Available online at www.sciencedirect.com
SCIENCE DIRECT
Aquaculture 252 (2006) 348–355
Aquaculture
www.elsevier.com/locate/aqua-online

Growth of redclaw crayfish (*Cherax quadricarinatus*) in a three-dimensional compartments system: Does a neighbor matter?

Assaf Barki [a,*], Ilan Karplus [a], Rivka Manor [b], Shmuel Parnes [b], Eliahu D. Aflalo [b], Amir Sagi [b]

[a] *Aquaculture Research Unit, Institute of Animal Science, Agricultural Research Organization, The Volcani Center, P.O. Box 6, Bet Dagan 50250, Israel*
[b] *Department of Life Sciences and the National Institute for Biotechnology in the Negev, Ben-Gurion University of the Negev, P.O. Box 653, Beer-Sheva 84105, Israel*

Received 14 April 2005; received in revised form 11 July 2005; accepted 14 July 2005

Abstract

Rearing crayfish in individual compartments could be a means of overcoming social-dependent density limitations in order to increase yields per unit area in intensive culture. Two experiments were conducted to evaluate the impact of neighbors on the growth of redclaw crayfish (*Cherax quadricarinatus*) males in three-dimensional units, consisting of 144 individual compartments, designed for intensive battery culture. The first experiment revealed significantly lower growth rates in crayfish surrounded by neighbors on all sides than in those reared with no neighbors in adjacent compartments, or with neighbors only in compartments on the same level but not above or below them. The second experiment revealed significantly lower growth rates in relatively small crayfish surrounded by large crayfish in a mixed-size unit than in those surrounded by similar-sized small crayfish in a uniform-size unit. No such effect was found for relatively large crayfish surrounded by small crayfish. The results clearly indicated interactions between crayfish in our system, despite them being housed in separate compartments. Growth was adversely affected by the presence of neighbors in adjacent compartments, especially vertically adjacent ones, and the presence of larger individuals in adjacent compartments. This social effect was attributed to partial tactile contact between neighbors in our system. The consequences of these findings for battery culture of crayfish are discussed.

Keywords: Redclaw crayfish; *Cherax quadricarinatus*; Growth; Growth inhibition; Social interactions; Individual compartments; Battery culture; Intensive culture

1. Introduction

Population density is a key factor in limiting the growth and survival of most cultured aquatic spe-

* Corresponding author. Tel.: +972 3 9683388; fax: +972 3 9605667.
E-mail address: barkia@agri.gov.il (A. Barki).

0044-8486/$ - see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.aquaculture.2005.07.012

cies, and this poses a problem especially for intensive culture systems, in which the aim is to maximize the number of animals in a limited space. The problem is more pronounced with benthic organisms, which do not utilize the water column. A desirable species for such systems would be tolerant of high densities; however, clawed crustaceans such as the benthic crayfish and lobsters are sensitive to crowding.

Many studies in crayfish have demonstrated an inverse relationship between density and growth, in both wild and cultured populations (for reviews see: Lowery, 1988; Aiken and Waddy, 1992); the latter include the three cultured *Cherax* species (e.g., Mills and McCloud, 1983; Morrissy, 1992; Morrissy et al., 1995; Verhoef and Austin, 1998a,b; Jones and Ruscoe, 2000). The effect of crowding may act through deterioration of water quality, decrease of essential resources such as food and shelter, or increased frequency of behavioral interactions (Aiken and Waddy, 1992). Whereas environmental factors and resource availability may be fairly well controlled in intensive facilities, social interactions are unavoidable in communal culture. The social factor has a particular impact in crustaceans since their growth is associated with vulnerability to cannibalism as a consequence of molting.

