Available online at www.sciencedirect.com

ScienceDirect

Aquaculture 274 (2008) 175 – 180

Aquaculture

www.elsevier.com/locate/aqua-online

Short communication

Effect of starvation during late megalopa stage of *Mithraculus forceps* (Brachyura: Majidae) on larval duration, synchronism of metamorphosis, survival to juvenile, and newly metamorphosed juvenile size

Joana Figueiredo [a,b,*], Gil Penha-Lopes [a], Luís Narciso [a], Junda Lin [b]

[a] *Laboratório Marítimo da Guia, IMAR, Departamento de Biologia Animal, Faculdade de Ciências da Universidade de Lisboa, Estrada do Guincho, 2750-374 Cascais, Portugal*

[b] *Florida Institute of Technology, Department of Biological Sciences, 150 W. University Boulevard, Melbourne, Florida 32901, USA*

Received 11 April 2007; received in revised form 29 October 2007; accepted 29 October 2007

Abstract

Larval resistance to temporary starvation is considered a key factor for successful development in the wild. Subjecting larvae to temporary starvation during early and/or late development is occasionally used in larviculture to reduce production costs.

Mithraculus forceps is a popular species in the marine aquarium industry for their ability to control nuisance algae in aquarium tanks; a larval culture methodology was previously proposed in order to avoid collection from the wild. In an attempt to reduce production/feeding costs of *M. forceps* larval culture (two zoea stages and a megalopa), larvae (megalopa stage) were starved after 7 and 8 days post-hatch (DPH); starvation treatments were compared with those of the control treatment where larvae were fed continuously. No differences were found in survival to juvenile, metamorphosis synchronism or larval duration between the treatments, which suggest that at least by day 7 DPH, megalopae have already achieved the point-of-reserve-saturation (PRS) and are able to successfully metamorphose to crab stage without feeding (facultative lecithotrophic); newly metamorphosed juveniles are slightly smaller (particularly the ones starved after 7DPH). This flexible way of development might be very advantageous in the wild and might allow the reduction of costs of larval culture in captivity.

Keywords: *Mithraculus forceps*; Starvation; Point-of-reserve-saturation; Megalopa

1. Introduction

The ability of crustacean larvae to tolerate temporary starvation periods is believed to be essential for survival in the wild, particularly in unstable habitats, where food availability varies (Anger, 2001). Anger and Dawirs (1981) applied indices of larval starvation tolerance to crustacean larvae-the point-of-no-return (PNR), i.e. the average time of initial food deprivation that will not allow larvae to survive even after being fed again; and the point-of-reserve-saturation (PRS), i.e. the minimum time of initial feeding after which a food-independent development to the next stage is possible. These two indices have been used to compare the degree of nutritional vulnerability in different species and developmental stages among decapod species (Anger et al., 1981; McConaugha, 1985; Anger, 1987, 1995a, 1995b, 2001).

Subjecting larvae to temporary starvation is occasionally used in larviculture to reduce production costs (Simões et al., 2002), particularly during early development. This is used for larvae that hatch with adequate energy reserves allowing for the delayed onset of exogenous feeding (Mikami and Takashima, 1993; Schuh and Diesel, 1995a,b; Diesel and Schuh, 1998; Giménez and Anger, 2005). Studies on the effect of temporary starvation during later development are less common (Harms, 1992; Anger, 1995a,b; Harvey, 1996; McWilliam and Phillips, 1997); once larvae in the

---

* Corresponding author. Laboratório Marítimo da Guia, IMAR, Departamento de Biologia Animal, Faculdade de Ciências da Universidade de Lisboa, Estrada do Guincho, 2750-374 Cascais, Portugal. Tel.: +351 214 869 211; fax: +351 214 869 720.

E-mail address: joana_figueiredo@portugalmail.pt (J. Figueiredo).

