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RESEARCH ARTICLE

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Amino and fatty acid dynamics of *Lysmata seticaudata* (Decapoda: Hippolytidae) embryos during early and late reproductive season

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Abstract The present study investigates amino and fatty acid dynamics of embryos of different-sized simultaneous hermaphrodite shrimp (SH) (*Lysmata seticaudata*) during early (ERS) and late reproductive seasons (LRS). A significant relative decrease in total amino acids and essential amino acids (EAA) was recorded ($P < 0.05$) during the development of embryos produced by shrimp collected during ERS and LRS. The content of non-essential amino acids (NEAA) showed a smaller variation, without a marked decrease. During the last embryonic stage, the major EAAs of embryos were, in decreasing magnitude, lysine and arginine, while the major NEAAs were glutamic acid and valine. A substantial decrease in lipid content ($P < 0.05$) was observed, and the quantitatively more important fatty acids were the saturates 16:0 and 18:0, the monounsaturates 18:1*n*-9 and 18:1*n*-7 and the polyunsaturates 20:4*n*-6 (arachidonic acid, ARA), 20:5*n*-3 (eicosapentaenoic acid, EPA) and 22:6*n*-3 (docosahexaenoic acid, DHA). Monounsaturates were used at a higher rate, and embryos produced by SH shrimp displayed similar consumption rates of saturated and polyunsaturated fatty acids. Considering individual fatty acids, no clear utilization pattern between different-sized SH shrimp in ERS and LRS was recorded. The inexistence of consistent differences between amino and fatty acid utilization during embryogenesis among different-sized SH shrimp in ERS and LRS emphasizes the variability affecting offspring in decapod crustaceans.

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Introduction

Marine ornamental shrimp of the genus *Lysmata* are among the most traded invertebrate organisms in the marine aquarium industry (Wabnitz et al. 2003). This popularity has led to a growing pressure by collectors of marine ornamental shrimp on their wild populations. In order to help minimize the ecological impacts associated with this practice, the rearing potential of several decapod species occurring in warm temperate and subtropical European waters has started to be evaluated (Calado et al. 2003a). The Monaco shrimp *Lysmata seticaudata* Risso, 1816 is one of these species, and its larval rearing has recently been achieved on a commercial scale (Calado et al. 2003b). To establish a suitable culture protocol for this species the number and biochemical composition of embryos produced in the laboratory must, at least, be similar to those produced in the wild. Calado and Narciso (2003) already quantified the seasonal variation on embryo production and brood loss in *L. seticaudata*. However, no study has ever addressed the embryos' biochemical composition or changes during the incubation period of the Monaco shrimp. Additionally, since this species' reproductive season extends from early March to late September (Dohrn 1950) and brood size increases with increasing shrimp size (Calado and Narciso 2003), it is also important to investigate the existence of any seasonal or parental size variation on the embryos' biochemical profile.

The objectives of the present study were: (1) to evaluate the dynamics of amino and fatty acid profiles during the embryogenesis of *L. seticaudata*, (2) compare the biochemical composition of embryos in the same development stage among similar-sized shrimp in early and late reproductive seasons, (3) and to compare the

embryos' biochemical composition among different-sized shrimp in early and late reproductive seasons.

Materials and methods

Sampling

Ovigerous Monaco shrimp (*Lysmata seticaudata*) were collected in a single, large tidal pool during spring tides at Cape Raso, 30 km west of Lisbon, in the months of March and April (early reproductive season—ERS) and of August and September (late reproductive season—LRS), 2001, using baited traps described by Calado and Narciso (2004). Total length (TL, distance between the rostrum anterior end and the telson posterior edge) of each ovigerous shrimp were measured with callipers to the nearest 0.05 mm. The shrimp were classified as small (40–44 mm TL), medium (48–52 mm TL) and large (58–62 mm TL) (Dohrn 1950). The egg mass was removed from the females, and eggs were classified according to the following criteria (modified from Kattner et al 1994): stage I—uniform yolk and no embryonic development visible; stage II—eyes clearly visible with 1/2 yolk consumed; and stage III—almost no yolk present and embryo fully developed. Thirty eggs were separated from each simultaneous hermaphrodite (SH) shrimp (18 SH, 3 per each embryonic stage in each reproductive season), and length and width were measured under a stereomicroscope (Olympus, model SZ6045TR) with a calibrated micrometer eyepiece. Egg samples were stored in liquid nitrogen for later biochemical analyses. In order to perform the biochemical analyses, different batches of eggs at the same stage of development were pooled.

Egg volume and water content

Egg volume was calculated using the formula for oblate spheroids $V = 1/6(\pi W^2 L)$ (Turner and Lawrence 1979). 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.

Protein and amino acid analyses

Protein concentration was determined (with 100 mg of wet tissue) on the washed TCA precipitate solubilized in 1 M sodium hydroxide (NaOH) for 24 h as described by Lowry et al. (1951), using the Bio-Rad protein assay (BIO-RAD). Bovine gamma globulin (BIO-RAD) was used as a standard.

In order to determinate the total amino acid profile, egg proteins were hydrolyzed with 6 N hydrochloric acid (containing 0.1% phenol) in a MLS-1200 Mega Microwave System (Milestone), at 800 W, 160°C for 10 min. The hydrolysis was performed under inert and anaerobic conditions to prevent oxidative degradation of amino acids. The hydrolysates were filtered and dissolved in sodium citrate buffer (pH 2.2). Amino acids were separated by ion exchange liquid chromatography in an automatic analyzer (Biochrom 20, Amersham Biosciences), equipped with a column filled with a polysulfonated resin (250×4.6 mm), using three sodium citrate buffers (Amersham Biosciences) of different pH (3.20, 4.25 and 6.45) and three different temperatures (50°C, 58°C and 95°C).

The detection of amino acids was done at 440 and 570 nm after reaction with ninhydrin (Amersham Biosciences). Amino acids were identified by comparison of their retention time with those of specific standards (Sigma) and quantified with the software EZChrom Chromatography Data System, vers. 6.7 (Scientific Software) using norleucine (Sigma) as internal standard.

Lipid and fatty acid analysis

Total lipids were extracted using the Bligh and Dyer (1959) method. The distribution of fatty acids was based on the experimental procedure of Lepage and Roy (1986), modified by Cohen et al. (1988). The fatty acid methyl esters were analyzed in a Varian 3400 gas chromatograph, equipped with an auto-sampler and fitted with a flame ionization detector. The separation was carried out with helium as carrier gas in a fused silica capillary column (Chrompack CPSil/88, 50 m×0.32 mm i.d.), programmed from 180°C to 200°C at 4°C min^{-1}, held for 10 min at 200°C and heated to 210°C for 14.5 min at 0.68°C min^{-1}, with a detector at 250°C. A split injector (100:1) at 250°C was used. Fatty acid methyl esters were identified by comparison of their retention time with those of chromatographic Sigma standards. Peak areas were determined using the Varian software, and the quantification was done using 21:0 (10 mg ml^{-1}) as an internal standard.

Statistical analysis

Significant differences between embryo volume, water content, total amino acid, total lipids and fatty acids at each embryonic stage from different-sized shrimp, in both ERS and LRS, were determined by a three-way ANOVA (embryonic stage×reproductive season×shrimp size), after checking the assumptions. Whenever significance was accepted ($P < 0.05$), the Tukey multi-comparison test was used (Zar 1996).

Results

Egg volume and water content

The average volume of embryos at the same development stage was not significantly different among small,

medium and large shrimp collected during ERS and LRS. In all size classes of both ERS and LRS shrimp, average embryo volume significantly increased ($P = 0.001$) from 0.062 to 0.136 mm^3 (119%) at embryonic stages I and III, respectively (Table 1).

A progressive and significant increase in the water content of embryos was also observed during their development (Fig. 1), with early and later stage embryos showing an average water content of 66% and 85%, respectively. Again, no significant differences among small, medium and large shrimp collected in ERS and LRS were recorded.

