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Shrimp larval quality in relation to broodstock condition

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Abstract

This review focuses on the different criteria currently used to assess offspring quality of penaeid shrimp and the factors that affect this characteristic. The term 'larval quality' generally refers to the physiological condition of the larvae and is related to survival and growth rates during several larval developmental stages. The criteria fit into five general categories, depending on the approach used: biochemical, morphological, behavioral, production and survival to stress tests. Several variables at the broodstock management level are known or suspected to affect larval quality. These include variables that can be more easily controlled by producers or researchers than others. Broodstock nutrition is probably the best reviewed aspect and is supported by many papers on the metabolism of several components during maturation, use of fresh vs. artificial food and specific requirements of particular components, such as lipids and vitamins. Endocrine control of reproduction has been widely studied in crustaceans. Eyestalk ablation still represents the most commonly used endocrine manipulation to induce maturation and spawning. Other alternatives are considered although few evaluate larval quality and none has been used in production. More recently, the use of captive broodstock and genetic improvement programs have gained importance. The effect of other biological characteristics of shrimp, such as age and size, season of the year when induced to intensive maturation conditions, time spent in maturation tanks and consecutive spawnings are also considered.

Keywords: Penaeid shrimp; Reproduction; Larvae; Offspring quality

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1. Introduction

Seed production from penaeid shrimp matured in captivity is continuously increasing and represents one of the most important strategies to shrimp farming activity. During the 1980s and 1990s, several reviews discussing the advances in this particular field were published. All of them recognize that serious gaps still exist for the optimization of shrimp maturation under controlled conditions. In the present review, we focus on the existing criteria of offspring quality with an emphasis on their link to broodstock conditions.

2. Criteria of offspring quality

The term larval quality is widely used to refer to the physiological condition, performance during culture (survival and growth) and resistance to stress tests (e.g., manipulation stress, changes in environmental conditions, resistance to pathogens). The search and establishment of universal criteria to assess larval quality is a major concern at both research and production levels. Egg and naupliar quality depends principally on the physiological condition of broodstock, but also on environmental conditions prevailing in spawning and hatching tanks. Larval and postlarval quality is based on criteria that include development from zoeal to postlarval stages and depend principally on larval culture conditions, although maternal effects may still have some influence. The naupliar stage represents the first larval stage and its quality is a direct reflection of broodstock condition, because at this stage there is still a strong dependence on the nutrients transferred from the female.

The criteria used to evaluate offspring quality can be separated into those that are applied a posteriori to determine the effect of a particular condition or treatment (i.e., diets, hormones, broodstock condition), and those that are evaluated a priori that are an attempt to predict the quality of further larval stages. Some criteria, such as hatching rate, can be used both ways.

The optimum environmental and management conditions of larviculture as well as nutritional requirements are the main factors that determine offspring quality from zoea to postlarva, and have been extensively reviewed previously (Léger and Sorgeloos, 1992; Liao, 1992; Smith et al., 1993; Treece and Fox, 1993; Jones et al., 1997a). Nevertheless, broodstock condition or maternal effects can also affect larval quality even in advanced stages such as postlarvae, and evidence of this relation will be addressed in the present review.

The offspring quality criteria analyzed in the present work were based on the majority of the criteria previously reviewed (Bray and Lawrence, 1991, 1992; Clifford, 1992; Fegan, 1992). Therefore, five general categories are proposed to cover different approaches to assess offspring quality: biochemical, morphological, behavioral, productive yields and survival to stress tests.

2.1. Biochemical composition

Eggs and nauplii are lecitotrophic and thus their development depends on biochemical reserves transferred to the eggs from the female. The initial level of reserves and the time-

course changes due to the use of reserves or the synthesis of structural components could determine further larval quality, hence they can be considered as predictive quality criteria. Evidences that associate the content of a specific component with offspring performance are summarized in Table 1. More advanced stages (i.e., zoea, mysis and postlarva) are also included, although their biochemical composition would reflect principally larval nutrition.

Lipids have an energetic and structural function during lecitotrophic development, a period in which they are gradually consumed (Cahu et al., 1988; Mourente et al., 1995; Palacios et al., 2001a). The association between lipid concentration and the physiological condition or performance of larvae is supported by several studies. Total lipid concentration was higher in batches of eggs that were able to develop to postlarvae (PL) than in batches with no further development after hatching (Hernández-Herrera et al., 2001). Quantitatively, triglycerides (TG) are the most important lipids for storing energy. In penaeid shrimp, they represent up to 50% of total lipids in eggs (Cahu et al., 1988; Palacios et al., 2001b) and from 20% to 30% in nauplii (Mourente et al., 1995; Wouters et al., 2001a). TG content was first proposed as a condition index for crustacean, fish and mollusk larvae by Fraser (1989). For crustaceans, TG has been associated with the physiological condition of larvae in terms of tolerance to pollutants (Fraser, 1989), survival during early molting (Ouellet et al., 1992), the rate of egg development (Wickins

Table 1
Biochemical composition of eggs or larvae related to a performance characteristic

Biochemical component	Stage	Related performance	Species	Reference
TG	Larvae and juveniles	Resistance to pollutant stress	*Homarus americanus*, *Callinectes sapidus*	Fraser, 1989
TG	Larvae	Survival during early molting	*Pandalus borealis*	Ouellet et al., 1992
TG	Eggs and larvae	Egg development rate	*Homarus gammarus*	Wickins et al., 1995
TG, proteins, carotenoids and glucose	Eggs and nauplii	Spawner condition and associated larval survival	*Litopenaeus vannamei*	Palacios et al., 1999a
Phospholipids	Eggs	Number of spawns per female	*Litopenaeus vannamei*	Cahu et al., 1994
EPA and DHA	Eggs	Fecundity, hatching rate	*Penaeus chinensis*	Xu et al., 1994
EPA in LPE, PS and PI	Eggs	Survival to zoeae	*Penaeus vannamei*	Palacios et al., 2001b
Total HUFA	Eggs	Hatching rate	*Macrobrachium rosenbergii*	Cavalli et al., 1999
Total HUFA	Eggs	Hatching rate	*Penaeus indicus*	Cahu et al., 1995
Lipids and carbohydrates	Eggs	Successful development to PL	*Litopenaeus vannamei*	Hernández-Herrera et al., 2001
Carotenoids in diet	Not measured	Survival to zoeae	*Litopenaeus vannamei*	Wyban et al., 1997
RNA/DNA ratio	PL	Feeding condition	*Litopenaeus vannamei*	Moss, 1995