0044-8486/$ - see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.aquaculture.2007.10.052

last stage of development achieve the PRS, we can stop feeding to reduce cost. However, the suitability of these procedures should be studied in what matters not only to larvae survival to juvenile and growth but also synchronism of metamorphosis and larval duration. It is important to have a good synchronism of metamorphosis to avoid larval size dispersion that could trigger competition and cannibalism (Polis, 1981; Smith and Reay, 1991; Hecht and Pienaar, 1993; Figueiredo and Narciso, 2006; Penha-Lopes et al., 2007). A long larval duration increases costs associated with man-power, electricity, diets, etc. Previous studies have shown that crustacean larvae subjected to temporary starvation may decrease survivorship, reduce growth rate and increase larval duration by performing mark-time moulting (Gore, 1985; Mikami et al., 1993; Schuh and Diesel, 1995a,b; Harvey, 1996; Diesel and Schuh, 1998; Calado et al., 2005; Giménez and Anger, 2005). These studies also showed that starvation impact on larval development is, in general, directly proportional to the time they are under those conditions (Mikami and Takashima, 1993; Giménez and Anger, 2005).

Marine ornamental crabs *M. forceps* (A. Milne Edwards, 1875) are popular in the aquarium industry for its ability to control nuisance algae. The direct effects of temperature, diet, stocking and prey densities on *M. forceps* larval and juvenile survival and growth were addressed by Penha-Lopes et al. (2005, 2006) who proposed a culture protocol to avoid collection from the wild. During the course of those experiments, G. Penha-Lopes noticed that the megalopae seem to feed less during the last two days prior to metamorphosis to newly metamorphosed juvenile (i.e. first crab stage); Anger and Dietrich (1984) reported some crustacean larvae reduce feeding rate in the pre-moult stage.

In an attempt to improve larval culture methodology of *M. forceps* and reduce production costs, we will examine if their megalopae require food 1 or 2 days prior to metamorphosis to crab. The suitability of this procedure will be evaluated based on survival to newly metamorphosed juvenile, metamorphosis synchronism, larval duration and newly metamorphosed juveõnile size.

2. Materials and methods

2.1. Larvae culture

Experiments were carried out using a larval rearing system developed and described by Calado et al. (2003), and already used to culture *M. forceps* larvae by Rhyne et al. (2005) and Penha-Lopes et al. (2005). This system uses cylindrico-conical tanks and its main features are the "upwelling" flow that allows larvae and prey to be maintained in suspension and the use of screens that allow removing the prey from the tank without manipulation of the larvae. A photoperiod of 14L: 10D, salinity 35, and pH 8.0–8.2 were maintained for all experiments. *M. forceps* larvae development includes two zoeal stages (2 days per zoeal stage) followed by a megalopa (4 to 6 days).

In the control treatment, larvae were stocked in 10 l tanks at 10 larvae l^{-1} ($N=100$) and raised at 28 °C, and fed newly hatched *Artemia* nauplii at a density of 7 ml^{-1} (prey was renewed daily) until 15 day post-hatch (DPH) (according to the protocol proposed by Penha-Lopes et al. 2005, 2006). In the starvation treatments, larvae were raised under the same conditions except that they were starved after 7 or 8 DPH (2 and 1 day prior to first larvae undergoing metamorphosis, respectively). Four replicates were done for each treatment.

After the appearance of the first newly metamorphosed juvenile (crab), presence of crabs was checked daily, and crabs were removed from the system and recorded. At 9 DPH, a sample of 10 newly metamorphosed crabs from each replicate tank was used for measurements of carapace length (CL) and carapace width (CW) using an Olympus® SZ6045TR to the nearest 0.01 mm.

2.2. Statistical analysis

Models can be an advantageous approach when comparing to the traditionally used analysis of variance (Leung and Shang, 1989; Jorgensen and Bendoricchio, 2001; Figueiredo and Narciso, 2006; Penha-Lopes et al., 2007). Pinheiro and Bates (2000) developed the library "nlme" (non-linear mixed-effects models) for R 2.1.1. that allows predicting survival to juvenile through time and to statistically test final survival to juvenile, metamorphosis synchronism and larval duration (analysis of variance are incorporated on the development of the model). The percentage of larvae that survived to juvenile during the experiments (cumulative survivorship) was modelled using an asymptotic model (Eq. (1)) was used to describe the effect of late larval starvation on the survival to juvenile (y in %) through time (*x* in DPH):

$$y(x) = \phi_1 \times \left(1 - e^{\left(-e^{\phi_2} \times (x-\phi_3)\right)}\right), \quad y \leq 0. \tag{1}$$

In this formulation the model's parameters (estimated using maximum likelihood) are:

Φ_1 is the asymptote as $x \to +\infty$ (Time $\to +\infty$) and represents the maximum survival to juvenile (%);
Φ_2 is the logarithm of the rate of increase, corresponding to a half-life of $t_{0.5} = \log^2/\exp(\Phi_2)$, which gives an idea on the synchrony of metamorphosis (greater values indicate greater synchrony);
Φ_3 is the time (x) at which percent metamorphosis (y)=0, i.e., the day metamorphosis to crab began and gives an idea of larval duration.