Protein and amino acid contents

The embryos produced by small- and medium-sized SH shrimp in LRS displayed the highest decrease in protein content during their embryonic development (12.03% and 7.47%, respectively). Embryos of larger sized shrimp in ERS and LRS presented similar percentages of protein utilization during their development (3.88% and 4.26%, respectively) (Fig. 2).

A significant decrease in the content of total amino acids (TAA) and essential amino acids (EAA) was recorded during the development of embryos produced by all shrimp collected during ERS and LRS (Tables 2, 3). The content of non-essential amino acids (NEAA) showed a smaller variation, without a marked decrease pattern (Tables 2, 3).

During the last embryonic stage, the major EAAs of embryos produced by all shrimp in ERS and LRS were, in decreasing magnitude, lysine and arginine, while the major NEAAs were glutamic acid and valine (Tables 2, 3). The EAA lysine was significantly ($P = 0.015$) more used in embryos produced by shrimp in LRS, with small-sized SH shrimp using up to 15.5% of its initial content (Fig. 3). Valine was the most significantly ($P = 0.003$) used NEAA, with shrimp in LRS showing the highest utilization percentages (15.50%, 9.11% and 7.43% for small-, medium- and large-sized SH, respectively) (Fig. 3). Although in ERS large SH shrimp showed the highest utilization percentage of TAA (4.08%), small- and medium-sized SH shrimp displayed the highest TAA utilization values in LRS (12.70% and 7.31%, respectively). These utilization percentages were significantly ($P = 0.026$) different for small- and medium-sized SH shrimp, while large SH shrimp showed similar values in both ERS and LRS (Fig. 3).

Lipid and fatty acid contents

The embryos of all SH shrimp in ERS and LRS showed similar and significant ($P = 0.002$) decreases in their lipid content, with lipid utilization percentages varying between 59.6% and 66.5% (Fig. 2). The fatty acid composition of embryos produced by different-sized SH shrimp in ERS and LRS are displayed in Tables 4 and 5. The quantitatively more important fatty acids were the

Table 1 *Lysmata seticaudata*. Volume (mm^3) and volume increase (%) of embryos from small, medium and large simultaneous hermaphroditic (*SH*) shrimp in early and late reproductive seasons (*ERS* and *LRS*, respectively). Values are means (±SD, $n = 90$). *Different superscript letters* within rows and columns represent significant differences ($P < 0.001$)

	Embryo volume (mm^3)			Embryo volume increase (%)
	Stage I	Stage II	Stage III	Stage I–III
ERS small SH	0.063 ± 0.003^a	0.101 ± 0.007^b	0.137 ± 0.010^c	118.48 ± 2.73
ERS medium SH	0.062 ± 0.005^a	0.102 ± 0.006^b	0.139 ± 0.012^c	125.39 ± 3.40
ERS large SH	0.061 ± 0.004^a	0.100 ± 0.006^b	0.136 ± 0.009^c	124.16 ± 2.54
LRS small SH	0.062 ± 0.003^a	0.102 ± 0.010^b	0.135 ± 0.015^c	116.11 ± 4.21
LRS medium SH	0.062 ± 0.006^a	0.102 ± 0.003^b	0.136 ± 0.008^c	118.80 ± 3.10
LRS large SH	0.063 ± 0.003^a	0.096 ± 0.004^b	0.134 ± 0.012^c	112.70 ± 3.34

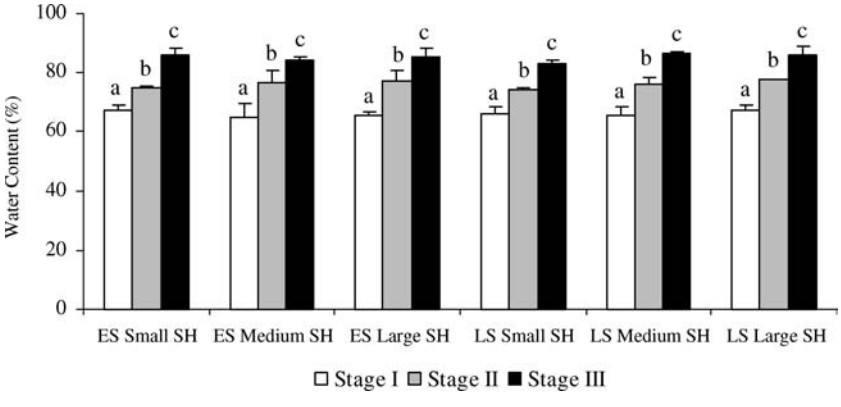

Fig. 1 *Lysmata seticaudata*. Water content (% wet weight) of embryos from small, medium and large simultaneous hermaphroditic (*SH*) shrimp in early and late reproductive seasons (*ES* and *LS*, respectively). Values are means (+SD, $n = 3$). *Different letters above bars* represent significant differences ($P < 0.001$)

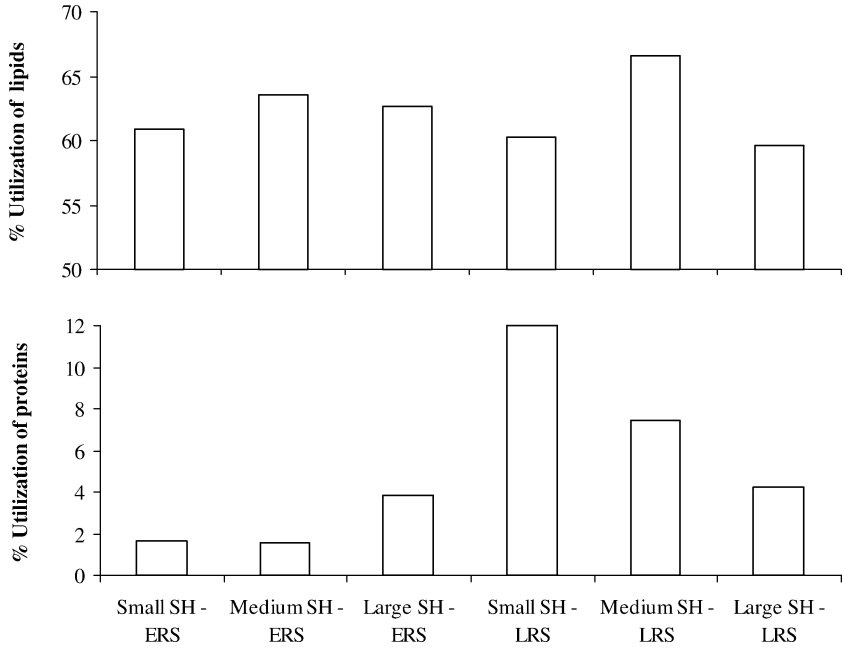

Fig. 2 *Lysmata seticaudata*. Percent utilization of lipid (*upper panel*) and protein (*lower panel*) content during embryonic development of small, medium and large simultaneous hermaphroditic (*SH*) shrimp in early and late reproductive seasons (*ERS* and *LRS*, respectively)

saturates (SFA) 16:0 and 18:0, the monounsaturates (MUFA) 18:1*n*-9 and 18:1*n*-7, and the polyunsaturates (PUFA) 20:4*n*-6 (arachidonic acid, ARA), 20:5*n*-3 (eicosapentaenoic acid, EPA) and 22:6*n*-3 (docosahexaenoic acid, DHA). Monounsaturates were used at a higher rate (up to 67.87% of utilization) during embryonic development (Fig. 4). Embryos displayed a similar consumption rate of SFA and PUFA during their development in ERS and LRS. Medium-sized SH shrimp in LRS displayed the highest fatty acid utilization percentage (Fig. 4). Considering individual fatty acids, no clear utilization pattern between different-sized shrimp in ERS and LRS could be establish for 16:0, 18:0, 18:1*n*-9 or 18:1*n*-7. A preferential consumption of ARA and EPA was recorded in embryos produced in LRS, while in general DHA was more consumed in ERS (Fig. 5).