TG: triglycerides, EPA: eicosapentaenoic acid, DHA: docosahexaenoic acid, LPE: lysophosphatidylethanolamine or plasmalogens, PS: phosphatidylserine, PI: phosphatidylinositol, HUFA: highly unsaturated fatty acids.

et al., 1995), spawner condition and resulting larval quality (Palacios et al., 1999a), and survival to zoeae (Palacios et al., 2001b). In addition to TG, phospholipids have specific functions during larval development (for review, see Coutteau et al., 1997), and thus their content should also be related to larval quality. Cahu et al. (1994) observed that broodstock fed diets with a high content of phospholipids had a higher spawning frequency and produced eggs with increased phospholipids content, but, unfortunately, viability of resulting larvae was not tested. Bray et al. (1990a) observed an increased hatching rate when broodstock diet was supplemented with soybean lecithin, although levels of phospholipids in eggs or nauplii were not measured. The importance of phospholipids during lecitotrophic stages remains to be established, although their nutritional requirements have been extensively studied for larval and postlarval stages nutrition (Kanazawa et al., 1985; Coutteau et al., 1996, 1997; Kontara et al., 1997; Paibulkichakul et al., 1998).

In addition to absolute levels of TG and phospholipids, the composition of fatty acids in eggs, particularly that of highly unsaturated fatty acids (HUFA), has been shown to be correlated to fecundity, fertilization and hatching rates (Xu et al., 1994; Cahu et al., 1995; Cavalli et al., 1999; Wouters et al., 1999). From these results, it seems clear that the level of HUFA could be a predictive criterion useful in assessing spawn quality, although its importance in further larval development remains to be analyzed. The role of the different HUFAs in the particular lipid classes has not been thoroughly studied. Eggs with high survival to zoeae had a higher content of eicosapentaenoic acid (EPA) in several phospholipid classes (Palacios et al., 2001b). However, in the same study, docosahexaenoic acid (DHA) was not associated with survival to zoeae, probably because high levels (at least 15% of the total fatty acids) were present both in eggs that developed to zoeae and in those that did not.

Lipids are stored in the ovaries and transferred to the eggs mainly in the form of vitellin. The fate of vitellin, or its precursor vitellogenin, during ovary development, and the hormonal control for its synthesis and incorporation into the ovaries have also been extensively analyzed (Yano and Chinzei, 1987; Quackenbush, 1989, 1992; Browdy et al., 1990; Vazquez-Boucard, 1990; Mendoza, 1992; Quinitio and Millamena, 1992; Shafir et al., 1992). There are also some studies on vitellin levels in eggs and early larvae (Quackenbush, 1989; Vazquez-Boucard, 1990; Lee et al., 1995), but there is no evidence of its suitability as an indicator of further larval performance, although theoretically this could be a promising approach as a predictive quality criterion in eggs. It remains to be established whether the levels of vitellin in eggs, measured by ELISA as the content of apoprotein (Mendoza et al., 1993; Lee and Watson, 1994), can be associated with spawn quality, or if in addition the lipid composition of the vitellin should be taken into account.

Proteins are the most abundant component of eggs and nauplii in penaeid shrimp (Chu and Ovsianico-Koulikowsky, 1994; Mourente et al., 1995; Lemos and Rodriguez, 1998; Palacios et al., 1999a). In addition to their structural role, an energetic use of protein in advanced naupliar substages has been suggested by a study measuring the oxygen consumption/nitrogen excretion ratio (Chu and Ovsianico-Koulikowsky, 1994). Total protein levels in nauplii, but not in eggs, were affected by broodstock condition and associated to larval quality (Palacios et al., 1999a). However, no further evidence of the relationship between total protein levels and spawn or larval quality was found. Specific proteins, such as the apoprotein fraction of vitellin (discussed above) and digestive or

metabolic enzymes, could be more adequate predictive indicators of larval quality. The ontogeny of digestive enzymes in first feeding penaeid larvae was analyzed in detail (for review, see Jones et al., 1997b) and their concentration and activity in zoeal and myses stages should be related to larval quality.

Carotenoids, which also form part of the vitellin, are known to be essential for enhancing maturation, reproductive performance and offspring quality (for reviews, see Harrison, 1990; Wouters et al., 2001b). The levels of carotenoids, particularly astaxanthin, decrease from eggs to zoeae, suggesting a catabolism or oxidation during this period (Dall, 1995). Their protective role as natural antioxidants against biochemical components or light, particularly for HUFA (Wouters et al., 2001b), should have a determinant effect on development. In accordance, when paprika was added to broodstock diet, an increase in survival to zoeae was observed (Wyban et al., 1997) and, although not quantified, carotenoid egg content probably increased. Wyban et al. (1997) suggested that the decline in larval quality under repetitive spawning is caused by a reduction in the levels of pigments in the egg. In a similar context, carotenoid levels were lower in eggs and nauplii obtained from females that had spent more time in maturation tanks, and this was also associated with a further lower larval performance (Palacios et al., 1999a). Moreover, eggs with higher carotenoid content in eggs resulted in higher survival to zoeal III substage (Palacios et al., 2001b), suggesting that carotenoids levels, similar to lipids levels, can be used as both predictive and final criteria.

Carbohydrates are minor components of eggs and nauplii (Chu and Ovsianico-Koulikowsky, 1994; Mourente et al., 1995; Lemos and Rodriguez, 1998; Hernández-Herrera et al., 2001) and thus represent only a limited energy reserve. However, some specific functions such as chitin synthesis during the frequent molting cycles of larvae could determine larval performance and justify its analysis. The free glucose levels in eggs and nauplii were affected by spawner condition (Palacios et al., 1998, 1999a). In addition, total carbohydrate concentration in batches of eggs that developed to PL was higher than in batches with no further development (Hernández-Herrera et al., 2001).