The effect of the late megalopa starvation on maximum survival to juvenile (Φ_1), synchronism of metamorphosis (Φ_2), and larval duration (Φ_3) were tested using analysis of variance (incorporated on the development of the model on "nlme", described in detail by Pinheiro and Bates 2000). The development of

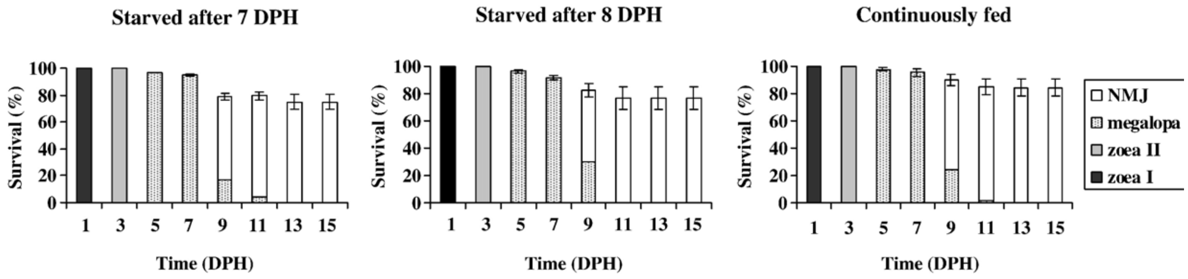

Fig. 1. Average (±standard error) survival (%) and larval development of *Mithraculus forceps* larvae starved after 7 and 8 days post-hatch (DPH) and fed continuously (control) (NMJ — newly metamorphosed juvenile, crab stage).

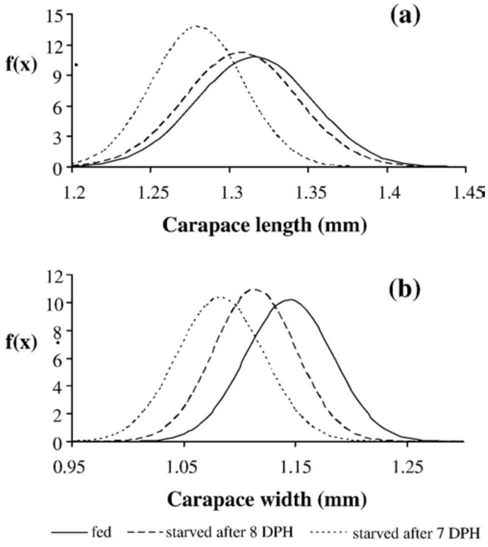

Fig. 2. Modelling carapace length (a) and carapace width (b) (mm) of newly metamorphosed juveniles that were reared under different conditions: continuously fed (control — solid line); starved after 7 DPH (pointed line); and starved after 8 DPH (dashed line) (DPH — days post-hatch).

the model includes the performance of consecutive goodness-of-fit tests. A model was considered to be well fit when standardized residuals were inside 95% confidence level (between −1.96 and 1.96) and randomly distributed around zero.

CL and CW of newly metamorphosed juvenile (NMJ) from the different treatments were compared using one-way-ANOVA's, followed by Tukey test if significant differences were found. Prior to ANOVA tests, data were checked for homogeneity of variances (Cochran's test) and normality (Shapiro–Wilk's test), and whenever necessary, data were appropriately transformed (Pestana and Velosa, 2006).

