA (Zar 1984). When lines proved to be parallel, a common slope, b_c, was computed. With b_c and the mean values of X and Y, new intercepts were estimated (a^*). The reproductive output, expressed as percent reduction of female weight after oviposition, is given by the formula:

$$\text{RO} = [1 - (a_o^*/a_{no}^*)] \times 100 \ ,$$

where RO is reproductive output, a_o^* and a_{no}^* are the intercepts of the CL–weight regressions of the ovigerous and nonovigerous females, respectively (Morizur et al. 1981; Somerton and Meyers 1983). For female body–ovary relationship a similar approach was used after the ANCOVA test showed that the regressions for the ovigerous and nonovigerous females were parallel (Zar 1984). Statistical treatment was carried out using the computer packages STATGRAPHICS and BIOM.

Results

Fecundity

The fecundity (number of eggs) per brood of *Callianassa tyrrhena* is significantly correlated to the CL and DW of the females (Table 1, Eqs. 1 and 2; Fig. 1). Nevertheless, the percentage of the variation explained by the equations is generally lower than that found in the majority of decapod species. This is especially true for the variation explained by the CL (55%), while the DW of the individuals explains a higher percentage (75%). The slopes of these regressions do not deviate from isometry, ($b = 3$ or 1) for female size expressed as CL and DW, respectively (Student's *t*-test, $P > 0.05$).

A mean brood size (number of eggs per female) is estimated at about 270, with a range from 56 to 1128 eggs.

Table 1 *Callianassa tyrrhena*. Summary of regression equations of the three methods used in the determination of the reproductive output. Regressions 1 to 11 are isometric, while 12 to 15 are positive allometric (Student's *t*-test) (*EN* egg number; *EM* egg mass; *B* body; *WW* wet weight; *DW* dry weight; *AFDW* ash-free dry weight; *CL* carapace length; *O* ovary; *r* correlation coefficient; *N* sample size) CL in mm, all weights in mg

Regression equation	r	N
Fecundity		
1. logEN = −0.148 + 2.856 logCL	0.758	59
2. logEN = 0.640 + 0.902 logB DW	0.817	58
Female body–egg mass weight relationships		
3. logEM WW = −0.398 + 0.861 logB WW	0.659	41
4. logEM WW = −0.523 + 0.905 logB DW	0.785	40
5. logEM AFDW = −0.283 + 0.881 logB AFDW	0.774	39
Female CL–weight relationships		
Nonovigerous		
6. logB WW = −0.069 + 3.111 logCL	0.963	25
7. logB DW = −0.904 + 3.290 logCL	0.970	25
8. logB AFDW = −1.158 + 3.327 logCL	0.925	25
Ovigerous		
9. logB WW = 0.100 + 2.896 logCL	0.974	60
10. logB DW = −1.034 + 3.346 logCL	0.968	59
11. logB AFDW = −1.063 + 3.063 logCL	0.927	59
Female body–ovary weight relationships		
Nonovigerous		
12. logO WW = −3.186 + 1.755 logB WW	0.737	58
13. logO DW = −2.824 + 1.755 logB DW	0.686	58
Ovigerous		
14. logO WW = −4.998 + 2.021 logB WW	9.621	45
15. logO DW = −3.321 + 1.604 logB DW	0.497	45

Reproductive output

Female body–egg mass weight relationship

The regressions of the egg mass versus female WW, DW and AFDW are given in Eqs. 3, 4 and 5 of Table 1 and in Fig. 2. Isometry is also shown in all these regressions (Student's *t*-test, $P > 0.05$), and correlation coefficients are statistically significant, although the variance is high. Isometry indicates that an estimation of the reproductive output as a consistent percentage of the female weight is feasible. With $b = 1$, new intercepts were estimated the antilogs of which represent the values of the brood weight when the female weight is equal to 1 mg ($\log 1 = 0$). Thus, the reproductive output estimated by the first method is 17.1, 19.6 and 33.1% of the WW, DW and AFDW of the females, respectively (Table 2).

Female CL–weight relationship

On this occasion weight loss of females was examined as an expression of reproductive output. As the samples were taken at the beginning of the reproductive season, we were able to use data from females just before and after oviposition. Thus, in this data set, a loss in female body weight could be attributed to egg laying. The CL–weight regression equations for nonovigerous females with gravid ovaries and for newly berried females are given in Eqs. 6 to 11 of Table 1.