The RNA/DNA ratio is used as an index of growth in fish because it reflects the amount of synthetic machinery per cell (Bückley, 1984). In penaeid shrimp, the RNA/DNA ratio was lower for fasted PL, and thus was proposed as an index of PL quality (Moss, 1995). However, the use of this ratio in *Homarus americanus* failed to detect differences between dietary treatments, which nonetheless influenced PL dry weight (Juinio et al., 1991). Its suitability in general and particularly in earlier stages remains to be established.

2.2. Morphology

This category groups variables such as size, weight, occurrence of deformities, color, muscle/gut ratio, gill and digestive system morphology, and presence of bacteria, fungi, protozoa and viruses (Villalón, 1991; Wyban and Sweeney, 1991; Bray and Lawrence, 1992; Clifford, 1992; Fegan, 1992; Treece and Fox, 1993). In this review, we will focus only on size or weight measurements from egg to postlarva. Egg size estimated either as volume or diameter could reflect the yolk content, and should be a rough equivalent of the quantity of reserves, with the advantage of being easier and quicker to assess. This approach was addressed by Clarke (1993) in nine species of polar shrimp on a within

species (between female) basis. He obtained a significant correlation between egg volume and several measures of yolk content (dry mass, organic matter, carbon, nitrogen). In penaeid shrimp, Bray and Lawrence (1991) stated that no experimental evidence relating egg size as a predictive criterion to larval viability is available. In more recent studies, we evaluated egg diameter in several experimental conditions, but found no correlation with the biochemical composition or other offspring quality criteria (Palacios et al., 1998, 1999a; Hernández-Herrera, 2001).

Nauplius length can be a more promising approach because it increases with development (Wyban and Sweeney, 1991; Palacios et al., 2001a), and thus reflects the degree of development at a given moment. This would be equivalent to reporting the percentage of nauplii classified in different developmental stages sampled at a particular time. However, length measurements have the advantage of producing a normal distribution and can be an indicator of development within a particular naupliar substage. This is of importance because if the content of a particular nutrient, such as TG, is measured in nauplii, its decrease should be related to naupliar development. Thus, late nauplii will have less reserves than recently hatched ones. We proposed a naupliar condition index which combines TG concentration, hatching rate and nauplius length (Palacios et al., 1998, 1999a). This index was affected by the broodstock condition and proved to be useful as a predictive criterion of larval survival (Palacios et al., 1999a).

Zoea length was proposed by Bray et al. (1990b) as an index of larval quality for broodstock nutrition studies, although they acknowledge that a low number of spawns was considered in their study. Wouters et al. (1999) were able to relate higher values of zoea length to increased larval survival, suggesting that zoea length could indeed be used as a predictive criteria. However, other studies have failed to obtain a similar relationship (Hernández-Herrera, 2001).

Postlarval size (length, dry or wet weight) is a direct indicator of growth, and thus several nutritional studies have successfully used this criterion to evaluate diets (Samocha et al., 1989; Bray and Lawrence, 1992; Gallardo et al., 1995; Coutteau et al., 1996; Kontara et al., 1997; Wouters et al., 1997; Paibulkichakul et al., 1998). Increased growth and reduced variability in size during postlarval stages has in turn been related to further growth to juvenile stages (Castille et al., 1993).

2.3. Behavior

The positive phototropism displayed by nauplii is commonly used to harvest larvae after hatching, on the premise that it is a predictive, although indirect, indicator of naupliar quality (Bray and Lawrence, 1991; Smith et al., 1993; Treece and Fox, 1993). In an attempt to prove if this procedure was adequate for selecting viable nauplii, Ibarra et al. (1998a) evaluated larvae batches selected by positive phototropism and batches of the remnant nauplii. They observed that selected nauplii had a better survival to zoeal stage than remnant nauplii. However, there were no significant differences between both batches for survival or size after zoeal stage, because of large mortalities occurring from zoea III to mysis I in the selected batch. As all batches received the same feeding rate irrespective of surviving larvae (density), this appears to indicate that even for nauplii with a good initial condition, further survival and growth depends on optimal nutrition conditions.

Swimming activity is used at various stages of larviculture (Villalón, 1991; Clifford, 1992; Smith et al., 1993; Treece and Fox, 1993) and it seems obvious that poor activity or erratic swimming would suggest a lower physiological condition or illness, although this behavior can usually be appreciated only during critical conditions.

2.4. Production or yields

This category groups the characteristics usually applied at production level. Higher fecundity, fertilization and hatching rates are the main goals of a maturation facility, and correspond to a higher nauplii output. The majority of the studies evaluating the reproductive performance base their success on these production criteria. The evaluation of production criteria could be better justified if a relation between these and further larval performance is found. Bray and Lawrence (1991) proposed that the hatching rate should be a predictive criterion for further larval performance. Recently, a positive correlation between survival to postlarvae and hatching rate or number of nauplii was established (Hernández-Herrera et al., 2001). However, in the same study, no relationship between fecundity or fertilization rate and further larval performance was found.

Survival of larvae from one stage to the next is routinely monitored during larviculture as a final criterion, and lower values are accepted as direct indicators of a generally poor quality (Bray and Lawrence, 1992). The high correlation between survival to postlarvae and early survival to zoeae was recently considered in a predictive way from which a "cut-off point" could be established (Hernández-Herrera et al., 2001).