Increasing habitat complexity through provision of artificial shelters has been demonstrated to significantly improve survival and production in communally cultured redclaw crayfish (*Cherax quadricarinatus*) (Jones and Ruscoe, 2001). Of all tested shelter types, the one with the highest capacity to separate many individuals (mesh bundles) yielded the best results (Jones and Ruscoe, 2001), indicating the importance of eliminating social interactions through direct contact. Thus, a logical and straightforward means of overcoming density limitations imposed by social interaction is rearing crayfish in individual compartments. On the commercial scale, this method is termed 'battery culture'. Density has been demonstrated to affect growth in *C. quadricarinatus* at all growth stages: first month post release (Barki and Karplus, 2004); nursery stage (Naranjo-Páramo et al., 2004); and grow-out (Pinto and Rouse, 1996; Jones and Ruscoe, 2000). However, this method would be most beneficial during the fattening (grow-out) stage in intensive systems, when spacing out the growing animals is no longer possible because of space limitations. Previous attempts to rear the American lobster, *Homarus americanus* (van Olst et al., 1980), and the marron crayfish, *Cherax tenuimanus* (Morrissy et al., 1995), in battery culture systems proved unsuccessful. Studies on possible growth-limiting factors have addressed the effect of compartment size, and determined the appropriate sizes for unrestricted growth in the American lobster (Aiken and Waddy, 1978; van Olst and Carlberg, 1978) and in various crayfishes (Goyert and Avault, 1978; Jussila, 1997), including the redclaw crayfish (Manor et al., 2002). Morrissy (2002) attributed the poor growth in such intensive systems primarily to nutritional deficiencies caused by inadequate artificial feeds and lack of the natural food that is available in outdoor earthen ponds.

In the present study we evaluated the growth performance of male *C. quadricarinatus* in individual compartments in the context of possible effects of the social environment, by using three-dimensional (3D) units comprising individual compartments designed for intensive battery culture. The main advantage of a 3D system is its high yield per bottom area of the tank, gained by utilizing the whole water volume for the benthic crayfish. However, the need for water to flow into the internal compartments in such a system dictates a compartment design that enables chemical contact via waterborne substances as well as visual and limited tactile contact between neighboring individuals. We have recently investigated the importance of the various sensory modalities in mediating growth inhibition in *C. quadricarinatus*, by using an experimental setup based on observation of pairs of males in the laboratory (Karplus and Barki, 2004). Growth inhibition in the smaller individual was evident when there was full contact between conspecifics, whereas visual and/or chemical cues were not sufficient to elicit that social effect. The results obtained from observation of pairs of males suggest that redclaw crayfish might be suitable for individual rearing that allowed visual and chemical contact. The specific purpose of the present study was to elucidate the impact of neighbors on crayfish growth in individual compartments within multiple-neighbor 3D units designed for battery culture.

2. Materials and methods

2.1. The individual-compartment units

The experiments were conducted in three comparted units submerged within a 1 m deep, 15 m long tank in a greenhouse. Each unit was a 1 m^3 cubic structure that contained 144 individual compartments arranged in nine layers of 16 (4×4) square compartments (Figs. 1 and 2). The internal horizontal area of each compartment was 484 cm^2 (22×22 cm), which is appropriate for growth to marketable size (Manor et al., 2002). The vertical and horizontal walls of the compartments had narrow slits (approximately 4 mm) to allow the passage of water. Each compartment had its own feed inlet at the end of a pipe leading to the top of the unit at the water surface.

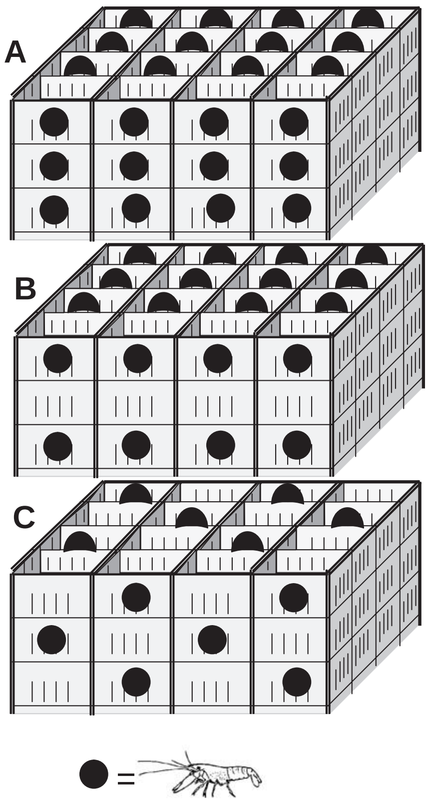

Fig. 1. The three individual-compartment units used for experiment 1, illustrating the stocking design of *C. quadricarinatus* males according to the following treatments: A—all-neighbor; B—horizontal-neighbor; C—no-neighbor. Only three of the nine storeys of each unit are depicted.