There is a close correlation in all the length–weight relationships. The pairs of regressions (equations for nonovigerous and ovigerous shrimps) were compared for equality of slopes and elevations (ANCOVA). Wet weight regressions are identical (equal slopes and elevations). It seems therefore that we cannot measure a significant loss in female body WW due to oviposition (Fig. 3A). On the contrary, the pairs of the regressions for DW and AFDW are parallel (same slopes, different elevations), with the nonovigerous females heavier in both cases (Fig. 3B, C). For the two latter pairs of equations the common slopes were estimated.

A second approach in estimating the reproductive output in DW and AFDW was thus feasible; using the common slope, we calculated the new intercepts and finally the ratio of the weights of the females of the same CL. Ovigerous females proved to have 82.9 and 74.5% of the DW and the AFDW, respectively, of equal-sized nonovigerous females with gravid ovaries. This means that the corresponding weight loss due to oviposition was 17.1 and 25.5% of the female weight before oviposition. If this loss is expressed as a percentage of the

Fig. 1 *Callianassa tyrrhena*. Number of eggs per brood versus **A** carapace (*CL*) length and **B** dry weight (*DW*) of female body, plotted on logarithmic scales
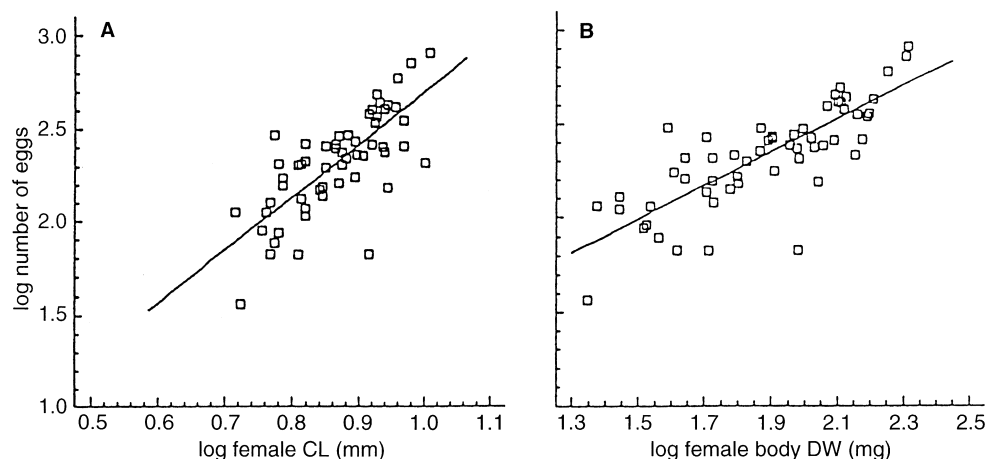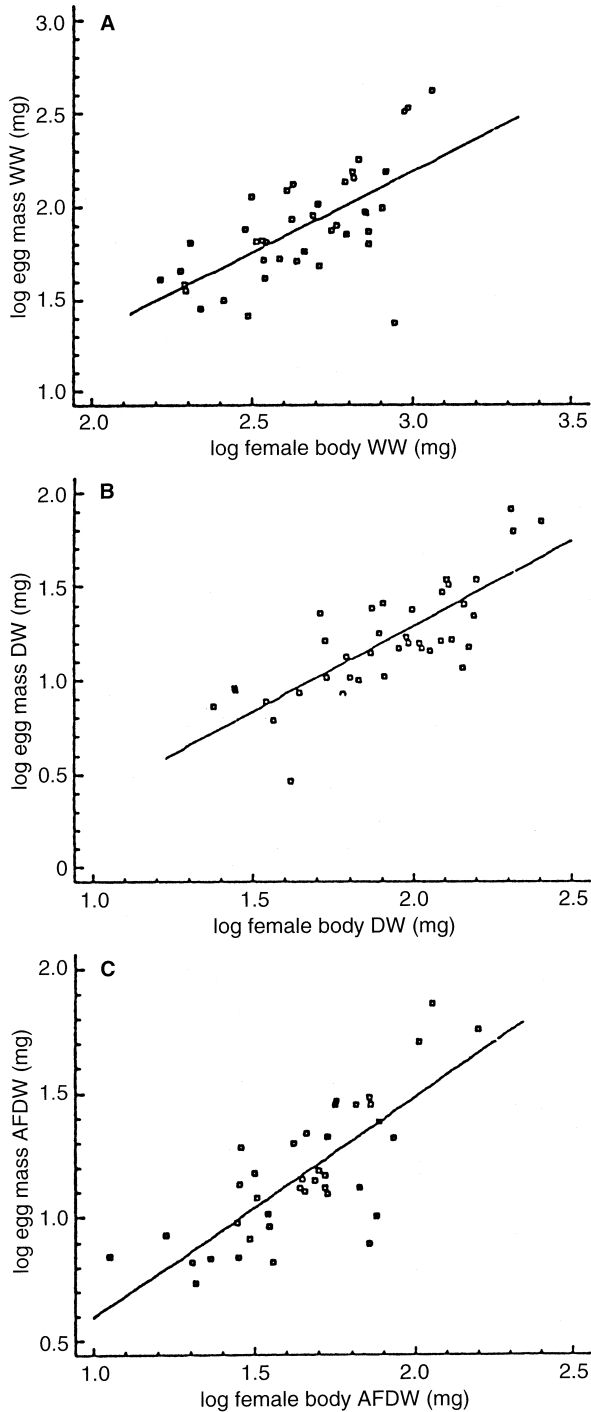
Fig. 2 *Callianassa tyrrhena*. Egg mass weight versus female body weight in **A** wet, **B** dry and **C** ash-free dry weight (*WW, DW* and *AFDW*, respectively), plotted on logarithmic scales

