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Reproductive performance, biochemical composition and fatty acid profile of wild-caught and 2nd generation domesticated *Farfantepenaeus duorarum* (Burkenroad, 1939) broodstock

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Abstract:

A 30-day trial was performed to evaluate the reproductive performance of wild and 2nd generation domesticated *Farfantepenaeus duorarum* broodstock. Changes in biochemical composition and fatty acids (FA) profile in the 1st and 4th spawn order females were used as indicators of nutritional condition. Wild population of *F. duorarum* presented significantly better reproductive outcomes as compared to domesticated ones. Wild spawners achieved significantly higher number of eggs per spawn, number of egg per spawn per g of spawner's body weight and number of nauplii per spawn ($P < 0.05$). Latency period was significantly shorter (P0.05) for wild than for domesticated females (11 vs 17 days). Wild spawners also presented less mortality (6 vs 12%), higher number of total spawns (51 vs 33), spawns per ablated and per spawning females as well as higher total eggs and nauplii production. On the other hand, domesticated females presented higher number of females that spawned at least once (89 vs 76%). The higher spawning activity was reflected in lower levels of acylglycerides (AG) and cholesterol content in wild hepatopancreas (HP) and ovary (OV) (Pb0.05). FA profile, mainly represented by ARA, EPA and sum of n−3 were higher in hepatopancreas and ovary of wild females, however lower levels were detected in eggs as a result of a high spawning activity. Multivariate analysis performed to detected simultaneous variation in biochemical variables indicated AG as variation pattern's responsive.

Highlights

► Original paper comparing the reproductive performance of wild and G2 *F. duorarum*. ► Interesting findings using biochemical composition/FA profile as a nutritional index. ► Multivariate analysis method contributed to explain the results. ► Wild population performed better reproductive performance.

Keywords: Fatty acids ; *F. duorarum* ; Lipids ; Pink shrimp ; Nutrition ; Reproduction

1. Introduction

Penaeid shrimp is a valuable ecological and economic resource, but the majority of its production, research and development efforts have been directed to only a few candidate species. Since current hatcheries predominantly focus on *Litopenaeus vannamei* and *Penaeus monodon*, the two most studied species, availability of other penaeid larvae and postlarvae are limited, depending mostly upon wild stocks. In addition, a variety of indigenous shrimp species, valuable for aquaculture as a source of possible virus-free and virus-resistant stocks, may present higher growth rates under specific environmental conditions, as well as better acceptance in local markets (Peixoto et al., 2011).

The pink shrimp *Farfantepenaeus duorarum* is naturally distributed in the western Atlantic Ocean from Maryland (EUA), through Gulf of Mexico until Ascensión Bay in Quintana Roo, Mexico (Pérez-Farfante, 1969). In recent years the relative importance of cultivating *F. duorarum* has increased due to signs of depletion in thewild fishery, inwhichwas a very important resource in southern Gulf of Mexico, but is currently collapsed (Arreguin-Sanchez et al., 2008). High yields were obtained during the early 70s, with approximately 27,000 t per year, of which 90% was *F. duorarum*, however yields dropped below 3000 t per year (Arreguin-Sanchez et al., 2008). Hypotheses suggested that this collapse is essentially represented by pollution in nursery areas (Arreguín-Sánchez et al., 1997); estuary and off-shore over-fishing (Gracia, 1995, 1997).

Previous studies have been considered *F. duorarum* for shrimp farming (Cripe, 1994; Gullian et al., 2010; Samocha et al., 2008)mainly focused on the localmarket value (López-Téllez et al., 2000). However, high costs associated with the capture of the wild stocks remain unsolved (Menasveta et al., 1993). To overcome this problem, research efforts have been performed in many penaeid species comparing wild vs domesticated stocks and evaluating several characteristics of reproductive

performance and spawn quality such as zootechnical parameters (Cavalli et al., 1997; Coman et al., 2006; Keys and Crocos, 2006; Menasveta et al., 1993; Palacios et al., 1999a), indicators of nutritional condition of broodstock, based on biochemical composition of hepatopancreas, hemolymph and/or ovary (Marsden et al., 2007; Nakayama et al., 2008; Palacios et al., 2000; Peixoto et al., 2008) or biochemical composition of eggs and nauplii as indicators of spawn quality (Palacios et al., 1998, 1999b; Regunathan, 2008). On the other hand, no studies had integrated all these approaches in the same work, clarifying the whole metabolic pathway of nutrients from food stored in hepatopancreas (HP), transported through the hemolymph to ovaries (OV), and then transferred to eggs and metabolized during their development to nauplii; as well as the associated reproductive performance and spawn quality.

Understanding the effect of different food sources on reproductive output will enable broodstock performance to be improved. Differences in food items ingested prior to ablation in wild such as benthos, rotifers, copepods, polychaetes, bivalves and other small crustaceans (Schwamborn and Criales, 2000; Soares et al., 2004, 2005); or in captivity such as pelleted feed, squid and mussels (Browdy, 1998; Cavalli et al., 1997; Marsden et al., 1992; Peixoto et al., 2008) may often give the broodstock an adequate nutrition. However, limitation in certain dietary nutrients occurs due to a seasonal and storage factors (Bray and Lawrence, 1992; Wouters et al., 2001a).

Spawning frequency is often used as an index of reproductive performance which is turn based on multiple spawning capacities that could be a desirable trait (Ibarra et al., 1997). However, it could also involve a decrease in spawn quality over consecutive spawns (Emmerson, 1980; Hansford and Marsden, 1995; Wouters et al., 1999), although this is not necessarily the case (Arcos et al., 2005a; Browdy and Samocha, 1985; Palacios and Racotta, 2003). So, rather than evaluating the spawning frequency itself, the analysis of the potential effect of spawn quality over consecutive spawns could be a useful tool to select the best condition or diet for optimal reproductive performance (Coman and Crocos, 2003; Marsden et al., 1997; Palacios et al., 1999a). Biochemical composition has been used as a tool to compare the physiological and immunological condition of *F. duorarum* wild population (Rosas et al., 2007), but few studies focused on broodstock and its relation with multiple spawns. Thus, the aim of this study is to evaluate the reproductive performance of wild-caught and domesticated *F. duorarum* broodstock using biochemical composition and FA profile as indicators of shrimp nutritional condition.

2. Materials and methods

2.1. Wild-caught broodstock

Wild adult *F. duorarum* were captured by bottom otter trawl in 15–25 m deep waters, off the coast of Campeche (19° 50′ N/91° 30′ W), Mexico. Animals were transported to the laboratory, selected based on body morphological integrity and acclimated for 1 week before the start of experiment.

2.2. Domesticated broodstock

Second generation tank-reared domesticated *F. duorarum* broodstock were raised at Unidad Multidiciplinaria de Docencia e Investigación (UMDI), Universidad Nacional Autónoma de México (UNAM), located at Sisal Beach (21°09′5/N and 90°02′5/W), Yucatán, Mexico. The two-stage culture system consisted of indoor 400 L larviculture tanks (nursery: until PL 20 stage) and 20,000 L round lined outdoor tanks covered by shade cloth, where PL were later transferred (grow-out tanks). The grow-out tank-reared culture system (20,000 L circular lined tanks; 1 m deep) consisted of water exchange about 25% per day and animals were fed *ad libitum* twice a day (09:00 and 17:00 h) with 35% crude protein dry pellets (Malta Clayton, Inc., Culiacan, Sinaloa, Mexico) during 15 months. Temperature, salinity, pH and dissolved oxygen (Hach HQ40d, Hach Company, Loveland, Colorado, USA) were monitored daily at 09:00 h and varied between 17–32 °C, 33–42 ppt, 7.4–8.5, and 3.9–6.9 mg L^{-1}, respectively. Animals were transported to the maturation room and selected followed by wild breeders.

2.3. Experimental design

During 30 days, reproductive performance trial was performed using four 12,000 L round lined maturation tank with recirculation system maintaining temperature stable (28 ± 1 °C). In each tank, groups of 17 females and 35 males from each source were stocked (female to male ratio 1:2 and stocking density of 4.3 shrimp m^{-2}). Two tanks were used to collect samples for biochemistry and FA and another two were used for trials on reproductive performance. Each female was considered an experimental unit (Nakayama et al., 2008). Animals were fed *ad libitum* three times per day (09:00, 01:00 and 20:00 h) alternating frozen squid, mussels, Artemia biomass and polychaetes.

