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Lipid dynamics during the embryonic development of *Plesionika martia martia* (Decapoda; Pandalidae), *Palaemon serratus* and *P. elegans* (Decapoda; Palaemonidae): relation to metabolic consumption

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ABSTRACT: The present study examines the changes in volume and lipid biochemistry during the embryonic development of 3 temperate caridean species—*Plesionika martia martia*, *Palaemon serratus* and *P. elegans*—with similar reproductive strategies but occupying different ecological niches. Egg volume, water content and lipid embryonic metabolism are analysed and discussed in relation to early life history and environmental conditions. An increase in egg volume and water content during embryogenesis was noted in all species, although it was larger in *P. serratus*. *P. serratus* also had the largest eggs, followed by *P. elegans* and *P. martia martia*. The quantitatively most important fatty acids (FA) in the eggs are the saturates (SFA) 14:0, 16:0 and 18:0, the monounsaturates (MUFA) 16:1(n-7), 18:1(n-9) and 18:1(n-7), and the polyunsaturates (PUFA) 18:2(n-6), 18:3(n-3), 20:4(n-6), 20:5(n-3) (eicosapentaenoic acid, EPA) and 22:6(n-3) (docosahexaenoic acid, DHA). Looking at the predominant FA, there appears to be a higher similarity between *P. martia martia* and *P. serratus.* The eggs of these species present similar levels of SFA, highly unsaturated (HUFA) and (n-3) FA but *P. martia martia* eggs have an extremely elevated MUFA and a low PUFA content. *P. elegans* has high levels of SFA, PUFA, HUFA and (n-3) FA. *P. serratus* and particularly *P. martia martia* eggs are characterised by a higher DHA:EPA ratio than *P. elegans*. The similarity between the FA profile of *P. martia martia* and *P. serratus* eggs may suggest that these 2 species are exposed to more comparable environmental conditions than *P. elegans*. As for the utilisation of FA classes during embryonic development, all species showed the same trend—MUFA were found to be the major energetic fuel during embryonic development while SFA and HUFA seemed to be conserved. A steady decrease in total lipids, particularly tri- (TAG) and diacylglycerol (DAG), and FA contents was noted in the 3 species. The utilisation of these lipid classes during the incubation period was comparatively low in *P. martia martia* and *P. elegans* in relation to *P. serratus* eggs. This may suggest a higher dependence of the newly hatched larvae of *P. martia martia* and *P. elegans* on their lipid reserves and has been interpreted as an adaptation to the early life history of these species, during which there might be a reduced availability of food.

KEY WORDS: Lipids · Fatty acid composition · Eggs · Caridea · Early life history · Environmental conditions

INTRODUCTION

Lipids are considered the most important source of metabolic energy in decapod and other crustacean eggs. In marine demersal eggs of crustaceans and molluscs, 60 to 88% of the energy is drawn from fat oxidation during embryonic development (Pandian 1970a,b). The lipid content of decapod eggs may vary

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from 3.2 to 20.2% of the wet weight and considerable changes in these values occur during development. The fact that the amount of lipid reserves transferred from the female to the eggs may exceed 60% of that remaining in the female's body indicates that the lipid metabolism of the female is geared to the provision of egg lipid (Herring 1973).

Given that they are the main source of metabolic energy throughout embryonic development, the amount of lipids in the egg generally correlates with the size of the egg and with the time interval between spawning and hatching or larval first feeding (Herring 1973, Rainuzzo et al. 1997). In species with an abbreviated larval development, large energy reserves need to be provided for the developing embryo (Herring 1974). Phospholipids (PL) are of vital importance in maintaining the structural and physiological integrity of cellular membranes and, in crustaceans, glycerophospholipids are also crucial for the transport of substances via the hemolymph (Chapelle 1986).

The patterns of utilisation of specific lipid classes and fatty acids (FA) may be species-dependent and may reflect particular nutritional or environmental requirements. Relationships have been found between the ecology of the species and their lipid profile, with the egg FA profile reflecting the adult's diet and colder and/or deeper water species showing a higher degree of unsaturation in their FA profile (Narciso 1999). The crustaceans consist of a wide range of species adapted to a great variety of environmental conditions and there is evidence of adaptative mechanisms to changing environmental conditions in the metabolism of PL. It has long been recognised that the (n-3) requirements of marine animals represent one of the adaptation mechanisms to changes in environmental factors, particularly temperature, and to a much lower degree, salinity. The requirement for high levels of polyunsaturated fatty acids (PUFA) from the (n-3) series, particularly 20:5(n-3) (EPA; eicosapentaenoic acid) and 22:6(n-3) (DHA; docosahexaenoic acid) is explained by the fact that the (n-3) polyunsaturated structure permits greater flexibility of membranes and maintenance of the required physical properties at lower temperatures (Chapelle 1986).

Until now, few studies have examined the lipid composition of crustacean eggs (e.g. Dawson & Barnes 1966, Pandian 1970a, Achitiv & Barnes 1976, Amsler & George 1984, Biesiot & Perry 1995) and even fewer have looked at the FA depletion during embryonic development (Clarke et al. 1990, Kattner et al. 1994, Wehrtmann & Graeve 1998, Wehrtmann & Kattner 1998, Nates & McKenney 2000, Narciso & Morais 2001). A lot of research has been conducted to determine the essential FA requirements of crustacean species with aquaculture potential; a great deal of this research has focused on the quantitative and qualitative lipid requirements of commercially important species and relatively few studies have examined other crustacean species (D'Abramo & Sheen 1993, Fox et al. 1994).

The present study examines changes in the egg lipid composition and FA profile of 3 temperate caridean species—*Plesionika martia martia*, *Palaemon serratus* and *Palaemon elegans*. These species were chosen because they occupy different ecological niches, although they have a similar reproductive strategy. The effect of the environmental conditions and early life history in the lipid embryonic metabolism of these species is analysed.