Discussion and conclusions

A significant increase in egg volume is generally associated with an increase in water content and wet weight, and is accompanied by a decrease in dry weight during the embryonic development of crustacean decapods (Clarke et al. 1990; Wehrtmann and Graeve 1998; Wehrtmann and Kattner 1998; Garcia-Guerrero et al. 2003a, 2003b). However, researchers have not yet clarified if water content increase is entirely caused by water absorption, or if it is also a result of respiration and metabolic water retention (Amsler and George 1984).

Rosa et al. (2003) and Mente et al. (2002) emphasized the absence of studies addressing amino acid dynamics during embryonic development and adult life of decapod crustaceans, respectively. Rosa et al. (2003) noted a significant increase in the content of TAA, EAA and NEAA for Norway lobster (*Nephrops norvegicus*) eggs during embryonic development and a larger variation in the content of NEAA. The dynamics presented for *Lysmata seticaudata* embryos in ERS and LRS appear to contradict those described by Rosa et al. (2003), since the present work records a decrease in TAA, EAA and NEAA content, and displays a larger variation in the content of EAA than of NEAA. These differences in amino acid dynamics during embryogenesis can be related with the phylogenetic distance of these two decapod species and different early life strategies. According to the classification proposed by Martin and Davis (2001), *N. norvegicus* and *L. seticaudata* belong to different infraorders (Astacidea and Caridea, respectively). While the genus *Nephrops* is known to display a reduced number of larval stages (three zoeal stages) and a morphologically well-developed first larval stage (with all pereiopods already functional) (Williamson 1983), the genus *Lysmata* displays a long larval series (nine or more larval stages) and a first larval stage clearly less developed than that of *Nephrops* (Calado et al. 2004). Therefore, the early life strategy of *Nephrops* may require higher levels of energy during embryogenesis.

The lipid content of decapod crustaceans has been found to significantly decrease during embryonic development (Petersen and Anger 1997; Morais et al. 2002; Rosa et al. 2003). This decrease was also registered in the present work and is explained by the fact that lipids are the primary energy source of incubating embryos (Harrison 1990). In general, the fatty acid consumption pattern during embryonic development recorded in the present study agrees with those described by Clarke et al. (1990), Wehrtmann and Graeve (1998), Wehrtmann and Kattner (1998), Morais et al. (2002) and Rosa et al. (2003).

Although ARA, EPA and DHA are considered to be essential fatty acids for decapod crustaceans

Table 2 *Lysmata seticaudata*. Total amino acid composition (*TAA*, % wet weight) and protein content (% wet weight) of eggs at different stages of embryonic development from small, medium and large simultaneous hermaphroditic (*SH*) Monaco shrimp in early reproductive season (*ERS*). Values are means (+SD) of triplicate samples. *Different superscript letters* within rows represent significant differences ($P < 0.05$)

Amino acids (%WW)	Small SH			Medium SH			Large SH		
	I	II	III	I	II	III	I	II	III
Essential amino acids (EAA)									
Threonine	$2.39 + 0.12^{a}$	$2.25 + 0.08^{a}$	$2.16 + 0.05^{b}$	$2.33 + 0.14^{a}$	$2.28 + 0.06^{a}$	$2.13 + 0.06^{b}$	$2.05 + 0.03^{c}$	$1.90 + 0.06^{d}$	$1.89 + 0.05^{e}$
Methionine	$1.96 + 0.11^{a}$	$1.61 + 0.04^{b}$	$1.33 + 0.03^{c}$	$1.93 + 0.12^{a}$	$1.59 + 0.09^{b}$	$1.38 + 0.07^{c}$	$1.64 + 0.05^{b}$	$1.43 + 0.03^{d}$	$1.36 + 0.01^{c}$
Isoleucine	$2.44 + 0.12^{a}$	$2.24 + 0.05^{b}$	$2.06 + 0.05^{c}$	$2.52 + 0.15^{a}$	$2.30 + 0.08^{b}$	$2.14 + 0.06^{bc}$	$2.20 + 0.06^{b}$	$2.13 + 0.06^{bc}$	$2.04 + 0.05^{c}$
Leucine	$3.64 + 0.17^{a}$	$3.42 + 0.09^{b}$	$3.33 + 0.07^{c}$	$3.63 + 0.22^{a}$	$3.50 + 0.09^{b}$	$3.33 + 0.08^{c}$	$3.15 + 0.07^{d}$	$3.09 + 0.10^{d}$	$3.00 + 0.15^{e}$
Phenylalanine	$2.30 + 0.10^{a}$	$2.13 + 0.04^{b}$	$2.19 + 0.06^{b}$	$2.26 + 0.12^{ab}$	$2.18 + 0.05^{b}$	$2.12 + 0.04^{b}$	$1.99 + 0.03^{c}$	$1.88 + 0.05^{d}$	$1.88 + 0.04^{d}$
Lysine	$4.19 + 0.19^{a}$	$4.11 + 0.13^{a}$	$4.07 + 0.09^{b}$	$4.22 + 0.23^{a}$	$4.26 + 0.09^{a}$	$4.05 + 0.15^{b}$	$3.62 + 0.03^{c}$	$3.65 + 0.13^{c}$	$3.58 + 0.26^{c}$
Histidine	$1.53 + 0.07^{a}$	$1.45 + 0.06^{a}$	$1.36 + 0.05^{b}$	$1.58 + 0.05^{c}$	$1.49 + 0.05^{a}$	$1.42 + 0.04^{a}$	$1.31 + 0.01^{b}$	$1.31 + 0.04^{b}$	$1.28 + 0.06^{b}$
Arginine	$3.89 + 0.17^{a}$	$3.76 + 0.12^{a}$	$3.88 + 0.09^{a}$	$3.83 + 0.20^{a}$	$3.93 + 0.05^{a}$	$3.83 + 0.08^{a}$	$3.34 + 0.02^{b}$	$3.39 + 0.14^{b}$	$3.36 + 0.21^{b}$
ΣEAA	$22.34 + 1.07^{a}$	$20.98 + 0.60^{b}$	$20.37 + 0.49^{b}$	$22.30 + 1.23^{a}$	$21.53 + 0.57^{a}$	$20.40 + 0.58^{b}$	$19.30 + 0.30^{c}$	$18.79 + 0.62^{c}$	$18.38 + 0.83^{c}$
Non-essential amino acids (NEAA)									
Aspartic acid	$4.07 + 0.10^{a}$	$4.07 + 0.13^{a}$	$4.21 + 0.08^{b}$	$4.02 + 0.23^{a}$	$4.13 + 0.04^{a}$	$4.06 + 0.04^{a}$	$3.54 + 0.04^{c}$	$3.49 + 0.11^{c}$	$3.48 + 0.19^{c}$
Serine	$3.43 + 0.18^{a}$	$2.85 + 0.09^{b}$	$2.27 + 0.04^{c}$	$3.22 + 0.21^{a}$	$2.75 + 0.19^{b}$	$2.29 + 0.15^{c}$	$2.70 + 0.08^{b}$	$2.31 + 0.08^{c}$	$2.10 + 0.10^{d}$
Glutamic acid	$6.70 + 0.23^{a}$	$6.38 + 0.11^{b}$	$6.34 + 0.12^{b}$	$6.48 + 0.10^{ab}$	$6.56 + 0.09^{a}$	$6.22 + 0.12^{c}$	$6.37 + 0.10^{b}$	$5.58 + 0.16^{d}$	$5.53 + 0.24^{d}$
Glycine	$2.15 + 0.10^{a}$	$2.56 + 0.05^{b}$	$3.54 + 0.10^{c}$	$2.30 + 0.11^{d}$	$2.82 + 0.14^{e}$	$3.26 + 0.13^{f}$	$2.32 + 0.06^{d}$	$2.31 + 0.06^{d}$	$2.66 + 0.05^{e}$
Alanine	$2.52 + 0.11^{a}$	$2.72 + 0.03^{b}$	$3.03 + 0.06^{c}$	$2.51 + 0.13^{a}$	$2.80 + 0.02^{d}$	$2.94 + 0.01^{c}$	$2.70 + 0.17^{b}$	$2.55 + 0.11^{a}$	$2.71 + 0.10^{b}$
Cystine	$0.23 + 0.00^{a}$	$0.28 + 0.12^{a}$	$0.22 + 0.01^{a}$	$0.17 + 0.01^{b}$	$0.20 + 0.02^{a}$	$0.17 + 0.00^{b}$	$0.22 + 0.01^{a}$	$0.20 + 0.05^{a}$	$0.26 + 0.07^{a}$
Valine	$5.12 + 0.24^{a}$	$4.73 + 0.07^{b}$	$4.30 + 0.08^{c}$	$5.27 + 0.36^{a}$	$4.85 + 0.20^{b}$	$4.49 + 0.15^{c}$	$4.78 + 0.11^{b}$	$4.40 + 0.12^{c}$	$4.37 + 0.06^{c}$
Tyrosine	$2.13 + 0.09^{a}$	$2.01 + 0.04^{a}$	$1.93 + 0.03^{b}$	$2.09 + 0.14^{a}$	$2.04 + 0.05^{a}$	$1.99 + 0.01^{ab}$	$1.94 + 0.05$	$1.84 + 0.06$	$1.85 + 0.01$
Proline	$2.31 + 0.08^{a}$	$3.00 + 0.13^{b}$	$3.94 + 0.14^{c}$	$2.26 + 0.17^{a}$	$3.14 + 0.07^{b}$	$4.07 + 0.67^{c}$	$2.81 + 0.12^{d}$	$2.85 + 0.05^{d}$	$3.44 + 0.06^{e}$
ΣNEAA	$28.65 + 0.36^{a}$	$28.58 + 0.16^{a}$	$29.78 + 0.39^{b}$	$28.32 + 0.76^{a}$	$29.30 + 0.40^{b}$	$29.49 + 0.22^{b}$	$27.38 + 0.30^{c}$	$25.54 + 0.65^{d}$	$26.40 + 0.19^{e}$
ΣTAA	$50.98 + 2.42^{a}$	$49.56 + 0.77^{a}$	$50.15 + 0.88^{a}$	$50.62 + 1.01^{a}$	$50.83 + 0.96^{a}$	$49.88 + 0.36^{a}$	$46.68 + 1.00^{b}$	$44.32 + 1.28^{c}$	$44.78 + 1.01^{c}$
Protein	$52.14 + 2.50^{a}$	$50.70 + 0.80^{a}$	$51.27 + 0.93^{a}$	$52.02 + 2.09^{a}$	$52.17 + 1.02^{a}$	$51.19 + 0.47^{a}$	$47.77 + 0.91^{b}$	$45.42 + 1.39^{c}$	$45.92 + 1.11^{c}$