2.5. Survival to stress tests

Stress tests are applied principally in PL stages and are generally based on the exposure of shrimp to environmentally adverse conditions. The salinity stress test is by far the most commonly used test (Villalón, 1991; Clifford, 1992; Fegan, 1992; Bray and Lawrence, 1992). However, there is no reported evidence that the results of these stress tests are associated to performance during culture and growout (Aquacop et al., 1991; Fegan, 1992; Samocha et al., 1998). Table 2 summarizes the levels and duration of low salinity exposure used for different penaeid species as a function of PL age. Fewer studies have focused on early PL stages, during which changes in salinity level must be milder than in advanced PL stages (from 15 days old), when freshwater is generally used. The relation between low salinity tolerance and age was demonstrated in previous studies (Charmantier et al., 1988; Tackaert et al., 1989; Aquacop et al., 1991; Samocha et al., 1998) and this relation depends on increased osmoregulatory capacities through PL development (Charmantier et al., 1988). Despite its controversial application as a predictive indicator of performance during growout, low salinity stress tests have been widely used as a final criterion to evaluate different diets. The diet that results in a higher survival and growth, sometimes also results in PL that are more resistant to a stress test (Tackaert et al., 1989; Rees et al., 1994; Gallardo et al., 1995; Kontara et al., 1997; Paibulkichakul et al., 1998). However, this increased resistance to a stress test in relation to a particular diet has not always been proven (Tackaert et al., 1989; Rees et al., 1994; Coutteau et al., 1996; Wouters et al., 1997). This discrepancy could be a consequence of the age of the PL; as resistance to low

Table 2
Levels of salinity (ppt) and exposure times used for survival stress test for different ages and species of postlarvae (PL)

Age	Salinity	Time	Survival	Species	Reference
PL1–PL2	16.8	2 h	50% LC50	*L. vannamei*	Samocha et al., 1998
PL1–PL2	18	30 min[a]	61–89%	*L. vannamei*	Hernández-Herrera et al., 2001[b]
PL2	20	2 h	<5%	*L. vannamei*	Aquacop et al., 1991
PL5	8.3	2 h	50% LC50	*L. vannamei*	Samocha et al., 1998
PL5	14	30 min	0–85%	*P. monodon*	Tackaert et al., 1989[c]
PL5	16	1 h[a]	45–96%	*L. setiferus*	Gallardo et al., 1995[c]
PL5	20	2 h	~ 40%	*L. vannamei*	Aquacop et al., 1991
PL5	21	1 h	45–96%	*P. monodon*	Tackaert et al., 1989[c]
PL10	0	1 h	18–36%	*L. vannamei*	Wouters et al., 1997[c]
PL10	10	1 h	70–98%	*P. monodon*	Rees et al., 1994[c]
PL10	10	2 h	23–95%	*P. monodon*	Rees et al., 1994[c]
PL10	10	2 h	~ 25%	*L. vannamei*	Aquacop et al., 1991
PL10	14	30 min	36–97%	*P. monodon*	Tackaert et al., 1989[c]
PL10	14	1 h	24–68%	*P. monodon*	Tackaert et al., 1989[c]
PL15	0	30 min	50–96%	*P. monodon*	Tackaert et al., 1989[c]
PL15	0	30 min[a]	39–89%	*L. vannamei*	Palacios et al., 1999a[b]
PL15	0	1 h	0–20%	*P. monodon*	Tackaert et al., 1989[c]
PL15	5	2 h	~ 70%	*L. vannamei*	Aquacop et al., 1991
PL17	0[d]	30 min[a]	77–90%	*P. japonicus*	Tackaert et al., 1991[c]
PL18	0[d]	1 h[a]	86–93%	*L. vannamei*	Coutteau et al., 1996[c]
PL20	0	30 min[a]	43–64%	*L. vannamei*	Hernández-Herrera et al., 2001[b]
PL20	2	2 h	>90%	*L. vannamei*	Aquacop et al., 1991
PL31	0[d]	30 min[a]	43–87%	*P. japonicus*	Tackaert et al., 1991[c]
PL41	0[d]	1 h[a]	90–95%	*L. vannamei*	Coutteau et al., 1996[c]

Adapted from Hernández-Herrera, 2001.
[a] With recuperation in sea water.
[b] In relation to broodstock condition.
[c] In relation to postlarval diet.
[d] In deionized water.

salinity is more importantly affected by diet at an early (5–10 days old) than at a late age (15 days old or more) (Tackaert et al., 1989; Rees et al., 1994). In addition, species-specific differences could also play an important role. It was suggested that the euryhaline *Litopenaeus vannamei* is less susceptible to low salinity stress tests than *Penaeus japonicus* (Coutteau et al., 1996).

In addition, the survival to a salinity stress test is an individual measure of diverse complex processes, which include the shrimp nutritional status and its ability for nutrient mobilization under a sudden stress, the degree of development of the PL, related to the osmoregulatory capacity of gills, the local energy storage in the gills needed to maintain the high energy expenditure for the ATPase pumps, and probably genetic variations that affect the activity of the different enzymes involved in these processes. In this regard, a positive relation between the general glucose and TG levels of the PL and the survival to a salinity stress test has been found (Palacios et al., 1999a). In crab, the posterior gills, where the

major part of the osmoregulation process occurs, have been reported to accumulate higher levels of glycogen (Chausson and Regnault, 1995). A more profound study of this complex mechanism may shed some light on the reasons for such discrepancies in the literature.

Another application for the salinity stress test could be as a predictive criterion at early PL stages for further PL performance. A significant correlation was found between survival to a salinity stress test applied on PL10 and survival during larviculture to PL15 ($r=0.73$, $P<0.001$; Rees et al., 1994). Similarly, the survival to a salinity stress test applied on PL2 was also related to the survival to PL20 ($r=0.45$, $P<0.01$; Hernández-Herrera et al., 2001).

Other stress tests have been used in PL stages, such as the exposure to formalin (Clifford, 1992; Samocha et al., 1998), low temperature and low salinity combinations (Clifford, 1992; Fegan, 1992) and low dissolved oxygen levels (Ibarra et al., 1998b). In *Macrobrachium rosenbergii* larvae, a high ammonia stress test was recently tested in relation to the quality of broodstock (Cavalli et al., 1999, 2000a) and larval nutrition (Cavalli et al., 2000b). It was concluded that this stress test is a sensitive and reproducible criterion for the establishment of larval quality (Cavalli et al., 2000b). In penaeids, its suitability as a predictive stress test to evaluate further larval quality has been recently analyzed and we found that survival of zoeae to an ammonia stress test is related to the survival to PL during larviculture (Hernández-Herrera et al., 1999, 2001).

3. Broodstock condition

Some characteristics or conditions of spawners, such as nutrition, size and age of shrimp, broodstock origin, and possible endocrine manipulations, can be defined or controlled by producers and researchers. Others such as genetic variability or consequences during intensive reproduction conditions cannot be so easily controlled.