2.4. Reproductive performance

Before the start of the trial, each female was weighed, unilaterally eyestalk ablated and tagged using silicon eye rings. Females with mature ovaries (ready-to-spawn) were identified daily at 18:00 h and transferred into separated 100 L circular tanks located in a temperature controlled spawning room (28–29 °C). Gentle aeration was supplied to each tank. The number of eggs and nauplii was estimated from five 4.7 mL replicate samples taken in spawning tanks, collected after gentle swirling. Fertilized and hatch rates of viable spawning were determined (Primavera and Posadas, 1981). Reproductive performance was evaluated in terms of latency period (interval between eyestalk ablation and first spawn), females that spawn at least once (%), mortality (%), total spawns, unfertilized spawns, number of spawns per ablated females, number of spawns per spawning female, maximum spawn order, number of egg and nauplii per spawn, fertilization and hatching rate. Larval body length and weight from first spawns of different origins were also measured in stages of $zoea_I$, $mysis_I$ and PL_I.

2.5. Samples collection

HP and OV were collected from wild and domesticated ripe females in the 1st and 4th spawn order. HP and OV were removed through an incision on the back of the cephalothorax and dorsal region of the entire abdomen length, respectively. The samples were weighed, placed in a 1.5 mL Eppendorf tube, immediately frozen in liquid nitrogen and preserved at −80 °C for further biochemical and FA analysis. Hepatosomatic index (HSI) and gonadosomatic index (GSI) were calculated as a percentage of the hepatopancreas and ovarian weight, respectively, relative to the body weight.

Hemolymph (100 μL) was sampled according to Pascual et al. (2003) to assess hemocyanin and biochemical composition. Eggs and nauplii were collected directly from spawning and hatching tanks, respectively. The samples were carefully dried with a scarf paper, weighed, placed in a 1.5 mL Eppendorf tube, immediately frozen in liquid nitrogen and also preserved at −80 °C for further analysis. Number of samples collected (according availability of spawns over time) for domesticated 1st and 4th spawns and wild 1st and 4th spawns were: HP, hemolymph and OV: 6, 6, 5 and 3; eggs and nauplii: 6, 6, 9 and 6, respectively.

2.6. Biochemical composition

Changes in metabolite levels of wild and domesticated broodstock at different spawn order (1st and 4th) were performed in hemolymph (acylglycerides "AG", cholesterol, glucose and total soluble proteins "TSP") and in HP, OV, eggs and nauplii (AG, cholesterol and

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TSP). The indices including acylglycerides/total soluble protein (AG: TSP) and acylglycerides/cholesterol (AG:C) were calculated in HP, OV, eggs and nauplii using the metabolite data following specification given by Mourente and Rodríguez (1997) and Palacios et al. (1998).

HP, OV, eggs and nauplii were homogenized in 500 ml of distilled water for 2 min. Aliquots of 10 μL were taken to determine AG and cholesterol with 200 μL of reactive solution (kits ELITech TGML-0427 and ELITech CHSL-0507, respectively; ELITech Group, Puteaux, France). The remaining sample was centrifuged at 800 *g* for 20 min at 4 °C, and 10 μL of the supernatant was collected in Eppendorf tubes to determine TSP with 200 μL of reactive solution (Bradford, 1976). Solutions were placed in microplates and incubated in an oven for 7, 5 and 5 min in 37, 37 and 24 °C for AG, cholesterol and TSP, respectively. Immediately, samples were read in an ELISA lector (Biorad 550, Bio-Rad Inc., Richmond, CA, USA) at 500 nm of absorbance length for AG and cholesterol; and 595 nm for total protein. A blank was considered with distilled water and the final concentrations ($\mu g\ g^{-1}$) were calculated from a calibration curve, in which the standard was the substrate that acts as the reagent in the kit.

To obtain metabolite concentrations in hemolymph, it was extracted and diluted using anticoagulant solution (Vargas-Albores et al., 1993) considering a hemolymph-anticoagulant ratio equal to 1:2. The hemolymph plus anticoagulant was centrifuged at 800 *g* for 3 min at 4 °C and the supernatant was collected in Eppendorf tubes. Glucose (kit ELITech GPSL-5505, ELITech Group, Puteaux, France), cholesterol, AG and TSP (Bradford, 1976) determinations were made in aliquots of 10 μL with 200 μL of reactive solution. Samples were immediately placed in microplates, incubated and read in an ELISA lector. Anticoagulant solution was used as a blank. Same incubation time, absorbance length and calculations of final concentration ($\mu g\ mL^{-1}$) were made as described above, except by glucose with 2 min of incubation time in 37 °C at 500 nm of absorbance length.

For hemocyanin measurements, 10 μL of hemolymph was immediately diluted in 990 μL of distilled water in a 10 mm cuvette for UV-wavelength spectroscopy (1.0 mL; 1 cm path length), and the absorbance was measured at 335 nm. The final concentration ($mmol\ L^{-1}$) was determined according to Chen and Cheng (1993) using the coefficient of extinction of hemocyanin (17.26) and factor of dilution (1:100).

2.7. Fatty acid profile

The FA profile of 1st and 4th spawn order (HP and OV samples) and 1st to 4th spawn order (eggs samples) were measured in wild and domesticated populations. Pooled samples were maintained at −80 °C and then freeze-dried prior to analysis. Number of organisms or spawns per pooled sample is given in Section 2.5, except by eggs from 1st to 4th in both domesticated and wild with 9, 6, 6 and 6 spawns per pooled sample, respectively. Samples were homogenized and 50 to 100 mg subsamples were taken. Lipids were extracted with methylene chloride: methanol (2:1, v/v) according to a modification of Folch extraction procedure (Folch et al., 1957). Lipid extracts were saponified with 20% KOH:Methanol (w:v) and free FA were recovered in hexane from acidified saponifiable fraction (pH = 1–2). FA methyl esters (FAME) were obtained by esterification with 10% BF_3 in methanol (Fluka-Boron trifluoride-methanol solution, 15716, Sigma-Aldrich Co., St Louis, Missouri, USA) for 60 min at 80 °C. FAME were analyzed by capillary gas chromatography in a Perkin Elmer Clarus 500 GC (Perkin Elmer Inc., Shelton, Connecticut, USA) equipped with a Perkin Elmer Elite-WAX capillary column (30 m × 0.25 mm × 0.25 μm film thickness, crossbond—PEG, Perkin Elmer Inc., Shelton, Connecticut, USA) and a flame ionization detector (FID). Hydrogen was used as carrier gas with a flow rate of $40\ mL\ min^{-1}$. Injector and detector temperatures were programmed to 280 °C and 250 °C, respectively. Column temperature was programmed from 40 to 200 °C at 20 °C min^{-1} and from 200 to 250 °C at 2.5 °C min^{-1}. FAME were identified by comparing retention times with reference standards (Supelco 37 Component FAME Mix, 47885-U and Fluka-Nonadecanoic acid, 72332, Sigma-Aldrich Co., St Louis, Missouri, USA) and results were reported as area percentages.

2.8. Statistical analysis

Two-way ANOVA followed by a Tukey test for unequal *N* post-hoc mean comparisons were performed to assess significant differences in biochemical composition, HSI and GSI, using origin (O: wild and domesticated) and spawn order (S: first and fourth spawn order) as categorical factors in the model. For reproductive performance Student's t-test was applied to find the differences among the treatments when data were homogeneous and normality distributed (Zar, 1984). Percentage data were arcsin transformed, but only original values were presented. Differences were considered significant at $P<0.05$ (Sokal and Rohlf, 1995).

Multivariate analysis using Empirical Orthogonal Function "EOF" (Von Storch and Zwiers, 2001) was performed to detected simultaneous variation on biochemical parameters, determining the underlying patterns of temporal variation (1st and 4th spawn order) of AG, cholesterol and TSP performed in HP, OV, hemolymph, eggs and nauplii. Using Matlab 5.3 software (MathWorks Inc., Natick, MA, USA), the EOF analysis allowed us to identify not only the joint variation patterns, but we were also able to maximize the overall variance and capture the more energetic modes of variation (three in total), where "mode 1" is the most energetic mode (for review, see Gomez-Valdes and Jeronimo, 2009). Furthermore, this analysis detected the variation pattern responsive described as the most energetic variable (MEV), expressed in % of the total mode 1 energy retention. EOF analysis were performed using $x_n = \frac{x-\bar{x}}{\sigma}$ transformed data where x_n is the new data, with the aim to normalized variables with different scale (i.e. $mg\ dL^{-1}$ and $mg\ g^{-1}$). In addition, nutritional status pyramids were built using $log_{10}+1$ transformed data from AG, cholesterol and TSP biochemical data from all tissues.