For all treatments, CL and CW of newly metamorphosed juveniles were modelled using Gaussian models since they can provide information on juvenile size obtained at the end of the larval culture (and that then will be used to initiate grow out) to producers. The graph of the Gaussian density function (Eq. (2)) can give us an idea of the most and least common sizes that we expect to obtain (Pestana and Velosa, 2006).

$$f(x) = \frac{1}{\sqrt{2\times\pi\times\sigma}} \times \exp\left(-0.5 \times \left(\frac{(x-\mu)}{\sigma}\right)^2\right). \quad (2)$$

Gaussian distribution function (Eq. (3)) allows estimation of how many juveniles will be obtained until a certain size (multiplying $P[X<x]$ by the maximum number of juveniles that will be obtained), larger than a certain size (multiplying $P[X>x]$ by the maximum number of juveniles that will be obtained), and between sizes y and x (multiplying $[P(X<x)-P(X<y)]$ by the maximum number of juveniles that will be obtained) (Pestana and Velosa, 2006).

$$F(x) = P(X<x) = \int_{-\infty}^{x} \frac{1}{\sqrt{2\times\pi\times\sigma}} \times \exp\left(-0.5 \times \left(\frac{(x-\mu)}{\sigma}\right)^2\right) dx$$

and

$$F(x) = P(X>x) = \int_{x}^{+\infty} \frac{1}{\sqrt{2\times\pi\times\sigma}} \times \exp\left(-0.5 \times \left(\frac{(x-\mu)}{\sigma}\right)^2\right) dx. \quad (3)$$

Parameters of the Gaussian model (μ and σ) were estimated by maximum likelihood (average and standard deviation of the sample, respectively) (Pestana and Velosa, 2006). Goodness of fit was tested by performing chi-square adjustment tests with Statistica 7.0.

Results were considered statistically significant when p-values were lower than 0.05 (Sokal and Rohlf, 1995).

3. Results

Mithraculus forceps larval development and survival (until 15 days post-hatch) for each treatment are represented in Fig. 1. The model that best described the effect of the tested starvation periods on percent survival to newly metamorphosed juveniles (Fig. 1) was:

$$\text{Survival to NMJ }(\%) = (82.02) \times \left(1 - e^{-e^{(0.39)\times(\text{DPH}-8)}}\right),\ y \geq 0. \quad (4)$$

The development of this model with "nlme" provided the following results: late megalopa starvation did not significantly influence survival to juvenile ($\Phi_1=82.02\%$, $p>0.83$), synchronism on metamorphosis ($\Phi_2=0.39$, $p>0.87$) or larval duration ($\Phi_3=8$ DPH, $p>0.79$). The standard error of the estimated parameters is 3.84, 0.22 and 0.00, respectively for Φ_1, Φ_2, and Φ_3.

Newly metamorphosed juvenile CW and CL were significantly different between the treatments (both $p<0.001$). Newly metamorphosed juveniles that were fed throughout larval development had similar CL to those starved after 8 DPH (1.32±0.01 and 1.31±0.01 mm, respectively, $p>0.60$), and both were larger than those starved after 7 DPH (1.28±0.01 mm, both $p<0.001$). CW of the newly metamorphosed were significantly different between all the treatments (all $p<0.01$); individuals fed continuously measured 1.14±0.01 mm CW, while the ones starved after 8 DPH and 7 DPH measured 1.11±0.01 and 1.08±0.01 mm, respectively. These results are reflected in the Gaussian models developed (Fig. 2, whose parameters estimated by maximum likelihood and adjustment tests results are listed in Table 1).

4. Discussion

Traditionally only survival to juvenile (or even just percent survival) and growth are studied to optimize a larval culture

Table 1
Gaussian parameters (μ and σ) and Chi-square adjustment tests (Q-statistic; df — degrees of freedom) for treatments where larvae were always fed, starved after 8 DPH and starved after 7 DPH

Starvation period	CL					CW				
	Gaussian parameters		Chi-square adjustment test			Gaussian parameters		Chi-square adjustment test		
	μ	σ	Q	df	p-value	μ	σ	Q	df	p-value
No	1.32	0.04	2.544	2	0.280	1.14	0.04	7.617	3	0.055
After 8 DPH	1.31	0.04	1.710	3	0.635	1.11	0.04	2.289	3	0.515
After 7 DPH	1.28	0.03	0.051	2	0.975	1.08	0.04	2.443	6	0.875