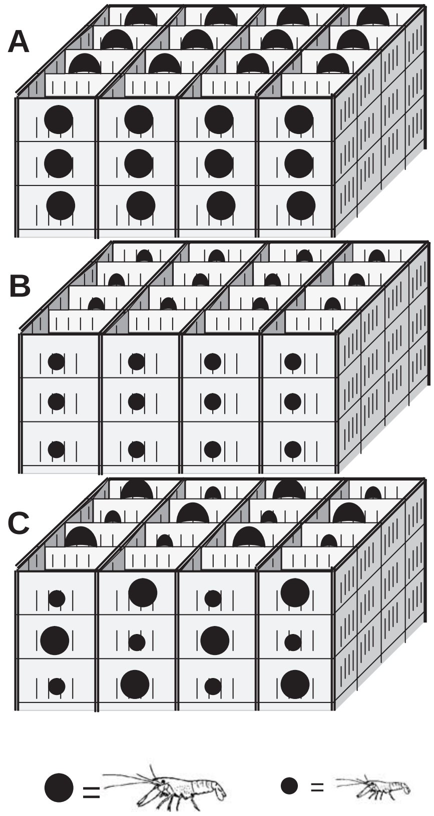

Fig. 2. The three individual-compartment units used for experiment 2, illustrating the stocking design of *C. quadricarinatus* males according to the following treatments: A—large males, uniform size; B—small males, uniform size; C—large and small males, mixed size. Only three out of the nine storeys of each unit are depicted.

The crayfish were daily fed through these pipes with extruded sinking fish pellets, 2 mm in diameter, containing 42% protein, 12% fat, 1.7% fiber, 2% calcium, 1.5% phosphorus and 9.2% ash, manufactured by Raanan Marketing (R.M.D. Ltd Israel). The daily ration was approximately 2% of the crayfish body mass in the unit.

Water was re-circulated through a biofilter and aerated by air stones distributed along the tank. Water temperatures (measured daily) varied gradually in the course of the experiments, with the lowest mean values during May (22.7 ± 0.8 °C; measured in experiment 1) and November (22.9 ± 1.5 °C; measured in experiment 2) and the highest during August (28.3 ± 0.8 °C). Water quality parameters were measured monthly: dissolved oxygen exceeded 7.5 mg

l^{-1}, ammonium was at an undetectable level, the nitrite level did not exceed 0.05 mg l^{-1}, and pH was 7–7.2.

2.2. Experiment 1

In this experiment we investigated the effect of the presence of crayfish in neighboring compartments on growth. Male redclaws (initial weight 16.5 ± 4.6 g) were weighed monthly for 158 days, between May and October. We tested only males, which grow faster than females while socially isolated in individual cells (Manor et al., 2002). The males were stocked according to the following treatments, each of which occupied a separate unit: (i) 'all-neighbor'—adjacent neighbors in all possible directions, i.e., a completely stocked unit (n = 144) (Fig 1A); (ii) 'horizontal neighbor'—adjacent neighbors only in the horizontal direction, i.e., five stocked storeys alternated with four unstocked ones (n = 80) (Fig 1B); (iii) 'no-neighbor'—no adjacent neighbors, i.e., alternating compartments in each storey were occupied, in a pattern like a chess board, so that all compartment partitions–horizontal and vertical–faced an empty compartment (n = 72) (Fig. 1C). Crayfish that escaped or died were replaced with other males in order to maintain a constant number of neighbors. Only males that resided within the compartments for at least 4 of the 5 months of the experiment were included in the analysis.