3.1. Broodstock nutrition

This is probably the most researched topic in shrimp maturation, and as such, it has been extensively reviewed by other authors (Harrison, 1990; Bray and Lawrence, 1992; Browdy, 1992; Benzie, 1997; Wouters et al., 2001b). In general, broodstock nutrition studies range form supplementation of specific nutrients, comparison of food with different levels of essential nutrients and the use of artificial vs. fresh food. The variation in tissue levels of several biochemical components during gonad development also represents a useful approach for understanding broodstock nutritional requirements. In general, the studies on broodstock nutrition evaluate the resulting reproductive performance (gonad maturation, number of spawns per female, fecundity) and early offspring quality (fertilization and hatching rate, number of nauplii, egg and nauplius biochemical composition). A possible maternal influence on further feeding larvae should not be underestimated. However, there are few studies that analyze the influence of broodstock diet on survival to zoeae (Marsden et al., 1997; Wyban et al., 1997) and myses stage of penaeids (Wouters et al., 1999), or on survival, growth, and resistance to ammonia stress test of 8-day-old larvae of *M. rosenbergii* (Cavalli et al., 1999, 2000a).

3.2. Spawner size and age

Spawner size (weight or length) is probably the most widely used criterion for broodstock selection and it varies with the species. For example, for *Penaeus monodon*, the average weight of a wild spawner is 75 g, and thus the average weight recommended even for captive populations is over 60 g (Aquacop, 1983; Yano, 1993) or around 90 g (Bray and Lawrence, 1992). For males, 40 g individuals with mature sperm can be found (Primavera, 1985), although the recommended value is 60 g (Bray and Lawrence, 1992). For *L. vannamei*, 30–45 g organisms can be used for production (Aquacop, 1983), although other authors recommended that males should be over 40 g and females over 45 g (Wyban and Sweeney, 1991; Bray and Lawrence, 1992; Robertson et al., 1993). Fecundity (number of eggs per spawn) is positively correlated to the spawner size (Emmerson, 1980; Ottogalli et al., 1988; Hansford and Marsden, 1995; Palacios et al., 1998). The number of spawns per time unit (spawning frequency) has also been reported to be higher for larger females (Menasveta et al., 1994; Palacios et al., 1999b, 2000). Thus, the final yield (number of eggs/female/time unit) should be higher for larger females, and this should have an effect on the total number of larvae produced over a period of time. In accordance, total nauplii and zoeae production was higher for relatively larger females (Menasveta et al., 1994; Cavalli et al., 1997). These results clearly justify the selection of the largest individuals for hatchery use as long as the resulting offspring quality is not affected. Menasveta et al. (1994) found no difference in fertilization, hatching, and metamorphosis to zoeae between small and large individuals of *P. monodon* ranging from 86 to 140 g. In contrast, for females of the same species ranging from 60 to 200 g, Hansford and Marsden (1995) obtained a low but significant negative correlation ($r = -0.17$, $P < 0.01$) between hatching rate and spawner size. For *Penaeus paulensis* females of 18–25 g, Cavalli et al. (1997) also obtained lower values of fertilization, hatching and zoea length for larger individuals, although the total nauplii production was still higher for the larger shrimp. In *L. vannamei* (43–56 g), no relation between spawner size and production was obtained, although some biochemical variables in eggs and nauplii were negatively correlated to spawner size (Palacios et al., 1998). Although further larval (and PL) quality has not yet been evaluated in relation to spawner size, at present, it seems that the use of larger individuals is well justified, although for pond-reared populations, this could imply an increase in the cost of growout.

Size is closely related to the age of spawners, but the size of same-age populations can vary in relation to growout or site conditions. Age has also been reported to influence reproductive performance and offspring quality, although few studies have systematically compared age per se. For *Penaeus semisulcatus*, Crocos and Coman (1997) reported that spawning frequency, and hence number of eggs, nauplii, and zoeae per female, increased from 6- to 12-month-old shrimp and then decreased at 14 months. However, hatching and metamorphosis to zoeae was not affected by broodstock age except for lower hatching rates in 6-month-old organisms. In *Litopenaeus stylirostris*, Ottogalli et al. (1988) observed that young (5–7 months) and old (more than 12 months) individuals had lower fertilization rates than intermediate ones (8–12 months). Cavalli et al. (1997) attributed some of the differences between large and small wild shrimp to an age effect, with older shrimp (15 months or more) having a lower spawning frequency, fecundity, fertilization

and hatching rate. In general, it can be concluded that the beneficial effect of selecting the largest individuals is limited by an age effect (see also Rothlisberg, 1998).

3.3. Broodstock origin

This section refers principally to the use of wild vs. pond-reared spawner populations, although differences can also exist within shrimp captured from different sites for wild populations, or from different growout conditions for pond-reared populations. Presently, the use of pond-reared populations is increasing because of the associated advantages over wild populations, such as ecological and sanitary safety, feasibility of genetic improvement programs and continuous year-round availability. The use of captive stocks, their advantages, the future directions and comparisons between wild and pond-reared stocks were reviewed by Browdy (1996, 1998).

A lower fecundity has been commonly observed for pond-reared broodstock, but this could be an effect of differences in shrimp size rather than source (Menasveta et al., 1993, 1994; Cavalli et al., 1997; Palacios et al., 2000). However, when comparing shrimp of similar size, some studies report lower fecundity for pond-reared shrimp (Browdy et al., 1986), while others obtained similar values for both origins (Menasveta et al., 1994; Preston et al., 1999). Spawning frequency has also been reported to be lower for pond-reared shrimp (Cavalli et al., 1997; Palacios et al., 1999b), but this also seems to be related to size, because no differences were observed when shrimp of similar size were compared (Menasveta et al., 1994).