protocol (Calado et al., 2005; Penha-Lopes et al., 2005). However, to effectively address larval culture issues, there are other important criteria such as larval duration and synchrony of metamorphosis that need to be taken in account (Figueiredo and Narciso, 2006). In some invertebrates, a delayed metamorphosis to juvenile (longer larval duration) can influence their performance during grow out (Roberts and Lapworth, 2001) by reducing juvenile growth and survival, increasing time to maturation and reducing adult fecundity (Qian et al., 1990; Pechenik et al., 1993). It has also been demonstrated for several decapod species that asynchronous larval development causes size dispersion, increase in mortality due to food competition and cannibalism by larger larvae upon smaller ones (Polis, 1981; Gebauer et al., 2003). Metamorphosis asynchrony and size dispersion can also affect efficiency of juvenile culture. Coupled with the aggressive behaviour of larger crabs towards smaller conspecifics, different size crabs require different prey sizes and nutritional profile (e.g. Sainte-Marie and Lafrance, 2002).

The ideal conditions to raise *M. forceps* larvae would be those promoting high survival to juvenile, high synchronism of metamorphosis, and short larval duration, which means in an asymptotic model, a high Φ_1, high Φ_2 and low Φ_3, respectively. The conditions that promote optimal growth are those that allow newly metamorphosed juveniles to achieve a large CL and CW with all individuals growing to a similar size, which means in a Gaussian model, a high μ (newly metamorphosed juvenile CL and CW average) and a small σ (CL and CW standard deviation), respectively. A larger newly metamorphosed juvenile may reach adult size earlier (assuming that all juveniles grow at the same rate, independently of newly metamorphosed juvenile size) and therefore reduce grow-out period. A smaller range of newly metamorphosed juveniles CL and CW may imply that newly metamorphosed juveniles have similar conditions, thereby decreasing the risk of competition and cannibalism during juvenile culture (Polis, 1981; Smith and Reay, 1991; Hecht and Pienaar, 1993; Figueiredo et al., 2006; Penha-Lopes et al., 2007).

Modelling has been used to improve culture methodologies in captivity (Leung and Shang, 1989; Jorgensen and Bendoricchio, 2001). Models can be used as a decision support contributing to reduce production costs in aquaculture farms (Forsberg and Guttormsen, 2006). In aquaculture the main goal is to achieve high productivity at low cost. Since live prey culture is considered one of the most expensive and laborious activities of a hatchery, not providing *Artemia* nauplii to *M. forceps* larvae after 7 and 8 DPH (when considering 13 days of culture, 7 and 6 days of culture, respectively) could reduce *M. forceps* larval culture costs. Food is a key factor controlling survival, intermoult period and growth rate in crustacean larval culture (Mikami et al., 1993). In this study, *M. forceps* larvae subjected to starvation after 7 and 8 DPH (starting two and one day prior to metamorphosis to crab begins, respectively) displayed similar survival to juvenile, metamorphosis synchronism and larval duration to those continuously fed. Carapace width of newly metamorphosed juvenile subjected to starvation slightly decreases for every additional day of starvation but their size dispersion is similar (see Fig. 2) which means that food competition and cannibalism might not increase when megalopae are exposed to temporary starvation periods. Despite maintaining good survival, when starved after 7 DPH, larval growth is affected: average CL significantly reduces when compared with larvae starved after 8 DPH or continuously fed; and average CW is significantly smaller than the one displayed by continuously fed larvae. According to Knowlton (1974), larvae prioritize their energy use for (1) maintenance (survival), (2) moult and (3) growth. In optimal conditions larvae grow; in sub-optimal animals survive and moult (metamorphose) but do not grow. Subjecting megalopae to starvation after 7 and 8 DPH did not affect their survival and moulting period, but it also did not allow them to store enough energy that could then be used for growth (Fig. 2). From the biological perspective, the results suggest that if we fed *M. forceps* larvae with 7 *Artemia* nauplii ml^{-1}, by day 7 post-hatch, megalopae have already achieved the point-of-reserve-saturation. In other words, megalopae at 7 DPH have gained sufficient organic matter or energy to successfully metamorphose to crab stage (Anger, 2001). Based on this experiment, we cannot determine if the PRS was achieved at 7 DPH or previously. Nutrition is known to primarily affect size increment at ecdysis, and has less importance on moulting frequency (Anger, 2001). As previous studies in other decapods have already showed, the greater the starvation period, the greater was the impact on larval development and growth (Mikami and Takashima, 1993; Mikami et al., 1993; Anger, 2001; Giménez and Anger, 2005).