3. Results

3.1. Reproductive performance

Results of reproductive performance and morphometric parameters are given in Table 1. Wild spawners achieved significantly better results ($P<0.05$) in terms of number of egg per spawn, number of egg per spawn per g of spawner's body weight and number of nauplii per spawn compared to domesticated spawners (71.9, 2.6 and 51.9×10^3 for wild spawners and 33.5, 1.7 and 25.6×10^3 for domesticated ones, respectively). Latency period was significantly shorter for wild than for domesticated females (11 vs 17 days). Wild spawners also presented less mortality (6 vs 12%), higher number of total spawns (51 vs 33), spawns per ablated and per spawning females (3.0 and 3.9 for wild and 1.9 and 2.2 for domesticated, respectively) and achieved better total eggs and nauplii production (3306 and 2334 for wild and 1,071 and 487×10^3 for domesticated females). On the other hand, domesticated females presented higher number of females that spawned at least once (89 vs 76%). Number of nauplii per spawn per g of spawner's body weight, females weight, fertilization rate and hatch rate presented no significant differences between treatments ($P>0.05$). Larval weight and length (zoea, mysis and postlarvae stage I) were significantly higher coming from wild compared to domesticated females ($P<0.05$).

Cumulative spawning given in Fig. 1 indicated that wild females started to spawn on the 3rd day, unlike domesticated ones that did on the 8th day and maintained a higher spawn rate until the end of the experiment. Number of eggs per spawn order and maximum spawn order is given in Fig. 2. Overall results showed that wild females increased the number of eggs per spawn over time whereas domesticated ones decreased their production. Wild females presented

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Table 1
Reproductive performance and morphometric parameters (means ± SD) of domesticated (G2) and wild F. duorarum broodstock in a 30-d experimental period.

	Domesticated	Wild	Significance level
Reproductive parameters			
Female mortality (%)	12	6	NA
Total spawns	33	51	NA
Unfertilized spawns	4	3	NA
Number of spawn/ablated female	1.9	3.0	NA
Number of spawn/spawning female	2.2	3.9	NA
Latency period (days)	17 ± 7^{a}	11 ± 8^{b}	*
Spawning females[1] (%)	89	76	NA
Number of egg per spawn ($\times 10^3$)	33.5 ± 11.2^{b}	71.9 ± 34.5^{a}	***
Number of egg per spawn ($\times 10^3$) per g of female's body weight	1.7 ± 0.6^{b}	2.6 ± 1.3^{a}	***
Fertilization rate (%)	73.3 ± 24.2	85.1 ± 14.8	ns
Number of nauplii per spawn ($\times 10^3$)	25.6 ± 12.5^{b}	51.9 ± 31.8^{a}	***
Number of nauplii per spawn ($\times 10^3$) per g of spawner's body weight	1.3 ± 0.6	1.8 ± 1.1	ns
Hatch rate (%)	70.6 ± 19.2	68.1 ± 21.8	ns
Total eggs production ($\times 10^3$)	1071.8	3306.8	NA
Total nauplii production ($\times 10^3$)	487.5	2334.1	NA
Morphometric parameters			
Female weight (g)	19.6 ± 2.2	25.9 ± 5.0	ns
Zoea[2] weight (mg)	5.4 ± 0.3^{b}	6.4 ± 0.3^{a}	*
Zoea[2] length (μm)	911.5 ± 24.6^{b}	923.7 ± 28.5^{a}	***
Mysis[2] weight (mg)	56.2 ± 11.3^{b}	73.8 ± 12.1^{a}	***
Mysis[2] length (mm)	2.9 ± 1.3^{b}	3.2 ± 1.8^{a}	***
Postlarvae[2] weight (mg)	135.1 ± 21.5^{b}	151.1 ± 25.3^{a}	***
Postlarvae[2] length (mm)	4.4 ± 1.3^{b}	4.5 ± 1.8^{a}	***

Within rows, superscript letters indicate significant differences by Student's T test (*$P<0.05$; **$P<0.01$; ***$P<0.001$; *ns = no significant difference*).
NA = statistics not applicable
[1]Females that spawn at least once
[2]morphometric values of larval stage 1.

7 maximum consecutive spawns, whilst domesticated population only presented 4. HSI and GSI are shown in Fig. 3. No significant differences were observed ($P>0.05$), except by lower HSI in 1st spawn for wild females.

3.2. Biochemical composition and FA profile

The biochemical composition and FA profile results are given in Tables 2–4, respectively. Due to technical problems, FA measured in eggs from 4th spawn order was lost in domesticated samples. Significantly lower levels of AG in HP were observed in 1st spawn wild females than in domesticated females ($P<0.05$). Cholesterol levels (1st and 4th spawn order) were also lower in wild females than compared to domesticated ones ($P<0.05$). This trend were followed by lower ratios of AG:TSP and AG:C in 1st spawn wild population ($P<0.05$). On the other hand, TSP levels presented no significant differences between treatments ($P>0.05$). FA profile performed in HP

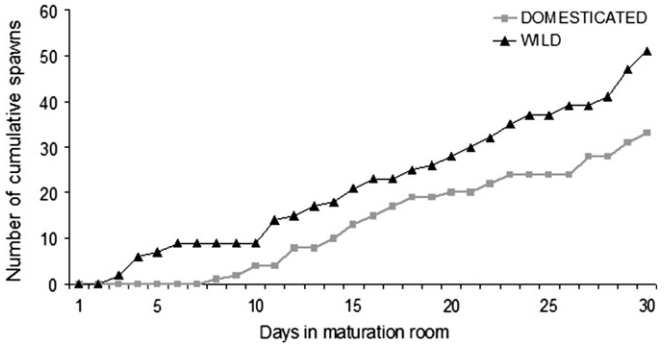

Fig. 1. Cumulative spawns of domesticated (G2) and wild *F. duorarum* broodstock in a 30-d experimental period from ablation.

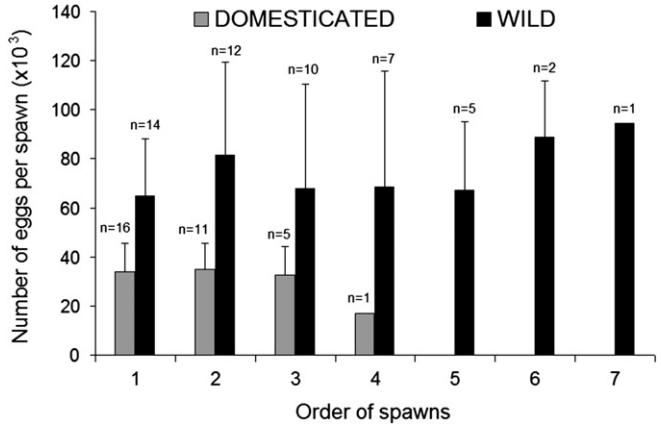

Fig. 2. Number of eggs per spawn (means ± SD) in each spawn order from domesticated (G2) and wild *F. duorarum* broodstock in a 30-d experimental period.

showed that linoleic acid (LA), linolenic acid (ALA) and docosahexaenoic acid (DHA) mean levels were higher in domesticated females (3.6, 1.1 and 9.7%, respectively) as compared to wild ones (2.3, 0.6 and 8.8%), whereas arachidonic acid (ARA), eicosapentanoic acid (EPA), sum of n-3 and sum of n-6 were higher in wild females (5.0, 10.0 and 19.4 and 7.8%, respectively) as compared to their domesticated counterparts (1.9, 3.3, 14.0 and 5.8%). ARA, sum of n-3 and sum n-6 levels decreased over time (1st to the 4th spawn order) in both populations. On the other hand, LA, ALA and DHA levels increased over time in wild females contrasting with DHA levels that substantially decreased in domesticated females (14.9 to 4.4%).