Growth was analyzed in terms of specific growth rate (SGR), calculated with the formula SGR = 100 $(\ln W_t - \ln W_0)t^{-1}$, in which W_0 and W_t are the mean initial and final weights, respectively, and t is the time in days. We tested for the effects of treatment and storey on SGR of male redclaw by means of two-way ANOVA at a significance level of $P<0.05$. Where a significant difference was found, multiple comparisons were performed by means of Tukey–Kramer honestly significant difference (HSD) test, to identify differences between specific treatments. Data of the daily growth rate (GR) are presented without the results of the statistical tests, which were similar to those obtained for SGR.

2.3. Experiment 2

We designed this experiment to investigate the effects of the relative size of the adjacent neighbors on crayfish growth. The individual compartments in three units were stocked according to the following treatments: (i) large males—uniform size (n = 144) (Fig 2A); (ii) small males—uniform size (n = 144) (Fig 2B); (iii) mixed size, with equal numbers of small and large males (n = 72 for each) in alternating compartments, so that each horizontal or vertical partition separated a male from a different-sized adjacent neighbor (Fig. 2C). The initial weights of the small and large males were 8.8 ± 1.5 and 23.1 ± 5.3 g, respectively. The experiment lasted for 93 days, between August and November, during which the crayfish were weighed monthly, as in the previous experiment. Crayfish that escaped or died were replaced with other males, which were not included in the analysis.

The effects of the following factors were tested by means of four-way ANOVA: (i) male size, i.e., small versus large; and (ii) size composition, i.e., uniform- versus mixed-size unit, with particular emphasis on the interaction between these factors; (iii) storey and (iv) location relative to the unit walls, i.e., external (12) versus internal (4) compartments in each storey, and the interaction between these two factors. Statistical analyses were performed with the JMP 5.1 statistical software (SAS, 2003).

3. Results

3.1. Experiment 1

The survival rates, i.e., the percentage of original crayfish found in the compartments at the end of the 5-month experiment, were 40.2% in the all-neighbor treatment, 63.7% in the horizontal-neighbor treatment and 79.2% in the no-neighbor treatment. The main reason for this reduction was the escape or passage of males into occupied compartments (which resulted in mortality through fighting) when the layers were not fitted properly one above the other.

Average daily growth rates and SGRs did not exceed 0.16 g day^{-1} and 0.57% day^{-1}, respectively, for all units (Fig. 3). ANOVA revealed a significant treatment effect ($F_{2,208}$ = 20.0, $P<0.001$) and storey effect ($F_{8,208}$ = 2.87, $P<0.01$), with significantly

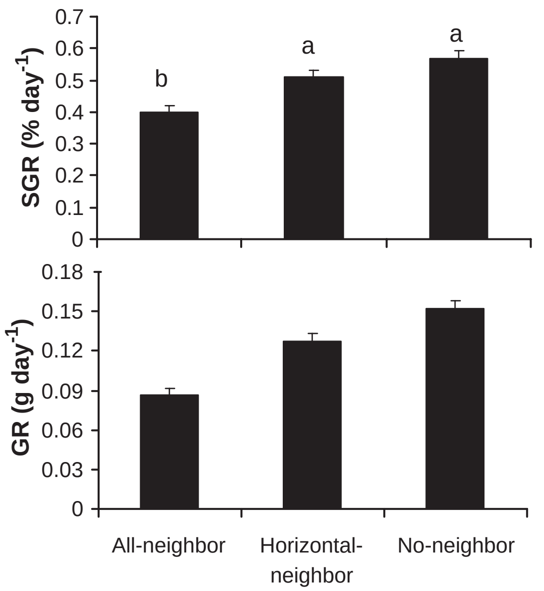

Fig. 3. Specific growth rates (SGR) and daily growth rates (GR) of *C. quadricarinatus* males in individual compartments, presented for the all-neighbor, horizontal-neighbor and no-neighbor treatments of experiment 1. Error bars represent S.E.M. Columns marked with different letters are significantly different (Tukey–Kramer HSD test, $P<0.05$).

lower SGR in the all-neighbor treatment (Fig. 3) and in the upper storey (Fig. 4) (Tukey–Kramer HSD, $P<0.05$).