Plesionika martia martia A. Milne-Edwards, 1883 (Decapoda; Caridea; Pandalidae) is an epibenthic species, occurring between a depth of 190 and 1214 m, being however more abundant between 200 and 700 m. It may have a total length of up to 17 cm (Lagardère 1971). In the western Mediterranean, pandalid shrimps are active predators of macroplankton species and the diet of *P. martia martia* consists mainly of benthopelagic eucarid crustaceans (Cartes 1993). Ovigerous females are found between March and November, and present blue coloured eggs (Lagardère 1971, Calado & Narciso 2002). It has a long larval development, presenting 11 zoeal stages (Kurian 1956, Barnich 1996).

Palaemon serratus (Pennant, 1777) (Decapoda; Caridea; Palaemonidae) is present in the infralitoral zone, in rocky substrates with algae and *Zostera* or in dark caves, up to a depth of 40 m (Udekem d'Acoz 1999). It has a total length of 7.5 to 11 cm. *P. serratus* is an omnivorous species, feeding mainly on algae (*Laminaria* and Rhodophyceae) and small crustaceans, and also on a minor proportion of small molluscs and polychaetes (Lagardère 1971). Egg-bearing females may be generally found all-year round (Lagardère 1971, Calado & Narciso 2002).

Palaemon elegans Rathke, 1837 (Decapoda; Caridea; Palaemonidae) is found in the intertidal zone, in sea grass beds or in rocky tidal pools, in the medium-litoral or even supra-litoral zone, occurring up to a depth of 5 m. It is typically a marine species that can tolerate slightly brackish waters, although some populations have been found living in waters with a very low salinity, tolerating salinities lower than 16 ppm (Udekem d'Acoz 1999). It has a total length of 3 to 6.5 cm. In the summer, *P. elegans* feeds mostly on filamentous algae and in the autumn they also start feeding on small crustaceans, particularly cyprids and *Balanus* sp. nauplii. Ovigerous females can be found from February to September (Lagardère 1971, Calado & Narciso 2002). Even though *P. serratus* and *P. elegans* may present 7 to 9 zoeal stages, depending on temperature and salinity conditions, 9 larval stages have been recorded

in the Portuguese coast (Fincham & Williamson 1978, Fincham 1983, dos Santos 1999).

MATERIALS AND METHODS

Egg-bearing females of *Plesionika martia martia* and *Palaemon serratus* were collected from February to June 2001 after being landed in Cascais, Portugal, by commercial fishing vessels. *Palaemon elegans* ovigerous females were captured with dip-nets in the intertidal zone of Cape Raso, Cascais, Portugal. The egg mass was removed from the females and eggs were classified according to the following criteria (modified from Kattner et al. 1994): (1) Stage 1—uniform yolk and no embryonic development visible; (2) Stage 2—eyes clearly visible with 1/2 yolk consumed; and (3) Stage 3—almost no yolk present and embryo fully developed.

Thirty eggs were separated from each female (9 females per species, 3 per each embryonic stage) and length (L) and width (W) were measured (Table 1) under a stereo microscope (Olympus®, Model SZ6045TR) with a calibrated micrometer eyepiece. The total length of each ovigerous female was measured with callipers rounded to the nearest 0.05 mm; the average female size for all embryonic stages was 82, 76 and 42 mm for *Plesionika martia martia*, *Palaemon serratus* and *Palaemon elegans*, respectively.

Egg volume (V) was calculated using the formula for oblate spheroids $V = {}^1/_6(\pi W^2 L)$ (Turner & Lawrence 1979). To determine significant differences between the egg volume of the 3 species at different embryonic stages, a 2-way analysis of variance (MANOVA) was conducted, after the assumptions had been checked. Whenever significance was accepted at $p < 0.05$, the Tukey multiple comparison test was used (Zar 1996).

Egg samples from each species and embryonic stage of development were stored in liquid nitrogen for later lipid analysis. Given the small size of each egg batch, batches of eggs at the same stage of development were pooled for biochemical analysis. Water content was determined in duplicate by measuring the dry weight of the egg samples in a high precision Sartorius Supermicro® balance (±0.2 µg), after freeze-drying in a Savant VP100®, and by relating it to the wet weight of the samples.

Total lipids were extracted using the Bligh & Dyer (1959) method, with samples being ground in a Potter homogeniser with chloroform:methanol:water (2:2:1.8). Lipid classes were resolved by thin layer chromatography (TLC) in plates coated with 0.25 mm silica gel G (Merck) and developed with hexane:diethylether:acetic acid (65:35:1). The developed plates were sprayed with 10% phosphomolybdic acid in ethanol. Lipid class identification was made by comparison with standards (Sigma). Quantification was performed using a scanner and the software Quantity One (Version 2.4) from PDI. For the FA analysis, the lipid extracts were saponified and esterified according to Metcalfe & Schmitz (1961) and the fatty acid methyl esters (FAME) were injected into a capillary column OmegaWax 320 WCOT (30 m fused silica, 0.32 internal diameter) installed in a Varian Star 3400CX gas-liquid chromatograph (GLC). Helium was used as carrier gas, at a flow rate of 1 ml min^{-1}; oven temperature was 180°C for 7 min and then 200°C (with a temperature gradient of 4°C min^{-1}) over a period of 71 min. Both the split injector Varian 8200 CX (100:1) and the FID detector were set at 250°C. GLC data acquisition and handling was done through a Varian integrator 4290 connected to the GLC. Peak quantification was carried out with a Star Chromatography workstation installed in an IBM PS/1. Peak identification was carried out

Table 1. *Plesionika martia martia*, *Palaemon serratus* and *Palaemon elegans.* Size of eggs (length and width in mm), total lipid (% dry weight) and lipid class composition (% of total lipids) at different stages of embryonic development. Values are means ± SD (n = 90 for egg size and n = 3 for lipid analysis). TAG: triacylglycerol, PL: phospholipids, DAG: diacylglycerol, MAG: monoacylglycerol, FFA: free fatty acids, FC: free cholesterol, CE: cholesterol ester