From the aquaculture perspective, we believe starving *M. forceps* larvae after 7DPH is already subjecting the larvae to sub-optimal conditions since growth is already significantly affected. This effect of starvation during larval development is thus carried over to juvenile stage since it affects their size and presumably their fitness (Giménez, 2004; Anger, 2006; Gimenez, 2006). Considering these aspects, the best compromise between cost and profit might be starving them after 8DPH (saving at least 5 days of *Artemia* nauplii feeding). A greater period of starvation produces a smaller newly metamorphosed juvenile that might require more time to achieve commercial size (1 cm CW); there may be reduced costs during larval culture but over-expenditure during juvenile grow out. However further long-term studies that could produce bio-economic data are needed to validate this suggestion.

Food availability in the plankton is considered a main factor accounting for fluctuations in abundance of planktotrophic larvae (Thorson, 1950). Decapod larvae are able to sustain short periods of starvation if larvae previously acquire nutritional reserves to reach the PRS; larvae accumulate biomass to be used as energy source during subsequent development (Gore, 1985; Anger, 2001; Liddy et al., 2004). Larvae of many species of benthic marine invertebrates can delay settlement and metamorphosis in the absence of often highly specific external cues, such as prey items (Harvey, 1996). This study shows that at least by 7 DPH, *M. forceps* megalopae (fed with 7 *Artemia* nauplii ml^{-1}) are facultative lecitotrophic i.e., are tolerant to temporary starvation but retain the ability to capture and ingest prey when it becomes available. Lecithotrophy is generally considered an adaptation to low or unpredictable food production in the environment where larval development takes place. It is usually more frequent in areas where nutritionally unpredictable conditions prevail such as high latitudes and freshwater environments (Anger, 1995a, 2001); however, even highly productive areas experience temporal or spatial variability in the plankton leading to a transitory or local occurrence of food limitation. A highly flexible mode of development can be determinant for survival, development and growth of larvae and other zooplankton in the wild (Thorson, 1950; Anger, 2001; Giménez and Anger, 2005); *M. forceps* megalopae ability to cope with short periods of lack of food might allow them to survive and metamorphose in areas with temporary food limitations.

Acknowledgments

We would like to thank Fundação para a Ciência e a Tecnologia (Scholarship #SFRH/BD/17130/2004), Fundação Calouste Gulbenkian, Portugal, (# 40739) and European Social Fund and Portuguese Government (# 1/3.2/PRODEP/2003) for their financial support. We are also grateful to J. Anto for making valuable suggestions during the writing process.

References

Anger, K., 1987. The D_0 threshold: a critical point in the larval development of decapod crustaceans. J. Exp. Mar. Biol. Ecol. 108, 15–30.

Anger, K., 1995a. Developmental biology of *Armases miersii* (Grapsidae), a crab breeding in supratidal rock pools. I. Facultative lecithotrophy of larval stages. Mar. Ecol. Prog. Ser. 117, 75–81.

Anger, K., 1995b. Starvation resistance in larvae of semisterrestrial crab, *Sesarma curacaoense* (Decapoda: Grapsidae). J. Exp. Mar. Biol. Ecol. 187, 161–174.

Anger, K., 2001. The Biology of Decapod Crustacean Larvae — Crustacean Issues, vol. 14. AA Balkema Publishers, Rotterdam, Netherlands. 419 pp.

Anger, K., 2006. Contributions of larval biology to crustacean research: a review. Invert. Reprod. Dev. 49, 175–205.

Anger, K., Dawirs, R.R., 1981. Influence of starvation on the larval development of *Hyas araneus* (Decapoda, Majidae). Helgol. Meersunters 34, 287–311.

Anger, K., Dietrich, A., 1984. Feeding rates and gross growth efficiencies in *Hyas araneus* L. larvae (Decapoda: Majidae) reared in the laboratory. J. Exp. Mar. Biol. Ecol. 77, 169–181.