Offspring quality should also be considered in comparing wild and pond-reared populations. Fertilization rates have been reported to be comparable (Browdy et al., 1986; Menasveta et al., 1993, 1994; Palacios et al., 2000) or higher for pond-reared shrimp (Cavalli et al., 1997; Palacios et al., 1999b). Results of hatching rate are conflicting since they have been reported to be equal (Browdy et al., 1986; Menasveta et al., 1993, 1994), higher for pond-reared shrimp (Cavalli et al., 1997; Palacios and Racotta, 1999; Palacios et al., 1999b) or higher for wild shrimp (Makinouchi and Hirata, 1995; Ramos et al., 1995; Mendoza, 1997; Preston et al., 1999). As mentioned in Section 3.2, size can also influence fertilization and hatching rates and could partially explain some of the controversies found between origins. From studies in which shrimps with comparable size were used, fertilization and hatching rates were equal or lower for pond-reared shrimp (Browdy et al., 1986; Menasveta et al., 1994; Makinouchi and Hirata, 1995; Preston et al., 1999). When other criteria of offspring quality were analyzed, eggs resulting from wild and pond-reared spawners were comparable in their biochemical composition (Palacios and Racotta, 1999), or were of lower quality for pond-reared spawners in terms of deformities and bacterial load (Sahul-Hameed, 1997).

Few studies have evaluated further larval quality between broodstock of different origins. Menasveta et al. (1993, 1994) found no difference on the metamorphosis to zoeae between wild and pond-reared shrimp. In a recent study, we observed that larvae from pond-reared spawners had a higher resistance to ammonia stress, survival to PL, and resistance to a salinity stress test in PL2 (Hernández-Herrera et al., 1999). However, only one collective spawn (from 10 females) for each origin was considered and it was reared to PL with no replicates.

In terms of costs, Menasveta et al. (1993) concluded that the greater expense in wild individuals of *P. monodon* is justified by the larger number of larvae that can be obtained. However, this is not always true and could depend on the site of capture of wild stock (Menasveta et al., 1994). Preston et al. (1999) estimated that the cost of producing larvae for stocking a one-hectare pond is twice as much if using wild rather than pond-reared spawners of *P. japonicus*.

3.4. Endocrine manipulations

Endocrine control of reproduction has been widely studied in crustaceans and considered in recent reviews for penaeid shrimp (Laufer and Landau, 1991; Quackenbush, 1991; Browdy, 1992; Chang, 1992; Yano, 1993, 1998; Benzie, 1997). Presently, the unilateral eyestalk ablation technique is still the most used method to induce maturation and spawning, at least for the two more widely cultured species, *P. monodon* and *L. vannamei*. It is based on the partial elimination of the sinus gland which produces and stores the gonad-inhibiting hormone (GIH), also called vitellogenesis-inhibiting hormone (VIH) (Primavera, 1985; Laufer and Landau, 1991; Browdy, 1992; Yano, 1993). This procedure is clearly justified by the well-known increase in reproductive output in quantitative terms, based principally on a shorter latency to first spawn, and on a higher spawning frequency (Chamberlain and Lawrence, 1981; Yano, 1984; Primavera, 1985; Browdy and Samocha, 1985a; Browdy et al., 1986; Gendrop-Funes and Valenzuela-Espinoza, 1995; Palacios et al., 1999c). When comparing between ablated and nonablated spawners, fecundity was reported to be higher (Chamberlain and Lawrence, 1981; Rothlisberg et al., 1991), lower (Browdy and Samocha, 1985b; Browdy et al., 1986; Muthu et al., 1986) or not different for ablated shrimp (Makinouchi and Honculada-Primavera, 1987; Redón and San Feliu, 1993; Yano, 1993; Gendrop-Funes and Valenzuela-Espinoza, 1995; Palacios et al., 1999c). However, even if fecundity was lower for eyestalk ablated females, the higher spawning frequency from ablated females yield a higher number of larvae per female.

The consequences of eyestalk ablation on offspring quality are still controversial. Fertilization and hatching rates were not considerably affected by eyestalk ablation (Chamberlain and Lawrence, 1981; Yano, 1984; Browdy and Samocha, 1985a,b; Browdy et al., 1986; Muthu et al., 1986; Rothlisberg et al., 1991; Gendrop-Funes and Valenzuela-Espinoza, 1995; Palacios et al., 1999c) or were lower for eyestalk-ablated females (Makinouchi and Honculada-Primavera, 1987; Vogt et al., 1989; Redón and San Feliu, 1993; Yano, 1993). In some studies, where the evaluation of further larval quality was made, metamorphosis to zoeae (Browdy and Samocha, 1985a,b; Rothlisberg et al., 1991; Gendrop-Funes and Valenzuela-Espinoza, 1995) and survival to PL (Vogt et al., 1989; Palacios et al., 1999c) were not affected by eyestalk ablation. Browdy (1992) concluded that some of the apparent contradictions might be associated with differences in the maturation conditions, and also probably to a decrease in the tolerance of ablated shrimp to suboptimal conditions. Decreased offspring quality might not be a direct consequence of eyestalk ablation, but an effect of forced reproduction during a short period of time. Forced reproduction could have a more important effect on eyestalk-ablated shrimp compared to intact animals (Emmerson, 1980; Browdy and Samocha, 1985b; Palacios et al., 1999c), and this possibility will be addressed in Section 3.5.

When considering the influence of eyestalk ablation on spawn quality, the physiological consequences on the spawner itself should also be analyzed. Removal of one eyestalk has many potential secondary effects because the levels of other hormones such as molt-inhibiting hormone (MIH) and crustacean hyperglycemic hormone (CHH) (Fingerman, 1987; Huberman et al., 1995) are also diminished. The concomitant decrease in the levels of GIH and MIH as a result of eyestalk ablation forces the female to reproduce and to molt more frequently, both of which require a larger amount of energy. This increased demand of energy appears to be at least partially compensated by an increase in food intake (Anilkumar and Adiyodi, 1980; Peter-Marian and Murugadass, 1991; Rosas et al., 1993) and by a more efficient physiological use of energy (Peter-Marian and Murugadass, 1991; Rosas et al., 1993). The reduction of CHH also affects carbohydrate (Fingerman, 1987; Keller and Sedlmeier, 1988; Santos and Keller, 1993) and lipid (Santos et al., 1997) metabolism. CHH has also been proposed to stimulate vitellogenesis (Tensen et al., 1989). Several authors have reported an increase of biochemical reserves in the ovaries, especially lipids, as a result of eyestalk ablation (Teshima et al., 1988; Millamena and Pascual, 1990; Millamena et al., 1993; Palacios et al., 1999c). Thus, the decrease in CHH levels by ablation apparently does not affect the normal metabolic processes involved in vitellogenesis. The increase in spawning frequency produced by eyestalk ablation could alter the long-term accumulation of reserves and their subsequent transfer to eggs. Nevertheless, the accumulation of lipids in the ovaries was not affected even if ablated animals had a previous higher number of spawns (Palacios et al., 1999c). Furthermore, the transfer of nutrients to the eggs was also not affected by ablation, as shown by a similar concentration of several biochemical components in eggs and nauplii from ablated or unablated spawners (Rothlisberg et al., 1991; Palacios et al., 1999c).