Table 2 *Callianassa tyrrhena*. Summary of estimations of the reproductive output as a percentage of body weight of the ovigerous female. Minimum and maximum values of the reproductive output in the method based on ovarian weight loss refer to individuals of 100 and 2000 mg for wet weight and 25 and 400 mg for dry weight (*WW* wet weight; *DW* dry weight; *AFDW* ash-free dry weight; – not tested)

Method	WW	DW	AFDW
Egg mass vs body weight	17.1	19.6	33.1
Female body weight loss	0	20.6	34.2
Ovarian weight loss (min.)	2.0	1.7	–
(max.)	22.9	14.6	–
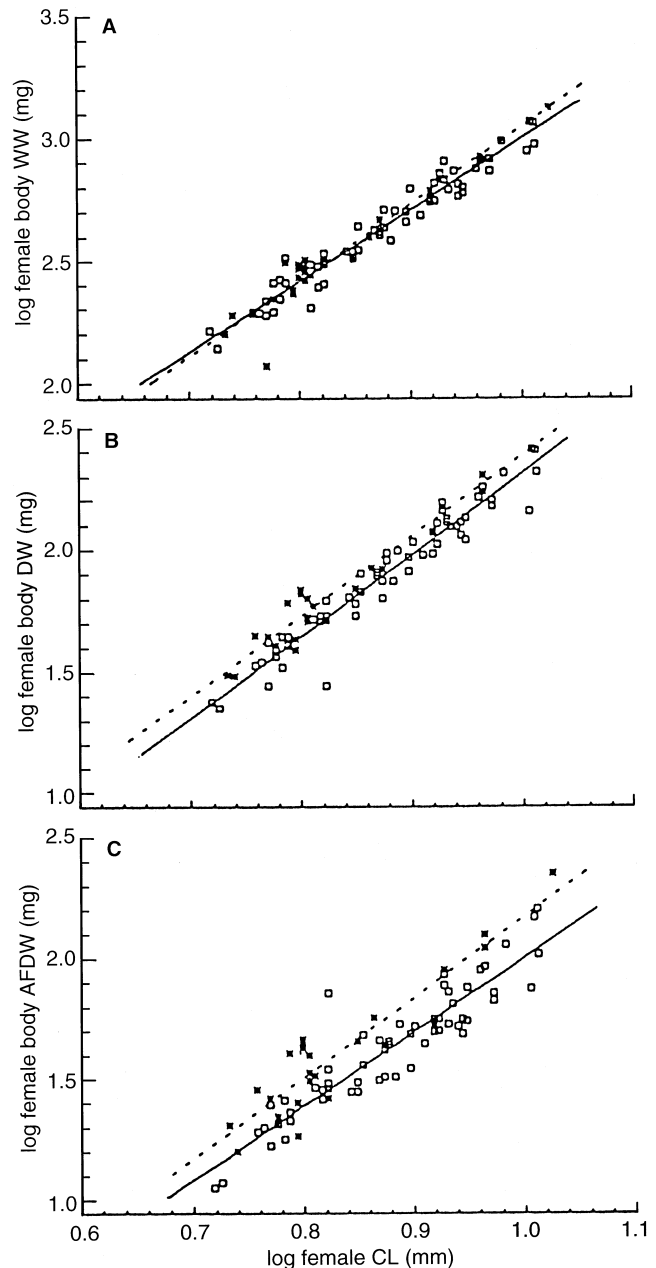
Fig. 3 *Callianassa tyrrhena*. Female length–weight relationships in **A** wet, **B** dry and **C** ash-free dry weight, plotted on logarithmic scales (*Asterisks* and *dashed lines* for nonovigerous; *squares* and *solid lines* for ovigerous females)

ovigerous female body, then a second estimation of the reproductive output is 20.6 and 34.2% for DW and AFDW, respectively (Table 2).