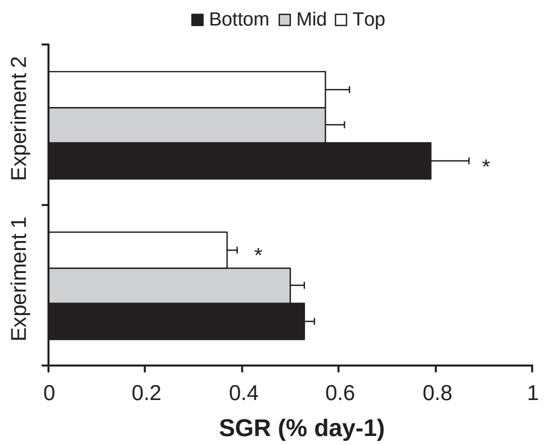

Fig. 4. Specific growth rates (SGR) of *C. quadricarinatus* males in individual compartments at the bottom, middle (5th) and top storeys of the nine-storey battery culture units. Error bars represent S.E.M. An asterisk denotes a storey that significantly differed from all other storeys.

3.2. Experiment 2

The survival rate of large crayfish was 84.7% in both the uniform-size and the mixed-size units, and those of small crayfish were 63.2% and 72.2%, respectively.

The average daily growth rates and SGRs did not exceed 0.14 g day^{-1} and 0.86% day^{-1}, respectively, for all units (Fig. 5). There were significant main effects for both the size of the crayfish ($F_{1,305}$= 108.1, $P<0.001$) and the size composition of the unit ($F_{1,305}=8.5$, $P<0.01$). However, a significant interaction between size and size composition ($F_{1,305}=12.4$, $P<0.001$) was found, which revealed that the SGRs of small males were influenced by the relative size of the neighbors, being lower in the mixed-size treatment (i.e., in the presence of larger neighbors), whereas those of large males were similar in the uniform- and mixed-size units (Fig. 5). There was also a significant main effect of the storey factor ($F_{8,305}=2.5$, $P<0.05$), with higher SGRs in the lowest storey (Fig. 4) (Tukey–Kramer HSD, $P<0.05$).

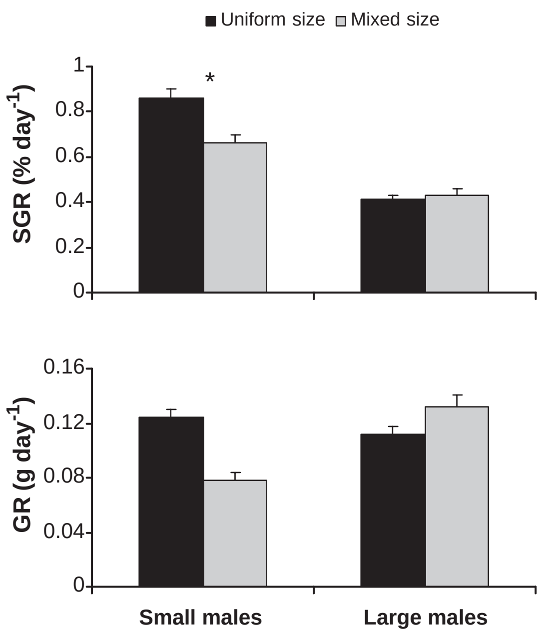

Fig. 5. Specific growth rates (SGR) and daily growth rates (GR) of *C. quadricarinatus* males in individual compartments, presented for the large males—uniform-size, small males—uniform-size and mixed-size treatments of experiment 2. Error bars represent S.E.M. The asterisk denotes significant difference between coupled columns.

However, there was no significant difference in SGR between internal and external compartments, and no interaction of this factor with the storey factor.