	Plesionika martia martia			*Palaemon serratus*			*Palaemon elegans*		
	1	2	3	1	2	3	1	2	3
Egg length	0.58±0.03	0.65±0.03	0.77±0.04	0.66±0.02	0.86±0.03	1.15±0.07	0.66±0.03	0.76±0.02	0.87±0.03
Egg width	0.43±0.03	0.48±0.02	0.55±0.04	0.56±0.02	0.63±0.02	0.71±0.05	0.52±0.02	0.57±0.01	0.60±0.02
Total lipid	17.5±0.9	13.4±1.1	7.2±1.3	17.7±0.7	14.8±1.6	4.1±1.2	19.5±1.8	15.2±2.3	8.1±0.8
TAG	46.7±6.9	39.4±6.5	3.9±1.6	50.0±5.8	39.7±8.0	2.4±0.8	42.0±6.8	51.3±7.6	6.8±3.4
PL	16.5±2.6	16.2±5.1	10.9±2.7	7.8±0.8	10.0±2.9	15.8±5.3	6.2±1.0	7.0±0.7	9.4±1.8
DAG	6.3±1.7	6.4±2.2	2.5±1.1	5.1±0.3	7.4±1.6	1.6±0.7	6.5±0.4	5.6±1.1	1.1±0.5
MAG	2.7±2.2	3.2±2.9	2.3±0.3	2.0±0.5	1.9±0.9	3.4±1.3	2.1±0.9	1.6±0.1	1.3±0.4
FFA	8.9±3.0	11.7±0.8	37.7±8.3	20.7±2.3	16.4±7.9	48.9±5.3	29.7±4.1	20.9±9.1	55.4±6.7
FC	8.7±2.2	10.7±3.0	10.8±3.2	5.8±0.3	10.7±2.7	9.3±1.2	5.3±0.8	6.9±2.7	9.6±2.0
CE	10.2±1.5	12.5±1.6	31.9±0.7	8.7±5.6	9.5±1.8	18.6±5.7	8.3±1.6	6.8±0.9	16.5±3.4

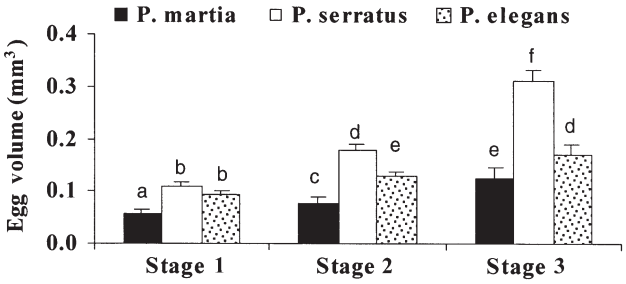

Fig. 1. *Plesionika martia martia*, *Palaemon serratus* and *Palaemon elegans.* Volume (mm^3) of eggs at different stages of embryonic development (n = 90 for each species). Different letters represent statistically significant differences ($p < 0.0001$)

using as reference well-characterised cod liver oil chromatograms. Triplicate samples were analysed.

RESULTS

The changes in egg volume with developmental stage can be seen in Fig. 1. The results showed a significant increase in egg volume during embryonic development in the 3 analysed species ($p < 0.0001$). Significant differences were also found between the 3 species in each embryonic stage ($p < 0.0001$), with the exception of the 2 *Palaemon* species in Stage 1 ($p \geq 0.05$). At the start of embryonic development, *Palaemon serratus* had the largest eggs (0.11 ± 0.009 mm^3), followed by *Palaemon elegans* (0.09 ± 0.007 mm^3), while *Plesionika martia martia* presented the eggs with the smallest volume (0.06 ± 0.008 mm^3). During embryogenesis, there was a much greater volume increment in *P. serratus* eggs (188%) than in *P. elegans* or *P. martia martia* (79 and 121%, respectively). Hence, just before hatching, *P. serratus* eggs had a significantly higher volume (0.31 ± 0.05 mm^3), followed by *P. elegans* (0.17 ± 0.01 mm^3) and *P. martia martia* (0.12 ± 0.02 mm^3).

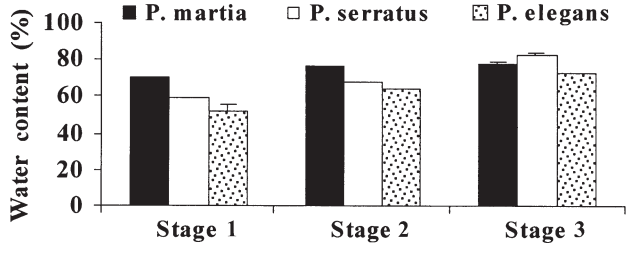

Fig. 2. *Plesionika martia martia*, *Palaemon serratus* and *Palaemon elegans.* Water content (% of wet weight) of eggs at different stages of embryonic development. Values are means ± SD (for each embryonic stage per species n = 2)

A progressive increase in the water content of the eggs was observed during embryonic development (Fig. 2). From the start of embryonic development to close to hatching, there was an increment from 70.2 ± 0.3 to 77.2 ± 1.5% in *Plesionika martia martia*, 59 ± 0.1 to 83.1 ± 0.3% in *Palaemon serratus* and 52.2 ± 3.9 to 72.9 ± 0.1% in *Palaemon elegans* eggs.

The lipid content of *Plesionika martia martia*, *Palaemon serratus* and *Palaemon elegans* eggs decreased considerably during embryonic development (Table 1), mainly between Stages 2 and 3. However, a higher lipid consumption was obtained in *P. serratus* (76.3%) in comparison to the other species (*P. martia martia*, 58.8%; *P. elegans*, 58.4%). The major lipid class in the early developmental stages of the 3 species analysed was triacylglycerol (TAG) (46.7, 50.0 and 42.0% in *P. martia martia*, *P. serratus* and *P. elegans*, respectively). The second most abundant classes were PL in *P. martia martia* (16.5%) and free fatty acids (FFA) in *P. serratus* and *P. elegans* (20.7 and 29.7%, respectively). A substantial decrease in the TAG and diacylglycerol (DAG) percentage was observed during development in the 3 species and it was also more pronounced from Stage 2 to 3. Concomitantly, an increase in the relative proportion of FFA and cholesterol esters (CE) was verified. Monoacylglycerols (MAG) presented an indistinct trend of variation during the development of the 3 species. Contrary to the PL percentages in *P. serratus* and *P. elegans* eggs, a decrease in the polar lipids was observed during embryonic development in *P. martia martia*.