Table 3 *Lysmata seticaudata*. Total amino acid composition (*TAA*, % wet weight) and protein content (% wet weight) of eggs at different stages of embryonic development from small, medium and large simultaneous hermaphroditic (*SH*) Monaco shrimp in late reproductive season (*LRS*). Values are means (+SD) of triplicate samples. *Different superscript letters* within rows represent significant differences ($P<0.05$) (*TAA* total amino acid)

Amino acids (%WW)	Small SH			Medium SH			Large SH		
	I	II	III	I	II	III	I	II	III
Essential amino acids (EAA)									
Threonine	$2.23+0.03^{a}$	$2.09+0.02^{b}$	$1.79+0.23^{c}$	$2.04+0.02^{b}$	$1.83+0.20^{c}$	$1.70+0.12^{c}$	$2.15+0.02^{d}$	$1.95+0.06^{c}$	$1.88+0.08^{c}$
Methionine	$1.86+0.08^{a}$	$1.58+0.02^{b}$	$1.24+0.08^{c}$	$1.70+0.00^{d}$	$1.31+0.12^{cf}$	$1.13+0.07^{e}$	$1.90+0.05^{a}$	$1.41+0.08^{f}$	$1.32+0.08^{f}$
Isoleucine	$2.50+0.06^{a}$	$2.27+0.01^{b}$	$1.93+0.16^{c}$	$2.27+0.05^{b}$	$1.95+0.15^{c}$	$1.83+0.13^{c}$	$2.46+0.04^{a}$	$2.17+0.08^{d}$	$2.03+0.09^{e}$
Leucine	$3.57+0.06^{a}$	$3.26+0.01^{b}$	$2.92+0.13^{c}$	$3.27+0.13^{d}$	$2.89+0.20^{c}$	$2.84+0.15^{c}$	$3.52+0.04^{a}$	$3.20+0.10^{b}$	$3.02+0.14^{e}$
Phenylalanine	$2.22+0.06^{a}$	$2.00+0.01^{b}$	$1.83+0.12^{c}$	$2.00+0.06^{b}$	$1.76+0.23^{c}$	$1.77+0.08^{c}$	$2.19+0.03^{a}$	$1.92+0.07^{b}$	$1.88+0.08^{bc}$
Lysine	$4.15+0.05^{a}$	$3.86+0.01^{b}$	$3.51+0.09^{c}$	$3.78+0.14^{b}$	$3.45+0.11^{c}$	$3.43+0.16^{c}$	$3.97+0.03^{d}$	$3.88+0.16^{bd}$	$3.67+0.27^{b}$
Histidine	$1.54+0.01^{a}$	$1.36+0.03^{b}$	$1.20+0.10^{c}$	$1.38+0.06^{b}$	$1.18+0.07^{c}$	$1.12+0.08^{c}$	$1.51+0.02^{a}$	$1.39+0.03^{b}$	$1.23+0.05^{c}$
Arginine	$3.79+0.09^{a}$	$3.59+0.00^{b}$	$3.28+0.25^{c}$	$3.44+0.19^{b}$	$3.17+0.20^{c}$	$3.23+0.16^{c}$	$3.68+0.05^{a}$	$3.49+0.13^{b}$	$3.35+0.17^{b}$
ΣEAA	$21.87+0.45^{a}$	$20.00+0.05^{b}$	$17.71+1.71^{c}$	$19.87+0.86^{b}$	$17.54+0.37^{c}$	$17.04+0.94^{c}$	$21.37+0.25^{a}$	$19.41+0.71^{bc}$	$18.38+0.98^{bc}$
Non-essential amino acids (NEAA)									
Aspartic acid	$3.89+0.02^{a}$	$3.69+0.02^{b}$	$3.42+0.13^{c}$	$3.56+0.19^{b}$	$3.30+0.20^{c}$	$3.36+0.18^{c}$	$3.72+0.02^{a}$	$3.64+0.12^{b}$	$3.57+0.21^{b}$
Serine	$3.04+0.11^{a}$	$2.54+0.06^{b}$	$1.93+0.22^{c}$	$2.79+0.16^{d}$	$2.07+0.22^{c}$	$1.76+0.09^{f}$	$2.98+0.09^{c}$	$2.25+0.10^{e}$	$2.01+0.10^{c}$
Glutamic acid	$6.42+0.23^{a}$	$6.40+0.048^{a}$	$5.48+0.54^{b}$	$6.14+0.59^{a}$	$5.73+0.58^{b}$	$5.43+0.01^{b}$	$6.28+0.35^{a}$	$6.09+0.43^{a}$	$6.05+0.64^{a}$
Glycine	$2.25+0.01^{a}$	$2.79+0.18^{b}$	$2.81+0.19^{b}$	$2.17+0.28^{a}$	$2.48+0.31^{c}$	$2.95+0.07^{b}$	$2.09+0.05^{d}$	$2.54+0.01^{c}$	$3.10+0.01^{e}$
Alanine	$2.53+0.08^{a}$	$2.72+0.08^{b}$	$2.75+0.12^{b}$	$2.42+0.17^{a}$	$2.52+0.27^{a}$	$2.80+0.07^{b}$	$2.44+0.08^{a}$	$2.81+0.06^{b}$	$2.75+0.04^{b}$
Cystine	$0.08+0.12^{a}$	$0.24+0.08^{b}$	$0.18+0.06^{b}$	$0.22+0.06^{b}$	$0.33+0.08^{c}$	$0.10+0.15^{a}$	$0.12+0.03^{a}$	$0.08+0.03^{a}$	$0.24+0.34^{b}$
Valine	$5.17+0.13^{a}$	$5.11+0.44^{a}$	$4.07+0.81^{b}$	$4.75+0.09^{c}$	$4.14+0.19^{b}$	$3.77+0.23^{d}$	$5.17+0.29^{a}$	$4.59+0.12^{a}$	$4.23+0.10^{b}$
Tyrosine	$2.12+0.04^{a}$	$1.99+0.02^{b}$	$1.77+0.09^{c}$	$1.92+0.05^{b}$	$1.75+0.21^{c}$	$1.70+0.10^{c}$	$2.05+0.03^{a}$	$1.89+0.05^{c}$	$1.85+0.07^{c}$
Proline	$2.53+0.04^{a}$	$2.67+0.88^{a}$	$3.43+0.27^{b}$	$1.85+0.40^{c}$	$2.68+0.54^{a}$	$3.40+0.13^{b}$	$2.26+0.16^{c}$	$3.32+0.06^{b}$	$4.39+0.08^{d}$
ΣNEAA	$28.03+0.62^{a}$	$28.15+0.23^{a}$	$25.85+1.07^{b}$	$25.82+2.28^{b}$	$25.00+1.84^{b}$	$25.31+0.87^{b}$	$27.12+0.42^{c}$	$27.13+0.64^{c}$	$28.19+0.66^{a}$
ΣTAA	$49.90+1.07^{a}$	$48.15+0.18^{a}$	$43.56+0.63^{bc}$	$45.69+1.14^{b}$	$42.55+1.22^{c}$	$42.35+1.81^{c}$	$48.49+0.62^{a}$	$46.53+1.35^{b}$	$46.56+1.64^{b}$
Protein	$51.18+1.12^{a}$	$49.31+0.18^{b}$	$45.02+0.82^{c}$	$46.88+1.02^{c}$	$43.62+1.41^{d}$	$43.38+1.90^{d}$	$49.70+0.21^{b}$	$47.70+1.56^{bc}$	$47.58+1.70^{bc}$