Endocrine alternatives to eyestalk ablation have been experimentally tested. These are based on injections or implants of hormones or endocrine glands extracts that are thought to be involved in the control of reproduction (Laufer and Sagi, 1991; Yano, 1993, 1998; Fingerman, 1997). In penaeid shrimp, female or male gonad development was induced by administration of thoracic ganglion extract (Yano et al., 1988; Yano, 1992), vertebrate-like steroids (Nagabhushanam and Kulkarni, 1981; Yano, 1985, 1987; Mendoza, 1992; Alfaro, 1996; Yashiro et al., 1998), methyl farnesoate (MF) (Tsukimura and Kamemoto, 1991; Laufer et al., 1997), serotonin (Vaca and Alfaro, 2000) and retinoids (Paniagua-Michel and Liñan-Cabello, 2000).

Another approach for identifying potential hormones that stimulate maturation is to detect active compounds in fresh foods that are typically used for broodstock feeding (Wouters et al., 2001b). For example, squid is commonly used as part of the maturation diet and a steroid-like compound found in this mollusk has been proposed to be responsible for its enhancing effect on maturation in shrimp (Mendoza et al., 1997). The use of polychaetes as an ingredient in maturation diet could be justified by their nutritional value in terms of essential fatty acids or amino acids (Lytle et al., 1990; Luis and Ponte, 1993), but also by their content of prostaglandins (D'Croz et al., 1988) or MF (Laufer et al., 1998). *Artemia* used for broodstock nutrition has also been proposed to contain an hormone-like substance that induces maturation, although it has not yet been identified (Naessens et al., 1997).

Despite this important research background on possible hormonal treatments to induce maturation and spawning in penaeid shrimp, several drawbacks could exist for production purposes: (1) injection of hormones or extracts could prove impractical unless it is clearly demonstrated that it has an advantage over eyestalk ablation. If repeated injections are used, the resulting stress (Racotta and Palacios, 1998) and other hormone-related effects could have even more side effects than eyestalk ablation. (2) Reproductive output and spawn and larval quality have not been evaluated in the majority of the studies mentioned above, and thus the different treatments have not yet been proven to be effective in terms of production. (3) At the production level, these procedures are not yet used because of high costs and a complicated procedure, compared to eyestalk ablation. The use of MF seems to be the most reliable alternative because it can be given directly through the diet and it has been reported that its administration results in a higher spawning frequency, and similar fertilization and hatching rates than untreated controls (Laufer et al., 1997). When combined with eyestalk-ablation, MF administration in the diet increased hatching and fertilization rates (Hall et al., 1999). Serotonin injection was also tested with promising results, although spawning frequency was higher for eyestalk-ablated females compared to serotonin-treated shrimp, without differences in fecundity, nauplii per spawn and fertilization and hatching rates (Vaca and Alfaro, 2000).

3.5. Reproductive exhaustion of spawners

This refers to the decline in reproductive capacity under intensive maturation conditions, both in males and females as a function of time spent in these conditions or as a consequence of successive rematurations. Table 3 summarizes the influence of time spent

Table 3
Consequences of reproductive exhaustion in terms of time elapsed in intensive reproduction conditions

Time in tanks	Consequence on broodstock condition, spawn or larval quality	Species	Reference
At 6–8 weeks	↓ hatching, ↓ fertilization, ↓ metamorphosis to zoeae	*P. monodon*	Simon, 1982
1–7 weeks	↓ sperm count, ↓ live sperm percent, ↑ abnormal sperm percent	*L. setiferus*	Leung-Trujillo and Lawrence, 1987
1–6 weeks	↓ hatching	*L. stylirostris*	Bray et al., 1990b
15–45 days	↓ spawning frequency	*L. schmitii*	Nascimento et al., 1991
5–40 days	↓ fertilization	*P. monodon*	Menasveta et al., 1993
1–14 weeks	↓ survival to zoeae	*L. vannamei*	Wyban et al., 1997
18–96 days	↑ body weight of spawners, ↑ fecundity, ↓ fertilization, ↓ glucose and TG in eggs, ↓ nauplius length and NCI	*L. vannamei*	Palacios et al., 1998
15–75 days	↑ body weight of spawners, ↓ spawning frequency, ↑ fecundity and number of nauplii, ↓ fertilization, =Hatching, ↓ biochemical components in eggs and nauplii, ↓ nauplius length and NCI, ↓ larval survival and salinity stress test	*L. vannamei*	Palacios et al., 1999a

↑ Significant increase, ↓ significant decrease.
NCI: naupliar condition index (see Section 2.2).

in maturation conditions on the spawner's physiological condition, its reproductive performance and associated spawn or larval quality. It seems clear that, after some time in an intensive maturation condition (approximately 3 months), broodstock should be replaced, although it has been suggested that unablated shrimp could be used longer, for 100–110 days compared to 70–80 days for ablated shrimp (Browdy and Samocha, 1985b). Nutrition could also partially counteract the negative influence of time, as shown by Wyban et al. (1997), who recovered the reproductive capacity of the broodstock by adding paprika to the diet. Due to year-round availability, pond-reared shrimp can allow a frequent 3-month replacement. The slightly lower performance of pond-reared broodstock could counteract the decline in reproductive output and resulting deterioration in larval quality of wild broodstock, which is used for long periods because of a shortage of their supply.