4. Discussion

The results of our study clearly demonstrate an effect of neighbors on growth of *C. quadricarinatus* males in individual compartments. This main finding emerged despite the evidently poor growth and survival rates, which reflected the technical and management difficulties inherent in the specific individual-compartment units used in this study.

The survival rates were much lower than would be expected in individual rearing, mainly because of technical problems that enabled some individuals to escape or to pass through into adjacent compartments and resulted in mortality through fighting. The fact that the survival rate was highest in the no-neighbor treatment and lowest in the all-neighbor treatment in experiment 1 is attributable to an increased tendency of the crayfish to escape (if it was made possible) and to the increased probability of passing into an occupied adjacent compartment with the increase in the number of adjacent neighbors. The lower survival of small crayfish compared with large crayfish in experiment 2 probably resulted from their smaller size which allowed them to pass through narrow spaces formed between unfitted adjacent layers. Previous studies comparing communally and individually reared crayfish reported higher survival rates in the later (Geddes et al., 1988; Du Boulay et al., 1993; Morrissy et al., 1995). In fact, high survival rate is supposed to be one of the major advantages of individual rearing systems.

The poor growth, on the other hand, reflected not only inadequacies in our specific rearing units (e.g., problems related to feed availability in each compartment) but most probably also a general shortcoming attributed to all individual rearing systems, i.e., inadequate artificial feed and lack of natural food (Morrissy, 2002). We compared the SGRs obtained in the present study with those reported in other studies of redclaw, but only with those of similar initial sizes and comparable rearing periods, because SGR decreases with size (Evans and Jussilla, 1997). For example, mixed-sex redclaw (17 g at stocking) reared in pen enclosures within an earthen pond for 140 days exhibited SGRs of 0.88%, 0.67% and 0.63% day^{-1} at densities of 3, 9 and 15 m^{-2}, respectively (Jones and Ruscoe, 2000), and redclaw (12.8 g at stocking) reared for 162 days at 12.5 m^{-2} exhibited SGRs between 0.51% and 0.63% day^{-1} under different shelter types (Jones and Ruscoe, 2001). These values are compared with SGR of 0.57% day^{-1} for the all-male population (16.5 g at stocking) reared for 158 days in the no-neighbor treatment in the present experiment 1 (Fig. 3). In an indoor recirculating system, mixed-sex redclaw juveniles (6.9 g at stocking) reared for 150 days grew at an SGR of 0.96% day^{-1} (Rodriguez-Canto et al., 2002), compared with 0.86% day^{-1} for 8.8 g juvenile males in the small-uniform-size treatment in the present experiment 2 (Fig. 4). In another separate-cell system, Manor et al. (2002) found SGRs of approximately 0.6% day^{-1} over 150 days for males stocked at 23.2 g, and of 1.2% day^{-1} over 98 days for males stocked at 10.7 g. These comparisons generally show slower growth in our battery culture units than in other systems. It is not possible to assess the extent to which the overall poor growth rate in the present study was attributable to inadequacies in the rearing units; however, we do believe that growth and survival could be improved in this system. For example, growth was better in the bottom storey than in the upper storeys, which is consistent with the findings of Manor et al. (2002), probably because feed particles sank through the grooved bottoms, from upper compartments into the bottom compartments; avoiding this could improve overall growth. In addition, the sub-optimal temperatures for redclaw (Jones, 1990) that prevailed in the present system during part of the experimental period probably affected overall growth adversely.

Notwithstanding the poor absolute growth, the differences among the growth rates in the various treatments indicated that there were interactions among males, despite the separate compartments. The first experiment showed that growth rates were significantly lower when crayfish were completely surrounded by neighbors, and were highest when there were no neighbors in adjacent compartments. Moreover, the significant difference between the all-neighbor and horizontal-neighbor treatments indicated that it was mainly the vertical neighbors who elicited this neighbor effect. It is conceivable that an individual could more easily avoid direct contact with its horizontal neighbors than with a neighbor in the compartment below, who might cling to the ceiling of the compartment, or nip small appendages such as pereiopods that passed through the slits in the floor. This result is in accordance with our previous finding (Karplus and Barki, 2004) that tactile physical contact, and not only chemical and/or visual contact, is necessary for inducing growth inhibition in *C. quadricarinatus*.