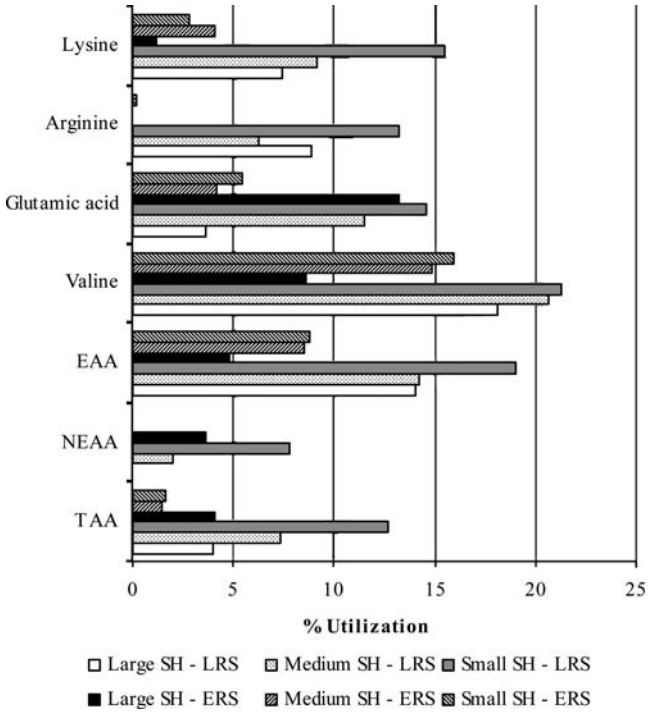

Fig. 3 *Lysmata seticaudata*. Percent utilization of selected amino acids during embryonic development of small, medium and large simultaneous hermaphroditic (*SH*) shrimp in early (*ERS*) and late reproductive seasons (*LRS*) (*EAA* essential amino acids; *NEAA* non-essential amino acids; *TAA* total amino acid)

(D'Abramo 1997; González-Félix et al. 2003a, 2003b) and are known to positively affect egg and larval quality when present in suitable amounts (Cavalli et al. 1999; Racotta et al. 2003; Smith et al. 2004), the present work has not revealed a preferential retention of these fatty acids during embryogenesis, as previously recorded by Anger (1998) and Heras et al. (2000) for decapod crustaceans and Soudant et al. (1998) for other marine invertebrates.

The inexistence of consistent differences between amino and fatty acid utilization during embryonic development among different-sized shrimp in ERS and LRS only emphasizes the already recognized intraspecific variability affecting offspring in decapod crustaceans. Since ovarian development in decapods can be supported by nutrients either provided by recent food intake or reserves stored in the midgut-gland (Krol et al. 1992; Ravid et al. 1999), the state of maternal nutrition may significantly affect yolk composition and utilization (Biesiot and Perry 1995). Nutritional and physiological condition can also significantly affect the embryos' biochemical profile (Hopkins et al. 1993; Wehrtmann and Kattner 1998). Amsler and George (1984) suggested that embryos spawned in ERS, following the winter, could present less reserves than those produced in the warmer months of LRS, when individuals are more active and may forage and find food more readily. Nevertheless, the present work has not confirmed the existence of such pattern in *L. seticaudata* embryos spawned in ERS and LRS, when water temperatures ranged between 14–15°C and 16–17°C, respectively.

Although no biochemical pattern could be established in the present work for embryos produced by different-sized shrimp in ERS and LRS, embryos in the same developmental stage displayed similar volumes, but different lipid and protein contents. These results support Jaeckle's (1995) assumption on the inaccuracy of using embryo size as a predictor of the energy available during embryogenesis. The temperature-related trends in lipid consumption recorded by Garcia-Guerrero et al. (2003b) for *Cherax quadricarinatus* were not noted in the present work, probably due to the lower temperature variation (2°C and 3°C between ERS and LRS), as opposed to the 9°C variation studied by these authors.

The unique sexual system displayed by genus *Lysmata*, simultaneous protandric hermaphroditism (Bauer 2000; Correa and Thiel 2003), and the apparent existence of complex social regulation (Lin and Zhang 2001) could have influenced embryo biochemical composition, since small shrimp in ERS would be those that had become SH in the previous year and would now produce their first embryos and small shrimp in LRS would be those that had become SH in that same reproductive season. The first embryos produced by these shrimp could be less viable (e.g. display less energetic reserves) if these new SH shrimp invested less energy in reproduction. As the present work confirmed, this was not the case, and the isometric egg production recorded by Calado and Narciso (2003) reinforces that the reproductive potential of *L. seticaudata* is not influenced by the temporal proximity of sex reversal to the reproductive season. The present work also verified the inexistence of senescence of larger SH shrimp in ERS and LRS, which will probably produce their last embryo batches during the analyzed reproductive season, again confirming the results of Calado and Narciso (2003) addressing embryo production.

Although the influence of age and/or size of reproductive shrimp and spawning season on offspring quality has been well documented for penaeid shrimp (Crocos and Coman 1997; Rothlisberg 1998; Racotta et al. 2003), the present results do not seem to indicate that this may also occur in the caridean *L. seticaudata*.

Since the results presented concern a single population and a single reproductive season, they should be interpreted cautiously, given that geographical and seasonal variations in embryonic biochemical dynamics can occur (Wehrtmann and Kattner 1998).