The FA analysis of *Plesionika martia martia*, *Palaemon serratus* and *Palaemon elegans* eggs (Table 2) revealed that the quantitatively most important FA are the saturates (SFA) 14:0, 16:0, 17:0 and 18:0, the monounsaturates (MUFA) 16:1(n-7), 18:1(n-9) and 18:1(n-7) and the PUFA 18:2(n-6), 18:3(n-3), 20:4(n-6) (ARA; arachidonic acid), 20:5(n-3) (EPA) and 22:6(n-3) (DHA). In spite of the similarity in terms of the most important FA in the different species, there are slight differences in the ordering of these FA by decreasing magnitude. Thus, in *P. martia martia* eggs, the most important fatty acids are 18:1(n-9), followed by 16:0, DHA, EPA and 16:1(n-7). *P. serratus* eggs are characterised by high levels of 18:1(n-9), followed by 16:0, 18:2(n-6), EPA, DHA and 16:1(n-7). As for the *P. elegans* eggs, the qualitatively most important FA are, by decreasing order of magnitude, EPA, 16:0, 18:1(n-9), 16:1(n-7), 18:1(n-7) and DHA. Furthermore, some FA appear in relatively high amounts in some species and not in others; this is the case of 20:1(n-9) in *P. martia martia* eggs, 18:2(n-6) and 20:2(n-6) in *P. serratus* eggs, and 22:5(n-3) in *P. elegans* eggs.

Looking at the egg composition in terms of the total FA classes, some interesting results were obtained.

Table 2. *Plesionika martia martia*, *Palaemon serratus* and *Palaemon elegans.* Fatty acid composition (µg mg^{-1} DW) of eggs at different stages of embryonic development. Values are means of triplicate samples ± SD. MUFA: monounsaturated fatty acids, PUFA: polyunsaturated fatty acids, HUFA: highly unsaturated fatty acids, DHA: docosahexaenoic acid, EPA: eicosa-pentaenoic acid, FAME: fatty acid methyl esters