In hemolymph, TSP levels presented no differences in 1st spawn between domesticated and wild and 4th spawn for wild (107.2, 95.7 and 100.7 mg mL^{-1}, respectively), but it was different in 4th spawn domesticated females ($P<0.05$) with higher levels (179.8 mg mL^{-1}). Lower levels of glucose (17.7 mg dL^{-1}) were observed in 1st spawn wild females and hemocyanin levels were both lower in 1st and 4th spawn wild females ($P<0.05$) than domesticated ones.

In OV, significantly lower levels of AG (15.8 mg g^{-1}) were observed in 1st spawn domesticated females. Other metabolites

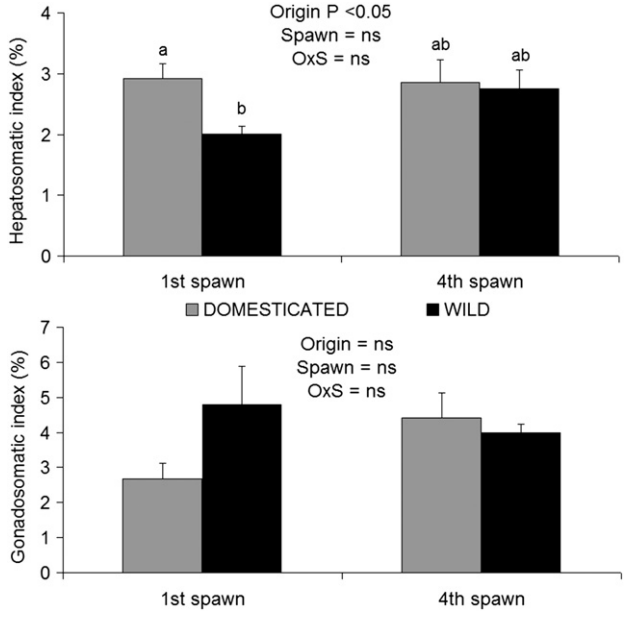

Fig. 3. Means (± SE) of hepatosomatic index and gonadosomatic index from 1st and 4th spawn order of domesticated (G2) and wild *F. duorarum* broodstock in a 30-d experimental period.

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Table 2
Means (±SE) of biochemical analysis performed in hepatopancreas, hemolymph, ovary, eggs and nauplii from 1st and 4th spawn order of domesticated (G2) and wild F. duorarum broodstock in a 30-d experimental period.

	Domesticated		Wild		Significance level[+]		
Variable	1st spawn	4th spawn	1st spawn	4th spawn	*Origin*	*Spawn*	*OxP*
Hepatopancreas	*(n = 6)*	*(n = 6)*	*(n = 5)*	*(n = 3)*			
Acylglycerides (mg g^{-1})	66.5 ± 10.3^{a}	32.7 ± 9.1^{b}	9.1 ± 2.0^{b}	91.0 ± 2.4^{a}	ns	*	***
Cholesterol (mg g^{-1})	2.2 ± 0.3^{ab}	2.7 ± 0.03^{a}	1.6 ± 0.2^{b}	1.4 ± 0.3^{b}	***	ns	ns
Total sol. protein (mg g^{-1})	28.2 ± 1.1	30.4 ± 0.5	30.4 ± 0.9	25.6 ± 1.5	ns	ns	**
AG:TSP	2.4 ± 0.4^{a}	1.6 ± 0.2^{b}	0.4 ± 0.5^{c}	2.4 ± 1.2^{a}	ns	*	***
AG:C	31.8 ± 5.6^{ab}	18.1 ± 1.9^{b}	6.9 ± 0.4^{c}	41.4 ± 21.7^{a}	ns	***	***
Hemolymph	*(n = 6)*	*(n = 6)*	*(n = 5)*	*(n = 3)*			
Acylglycerides (mg dL^{-1})	62.4 ± 10.4	53.5 ± 7.7	90.8 ± 25.2	65.8 ± 24.7	ns	ns	ns
Cholesterol (mg dL^{-1})	22.1 ± 4.1	24.0 ± 1.9	23.2 ± 2.6	30.6 ± 2.8	ns	ns	ns
Total sol. protein (mg mL^{-1})	107.2 ± 16.2^{b}	179.8 ± 16.0^{a}	95.7 ± 5.7^{b}	100.7 ± 22.5^{ab}	*	*	ns
Glucose (mg dL^{-1})	29.9 ± 3.3^{a}	23.5 ± 2.1^{ab}	17.7 ± 2.0^{b}	29.7 ± 6.0^{ab}	ns	ns	*
Hemocyanin (mmol L^{-1})	2.1 ± 0.2^{a}	2.2 ± 0.2^{a}	1.2 ± 0.3^{b}	1.3 ± 0.3^{b}	**	ns	ns
Ovary	*(n = 6)*	*(n = 6)*	*(n = 5)*	*(n = 3)*			
Acylglycerides (mg g^{-1})	15.8 ± 1.4^{b}	32.9 ± 6.5^{a}	26.5 ± 2.4^{ab}	34.4 ± 2.4^{a}	*	*	ns
Cholesterol (mg g^{-1})	0.6 ± 0.04	0.96 ± 0.2	1.0 ± 0.3	0.9 ± 0.2	ns	ns	ns
Total sol. protein (mg g^{-1})	25.9 ± 2.7	41.8 ± 7.1	38.9 ± 7.6	37.9 ± 1.7	ns	ns	ns
AG:TSP	0.7 ± 0.1	0.6 ± 0.1	0.8 ± 0.5	0.6 ± 0.2	ns	ns	ns
AG:C	29.5 ± 3.5	34.7 ± 6.8	37.3 ± 10.0	30.2 ± 12.9	ns	ns	ns
Eggs	*(n = 9)*	*(n = 6)*	*(n = 9)*	*(n = 6)*			
Acylglycerides (mg g^{-1})	19.5 ± 0.8^{b}	24.4 ± 0.9^{a}	24.7 ± 0.9^{a}	23.9 ± 1.3^{a}	*	*	**
Cholesterol (mg g^{-1})	7.4 ± 0.2	6.7 ± 0.8	6.8 ± 0.3	6.5 ± 0.4	ns	ns	ns
Total sol. protein (mg g^{-1})	122.2 ± 13.4^{b}	181.6 ± 17.9^{a}	113.7 ± 10.8^{b}	176.6 ± 32.8^{a}	ns	***	ns
AG:TSP	0.2 ± 0.2^{ab}	0.1 ± 0.1^{b}	0.2 ± 0.2^{ab}	0.4 ± 0.1^{a}	**	ns	ns
AG:C	2.7 ± 0.2^{b}	3.9 ± 0.3^{a}	3.7 ± 0.2^{a}	3.7 ± 0.3^{a}	ns	*	*
Nauplii	*(n = 9)*	*(n = 6)*	*(n = 9)*	*(n = 6)*			
Acylglycerides (mg g^{-1})	13.6 ± 0.5	12.3 ± 1.2	13.2 ± 0.6	13.9 ± 0.9	ns	ns	ns
Cholesterol (mg g^{-1})	3.2 ± 0.2^{b}	4.9 ± 0.8^{a}	3.7 ± 0.2^{b}	4.3 ± 0.2^{a}	ns	**	ns
Total sol. protein (mg g^{-1})	72.9 ± 5.5^{a}	62.5 ± 8.6^{a}	42.3 ± 2.3^{b}	33.2 ± 7.3^{b}	***	ns	ns
AG:TSP	0.6 ± 0.2	0.5 ± 0.3	0.3 ± 0.2	0.8 ± 0.3	ns	ns	ns
AG:C	4.4 ± 0.2^{a}	3.0 ± 0.3^{b}	3.7 ± 0.2^{ab}	3.3 ± 0.3^{ab}	ns	**	ns

Within rows, superscript letters indicate significant differences by Post-hoc Tukey test (P = 0.05).
[+]Bi-factorial ANOVA where **P<0.05; **P<0.01; ***P<0.001; ns = no significant difference*

presented no significant differences (P > 0.05). LA, ALA, DHA and sum of n-3 mean levels were higher in domesticated females (2.6, 0.8, 15.1 and 26.3%, respectively) as compared to wild ones (2.2, 0.5, 9.9 and 22.4%), whereas ARA, EPA and sum of n-6 were higher in wild females (4.9, 12.0 and 7.3%, respectively) than in their domesticated counterparts (3.3, 10.5 and 5.9%). Moreover, LA, ALA and sum of n-6 levels decreased over time in domesticated population, as well as ARA and EPA in wild ones. On the other hand, LA, sum of n-3 and mainly DHA (6.6 to 13.2%) increased over time in wild population (Table 3).