The high commercial value of ornamental shrimp of the genus *Lysmata* and the current efforts to establish culture protocols (Calado et al. 2003a) will certainly benefit from studies similar to the one presented here, since it is important to formulate well-balanced broodstock diets, thus optimizing egg production and larval quality. The influence of protein and energy level in lipid requirements must also be analyzed in more detail (Glencross et al. 2002). However, due to the scarcity of

Table 4 *Lysmata seticaudata*. Fatty acid composition (μg mg^{-1}dry weight) and lipid content (% dry weight) of eggs at different stages of embryonic development from small, medium and large simultaneous hermaphroditic (*SH*) Monaco shrimp in early reproductive season (*ERS*). Values are means (+SD) of triplicate samples. *Different superscript letters* within rows represent significant differences ($P < 0.05$)

Fatty acids (μg mg^{-1} DW)	Small SH			Medium SH			Large SH		
	I	II	III	I	II	III	I	II	III
14:0	$2.35 + 0.08^{a}$	$1.98 + 0.07^{b}$	$1.15 + 0.00^{c}$	$2.97 + 0.16^{d}$	$1.77 + 0.07^{e}$	$1.17 + 0.05^{c}$	$2.70 + 0.53^{d}$	$1.81 + 0.23^{be}$	$1.37 + 0.38^{f}$
16:0	$23.84 + 0.07^{a}$	$18.24 + 1.77^{b}$	$13.37 + 0.01^{c}$	$27.41 + 0.34^{d}$	$17.28 + 1.77^{b}$	$14.33 + 0.34^{e}$	$24.97 + 0.11^{a}$	$20.83 + 1.12^{f}$	$14.41 + 0.62^{e}$
17:0	$1.62 + 0.04^{a}$	$1.27 + 0.21^{b}$	$0.86 + 0.37^{c}$	$1.62 + 0.20^{a}$	$1.06 + 0.21^{cd}$	$1.14 + 0.05^{d}$	$1.31 + 0.05^{b}$	$1.33 + 0.17^{b}$	$1.04 + 0.11^{cd}$
18:0	$7.83 + 0.10^{a}$	$6.54 + 0.42^{b}$	$5.19 + 0.13^{b}$	$7.96 + 0.57^{a}$	$5.32 + 0.42^{c}$	$5.14 + 0.12^{c}$	$6.66 + 0.10^{b}$	$6.42 + 0.15^{b}$	$5.26 + 0.08^{c}$
ΣSaturated	$37.81 + 0.13^{a}$	$29.94 + 0.45^{b}$	$22.08 + 0.50^{c}$	$42.84 + 1.19^{d}$	$27.47 + 1.46^{b}$	$23.46 + 0.08^{d}$	$38.90 + 1.79^{a}$	$32.57 + 1.33^{e}$	$23.73 + 1.56^{cd}$
16:0 ant	$1.67 + 0.02^{a}$	$1.53 + 0.04^{b}$	$0.75 + 0.09^{c}$	$1.59 + 0.26^{ae}$	$0.79 + 0.05^{c}$	$0.86 + 0.01^{d}$	$1.46 + 0.27^{e}$	$0.95 + 0.24^{cd}$	$0.44 + 0.26^{f}$
ΣBranched	$2.33 + 0.02^{a}$	$2.00 + 0.06^{b}$	$1.04 + 0.10^{c}$	$2.48 + 0.37^{ae}$	$1.30 + 0.08^{d}$	$1.32 + 0.04^{d}$	$2.20 + 0.16^{e}$	$1.50 + 0.42^{f}$	$0.78 + 0.29^{g}$
16:1*n*-7	$9.55 + 0.15^{a}$	$8.05 + 0.21^{b}$	$4.33 + 0.24^{c}$	$12.88 + 2.58^{d}$	$6.90 + 0.32^{e}$	$4.81 + 0.19^{f}$	$13.75 + 0.06^{g}$	$8.50 + 0.33^{b}$	$4.26 + 0.20^{c}$
17:1*n*-8	$1.63 + 0.09^{a}$	$1.09 + 0.14^{b}$	$0.92 + 0.27^{bc}$	$1.63 + 0.17^{a}$	$0.80 + 0.14^{c}$	$0.72 + 0.02^{c}$	$1.27 + 0.19^{b}$	$1.12 + 0.17^{b}$	$0.75 + 0.18^{c}$
18:1*n*-9	$16.28 + 0.31^{a}$	$11.21 + 1.00^{b}$	$6.85 + 0.02^{c}$	$16.60 + 0.28^{a}$	$10.04 + 1.77^{b}$	$8.56 + 1.71^{c}$	$14.63 + 0.98^{d}$	$11.84 + 0.31^{b}$	$8.40 + 0.64^{c}$
18:1*n*-7	$6.47 + 0.30^{a}$	$5.34 + 0.49^{b}$	$4.38 + 0.08^{c}$	$7.25 + 0.95^{d}$	$4.75 + 0.49^{e}$	$4.85 + 0.37^{e}$	$7.25 + 0.45^{d}$	$6.50 + 1.83^{a}$	$4.14 + 0.34^{c}$
20:1*n*-7	$1.36 + 0.14^{a}$	$1.18 + 0.01^{b}$	$0.45 + 0.11^{c}$	$1.13 + 0.28^{b}$	$0.66 + 0.01^{b}$	$0.53 + 0.16^{cd}$	$1.07 + 0.18^{b}$	$0.77 + 0.12^{d}$	$0.55 + 0.15^{cd}$
ΣMonounsaturated	$36.45 + 0.45^{a}$	$27.99 + 1.12^{b}$	$17.50 + 0.51^{c}$	$41.47 + 0.56^{d}$	$24.46 + 1.12^{e}$	$20.30 + 2.30^{ce}$	$40.24 + 0.91^{d}$	$29.97 + 2.53^{b}$	$18.74 + 1.72^{c}$
16:4*n*-3	$3.53 + 0.25^{a}$	$2.95 + 0.20^{b}$	$1.40 + 0.14^{c}$	$2.19 + 0.31^{d}$	$1.08 + 0.20^{e}$	$1.01 + 0.13^{e}$	$2.34 + 0.14^{d}$	$1.68 + 0.59^{c}$	$1.11 + 0.36^{d}$
18:2*n*-6	$5.74 + 0.02^{a}$	$2.44 + 0.26^{b}$	$1.69 + 0.01^{c}$	$4.20 + 2.03^{d}$	$2.19 + 0.26^{e}$	$1.33 + 0.40^{c}$	$2.77 + 0.24^{b}$	$2.74 + 0.29^{b}$	$3.69 + 0.42^{f}$
18:3*n*-3	$3.92 + 0.40^{a}$	$2.15 + 0.45^{b}$	$1.27 + 0.09^{c}$	$5.09 + 0.48^{d}$	$1.51 + 0.45^{c}$	$1.45 + 0.42^{c}$	$2.15 + 0.13^{c}$	$2.23 + 0.98^{c}$	$2.06 + 0.55^{c}$
20:2*n*-6	$1.34 + 0.04^{a}$	$1.04 + 0.18^{b}$	$0.81 + 0.02^{c}$	$1.41 + 0.26^{a}$	$1.04 + 0.18^{b}$	$1.20 + 0.32^{a}$	$1.31 + 0.34^{a}$	$1.32 + 0.19^{a}$	$1.08 + 0.26^{b}$
20:4*n*-6	$6.73 + 0.06^{a}$	$5.61 + 0.25^{b}$	$4.06 + 0.14^{c}$	$6.33 + 0.85^{a}$	$5.20 + 0.25^{d}$	$4.62 + 0.20^{e}$	$5.68 + 0.43^{b}$	$4.98 + 0.87^{e}$	$4.35 + 0.65^{e}$
20:5*n*-3	$17.57 + 0.32^{a}$	$15.31 + 1.01^{b}$	$11.97 + 0.58^{c}$	$16.21 + 1.74^{ab}$	$15.23 + 1.99^{b}$	$11.83 + 0.64^{c}$	$16.43 + 1.68^{cb}$	$15.64 + 1.75^{b}$	$12.34 + 1.72^{c}$
22:5*n*-3	$2.76 + 0.02^{a}$	$1.87 + 0.09^{b}$	$1.20 + 0.06^{c}$	$2.89 + 0.33^{a}$	$2.35 + 0.09^{d}$	$1.93 + 0.17^{b}$	$3.58 + 1.57^{e}$	$2.59 + 0.42^{ad}$	$1.20 + 1.49^{b}$
22:6*n*-3	$12.70 + 0.40^{a}$	$13.27 + 0.71^{a}$	$8.01 + 0.00^{b}$	$11.99 + 1.91^{a}$	$8.02 + 0.74^{bc}$	$7.53 + 0.17^{c}$	$12.86 + 1.50^{a}$	$11.49 + 1.45^{a}$	$8.58 + 1.48^{bc}$
ΣPolyunsaturated	$57.61 + 0.26^{a}$	$47.44 + 1.83^{b}$	$31.63 + 0.94^{c}$	$53.85 + 3.02^{a}$	$38.73 + 1.83^{d}$	$32.79 + 0.32^{c}$	$50.82 + 3.34^{a}$	$45.13 + 4.85^{b}$	$35.75 + 4.09^{cd}$
Σ(*n*-3)	$42.56 + 0.22^{a}$	$37.14 + 1.85^{b}$	$24.55 + 0.76^{c}$	$40.80 + 0.43^{d}$	$29.47 + 1.85^{e}$	$24.87 + 0.50^{c}$	$40.16 + 4.62^{ad}$	$35.11 + 3.76^{b}$	$26.07 + 4.19^{c}$
Σ(*n*-6)	$15.05 + 0.04^{a}$	$10.30 + 0.02^{b}$	$7.08 + 0.18^{c}$	$13.05 + 3.45^{ab}$	$9.27 + 0.02^{d}$	$7.92 + 0.18^{e}$	$10.66 + 1.28^{bd}$	$10.02 + 1.09^{bd}$	$9.68 + 1.19^{bd}$
ΣTotal FA	$134.19 + 0.86^{a}$	$107.37 + 1.25^{b}$	$72.24 + 1.05^{c}$	$140.65 + 0.90^{d}$	$91.96 + 1.40^{e}$	$77.87 + 2.74^{f}$	$132.16 + 0.80^{a}$	$109.17 + 9.13^{b}$	$79.00 + 4.96^{f}$
Lipids (%DW)	$16.62 + 2.05^{a}$	$12.85 + 1.14^{b}$	$6.50 + 0.97^{c}$	$17.05 + 1.66^{a}$	$12.82 + 2.31^{b}$	$6.22 + 1.01^{c}$	$16.47 + 2.21^{a}$	$10.08 + 1.16^{b}$	$6.15 + 0.78^{c}$