Fatty acid	*Plesionika martia martia*			*Palaemon serratus*			*Palaemon elegans*		
	1	2	3	1	2	3	1	2	3
14:0	3.9±0.0	3.8±0.1	3.5±0.3	2.6±0.3	3.2±0.1	1.2±0.1	5.7±0.2	5.5±1.6	4.4±0.3
15:0	1.3±0.0	1.0±0.0	0.7±0.0	1.3±0.1	1.3±0.1	0.5±0.0	0.9±0.1	1.0±0.2	0.8±0.0
16:0	29.6±0.3	25.6±0.5	24.7±1.3	26.6±0.1	26.8±0.8	12.4±0.2	30.6±2.2	29.3±0.4	22.7±2.9
17:0	2.4±0.1	2.3±0.1	1.7±0.1	3.2±0.0	2.5±0.3	1.1±0.1	2.6±0.2	3.0±0.6	1.8±0.0
18:0	6.0±0.1	5.7±0.1	5.8±0.2	9.2±0.3	7.7±0.3	4.3±0.2	10.9±0.0	10.2±0.4	7.5±0.7
20:0	0.5±0.1	0.5±0.1	0.5±0.1	0.4±0.0	0.4±0.1	0.4±0.2	0.5±0.1	0.6±0.0	0.4±0.0
22:0	0.3±0.0	0.2±0.0	0.4±0.1	0.4±0.0	0.4±0.0	1.5±2.1	0.3±0.0	0.4±0.0	0.4±0.0
∑ Saturated	44.0±0.4	39.1±0.6	37.3±2.1	43.7±0.0	42.4±1.0	21.6±2.0	51.7±2.5	50.1±0.1	38.0±3.9
Iso 15:0	0.3±0.0	0.3±0.1	0.2±0.0	0.5±0.1	0.7±0.1	0.3±0.1	0.2±0.1	0.2±0.1	0.1±0.0
Iso 16:0	0.3±0.0	0.3±0.0	0.4±0.1	0.4±0.0	0.4±0.0	0.2±0.0	0.2±0.0	0.3±0.0	0.2±0.0
Iso 17:0	0.9±0.0	0.8±0.0	0.5±0.0	1.7±0.1	1.5±0.1	0.5±0.0	1.0±0.2	1.0±0.1	0.7±0.0
Anteiso 17:0	0.3±0.0	0.3±0.0	0.1±0.0	1.0±0.1	1.0±0.0	0.4±0.1	0.3±0.1	0.4±0.0	0.3±0.1
∑ Branched	1.9±0.0	1.7±0.0	1.2±0.1	3.8±0.3	3.6±0.1	1.4±0.1	1.8±0.5	2.0±0.3	1.3±0.1
16:1(n-7)	17.8±0.4	15.4±0.4	12.2±0.9	12.0±0.5	12.2±0.4	3.7±0.1	19.4±1.3	15.3±3.7	12.3±1.1
18:1(n-9)	45.1±0.5	35.1±0.8	32.4±1.9	43.3±0.9	49.5±1.6	13.0±0.6	20.0±3.4	18.4±2.0	13.0±0.9
18:1(n-7)	10.8±0.4	10.9±0.1	8.5±0.4	9.0±1.0	8.8±0.3	4.5±0.1	15.5±0.2	13.9±1.8	11.7±1.5
18:1(n-5)	0.3±0.0	0.4±0.0	0.2±0.0	0.3±0.0	0.3±0.0	0.0±0.0	0.3±0.0	0.3±0.0	0.2±0.0
20:1(n-9)	3.4±0.1	3.3±0.1	3.0±0.2	1.1±0.0	1.1±0.0	0.2±0.2	0.7±0.2	1.2±0.5	0.5±0.1
20:1(n-7)	0.6±0.1	0.9±0.1	0.3±0.0	0.6±0.1	0.6±0.0	0.0±0.0	1.1±0.3	1.0±0.3	0.7±0.1
20:1(n-5)	0.1±0.0	0.6±0.4	0.0±0.0	0.4±0.3	0.2±0.0	0.0±0.0	0.2±0.0	0.2±0.0	0.1±0.0
22:1(n-11)	1.0±0.0	0.4±0.0	1.4±0.1	0.2±0.0	0.1±0.0	0.0±0.0	0.1±0.0	0.1±0.0	0.1±0.0
22:1(n-9)	0.4±0.0	0.4±0.0	0.4±0.0	0.1±0.0	0.1±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
24:1(n-9)	0.4±0.0	0.4±0.0	0.3±0.0	0.1±0.0	0.1±0.0	0.0±0.0	0.1±0.0	0.1±0.0	0.0±0.0
∑ MUFA	80.7±1.3	68.4±0.4	59.2±3.6	67.6±1.2	73.1±2.4	21.4±1.0	57.9±4.8	50.4±2.8	38.8±3.6
16:2(n-4)	1.1±0.0	0.9±0.0	0.8±0.0	1.8±0.0	1.5±0.1	0.9±0.1	2.6±0.1	2.3±0.4	1.8±0.3
18:2(n-6)	4.9±0.1	2.5±0.1	2.9±0.3	26.9±2.6	25.3±0.9	10.0±0.5	6.1±2.0	6.6±2.6	4.4±0.8
18:3(n-3)	2.3±0.1	1.5±0.2	1.0±0.1	2.8±0.1	2.0±0.1	0.5±0.1	4.1±1.1	5.7±2.6	3.0±1.1
18:4(n-3)	0.8±0.0	0.6±0.1	0.4±0.0	0.8±0.1	0.5±0.2	0.1±0.1	3.0±0.1	2.9±0.1	1.8±0.5
20:2(n-6)	0.9±0.2	2.3±1.6	0.6±0.0	4.7±0.1	4.4±0.1	1.4±0.0	1.1±0.1	1.0±0.2	0.9±0.0
20:3(n-6)	0.2±0.1	1.3±0.5	0.2±0.1	0.7±0.1	0.6±0.0	0.0±0.0	0.7±0.0	0.6±0.0	0.5±0.1
20:4(n-6)	4.7±0.4	5.0±0.4	3.1±0.1	7.0±0.0	4.6±0.2	2.8±0.7	5.3±0.4	5.4±0.4	3.8±0.4
20:3(n-3)	0.6±0.3	2.4±1.1	0.4±0.0	0.7±0.2	0.7±0.0	2.3±0.1	0.9±0.1	1.3±0.4	1.1±0.7
20:4(n-3)	1.1±0.4	1.7±0.2	0.7±0.0	0.5±0.2	0.4±0.0	0.0±0.0	1.1±0.1	1.9±0.7	1.2±0.8
20:5(n-3)	22.6±4.1	23.5±0.5	18.9±1.1	25.7±1.7	23.8±0.7	17.9±2.3	54.6±1.0	43.0±9.3	38.8±6.8
21:5(n-3)	0.4±0.0	0.4±0.0	0.3±0.0	0.6±0.0	0.4±0.0	0.0±0.0	1.2±0.0	0.7±0.4	0.7±0.1
22:4(n-6)	0.7±0.0	0.6±0.0	0.5±0.0	0.8±0.0	0.6±0.0	0.1±0.1	0.5±0.0	0.4±0.0	0.3±0.0
22:5(n-6)	0.1±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
22:5(n-3)	1.4±0.0	1.5±0.0	1.1±0.1	2.1±0.2	1.8±0.0	0.2±0.2	3.5±0.7	3.0±0.6	2.0±0.1
22:6(n-3)	24.5±0.5	20.2±0.6	19.2±1.1	15.6±0.3	17.3±0.4	7.5±0.5	11.8±0.8	11.1±1.5	9.1±0.2
∑ PUFA	65.1±5.9	63.4±2.2	49.1±3.0	88.9±0.2	82.4±2.6	42.7±0.9	93.9±2.2	83.6±4.0	67.6 ±11.3
∑ HUFA	57.2±5.9	58.9±2.5	44.9±2.7	58.4±2.7	54.6±1.4	32.1±1.7	80.8±1.0	68.4±9.0	58.3±8.9
∑ Unsaturated	145.8±7.1	131.8±1.7	108.3±6.5	156.4±1.4	155.5±5.0	64.2±0.0	151.7±7.0	134.0±6.8	106.3±9.9
∑ (n-3)	53.6±5.3	51.9±0.1	41.9±2.4	48.7±2.6	46.9±1.4	28.5±2.3	80.1±0.6	69.6±7.0	57.7±9.8
∑ (n-6)	11.5±0.6	11.6±2.3	7.3±0.5	40.1±2.4	35.5±1.1	14.3±1.4	13.7±1.6	14.0±3.0	9.9±1.4
(n-3)/(n-6)	4.6±0.2	4.6±0.9	5.8±0.1	1.2±0.1	1.3±0.0	2.0±0.4	5.9±0.6	5.2±1.6	5.8±0.2
DHA:EPA	1.1±0.2	0.9±0.0	1.0±0.0	0.6±0.0	0.7±0.0	0.4±0.0	0.2±0.0	0.3±0.0	0.2±0.1
∑ Total FAME	191.7±7.6	172.6±1.2	146.8±8.7	203.9 ±1 .7	201.5±6.0	87.2±2.1	205.2±9.9	186.1±6.9	145.7± 9.9

Plesionika martia martia and *Palaemon serratus* have a higher resemblance with respect to the total SFA, (n-3) FA and highly unsaturated fatty acids (HUFA) content of their eggs. Nevertheless, *P. martia martia* eggs stand out by having elevated MUFA and reduced PUFA contents. *Palaemon elegans* eggs have high levels of both SFA, PUFA, HUFA and (n-3) FA, while *P. serratus* eggs show intermediate levels of most FA classes, with the exception of (n-6) FA, which they have in large amounts due to the abundance of 18:2(n-6).