Eggs from 1st spawn domesticated females presented significantly the lowest values of AG (P<0.05). TSP levels increased in 4th spawns eggs in both origins (P<0.05). In domesticated population, AG:TSP ratio was significantly lower and AG:C increased over time (P<0.05) (Table 2). FA profile measured in eggs (Table 4) showed that LA, ALA, ARA and sum of n-6 levels were similar and maintained stable over time in both treatments. On the other hand, EPA, DHA and sum of n-3 mean levels were higher in domesticated eggs (7.5, 10.1 and 18.4%, respectively) and increased over time as compared to low mean levels of wild ones (6.6, 8.5 and 15.7%) in which EPA, DHA and sum of n-3 levels decreased from 1st to the 2nd spawn order and then increased over time.

In nauplii, 1st spawn domesticated females presented the lowest levels of cholesterol with 3.2 mg g^{-1} although not significantly different with wild ones (3.7 mg g^{-1}). However, both 4th spawns origins presented significantly higher values with 4.9 and 4.3 mg g^{-1} for domesticated and wild, respectively (P<0.05). TSP levels were lower in wild population for both 1st and 4th spawn order (P<0.05). AG:C ratio decreased as the spawn order increased both in wild and domesticated females (P<0.05). AG and AG:TSP presented no differences between treatments (P > 0.05).

3.3. Multivariate analysis

EOF energetic modes of variation and percentage of the total mode 1 energy for the most energetic variable (MEV) are summarized in Table 5. Results indicated that overall variance was captured in more than 80% for mode 1, except by 1st spawn OV data for wild and domesticated as well as 4th spawn OV data for domesticated females. AG was the MEV and responded for most variance with energy retention with more than 85% in all cases. AG as MEV was also showed in Fig. 4 that includes the biochemical status of 1st and 4th spawn, indicating the same general trend for both origins in all tissues.

4. Discussion

4.1. Reproductive performance

In the past years, many studies reported a better reproductive performance in wild populations as compared to domesticated ones (Keys and Crocos, 2006; Menasveta et al., 1993; Mendoza, 1997; Regunathan, 2008). These results have been explained by the high pressure in natural selection suffered by wild populations (selecting the strongest and healthiest animals) as well as the consumption of high quality variety natural food items in wild. On the other hand, domesticated conditions offer a limited variety of food items, mainly based

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Table 3
Fatty acids profile (described as % of total fatty acids) measured in hepatopancreas and ovary from 1st and 4th spawn order of domesticated (G2) and wild *F. duorarum* broodstock in a 30-d experimental period.

	Hepatopancreas										Ovary									
	Domesticated					Wild					Domesticated					Wild				
Fatty acid	1st	4th	*Means*		*SD*	1st	4th	*Means*		*SD*	1st	4th	*Means*		*SD*	1st	4th	*Means*		*SD*
C14:0	2.8	3.8	*3.3*	±	*0.7*	2.2	3.5	*2.9*	±	*0.9*	1.8	2.3	*2.1*	±	*0.4*	3.4	2.0	*2.7*	±	*0.9*
C15:0	0.9	1.2	*1.1*	±	*0.2*	2.5	1.0	*1.7*	±	*1.1*	0.5	0.4	*0.5*	±	*0.1*	3.3	0.5	*1.9*	±	*2.0*
C16:0	28.5	30.4	*29.4*	±	*1.4*	20.3	31.9	*26.1*	±	*8.2*	21.7	24.3	*23.0*	±	*1.9*	20.7	21.7	*21.2*	±	*0.7*
C16:1 n-7	6.7	8.8	*7.7*	±	*1.5*	7.2	6.3	*6.7*	±	*0.7*	4.6	6.4	*5.5*	±	*1.3*	10.4	4.9	*7.6*	±	*3.9*
C17:0	1.1	1.3	*1.2*	±	*0.1*	4.3	1.5	*2.9*	±	*2.0*	1.1	1.0	*1.0*	±	*0.1*	3.6	0.9	*2.2*	±	*1.9*
C18:0	5.0	6.1	*5.6*	±	*0.8*	10.9	7.1	*9.0*	±	*2.7*	7.0	6.9	*6.9*	±	*0.1*	6.8	5.9	*6.4*	±	*0.6*
C18:1 n-7	8.0	9.5	*8.7*	±	*1.1*	4.6	5.4	*5.0*	±	*0.6*	5.5	4.6	*5.1*	±	*0.6*	5.4	5.3	*5.3*	±	*0.1*
C18:1 n-9	13.9	17.6	*15.8*	±	*2.6*	8.8	12.5	*10.6*	±	*2.6*	18.2	19.2	*18.7*	±	*0.8*	12.9	20.9	*16.9*	±	*5.7*
C18:2 n-6 (LA)	3.7	3.4	*3.6*	±	*0.3*	0.6	3.9	*2.3*	±	*2.3*	3.6	1.6	*2.6*	±	*1.4*	0.8	3.6	*2.2*	±	*2.0*
C18:3 n-3 (ALA)	1.3	0.8	*1.1*	±	*0.3*	0.4	0.8	*0.6*	±	*0.3*	1.0	0.5	*0.8*	±	*0.4*	0.5	0.6	*0.5*	±	*0.1*
C18:3 n-6	0.1	0.3	*0.2*	±	*0.1*	0.2	0.1	*0.1*	±	*0.1*	0.0	0.0	*0.0*	±	*0.0*	0.0	0.3	*0.1*	±	*0.2*
C20:0	0.2	0.2	*0.2*	±	*0.0*	0.4	0.3	*0.4*	±	*0.1*	0.5	0.5	*0.5*	±	*0.0*	0.5	0.5	*0.5*	±	*0.0*
C20:1 n-9	3.7	4.6	*4.2*	±	*0.6*	1.0	3.3	*2.2*	±	*1.6*	1.5	2.0	*1.8*	±	*0.3*	0.8	2.4	*1.6*	±	*1.1*
C20:2	1.0	0.9	*1.0*	±	*0.1*	1.7	0.8	*1.3*	±	*0.7*	0.6	0.5	*0.6*	±	*0.1*	1.1	0.8	*0.9*	±	*0.3*
C20:3 n-6	0.3	0.0	*0.1*	±	*0.2*	0.5	0.3	*0.4*	±	*0.1*	0.2	0.0	*0.1*	±	*0.1*	0.0	0.2	*0.1*	±	*0.2*
C20:4 n-6 (ARA)	2.3	1.6	*1.9*	±	*0.5*	8.0	2.0	*5.0*	±	*4.2*	3.2	3.3	*3.3*	±	*0.0*	6.4	3.3	*4.9*	±	*2.2*
C20:5 n-3 (EPA)	3.3	3.3	*3.3*	±	*0.0*	13.4	6.6	*10.0*	±	*4.8*	10.8	10.1	*10.5*	±	*0.5*	13.0	11.0	*12.0*	±	*1.4*
C22:6 n-3 (DHA)	14.9	4.4	*9.7*	±	*7.4*	8.0	9.5	*8.8*	±	*1.1*	15.6	14.5	*15.1*	±	*0.8*	6.6	13.2	*9.9*	±	*4.7*
∑ Saturated	38.5	43.0	*40.7*	±	*3.2*	40.6	45.4	*43.0*	±	*3.4*	32.6	35.5	*34.1*	±	*2.0*	38.2	31.6	*34.9*	±	*4.7*
∑ Monounsaturated	32.4	40.5	*36.4*	±	*5.8*	21.6	27.4	*24.5*	±	*4.1*	29.8	32.3	*31.0*	±	*1.7*	29.4	33.5	*31.5*	±	*2.9*
∑ n-3	19.5	8.6	*14.0*	±	*7.7*	21.8	17.0	*19.4*	±	*3.4*	27.5	25.1	*26.3*	±	*1.7*	20.0	24.8	*22.4*	±	*3.4*
∑ n-6	6.5	5.2	*5.8*	±	*0.9*	9.3	6.3	*7.8*	±	*2.1*	7.1	4.8	*5.9*	±	*1.6*	7.2	7.4	*7.3*	±	*0.2*
(n-3)/(n-6)	3.0	1.6	*2.3*	±	*1.0*	2.3	2.7	*2.5*	±	*0.2*	3.9	5.2	*4.6*	±	*0.9*	2.8	3.3	*3.1*	±	*0.4*

on dry commercial pellet and a relatively limited choice of fresh or frozen items such as squid, mussels, worms, Artemia biomass and others.