It is difficult to separate the effect of the number of spawns from time in production, so it is generally assumed that shrimp that have spent more time in the maturation tank have spawned more times. However, this relation is not so clear and Palacios (1999) observed that 80% of the females sampled in the first week were spawning for the first time. After 1 month, 50% of the females were having their first or second spawn, but the other half were on their third, fourth and even their seventh spawn. By the end of a 3-month period, there were still some females that were spawning for the first time. The sampling at a particular time within the production cycle produces females with a different spawning order; therefore, it is necessary to distinguish between the individual follow-up and the population or maturation tank follow-up, because each factor can affect the spawning quality in a different way. Table 4 summarizes some controversies in the spawn and larval quality reported as a consequence of consecutive spawning. The occurrence of a decline probably depends on the management of several of the controlled conditions (e.g., broodstock diet, use on eyestalk ablation, origin, environmental factors) and on genetic variability. For example, the use of an optimal diet counteracts the decrease in metamorphosis to zoeal stage resulting from consecutive spawns (Marsden et al., 1997; Wouters et al., 1999).

An important concern of the occurrence of multiple consecutive spawning is related to the contribution of each female to the overall nauplii production. Through individual female identification, Wyban and Sweeney (1991) reported that 10% of the females were responsible for 50% of the nauplii production. Similarly, Bray et al. (1990b) demonstrated that less than a quarter of females produced almost 70% of the larvae. Palacios et al. (1999b) observed that the nauplii production of one wild female with multiple spawns equaled the production of 30 wild females that had only one spawn, with a similar yield and spawn quality. Similarly, 6 pond-reared females with multiple spawns had a nauplii production almost equivalent to 91 females with only 1 spawn (Palacios et al., 1999b). Furthermore, of the total females stocked, 14% of the wild and 28% of the pond-reared females never mated, and 20% of wild and 34% of pond-reared females produced no viable spawns (Palacios et al., 1999b). Stocking with non-or low-producing females has a high cost of feeding and maintenance, so the selection of females based on their performance should be considered. For this reason, it has been proposed that the nonreproductive females should be replaced to improve total nauplii production (McGovern, 1988; Bray et al., 1990b). Cavalli et al. (1997) and Palacios et al. (1999b) proposed that females without spawning after 20–25 days should be replaced, although this can depend on species, broodstock availability and particular maturation conditions.

Table 4
Consequences of reproductive exhaustion in terms of consecutive spawns (spawning order)

Spawning order	Consequence on broodstock condition, spawn or larval quality	Species	Reference
1–8	↓ GSI, = fecundity and hatching	*P. kerathurus*	Lumare, 1979
1–4[a], 1–9[b]	↓ hatching, = fecundity and = nauplii/spawn	*P. indicus*	Emmerson, 1980
1–6[a]	= fecundity, ↓ hatching	*P. monodon*	Beard and Wickins, 1980
1–5, 1–3	= fecundity and hatching	*L. stylirostris*, *L. vannamei*	Chamberlain and Lawrence, 1981
1–3[a], 1–9[b]	↓ fecundity[a]; = fecundity[b] = fertilization and hatching = metamorphosis to zoeae	*P. semisulcatus*	Browdy and Samocha, 1985a,b
1–3	= fecundity, ↓ hatching	*L. stylirostris*	Bray et al., 1990b
1–3	↓ lipids in hepatopancreas	*P. japonicus*	Vazquez-Boucard, 1990
1–5	↓ fecundity and hatching, ↓ survival to zoeae	*P. monodon*	Hansford and Marsden, 1995
1–6	= fecundity, ↓ hatching, ↓ survival to zoeae	*P. monodon*	Marsden et al., 1997
1–3	↓ hatching	*L. stylirostris*	Mendoza, 1997
1–>10	= fertilization and hatching, ↑ nauplii per spawn	*L. vannamei*	Palacios et al., 1999b
1–25	↑ GSI, ↓ atresia occurrence	*L. vannamei*	Palacios et al., 1999d
1–5	↓ metamorphosis to zoeae	*L. vannamei*	Wouters et al., 1999
1–>9	↑ fecundity, nauplii per spawn, ↑ % viable spawns, ↑ body weight, ↑ GSI, = HIS, ↑ protein in hemolymph, hepatopancreas and ovaries, ↑ TG in hepatopancreas	*L. vannamei*	Palacios et al., 2000

GSI gonadosomatic index, HSI: hepatosomatic index, TG: triglycerides.
↑ Significant increase, ↓ significant decrease.
[a] In the same intermolt period.
[b] Between several molting cycles.

The reasons why some females produce only few spawns, while others produce numerous spawns of comparable quality under the same maturation conditions are unknown. It would be desirable to have a way to predict which females will produce more spawns. For example, if the initial physiological condition and thus the reserves of the female before stocking are determinant on the capacity for multiple spawns, a hemolymph or tissue sample could be used to evaluate the spawner condition and its production potential. Aquacop (1983) suggested that protein levels in hemolymph could be used as a predictive indicator of the spawning capabilities. We found (Palacios et al., 2000) that females that did not spawn had significantly lower levels of protein in the hemolymph, although these analyses were done at the end of the cycle, so they cannot be used as a predictive indicator. Our group is currently examining the possibility of a predictive metabolic indicator of spawning capacity. A long-term solution could be genetic selection, which is briefly discussed in Section 3.6.

3.6. Genetic variability

The implementation of genetic improvement programs are being considered not only for shrimp reproduction but in general for the overall shrimp farming process (for reviews, see Benzie, 1997, 1998; Browdy, 1998; Ibarra, 1999). There is evidence of individual (genetic)

differences in reproductive performance, and it has been observed that the progeny of females with multiple spawning capacities also present this characteristic (Wyban and Sweeney, 1991). These genetic differences are most probably related to physiological differences among females resulting from differences in endocrine regulation, metabolic pathways and digestive or assimilation capacity. Further studies and strategies are needed to establish the genetic variability of reproductive performance and offspring quality, and to evaluate the possibility of genetic programs to improve those traits.

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