When analysing the changes in the egg FA profile during embryonic development, a steady decrease in the total FA is observed. Again, as observed with total lipids, the most pronounced reduction occurred from Stage 2 to 3. The comparison of the total FA composition of the eggs in Stage 1 reveals that there is a similar level in the 3 species, with *Plesionika martia martia* presenting a just slightly lower FA content. Nevertheless, looking at the consumption rate during embryonic development, a much higher FA depletion was noted in *Palaemon serratus* eggs (57.3%), in comparison with *Palaemon elegans* (29.0%) and *P. martia martia* (23.4%).

Looking at the utilisation of FA during embryonic development (Fig. 3), it can be noted that the unsaturated fatty acids (UFA) are used up at a higher rate than SFA; within the UFA, MUFA are consumed more than PUFA. As for the consumption of (n-3) and (n-6) FA, a preferential use of (n-6) FA during development was detected in *Plesionika martia martia* and *Palaemon serratus* eggs, whereas both series were utilised at the same rate in *Palaemon elegans* eggs. As a result, an increase in the (n-3):(n-6) ratio was observed in *P. martia martia* and *P. serratus* during embryonic development, being this ratio kept constant in *P. elegans* eggs. In terms of the utilisation of individual FA, the results differ in the 3 species. In *P. martia martia* eggs, there was a preferential consumption (by order of decreasing magnitude) of 18:3(n-3), 18:2(n-6), ARA and 16:1(n-7); *P. serratus* eggs showed a faster depletion of 18:3(n-3), 20:1(n-9), 18:1(n-9) and 16:1(n-7), whereas the results point to a higher reduction in 16:1(n-7), 18:1(n-9), 20:1(n-9) and 18:0 in *P. elegans* eggs.

In all 3 species, there was a catabolism of both DHA and EPA during embryonic development. In *Plesionika martia martia* and *Palaemon serratus* eggs, DHA was slightly more depleted than EPA, while the inverse was observed in *Palaemon elegans*. However, the differences in the consumption rate of these 2 essential FA were small and the DHA:EPA ratio was kept relatively constant during the embryonic development of these shrimp species.

When the FA analysis results are expressed in terms of percentage of total FA (Table 3), some interesting observations can be made. Again, as expected, the results point to a higher similarity between *Plesionika martia martia* and *Palaemon serratus* eggs. One result that stands out is the stability that is maintained in the proportion of the different FA during the embryonic

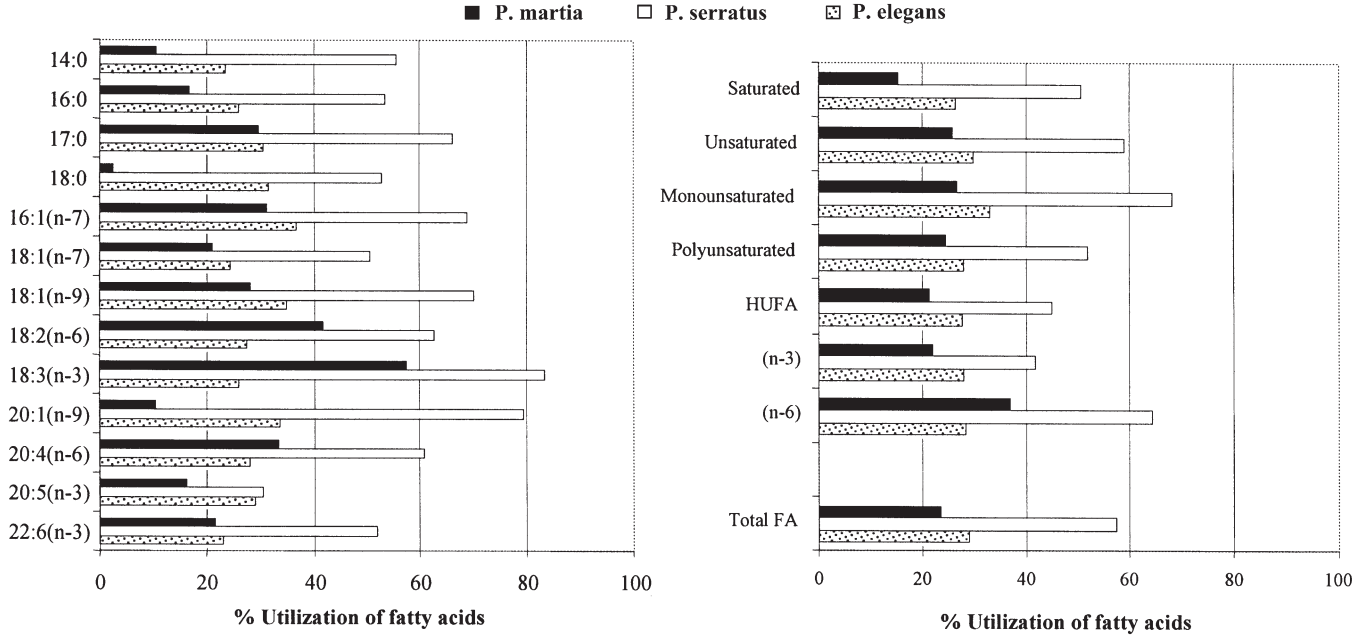

Fig. 3. *Plesionika martia martia*, *Palaemon serratus* and *Palaemon elegans*. Percentage of utilisation of selected fatty acids (FA), fatty acid classes and total fatty acid from the early to the later stage of embryonic development. HUFA: highly unsatuated fatty acids