The spawning frequency or number of spawns per time unit is considered as an important criterion to evaluate broodstock performance (Ibarra et al., 2007). In the present study, wild females had 1.7 times more spawns per spawning female than domesticated females. Wild females spawned 3.9 times per spawning female as an average, with a maximum of 7 spawns during 30 days compared to 4 reached by domesticated females. These values are higher than observed in wild or domesticated *Penaeus esculentus* (Keys and Crocos, 2006), *F. paulensis* (Peixoto et al., 2008) *Fenneropenaeus indicus* (Regunathan, 2008) and *L. stylirostris* (Mendoza, 1997) but similar than those reported for pond-reared *L. stylirostris* (Wabete et al., 2006), *L. vannamei* (Arcos et al., 2003) and wild and pond-reared *P. monodon* with max. of 7 and 3 maturations per female, respectively (Menasveta et al., 1993).

Latency period is directly related to the capacity of multiple spawning (Arcos et al., 2003; Palacios et al., 1999a) and a shorter latency period in wild females observed in this study (11 vs 17 days for wild and

Table 4
Fatty acids profile (described as % of total fatty acids) measured in eggs from 1st to 4th spawn order of domesticated (G2) and wild *F. duorarum* broodstock in a 30-d experimental period.

	Eggs													
	Domesticated							Wild						
Fatty acid	1st	2nd	3rd	4th	*Means*		*SD*	1st	2nd	3rd	4th	*Means*		*SD*
C14:0	1.5	2.0	2.3	NA	*1.9*	±	*0.4*	3.5	3.7	3.5	3.2	*3.5*	±	*0.2*
C15:0	0.7	0.6	0.6	NA	*0.6*	±	*0.1*	0.8	1.0	1.0	0.7	*0.9*	±	*0.1*
C16:0	27.6	25.6	26.0	NA	*26.4*	±	*1.1*	26.5	27.0	27.6	27.8	*27.2*	±	*0.6*
C16:1 n-7	5.2	5.7	5.6	NA	*5.5*	±	*0.3*	8.5	9.4	8.4	7.2	*8.4*	±	*0.9*
C17:0	1.7	1.4	1.4	NA	*1.5*	±	*0.2*	1.3	1.6	1.6	1.3	*1.5*	±	*0.2*
C18:0	10.6	8.9	8.9	NA	*9.5*	±	*1.0*	7.2	7.9	7.8	8.3	*7.8*	±	*0.4*
C18:1 n-7	7.0	6.7	5.8	NA	*6.5*	±	*0.6*	0.0	5.8	5.9	6.3	*4.5*	±	*3.0*
C18:1 n-9	20.0	19.7	19.2	NA	*19.6*	±	*0.4*	17.7	18.6	18.4	18.3	*18.2*	±	*0.4*
C18:2 n-6 (LA)	2.7	3.1	2.8	NA	*2.9*	±	*0.2*	2.5	2.8	2.6	2.6	*2.6*	±	*0.1*
C18:3 n-3 (ALA)	0.7	0.9	0.9	NA	*0.8*	±	*0.1*	0.6	0.6	0.6	0.7	*0.6*	±	*0.0*
C18:3 n-6	0.0	0.0	0.0	NA	*0.0*	±	*0.0*	0.1	0.1	0.1	0.0	*0.1*	±	*0.0*
C20:0	0.9	0.6	0.6	NA	*0.7*	±	*0.1*	0.6	0.6	0.6	0.6	*0.6*	±	*0.0*
C20:1 n-9	2.1	1.7	1.8	NA	*1.9*	±	*0.2*	2.4	2.1	2.3	2.2	*2.3*	±	*0.2*
C20:2	0.6	0.6	0.5	NA	*0.6*	±	*0.1*	0.5	0.5	0.5	0.4	*0.5*	±	*0.0*
C20:3 n-6	0.0	0.1	0.2	NA	*0.1*	±	*0.1*	0.2	0.2	0.2	0.1	*0.2*	±	*0.0*
C20:4 n-6 (ARA)	2.1	2.3	2.3	NA	*2.2*	±	*0.1*	1.9	2.0	1.9	1.7	*1.9*	±	*0.1*
C20:5 n-3 (EPA)	6.4	8.1	7.9	NA	*7.5*	±	*0.9*	7.0	5.9	6.4	6.9	*6.6*	±	*0.5*
C22:6 n-3 (DHA)	8.8	10.3	11.2	NA	*10.1*	±	*1.2*	10.9	6.9	7.3	9.0	*8.5*	±	*1.8*
∑ Saturated	43.0	39.1	39.8	NA	*40.6*	±	*2.1*	39.9	41.8	42.2	41.9	*41.5*	±	*1.1*
∑ Monounsaturated	34.2	33.7	32.4	NA	*33.4*	±	*0.9*	28.5	35.9	35.1	34.0	*33.4*	±	*3.3*
∑ n-3	16.0	19.3	20.0	NA	*18.4*	±	*2.2*	18.4	13.5	14.4	16.6	*15.7*	±	*2.2*
∑ n-6	4.7	5.5	5.3	NA	*5.2*	±	*0.4*	4.7	5.1	4.7	4.4	*4.7*	±	*0.3*
(n-3)/(n-6)	3.4	3.5	3.8	NA	*3.5*	±	*0.2*	3.9	2.7	3.0	3.8	*3.4*	±	*0.6*

NA = not available.

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Table 5
Multivariate analysis using Empirical Orthogonal Function (EOF) of acylglycerides (AG), cholesterol (chol.) and total soluble protein (TSP) biochemical data (first and fourth spawns) performed in hepatopancreas, hemolymph, ovary, eggs and nauplii from domesticated (G2) and wild *F. duorarum* broodstock in a 30-d experimental period. Data shows the more energetic modes of variation (Modes 1, 2 and 3) and percentage of the total mode 1 energy for the "most energetic variable" (MEV).

1st spawn order	Origin	EOF's energetic modes of variation (%)			MEV	MEV Mode 1 energy retention (%)		
Tissue		Mode 1	Mode 2	Mode 3		AG	Chol.	TSP
Hepatopancreas	Wild	84.5	8.5	7.1	AG	97.5	2.5	0.1
Hepatopancreas	Domesticated	97.8	1.7	0.6	AG	99.9	0.1	0.0
Hemolymph	Wild	92.5	6.7	0.7	AG	95.5	4.5	0.0
Hemolymph	Domesticated	94.5	4.5	1.0	AG	88.7	11.3	0.0
Ovary	Wild	67.9	25.0	7.1	AG	88.4	11.6	0.0
Ovary	Domesticated	63.3	34.1	2.6	AG	89.7	10.2	0.2
Eggs	Wild	92.0	4.7	3.3	AG	93.2	6.8	0.0
Eggs	Domesticated	90.7	5.7	3.6	AG	87.8	12.2	0.0
Nauplii	Wild	89.7	6.1	4.2	AG	93.0	7.0	0.0
Nauplii	Domesticated	89.8	6.6	3.6	AG	94.9	5.1	0.0
4th spawn order	Origin	EOF's energetic modes of variation (%)			MEV	MEV Mode 1 energy retention (%)		
Tissue		Mode 1	Mode 2	Mode 3		AG	Chol.	TSP
Hepatopancreas	Wild	98.1	1.2	0.7	AG	100.0	0.0	0.0
Hepatopancreas	Domesticated	94.3	3.5	2.2	AG	99.7	0.3	0.0
Hemolymph	Wild	84.4	15.1	0.4	AG	87.7	12.3	0.0
Hemolymph	Domesticated	92.4	6.3	1.4	AG	84.5	15.5	0.0
Ovary	Wild	82.2	17.7	0.1	AG	94.9	5.1	0.0
Ovary	Domesticated	76.9	18.0	5.1	AG	92.0	7.4	0.6
Eggs	Wild	93.9	3.6	2.5	AG	93.2	6.8	0.0
Eggs	Domesticated	92.4	4.7	2.8	AG	92.7	7.3	0.0
Nauplii	Wild	91.7	6.1	2.2	AG	91.5	8.5	0.0
Nauplii	Domesticated	83.1	11.3	5.6	AG	86.6	13.4	0.0

domesticated, respectively) is consistent with a higher spawning rate. The same trend was observed for other species such as *F. paulensis* (Cavalli et al., 1997), *P. monodon* (Menasveta et al., 1993) and *L. vannamei* (Palacios et al., 1999a) where wild females started spawning earlier and presented a higher spawning frequency than those kept in culture ponds. A better nutritional physiology condition of eyestalk ablated females from wild could be the main causative agent, increasing their capacity of multiple spawning.