Anger, K., Dawirs, R.R., Anger, V., Costlow, J.D., 1981. Effects of early starvation periods on zoea development of brachyuran crabs. Biol. Bull., Mar. Biol. Lab., Woods Hole 161, 199–212.

Calado, R., Narciso, L., Morais, S., Rhyne, A.L., Lin, J., 2003. A rearing system for the culture of ornamental decapod crustacean larvae. Aquaculture 218, 329–339.

Calado, R., Figueiredo, J., Rosa, R., Nunes, M.L., Narciso, L., 2005. Effects of temperature, density, and diet on development, survival, settlement synchronism, and fatty acid profile of the ornamental shrimp *Lysmata seticaudata*. Aquaculture 245, 221–237.

Diesel, R., Schuh, M., 1998. Effects of salinity and starvation on larval development of the crabs *Armases ricordi* and *A. roberti* (Decapoda: Grapsidae) from Jamaica, with notes on the biology and ecology of adults. J. Crust. Biol. 18, 423–436.

Figueiredo, J., Narciso, L., 2006. Productivity improvement of *Lysmata seticaudata* (Risso, 1816) larval rearing protocol through modelling. Aquaculture 261, 1249–1258.

Forsberg, O.I., Guttormsen, A.G., 2006. A pigmentation model for farmed Atlantic salmon: Nonlinear regression analysis of published experimental data. Aquaculture 253, 415–420.

Gebauer, P., Paschke, K., Anger, K., 2003. Delayed metamorphosis in decapod crustaceans. Evidence and consequences. Rev. Chil. Hist. Nat. 76, 169–175.

Giménez, L., 2004. Marine community ecology: importance of trait-mediated effects propagating through complex life cycles. Marine Ecology-Progress Series 283, 303–310.

Gimenez, L., 2006. Phenotypic links in complex life cycles: conclusions from studies with decapod crustaceans. Integr. Comp. Biol. 46, 615–622.

Giménez, L., Anger, K., 2005. Effects of temporary food limitation on survival and development of brachyuran crabs. J. Plankton Res. 27, 485–494.

Gore, R., 1985. Molting and growth in decapod larvae. In: Wenner, A.M. (Ed.), Crustacean Issues, vol. 2 — Larval Growth. AA Balkema Publishers, Rotterdam, Netherlands, pp. 1–65.

Harms, J., 1992. Laval development and delayed metamorphosis in the hermit crab *Clibanarius erythropus* (Latreille) (Crustacea, Diogenidae). J. Exp. Mar. Biol. Ecol. 156, 151–160.

Harvey, A.W., 1996. Delayed metamorphosis in Florida hermit crabs: multiple cues and constraints (Crustacea: Decapoda: Paguridae and Diogenidae). Mar. Ecol. Prog. Ser. 141, 27–36.

Hecht, T., Pienaar, A.G., 1993. A review of cannibalism and its implications in fish larviculture. J. World Aquacult. Soc. 24, 246–261.

Jorgensen, S.E., Bendoricchio, G., 2001. Fundamentals of Ecological Modelling, 3edn — Developments in Environmental Modelling 21. Elsevier Science B. V., Amsterdam. 530 pp.

Knowlton, R.E., 1974. Larval development processes and controlling factors in decapod Crustacea, with emphasis on Caridea. Thalassia Jugosl. 10, 139–158.

Leung, P., Shang, Y., 1989. Modeling prawn production management systems: a dynamic Markov decision approach. Agric. Systems 29, 5–20.

Liddy, G.C., Nelson, M.M., Nichols, P.D., Phillips, B.F., Maguire, G.B., 2004. The lipid composition on early stage western rock lobster (*Panulirus cygnus*) phyllosoma: importance of polar lipid and essential fatty acids. J. Shellfish Res. 23, 265–273.

McConaugha, J.R., 1985. Nutrition and larval growth. In: Wenner, A.M. (Ed.), Larval Growth. Balkema, Rotterdam, pp. 127–154.

McWilliam, P.S., Phillips, B.F., 1997. Metamorphosis of the final phyllosoma and secondary lecithotrophy in the puerulus of *Panulirus cygnus* George: a review. Mar. Freshwater Res. 48, 783–790.