Table 3. *Plesionika martia martia*, *Palaemon serratus* and *Palaemon elegans.* Relative fatty acid composition (% total lipids) of eggs at different stages of embryonic development (only the quantitatively most important fatty acids are represented). MUFA: monounsaturated fatty acids, PUFA: polyunsaturated fatty acids, HUFA: highly unsatuated fatty acids

Fatty acid	*Plesionika martia martia*			*Palaemon serratus*			*Palaemon elegans*		
	1	2	3	1	2	3	1	2	3
14:0	2.04	2.18	2.38	1.29	1.60	1.34	2.80	2.96	3.02
16:0	15.43	14.84	16.79	13.03	13.30	14.19	14.91	15.77	15.55
17:0	1.26	1.31	1.16	1.59	1.23	1.26	1.28	1.59	1.25
18:0	3.10	3.28	3.95	4.50	3.80	4.95	5.31	5.49	5.13
∑ Saturated	22.96	22.63	25.40	21.42	21.04	24.78	25.18	26.92	26.10
16:1(n-7)	9.26	8.93	8.33	5.90	6.05	4.28	9.44	8.20	8.41
18:1(n-9)	23.51	20.32	22.07	21.26	24.56	14.91	9.73	9.87	8.93
18:1(n-7)	5.63	6.33	5.81	4.43	4.37	5.10	7.55	7.49	8.03
20:1(n-9)	1.77	1.91	2.06	0.54	0.55	0.26	0.34	0.63	0.32
∑ MUFA	42.12	39.60	40.31	33.14	36.30	24.56	28.19	27.11	26.60
18:2(n-6)	2.55	1.42	1.94	13.18	12.56	11.50	2.96	3.54	3.03
18:3(n-3)	1.19	0.86	0.66	1.37	0.98	0.53	1.97	3.08	2.06
20:4(n-6)	2.45	2.90	2.13	3.46	2.29	3.16	2.60	2.89	2.63
20:5(n-3)	11.79	13.62	12.85	12.60	11.81	20.49	26.62	23.11	26.61
22:6(n-3)	12.78	11.72	13.09	7.66	8.58	8.64	5.75	5.96	6.24
∑ Unsaturated	76.08	76.35	73.77	76.72	77.18	73.58	73.94	72.02	72.98
∑ PUFA	33.96	36.75	33.46	43.58	40.89	49.01	45.75	44.91	46.38
∑ HUFA	29.81	34.12	30.61	28.66	27.09	36.82	39.36	36.74	40.02
∑ (n-3)	27.95	30.04	28.51	23.91	23.29	32.66	39.05	37.41	39.62
∑ (n-6)	6.01	6.71	4.95	19.68	17.60	16.35	6.70	7.50	6.76

development of *Palaemon elegans* eggs. In all species, there was a decrease in the percentages of both MUFA and UFA, mainly as a consequence of the decline on the proportions of 16:1(n-7) and 18:1(n-9). Total (n-6) FA, as well as 18:2(n-6) and 18:3(n-3), decrease their percentage during the embryonic development of *P. martia martia* and *P. serratus* but remain constant in *P. elegans* eggs. On the other hand, the SFA percentage (mainly 14:0 and 16:0) increases in all species. The proportions of PUFA and HUFA either increase or remain stable; DHA increases in all species, while EPA increases in *P. martia martia* and particularly in *P. serratus* eggs but remains constant in *P. elegans*.

DISCUSSION

Egg size has been correlated with lipid content, maternal investment and with the type of larval development in caridean decapods (Herring 1973, Clarke 1993, Wehrtmann & Graeve 1998). Normally, small eggs hatch in small larvae that pass through a large number of developmental stages, whereas large eggs hatch into a more advanced stage, with fewer larval stages, or directly into post-larvae (Herring 1974). However, most crustacean larvae hatch with little or no yolk reserves, have extremely high energetic and nutritional demands, and are therefore dependent on the availability of a suitable diet for growth and metamorphosis (McConaugha 1985). This is the case for the species analysed in the present study.

In general, deeper water species tend to produce a smaller number of large eggs, with a longer development period and more lipid reserves, as a way to offset the decrease in the probability of larval mortality with depth (King & Butler 1985, Mauchline 1988, Jaeckle 1995). In contrast, littoral species whose larvae are released and dispersed from the coastal nearshore zone have higher larval/post-larval mortality due to predation and drift; in this case, small eggs are usually produced as an adaptation to allow for larger brood sizes and greater egg production in shallow water species (Pollock & Melville-Smith 1993). In spite of the much higher depth at which *Plesionika martia martia* is found, the eggs of this species are smaller than the eggs of *Palaemon serratus* and *Palaemon elegans*. This

is probably a consequence of the type of larval development, which is similar in the 3 studied species, with several larval stages and a relatively long period of larval development.

An increase in egg volume during the incubation period has been reported to be typical in several crustacean species (Clarke et al. 1990, Biesiot & Perry 1995, Lardies & Wehrtmann 1996, Wehrtmann & Graeve 1998, Wehrtmann & Kattner 1998). In the present study, a significant increase in egg volume was also noted during embryogenesis (121, 188 and 79 % in *Plesionika martia martia*, *Palaemon serratus* and *Palaemon elegans*, respectively). This increase is within the range described for other decapod species and is generally associated with water uptake and a subsequent wet weight increase, accompanied by a decrease in dry weight (Pandian 1970a, Biesiot & Perry 1995, Lardies & Wehrtmann 1996, Wehrtmann & Kattner 1998). Nevertheless, it is not completely clear whether the increase in water content is caused entirely by the absorption of water. Given that water is a by-product of respiration, the retention of metabolic water is also likely (Amsler & George 1984).

In the present study, the increase in the egg water content of the 3 analysed species during embryonic development was comparable to other marine crustacean species (Pandian 1970a,b, Clarke et al. 1990, Petersen & Anger 1997, Wehrtmann & Graeve 1998). However, there appears to be a clear distinction between the different genera with *Plesionika martia martia* eggs having a higher water content at the earlier developmental stage than the 2 *Palaemon* species. In the latter species, a larger increase in water content is observed during embryonic development, with a relatively similar water content being measured in all 3 species just before hatching.