In a shrimp hatchery a large percentage of females in any production cycle spawned only once or sometimes never spawn, whereas only a small percentage is able to spawn several times (Cavalli et al., 1997; Palacios et al., 1999b). In contrast to other indicators of reproductive capacity, domesticated population presented a better performance in terms of spawning females than wild ones (89 vs 76% of females that spawned at least once). This result contrasted to Cavalli et al. (1997) in which the proportion of wild *F. paulensis* that never spawned was lower than for their domesticated counterparts.

The number of eggs and viable nauplii produced per spawns also represent quantitative criteria to evaluate broodstock performance and a way to exclude the poor strains, reducing costs in shrimp maintenance (Racotta et al., 2004). In the present study, both egg and nauplii production was higher for wild females. Furthermore, number of eggs per spawn increased over time in wild females whereas decreased for their domesticated counterparts (Fig. 2), corroborating with Peixoto et al. (2004) in which captive tank-reared *F. paulensis* females decreased the eggs production over time as compared to wild ones. A comparison of egg production per unit of body weight is presented in Table 6. In our study, *F. duorarum* outcomes, mainly represented by wild females, performed better results as compared with other wild populations as *F. indicus* (Regunathan, 2008), *P. semisulcatus* (Browdy et al., 1986), *F. paulensis* (Cavalli et al., 1997), *L. stylirostris* (Mendoza, 1997) and *P. esculentus* (Keys and Crocos, 2006). On the other hand, it was poorer than wild *P. monodon* (Menasveta et al., 1993) and *L. vannamei* (Ibarra et al., 1997). In contrast to reproductive quantitative output, spawn quality in terms of fertilization and hatch rates was not different between wild and domesticated populations. However zoea, mysis and postlavae weight and length, considered as indicators of larval quality (for review see Racotta et al., 2003, 2004; Arcos et al., 2005b), was higher in wild as compared to domesticated population, suggesting a superior quality that will be analyzed together with biochemical indicators of spawn and larval quality.

4.2. Biochemical composition and FA profile

Multiple spawning capacities could involve a decrease in spawn quality and nutrient storage (such as lipids and essential FA) over consecutive spawns (Emmerson, 1980; Palacios et al., 1999b, 2000). Substantial part of ovarian total lipids in the early stage of maturation must come from diet intake (Hoa et al., 2009) and sufficient levels will be accumulated in (i) HP and hemolymph to allow successive spawns (Palacios et al., 2000; Tseng et al., 2001) and (ii) in the egg yolk to guarantee the normal development of the embryos and prefeeding larvae (Teshima and Kanazawa, 1983; Wouters et al., 2001b). A large fraction of these lipids is composed by HUFA, especially DHA, EPA and ARA (Hoa et al., 2009). The importance of dietary HUFA for crustacean maturation and reproduction has been well described (Cahu et al., 1994, Harrison, 1990; Lytle et al., 1990; Teshima et al., 1988; Wouters et al., 2001c). ARA and EPA are essential components of cell membranes and precursors for 2-series and 3-series prostaglandins (Tahara and Yano, 2004), whereas DHA plays an important role as a source of energy and on the development of the central nervous system in crustaceans (Xu et al., 1994). On the other hand, the knowledge on a specific nutrient requirement for enhancement of reproductive performance remains limited and spawning outcomes could not be dependent to a single nutrient (Regunathan, 2008). For *F. duorarum* wild juveniles, previous studies in Celestún estuaries, Mexico, reported a preference on copepods and amphipods (Aragón-Axomulco et al., accepted for publication), lipids and protein-rich food items. Furthermore, amount and quality of broodstock food intake in wild is hard to measure.

The digestive gland HP is an important gland for storage of nutrients such as lipids (Cahu et al., 1994; Marsden et al., 2007), protein (Marsden et al., 2007; Palacios et al., 2000), carbohydrates (Arcos et al., 2003; Nakayama et al., 2008), carotenoids (Arcos et al., 2003), vitamins (Shiau and Wu, 2003), essential FA and amino acids (Cahu et al., 1994; Millamena and Pascual, 1990). Successive spawns imply a continuous transfer of nutrients to eggs and it is therefore expected to gradually deplete lipid reserves in HP as previously shown in *P. indicus* (Vazquez Boucard et al., 2004) and this would explain the 50% decrease in AG levels observed in the present study for domesticated females from the 1st to the 4th spawn. However this depletion is not always observed and could depend on adequate maturation conditions, particularly the diet (Palacios et al., 2000). This seems to be the case in wild females in which AG levels in HP of females at their 4th spawn were three-fold higher than in domesticated females. Moreover, the 10-fold increase observed from the 1st to the 4th spawn in wild females was mainly because they start with very low levels of AG at their first spawn, which also was observed for the sum of total FA (not shown), LA, ALA, DHA and also was related with low HSI. On the other hand, DHA levels and sum of n-3 in HP from domesticated females decreased between the 1st and the 4th spawn order possibly due to slow response to ablation in domesticated population, also corroborated with high HSI and low GSI. In *P. monodon*, lipid levels decreased to meet a need for rapid development of OV following eyestalk ablation in ablated females (Marsden et al., 2007). Thus the initial low levels of AG in our study in wild females could be explained by a more accentuated response to eyestalk ablation of wild population as compared to domesticated ones. Indeed, wild females spawned more promptly, had a higher number of

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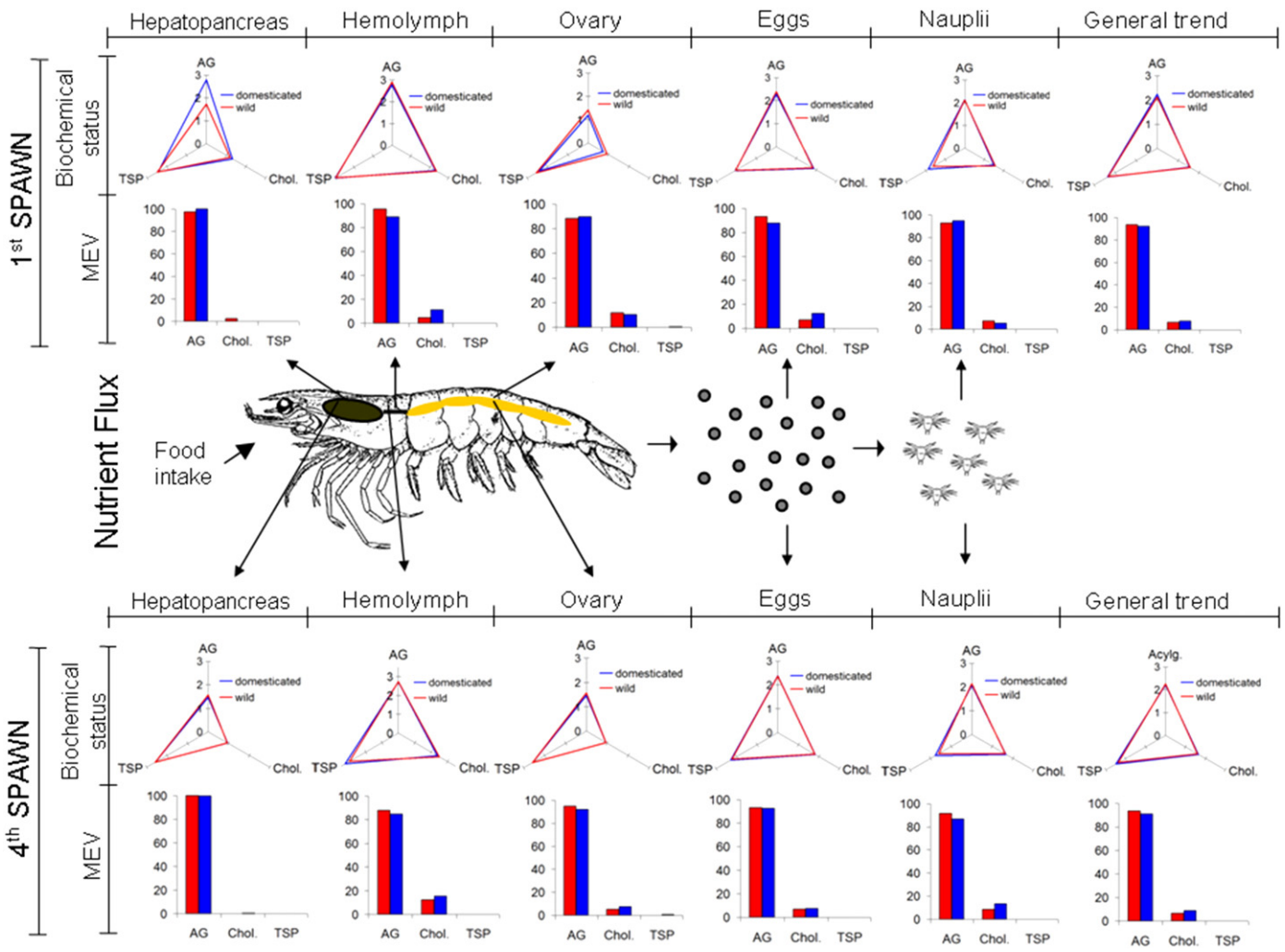