Female body–ovary weight relationship

Wet and dry ovarian weight regressed versus body weight of ovigerous and nonovigerous females (Table 1, Eqs. 12 to 15; Fig. 4) had the lowest correlation coefficient of all the biometrical relationships studied. No more than 54% of the variation in ovary weight can be explained by the variation in body WW. Another prominent feature of these size relationships is their positive allometry (Student's *t*-test, $P < 0.05$).

The results of the ANCOVA for the regressions of nonovigerous and ovigerous females showed that for both weight expressions, the pairs of regressions are parallel (same slopes, different elevations), with the ovaries of the nonovigerous females being heavier than those of the ovigerous females of the same weight (Fig. 4A, B). A constant percentage of the ovary that is extruded during oviposition is estimated as 91.9% of the WW and 85.1% of the DW of the ovary.

Because of the positive allometry exhibited in each of the above regressions, we cannot express the loss in ovary weight as a constant percentage of mother weight. Thus, no direct comparisons with the two previous methods can be made. Nevertheless, applying minimum and maximum values for WW and DW of the mother to Eqs. 12 and 13 (Table 1), and using the information on the percentage of ovary weight that leaves the body as eggs, we calculated a minimum and a maximum estimate of reproductive output (Table 2). The maximum value for the WW expression reaches the constant value of the first method, while the value of the DW expression is lower than that of both previous methods.

Discussion

The fecundity of *Callianassa tyrrhena* is determined by female body size and increases isometrically to size. About 55% of the variation of egg number is explained by the size of the individual. Different patterns in the relationship between fecundity and size of thalassinid species have appeared in the literature. In *Callianassa kraussi* fecundity increases with size up to 9 mm CL, while in larger females it decreases (Forbes 1977). In different populations of *Upogebia africana* there is a linear relationship between the number of eggs and CL on a logarithmic scale (Hill 1977; Hanekom and Erasmus 1989). Their correlation coefficients, from 0.66 to 0.77, are comparable to those of *C. tyrrhena* of the present study, whereas in *Upogebia pusilla* from different populations in the Adriatic Sea, the same values ranged from 0.47 to 0.77 (Dworschak 1988). Finally, in *Calocaris macandreae* no correlation was found; here the number of eggs ranges from 1 to 110 for comparable sized females, while a mean number of eggs per female has been estimated as low as 38 (Buchanan 1963).

No other studies on the above relationship in thalassinids are available. Nevertheless, there are some references which report on egg number per female: 4757 eggs for large females of *Upogebia deltaura* (16.6 to 18.9 mm CL) (Tunberg 1986), about 10 000 eggs in *Upogebia affinis* (Pearse 1945; Andryszak 1986); 8170 eggs in *Callianassa major* (Pohl 1946) and 660 to 1500 in *Callianassa filholi* (Devine 1966).