Table 5 *Lysmata seticaudata*. Fatty acid composition (μg mg^{-1} dry weight) and lipid content (% dry weight) of eggs at different stages of embryonic development from small, medium and large simultaneous hermaphroditic (*SH*) Monaco shrimp in late reproductive season (*LRS*). Values are means (+SD) of triplicate samples. *Different superscript letters* within rows represent significant differences ($P < 0.05$)

Fatty acids (μg mg^{-1} DW)	Small SH			Medium SH			Large SH		
	I	II	III	I	II	III	I	II	III
14:0	$2.65 + 0.20^{a}$	$1.67 + 0.03^{b}$	$1.39 + 0.29^{c}$	$2.53 + 0.40^{a}$	$2.38 + 0.15^{a}$	$1.43 + 0.30^{c}$	$2.08 + 0.25^{d}$	$1.92 + 0.21^{d}$	$1.37 + 0.37^{c}$
16:0	$28.17 + 0.38^{a}$	$20.20 + 0.14^{b}$	$14.69 + 0.50^{c}$	$28.90 + 0.41^{a}$	$26.56 + 0.80^{d}$	$12.91 + 0.13^{e}$	$32.26 + 0.44^{f}$	$21.66 + 0.28^{g}$	$18.93 + 0.25^{h}$
17:0	$1.41 + 0.07^{a}$	$1.34 + 0.02^{b}$	$1.06 + 0.09^{c}$	$1.81 + 0.25^{d}$	$1.68 + 0.05^{d}$	$0.79 + 0.12^{e}$	$1.80 + 0.08^{d}$	$1.27 + 0.14^{b}$	$0.90 + 0.07^{e}$
18:0	$8.31 + 0.06^{a}$	$6.53 + 0.05^{b}$	$5.37 + 0.07^{c}$	$8.14 + 0.41^{a}$	$8.32 + 0.04^{a}$	$4.65 + 0.05^{d}$	$8.71 + 0.07^{e}$	$6.36 + 0.23^{b}$	$5.52 + 0.06^{f}$
ΣSaturated	$43.44 + 0.85^{a}$	$32.01 + 0.14^{b}$	$24.20 + 1.20^{c}$	$43.69 + 0.08^{a}$	$41.63 + 1.50^{a}$	$21.08 + 0.28^{d}$	$48.04 + 1.03^{e}$	$33.39 + 0.11^{f}$	$28.22 + 1.35^{g}$
16:0 ant	$1.41 + 0.13^{a}$	$0.94 + 0.00^{b}$	$0.45 + 0.19^{c}$	$1.50 + 0.11^{a}$	$0.90 + 0.06^{b}$	$0.41 + 0.01^{c}$	$1.47 + 0.16^{a}$	$0.52 + 0.05^{d}$	$0.45 + 0.13^{d}$
ΣBranched	$2.01 + 0.15^{a}$	$1.47 + 0.02^{b}$	$0.80 + 0.22^{c}$	$2.12 + 0.14^{a}$	$2.24 + 0.49^{a}$	$0.74 + 0.03^{c}$	$2.16 + 0.19^{a}$	$0.96 + 0.08^{c}$	$0.80 + 0.56^{c}$
16:1*n*-7	$10.70 + 0.22^{a}$	$9.16 + 0.24^{b}$	$4.35 + 0.21^{c}$	$12.80 + 1.49^{d}$	$10.30 + 0.23^{a}$	$3.07 + 0.95^{c}$	$14.98 + 0.21^{e}$	$8.03 + 0.86^{b}$	$5.64 + 0.22^{f}$
17:1*n*-8	$1.81 + 0.10^{a}$	$1.27 + 0.02^{b}$	$0.76 + 0.14^{c}$	$1.99 + 0.06^{a}$	$1.51 + 0.01^{d}$	$0.44 + 0.15^{e}$	$1.88 + 0.12^{a}$	$1.32 + 0.04^{b}$	$0.65 + 0.07^{ce}$
18:1*n*-9	$16.74 + 0.40^{a}$	$11.67 + 0.16^{b}$	$8.57 + 0.52^{ce}$	$16.37 + 0.47^{a}$	$14.30 + 1.90^{a}$	$6.30 + 1.09^{e}$	$20.03 + 0.46^{d}$	$12.20 + 0.32^{b}$	$9.42 + 1.21^{e}$
18:1*n*-7	$8.00 + 0.71^{a}$	$5.65 + 0.28^{b}$	$4.22 + 0.93^{c}$	$8.84 + 0.36^{a}$	$7.06 + 0.68^{d}$	$3.79 + 0.38^{c}$	$8.78 + 0.82^{a}$	$7.20 + 0.30^{d}$	$4.72 + 0.80^{c}$
20:1*n*-7	$1.20 + 0.09^{a}$	$0.90 + 0.03^{b}$	$0.56 + 0.12^{c}$	$2.29 + 0.26^{d}$	$1.27 + 0.05^{a}$	$0.32 + 0.02^{e}$	$1.60 + 0.11^{f}$	$1.08 + 0.14^{b}$	$0.52 + 0.08^{c}$
ΣMonounsaturated	$40.38 + 1.31^{a}$	$30.66 + 0.90^{b}$	$19.11 + 1.51^{c}$	$44.69 + 3.29^{a}$	$36.48 + 2.45^{d}$	$14.36 + 0.39^{e}$	$50.06 + 1.41^{f}$	$31.36 + 2.09^{b}$	$21.77 + 1.98^{c}$
16:4*n*-3	$2.46 + 0.21^{a}$	$2.18 + 0.05^{b}$	$1.13 + 0.29^{c}$	$3.12 + 0.08^{d}$	$2.50 + 0.36^{a}$	$0.93 + 0.02^{c}$	$3.22 + 0.25^{d}$	$2.24 + 0.07^{b}$	$1.25 + 0.32^{c}$
18:2*n*-6	$7.69 + 0.27^{a}$	$2.44 + 0.12^{b}$	$3.76 + 0.34^{ce}$	$4.15 + 0.24^{c}$	$6.44 + 2.70^{d}$	$3.24 + 0.41^{e}$	$3.27 + 0.30^{e}$	$4.54 + 0.68^{c}$	$6.55 + 1.52^{d}$
18:3*n*-3	$6.26 + 0.45^{a}$	$2.59 + 0.34^{b}$	$2.10 + 0.50^{b}$	$5.40 + 1.27^{a}$	$4.11 + 0.56^{d}$	$1.37 + 0.43^{e}$	$4.52 + 0.47^{d}$	$4.86 + 0.81^{d}$	$2.35 + 0.53^{b}$
20:2*n*-6	$1.41 + 0.16^{a}$	$1.23 + 0.06^{b}$	$1.10 + 0.21^{c}$	$1.55 + 0.11^{d}$	$1.41 + 0.16^{a}$	$0.86 + 0.02^{e}$	$1.77 + 0.19^{d}$	$1.33 + 0.03^{a}$	$0.96 + 0.18^{ce}$
20:4*n*-6	$7.92 + 0.47^{a}$	$5.89 + 0.30^{b}$	$4.43 + 0.56^{c}$	$6.96 + 0.72^{d}$	$6.07 + 0.11^{b}$	$2.98 + 0.89^{e}$	$6.43 + 0.52^{db}$	$5.40 + 0.51^{b}$	$3.15 + 0.34^{e}$
20:5*n*-3	$18.64 + 1.19^{a}$	$15.67 + 0.67^{b}$	$12.59 + 1.46^{c}$	$23.20 + 0.50^{d}$	$18.51 + 2.17^{a}$	$9.18 + 0.38^{e}$	$22.75 + 1.33^{d}$	$17.87 + 0.59^{a}$	$13.15 + 1.81^{c}$
22:5*n*-3	$3.55 + 0.78^{a}$	$2.87 + 0.07^{b}$	$1.22 + 0.14^{c}$	$6.32 + 0.94^{d}$	$3.42 + 0.91^{a}$	$1.07 + 0.38^{c}$	$7.43 + 0.96^{d}$	$3.84 + 0.50^{a}$	$2.47 + 1.02^{ac}$
22:6*n*-3	$11.49 + 0.71^{a}$	$9.88 + 0.09^{b}$	$8.75 + 1.13^{c}$	$9.59 + 1.55^{ab}$	$9.85 + 1.53^{ab}$	$5.96 + 0.69^{d}$	$9.91 + 0.51^{c}$	$8.38 + 0.82^{c}$	$8.48 + 1.83^{c}$
ΣPolyunsaturated	$63.22 + 2.92^{a}$	$45.40 + 1.76^{b}$	$36.46 + 3.51^{c}$	$64.69 + 7.02^{a}$	$55.27 + 2.08^{d}$	$26.70 + 1.80^{e}$	$63.49 + 3.22^{a}$	$52.25 + 4.39^{d}$	$39.75 + 2.79^{c}$
Σ(*n*-3)	$45.03 + 2.71^{a}$	$34.88 + 1.23^{b}$	$26.59 + 3.45^{c}$	$50.95 + 5.01^{ad}$	$40.43 + 0.68^{a}$	$19.30 + 3.18^{f}$	$51.23 + 3.08^{d}$	$40.51 + 3.12^{a}$	$28.71 + 2.06^{c}$
Σ(*n*-6)	$18.19 + 0.86^{a}$	$10.52 + 0.53^{b}$	$9.87 + 1.02^{b}$	$13.74 + 1.01^{c}$	$14.84 + 2.76^{ac}$	$7.40 + 0.38^{d}$	$12.26 + 0.94^{a}$	$11.74 + 1.27^{b}$	$11.03 + 1.89^{b}$
ΣTotal FA	$149.05 + 3.75^{a}$	$109.54 + 2.53^{b}$	$80.57 + 4.36^{c}$	$155.19 + 5.37^{af}$	$135.61 + 5.14^{d}$	$62.88 + 5.51^{e}$	$163.76 + 4.05^{f}$	$117.96 + 6.45^{b}$	$90.54 + 4.75^{c}$
Lipids (% DW)	$18.33 + 1.47^{a}$	$12.32 + 1.23^{b}$	$7.28 + 0.89^{c}$	$17.58 + 2.10^{a}$	$10.74 + 1.55^{b}$	$5.88 + 0.78^{d}$	$18.37 + 1.13^{a}$	$10.64 + 1.44^{b}$	$7.41 + 1.25^{c}$