The lipid content of crustacean eggs has been typically found to decrease during development due to embryonic utilisation (Herring 1974, Wehrtmann & Graeve 1998, Wehrtmann & Kattner 1998). In the present study, a substantial decrease in the total lipid and FA content was also noted in the eggs of the 3 studied species. However, a higher percentage of lipid and FA utilisation was observed in *Palaemon serratus* eggs. These results suggest that both *Plesionika martia martia* and *Palaemon elegans* newly hatched larvae rely heavily on the endogenous lipid reserves, particularly for metabolic energetic purposes. An enhanced independence of the larvae on external energy sources has been interpreted as an adaptation to the early life history of the species (Wehrtmann & Graeve 1998). *P. serratus* inhabits a less fluctuating environment (infralittoral) than *P. elegans* (intertidal) and *P. martia martia* (deep sea). *P. elegans* larvae hatch in habitats characterised by strong currents and wave action and, consequently, must be adapted to a broader range of environmental conditions than *P. serratus*, as was demonstrated by Berglund (1980) and Berglund & Bengtsson (1981) in other intertidal and infralittoral *Palaemon* species. On the other hand, *P. martia martia*, like other deep-water pandalids, produce planktotrophic larvae that can migrate through the water column (Rothlisberg & Pearcy 1977, King & Buttler 1985). Consequently, these larvae are subjected to a great range of environmental factors during their vertical migration which may reduce their probability of survival (Mileikovsky 1971). Therefore, given the particular conditions to which newly hatched *P. elegans* and *P. martia martia* are submitted, a limited access to food immediately after hatching is likely. Nevertheless, in spite of this apparently similar strategy of *P. martia martia* and *P. elegans*, the egg FA profile of these 2 species is quite dissimilar, probably as a result of different diets and environmental conditions to which the females are submitted.

Egg lipids of the 3 investigated species also showed a clear trend of decreasing TAG and DAG during the early and late incubation period. In fact, neutral lipids, particularly TAG, are the major energy source and the predominant form of energy storage in the adult, egg and pre-feeding larva (Middleditch et al. 1979, Harrison 1990, Anger 1998). The utilisation of TAG during embryonic development implies a release of FA. The excess FFA can be diverted to growth at any point in larval development (Nates & McKenney 2000), given that the bioconversion and incorporation of FFA into polar lipids is higher than into neutral lipids during embryogenesis (Dall et al. 1993).

Taking into account the predominant FA in the eggs, there appears to be a higher similarity between *Plesionika martia martia* and *Palaemon serratus*. The eggs of these 2 species are also characterised by presenting higher levels of DHA and a lower EPA composition than the eggs of *Palaemon elegans*, which present an extremely elevated EPA content. Consequently, *P. martia martia* and *P. serratus* eggs have higher DHA:EPA ratios (1.1 and 0.6 at the start of the embryonic development, respectively) than *P. elegans* (0.2). In fact, with increasing depth (i.e. increase in pressure and decrease in temperature), there appears to be an increase in the DHA:EPA ratio of the eggs, as a result of the rise in the DHA level and a reduction in the EPA content (Kattner et al. 1994).

In spite of the occurrence of species-specific patterns of FA utilisation, the consumption of these compounds during embryonic development of the 3 studied species did not differ markedly from data collected by Clarke et al. (1990), Wehrtmann & Graeve (1998) and Wehrtmann & Kattner (1998). The most utilised SFA and MUFA were essentially the same as in all caridean shrimps—16:0 and 18:0, 16:1(n-7), 18:1(n-9) and

18:1(n-7). The PUFA consumption observed in developing eggs was mainly caused by the utilisation of 18:3(n-3) and 18:2(n-6).

The results concerning the utilisation of FA classes during embryonic development reveal the same trend in all the analysed species. UFA were always used up at a higher rate than SFA, with MUFA being preferentially used for energetic purposes, while HUFA were conserved. Since SFA are non-essential and can be synthesised de novo or obtained by desaturation of MUFA and HUFA (Sargent 1995, 1999), their pattern of consumption may either suggest a selective retainment during embryonic development or a partial utilisation and replacement (turnover).

The changes in the FA profile of *Palaemon serratus* eggs during embryonic development had been previously analysed by us (Narciso & Morais 2001). Although a similar trend of FA composition and depletion has been found in the present study, some small differences were encountered. Intraspecific differences have been attributed to female feeding ecology (Biesiot & Perry 1995), nutritional and physiological condition (Amsler & George 1984, Hopkins et al. 1993, Wehrtmann & Kattner 1998), differential demands on resource allocation (Jaeckle 1995), and geographic and seasonal variations in embryonic development (Wehrtmann & Kattner 1998).

It should be kept in mind that the present study has looked at single populations, at a single moment in time and with no knowledge of the nutritional and physiological condition of the females. Therefore, the lipid and FA composition and utilisation in the eggs should thus be interpreted with some caution.

In conclusion, although the studied species presented some similarities with other caridean shrimp and revealed some homogeneity in the quantitatively most important FA, species-specific differences in their order of magnitude were noticed. In this respect, a higher similarity was observed between *Plesionika martia martia* and *Palaemon serratus* eggs, comparatively with *Palaemon elegans*, probably due to comparable environmental conditions faced by females and newly hatched larvae. On the other hand, the depletion rate of total FA during embryogenesis suggests that *P. martia martia* and *P. elegans* developed a similar adaptive strategy to their early life history, with newly hatched larvae presenting a lower dependence on external energy sources. In the first case, the main catabolic substrate is MUFA while in the second both SFA and MUFA are probably the main energetic fuel available to the newly hatched larvae. Only further work on the lipid embryonic metabolism of different decapod populations at different times of the year, can help clarifying some of the questions raised in this study.

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