Compared to the above, the mean egg number per female in *Callianassa tyrrhena* (270 eggs) estimated in the present study is rather low. This can be related to the large egg size (mean maximum diameter of a mature egg is about 1.18 mm) (Thessalou-Legaki 1987). Although the data for the callianassids are very limited, the well-
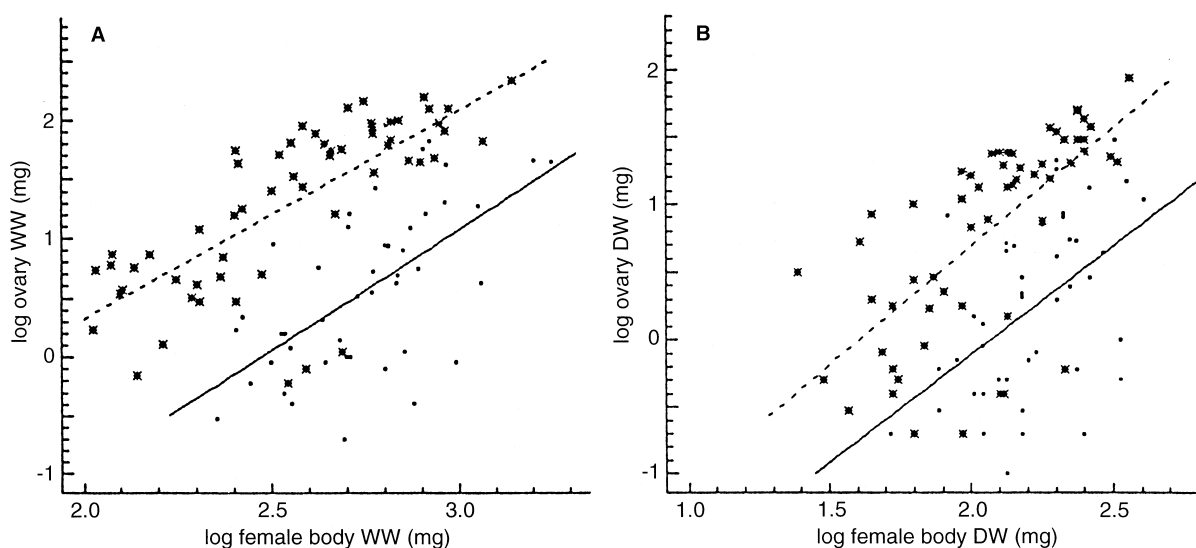

Fig. 4 *Callianassa tyrrhena.* Ovarian weight versus female body weight in **A** wet and **B** dry weight, plotted on logarithmic scales (*Asterisks and dashed lines* for nonovigerous; *squares and solid lines* for ovigerous females)

known inverse relationship between egg number and egg size (see Hines 1982; Anger 1995) seems to exist. The fecundity of *C. tyrrhena* is similar to that of *Callianassa kraussi* (122 eggs per female, 1.52 mm diameter, estimated from Forbes 1973), while in *Callianassa major* the eggs are much more numerous but smaller (0.88 mm) (Pohl 1946). Egg size determines the size and the developmental period of the larvae. Larger eggs produce larger larvae, which are more competitive in the plankton (Sastry 1983). A comprehensive study of literature data (Hines 1986; Anger 1995) showed that brachyuran species with direct or abbreviated development have large eggs. The larvae of *C. tyrrhena* show several characteristics of a shortened larval life: only a few days are needed for metamorphosis to megalopa, no significant size increment is exhibited between the two zoeal stages, and the hatched larvae can metamorphose using only their yolk reserves (Thessalou-Legaki 1990; Thessalou-Legaki et al. 1993). *Callianassa louisianensis* also produces large eggs and larvae with abbreviated planktonic development (two zoeae) (Felder et al. 1986), while in *C. kraussi* the planktonic phase seems to have been lost and the two zoeal stages molt in the burrows of the mother (Forbes 1973).

As already mentioned, the size of the female explains only a part of the fecundity of *Callianassa tyrrhena* and this is also true for other thalassind species. This weak relationship can be attributed to a variety of factors affecting the berried females. First, random losses of eggs can happen, even at the beginning of the incubation period, because of the burrowing mode of life. As these individuals continuously dig for food, they are in permanent contact with the burrow walls. Morphological characteristics can also contribute, as there are no protective pleura on the abdomen. In its natural habitat the fresh water palaemonid shrimp *Macrobrachium nobilii* loses more than 33% of the incubated eggs in the first 3 d after oviposition (Balasundaram and Pandian 1982; Kuris 1991). In the present study we consider the loss of eggs during the collection of the shrimps to be negligible because of the way of sampling. A second cause of variation in the observed fecundity of *C. tyrrhena* may be the fact that mature oocytes still remain in the ovaries after egg laying. Although there is a statistically significant percentage of the ovary left behind (as estimated by the weight loss of the ovary due to oviposition), there is variation in the amount which contributes to the total variation in fecundity. Kuris (1991), reviewing the causes of brood mortality in crustaceans, mentions that the retention of oocytes after oviposition is common in the decapods *Penaeus setiferus*, *Hemigrapsus oregonensis* and *Jasus novaehollandeae*. Third, there is a wide overlapping of female sizes in proximate year classes (Thessalou-Legaki 1987). Individuals reproducing for the first time could exhibit a reduced fecundity compared to equal-sized individuals which already reproduced once in the previous year. In the crab *Chionectes bairdi* the fecundity of the females reproducing for the second time is 30% higher than that of equally sized females re-

producing for the first time, because of the decreased yolk accumulation in prepubertal females (Somerton and Meyers 1983). In *C. tyrrhena* fecundity is better correlated to dry weight than to the carapace length of the individuals. We suggest that weight, especially that of the long abdomen, may represent more reliably the size of the individual. Unlike most decapods, the ovaries of callianassids are situated not in the cephalothorax but along the abdomen.