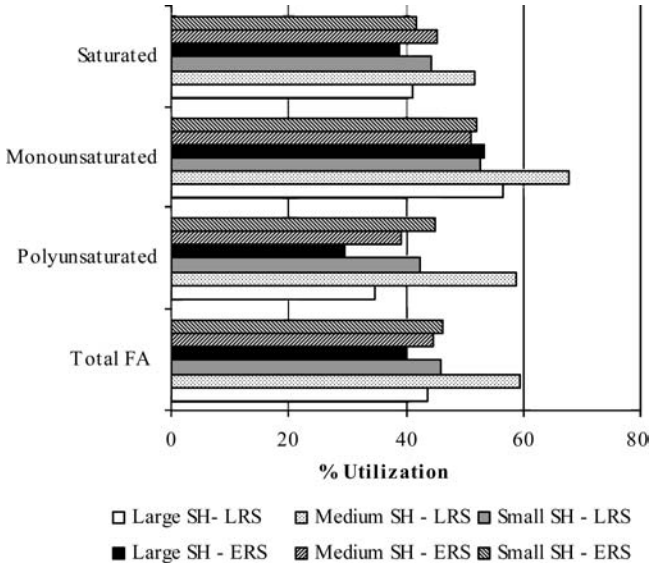

Fig. 4 *Lysmata seticaudata*. Percent utilization of fatty acid (*FA*) fractions during embryonic development of small, medium and large simultaneous hermaphroditic (*SH*) shrimp in early and late reproductive season (*ERS* and *LRS*, respectively)

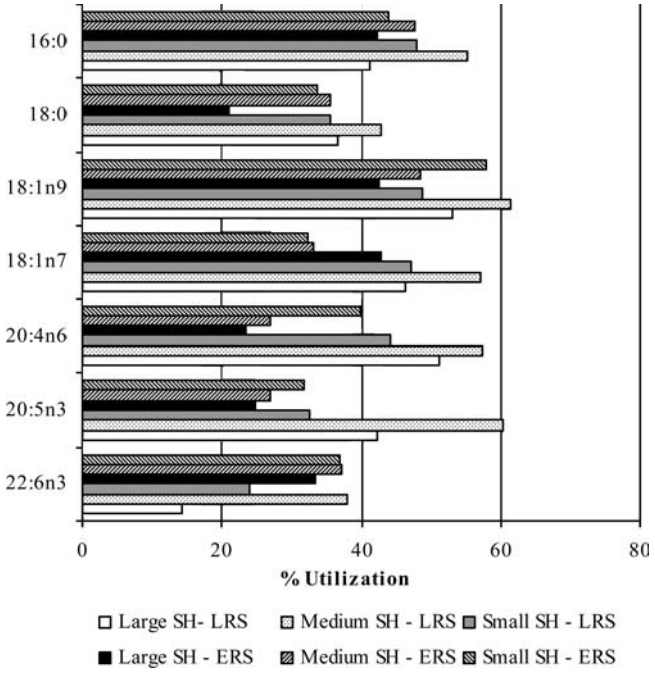

Fig. 5 *Lysmata seticaudata*. Percent utilization of selected fatty acids (*FA*) during embryonic development of small, medium and large simultaneous hermaphroditic (*SH*) shrimp in early and late reproductive seasons (*ERS* and *LRS*, respectively)

studies on decapod embryo physiology (Rosa et al. 2003) and the complex population ecology displayed by *Lysmata* species (Bauer 2002a, 2002b; Baldwin and Bauer 2003), only a combined effort of researchers working on decapod population dynamics, aquaculture, physiology and biochemistry will allow suitable culture protocols to be established.

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