Mikami, S., Takashima, F., 1993. Effects of starvation upon survival, growth and moulting interval of the larvae of the spiny lobster *Panulirus japonicus* (Decapoda, Palinuridae). Crustaceana 64, 137–142.

Mikami, S., Greenwood, J.G., Gillespie, N.C., 1993. The effect of starvation and feeding regimes on survival, intermoult period and growth of cultured *Panulirus japonicus* and *Thenus* sp. phyllosomas (Decapoda, Panuliridae and Scyllaridae). Crustaceana 68, 160–169.

Pechenik, J.A., Rittschof, D., Schmidt, A.R., 1993. Influence of delayed metamorphosis on survival and growth of juvenile barnacles *Balanus amphitrite*. Mar. Biol. 115, 287–294.

Penha-Lopes, G., Rhyne, A., Lin, J., Narciso, L., 2005. The larval rearing of the marine ornamental crab, *Mithraculus forceps* (A. Milne Edwards) (Decapoda: Brachyura: Majidae). Aquacult. Res. 36, 1313–1321.

Penha-Lopes, G., Rhyne, A.L., Lin, J., Narciso, L., 2006. Effects of temperature, stocking density and diet on the growth and survival of juvenile *Mithraculus forceps* (A. Milne Edwards) (Decapoda: Brachyura: Majidae). Aquacult. Res. 37, 398–408.

Penha-Lopes, G., Figueiredo, J., Narciso, L., 2007. Modelling survival and growth of *Mithraculus forceps*' larvae and juveniles (A. Milne Edwards, 1875) (Decapoda: Brachyura: Majidae) in aquaculture. Aquaculture 264, 285–296.

Pestana, D., Velosa, S.F., 2006. Introdução à Probabilidade e à Estatística, vol. I. Fundação Calouste Gulbenkian, Lisboa. 1157 pp.

Pinheiro, J.C., Bates, D.M., 2000. Mixed-Effects Models in S and S-PLUS — Statistics and Computing. Springer-Verlag, New York. 528 pp.

Polis, G.A., 1981. The evolution and dynamics of intraspecific predation. Annu. Rev. Ecol. Syst. 12, 225–251.

Qian, P.Y., McEdward, L.R., Chia, F.S., 1990. Effects of delayed settlement on survival, growth, and reproduction in the spionid polychaete, *Polydora ligni*. Invertebr. Reprod. Dev. 18, 147–152.

Rhyne, A., Penha-Lopes, G., Lin, J., 2005. Growth, development and survival of larval *Mithraculus sculptus* (Lamark) and *M. forceps* (A. Milne Edwards) (Decapoda: Brachyura: Majidae): economically important marine ornamental crabs. Aquaculture 245, 183–191.

Roberts, R.D., Lapworth, C., 2001. Effects of delayed metamorphosis on larval competence, and post-larval survival and growth, in the abalone *Haliotis iris* Gmelin. J. Exp. Mar. Biol. Ecol. 258, 1–13.

Sainte-Marie, B., Lafrance, M., 2002. Growth and survival of recently settled snow crab *Chionoecetes opilio* in relation to intra- and intercohort competition and cannibalism: a laboratory study. Mar. Ecol. Prog. Ser. 244, 191–203.

Schuh, M., Diesel, R., 1995a. Effects of salinity, and starvation on the larval development of *Armases* (=*Sesarma*) *miersii* (Rathbun, 1897), a semiterrestrial crab with abbreviated development (Decapoda: Grapsidae). J. Crust. Biol. 15, 205–213.

Schuh, M., Diesel, R., 1995b. Effects of salinity and starvation on the larval development of *Sesarma curacaoense* De Man, 1892, a mangrove crab with abbreviated development (Decapoda: Grapsidae). J. Crust. Biol. 15, 645–654.

Simões, F., Ribeiro, F., Jones, D.A., 2002. Feeding early larval stages of fire shrimp *Lysmata debelius* (Caridea, Hippolytidae). Aquacult. Int. 10, 349–360.

Smith, C., Reay, P., 1991. Cannibalism in teleost fish. Rev. Fish Biol. Fish. 1, 41–64.

Sokal, R., Rohlf, F., 1995. Biometry — The Principles and Practice of Statistics in Biological Research, 3rd edn. Freeman, NewYork. 887 pp.

Thorson, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. 25, 1–45.