The first two methods used for the estimation of the reproductive output of *Callianassa tyrrhena* gave similar results in the dry and ash-free dry weight expressions. There is however an important discrepancy where wet weight is involved. There appears to be no weight loss of the body of the female after oviposition, though the egg mass represents a constant percentage of the body (17%). Events related to oviposition could contribute to the above difference. A molt just prior to oviposition, and the subsequent absorption of water by the female body, could replace the weight loss due to oviposition. Tunberg (1986) found a strong correlation between ecdysis and berrying in *Upogebia deltaura*, indicating that the eggs are extruded shortly after ecdysis. Furthermore, swelling of the newly laid eggs, due to water uptake, increases their wet weight. It can be suggested therefore that the above discrepancy between the two methods is actually an expression of complex events that take place around oviposition. Thus the females of *C. tyrrhena* exhibit a replacement of their weight lost by oviposition (as shown by the second method) in order to enable them to carry an important egg mass which accounts for as much as 17% of their weight (as indicated by the first method).

Compared to other decapods, *Callianassa tyrrhena* shows a similar reproductive output, expressed in WW, to that of the polar shrimp *Chorismus antarcticus* (17.1%, Clarke 1979), but smaller than that of *Ovalipes punctatus* (28.6%, Du Preez and McLachlan 1984). Concerning DW, a wealth of information exists on the Brachyura. Hines (1982, 1988, 1991, 1992) in a series of papers on the reproductive output of this group, reported that there is a variation among nonpinnotherid species from 3.2% in *Portunus spinicarpus* to as high as 23.0% in *Chaceon quinquedeus*, with a mean reproductive output of about 10%. In contrast, the two pinnotherid species *Pinnotheres ostreum* and *Fabia subquadrata* have exceptionally high values of reproductive output (66 and 97%, respectively).

Because the ovary weight is positively allometric to body weight, the method based on ovary weight losses could not estimate the relative reproductive output as a percentage of body dry weight. It provided, however, a range from 1.7 to 14.6%, depending on the size of the reproducing female. These relationships were established during the long period of ovary maturation which, according to our observations, lasts more than 5 mo. We suggest that this positive allometry of the ovary is related to morphological/anatomical characteristics of the species. As in other callianassids, the ovary lies along the

abdomen which has a very soft and transparent exoskeleton that can be easily stretched. Thus, during maturation, the ovary is able to increase in width with no need for molting. This suggestion is supported by the observation of Felder and Lovett (1989) on the elasticity of the abdomen of *Callianassa louisianensis*. It is interesting to note that Hines (1992) attributes the large reproductive output of the two pinnotherid crabs to similar anatomical features that favour ovary development: unlike other brachyurans, their ovaries extend out of the cephalothorax into the abdomen, and exoskeleton calcification is greatly reduced, thus allowing for distension of the body. One may consider this ability an advantage to larger females; i.e., as a result, molting can be postponed for longer periods which allows more production to be directed into reproduction.

The only reference to the gonadosomatic index of other thalassinids is that of Dworschak (1988) for *Upogebia pusilla*. Great variation exists in his estimations since the material comes from different sites and seasons, but maximum values as high as 82.3% could be explained on the basis of possible positive allometry, as in the case of *Callianassa tyrrhena*. It is evident that positive allometry, seasonal variation and oocyte retention in the ovaries have to be taken into account when comparisons with the brood weight method are made. Only females close to oviposition should be used in order to avoid underestimations of the RO if females with unripe ovaries are included. Female size range has to be reported in order to eliminate confusion when interspecific comparisons are made. In any case, the gonadosomatic index, the potential RO (Stechey and Somers 1995), of a species with the reproductive characteristics of *C. tyrrhena* is an overestimation of the actual RO (brood mass) because a considerable number of oocytes are retained in the ovary after oviposition.

Each one of the three methods of RO estimation for *Callianassa tyrrhena* reflects different events in the life history of the species. The relationship of ovary to body weight is the result of the long period of ovary maturation and the age of the individuals. Events just prior to and after the oviposition determine the loss of female weight due to oviposition and the relative weight of the egg mass. The biometrical relationships used in the present study demonstrated the complexity of the reproductive biology of a crustacean in relation to the molting process or its inhibition.

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