Fig. 4. Scheme of nutrient flux performed using multivariate analysis and Empirical Orthogonal Function (EOF—mode 1) underlying patterns of temporal variation (first or fourth spawns) of acylglycerides (AG), cholesterol (chol.) and total soluble protein (TSP) biochemical data performed in hepatopancreas, hemolymph, ovary, eggs and nauplii from domesticated (G2) and wild *F. duorarum* broodstock. Data shows biochemical status and most energetic variable (MEV) from mode 1, expressed in %.

Table 6
Data from egg productivity (eggs per spawn per g of female's body weight) in some penaeid species.

Species and origin	Eggs per spawn per g of female's body weight ($\times 10^3$)	Female weight (g)	Reference
P. monodon (wild)	3.92	205.3	Menasveta et al. (1993)
P. monodon (pond-reared G2)	1.95	133.3	Menasveta et al. (1993)
L. vannamei (wild)	3.85	45.38	Ibarra et al. (1997)
L. vannamei (pond-reared)	2.67	33.76	Ibarra et al. (1997)
F. indicus (wild)	2.37	33.7	Regunathan (2008)
F. indicus (domesticated G2)	2.24	32.0	Regunathan (2008)
P. semisulcatus (wild)	2.14	41.6	Browdy et al. (1986)
P. semisulcatus (pond-reared G1)	1.98	38.9	Browdy et al. (1986)
L. stylirostris (wild)	1.92	58.8	Mendoza (1997)
L. stylirostris (pond-reared G5)	1.25	53.4	Mendoza (1997)
P. esculentus (wild)	0.8	58.0	Keys and Crocos (2006)
P. esculentus (tank-reared G1)	0.35	49.4	Keys and Crocos (2006)
P. esculentus (pond-reared G2)	0.77	42.7	Keys and Crocos (2006)
F. paulensis (wild)	1.99	54.9	Cavalli et al. (1997)
F. paulensis (pond-reared)	3.58	21.6	Cavalli et al. (1997)
F. duorarum (wild)	2.6	25.9	Present study
F. duorarum (tank-reared G2)	1.7	19.6	Present study

eggs per spawn, higher GSI, as well as high AG content in hemolymph and OV indicating a higher gonad development than domesticated ones. Furthermore, higher levels of AG in eggs of 1st spawn wild females compared to 1st spawn domesticated females also indicate a better transfer to eggs. This trend was followed in FA profile, mainly represented by DHA and sum of n-3. Eggs from wild females at their 1st spawn had higher levels (10.9 and 18.4%, respectively) as compared to their domesticated counterparts (8.8 and 16.0%). Moreover, its levels strongly decreased in the 1st to the 2nd spawn order and could not be sufficient to maintain stable levels, although it must be explained by an important increase of eggs production in the 2nd spawn order and over time (Fig. 2), resulting in final lower mean levels as compared to their domesticated counterparts. High mean levels of HUFA such as ARA and EPA were found in HP and OV from wild females (Table 3), possible due to a better nutrition in wild prior to maturation phase. Deficit in these HUFA contributed to decrease on embryogenesis (Clarke et al., 1990) and vitellogenesis (Wouters et al., 2001c).

Cholesterol is an important cell constituent in crustaceans, and is a precursor of steroid and molt hormones (D'Abramo, 1997). However, crustacean cells cannot synthesize cholesterol or other sterols *de novo* and need it from the diet (Teshima, 1972). The low levels of AG observed in HP from 1st spawn wild females as compared to domesticated ones was also observed in cholesterol content; although these

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differences were not seen in other tissues. Cholesterol is also an important component of lipoproteins (i.e. vitellogenin) involved in AG transfer into OV (Kanazawa and Teshima, 1971), and therefore its low levels of cholesterol in HP could be explained by a higher cholesterol turnover related to vitellogenin synthesis and transport to OV.

Hemocyanin plays a key role in oxygen transport and protein reserves in hemolymph (Chen and Cheng, 1993) and also participates in shrimp immune response (Pascual et al., 2003). Its levels are affected by the molting process (Bursey and Lane, 1971, Cheng et al., 2002) and dietary protein levels (Rosas and Carrillo, 2006). In the present study, hemocyanin levels of wild females were lower than domesticated ones. Such result could be related to a high protein turnover in wild shrimp, which is also suggested by a lower protein content level in nauplii obtained from wild spawners as a result of high spawning activity.

4.3. Multivariate analysis

EOF multivariate analysis (Jeronimo, 2007) is a tool to detect simultaneous variation in biochemical variables which many times is not seen in univariate analysis. EOF performed in our study allowed to detect AG as variation pattern responsive in 1st and 4th spawn order for all tissues, with more than 85% of energy retention (Table 5). Such result was corroborated with biochemical analysis performed in a univariate way, where AG showed a key role on nutrient flux and spawning activity. A scheme of nutrient flux, EOF's MEV (mode 1) and biochemical status of 1st and 4th spawn domesticated and wild females is given in Fig. 4. AG was also detected as the most responsive of variation retention in both origins and tissues, including the general trend. Biochemical status was represented by a pyramid where as more open is the pyramid better the animal nutritional condition is. Both origins showed the same general trend. Such result concluded that some specific nutrients such as essential FA could be more responsive than the metabolite changes measured in this study. Optimum ratios of HUFA will enable broodstock diets to be improved and enhance the reproductive outcomes in penaeid species (Coman et al., 2011; Wouters et al., 2001c). Multivariate analysis applied to broodstock nutrition seemed to be a tool to clarify nutrient traceability, detecting simultaneous variations. Further research is encouraged on this field.

5. Conclusion

In the present study wild population of *F. duorarum* presented better reproductive performance as compared to domesticated ones. Multiple spawning was reflected in some biochemical variables such as AG and cholesterol content in HP, hemolymph and OV. Higher content of some nutrients such as DHA and sum of n-3 in the 1st spawn order in domesticated females was related to a slow response to ablation whereas lower levels in wild populations was attributed to an accentuated response to eyestalk ablation, possible due to a better nutrition in wild prior to maturation phase. Additionally, wild females spawned more promptly, had a higher eggs production and a quickly gonad development as compared to domesticated ones.

Domestication of broodstock is common in shrimp industry to control production plan with successive generations (Coman et al., 2007). Our results and their practical implications should be taken in place for selecting *F. duorarum* broodstock origin in terms of reproductive performance and biochemical characteristics. However, domestication process using advanced generations (i.e. >G9) could be analyzed as it has shown advantages (Gitterle et al., 2005; Goyard et al., 2002; Wabete et al., 2006). On the other hand, nutritional problems in domesticated broodstock remain unresolved (Wouters et al., 2001a) and alternatives should be evaluated. The role of broodstock origin and nutritional history impacted on *F. duorarum* reproductive performance. Further research are encouraged to evaluate different food protocols and diets (i.e. dry pellets vs fresh food maturation diet and short-term vs long-term fresh food supplementation prior to ablation) aiming to improve *F. duorarum* outcomes.

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