Furthermore, the results of the present second experiment emphasized the importance of the neighbors' relative size in growth inhibition. Growth rates of small crayfish were lower when they were surrounded by larger neighbors than when their neighbors were of similar size, whereas large crayfish grew equally well in the uniform- and in the mixed-size units. That large individuals inhibit the growth of smaller conspecifics and not vice versa has been reported with regard to various crustaceans (Segal and Roe, 1975; Cobb et al., 1982; McLay, 1985; Ra'anan and Cohen, 1985; Karplus et al., 2000; Karplus, 2005) and was also shown between pairs of redclaw males (Karplus and Barki, 2004). Direct competition for food, in which competitively inferior (i.e., smaller) individuals obtain less food, is considered the major growth-controlling mechanism in communally held crustaceans. However, the present study, in which the crayfish could not directly compete for food, suggests that other social mechanisms, triggered by tactile contact, might also inhibit growth in *C. quadricarinatus*.

In conclusion, the principal lesson for those intending to implement individual rearing in battery culture is that the potential effects of social interaction are not to be underestimated; the premise that social effects are eliminated in such systems should be considered with caution. In practical terms, care must be taken to stock individuals of similar sizes and to prevent any tactile contact between neighbors. For 3D systems, a solid non-perforated or non-grooved compartment bottom would prevent tactile contact between vertical neighbors (the most damaging contact) and loss of feed particles that sink through the holes. Double vertical walls that created a minimal appropriate space between horizontally adjacent compartments would prevent contact between those neighbors.

Acknowledgements

We would like to thank the staff of Ben Farm at Be'er Tzofar, Israel for their support and for allowing us to use their facilities. This study was funded by grants from the Chief Scientist of the Israeli Ministry of Agriculture and Rural Development and from the ICA Foundation.

References

Aiken, D.E., Waddy, S.L., 1978. Space, density and growth of the lobster (*Homarus americanus*). Proc. Annu. Meet.-World Maric. Soc. 9, 461–467.

Aiken, D.E., Waddy, S.L., 1992. The growth process in crayfish. Rev. Aquat. Sci. 6, 335–381.

Barki, A., Karplus, I., 2004. Size rank and growth potential in redclaw crayfish (*Cherax quadricarinatus*): are stunted juveniles suitable for grow-out? Aquac. Res. 35, 559–567.

Cobb, J.S., Tamm, G.R., Wang, D., 1982. Behavioral mechanisms influencing molt frequency in the American lobster *Homarus americanus*. J. Exp. Mar. Biol. Ecol. 62, 185–200.

Du Boulay, A.J.H., Sayer, M.D.J., Holdich, D.M., 1993. Investigations into intensive culture of the Australian red claw crayfish *Cherax quadricarinatus*. Freshwater Crayfish 9, 70–78.

Evans, L.H., Jussilla, J., 1997. Freshwater crayfish growth under culture conditions: proposition for a standard reporting approach. J. World Aquac. Soc. 28, 11–19.

Geddes, M.C., Mills, B.J., Walker, K.F., 1988. Growth in the Australian freshwater crayfish, *Cherax destructor* Clark, under laboratory conditions. Aust. J. Mar. Freshw. Res. 39, 555–568.

Goyert, J.C., Avault Jr., J.W., 1978. Effects of container size on growth of crawfish (*Procambarus clarkii*) in a recirculating culture system. Freshwater Crayfish 4, 277–286.

Jones, C.M., 1990. The biology and aquaculture potential of the tropical freshwater crayfish *Cherax quadricarinatus*. Information Series, vol. Q190028. Queensland Department of Primary Industries, Brisbane. 109 pp.

Jones, C.M., Ruscoe, I.M., 2000. Assessment of stocking size and density in the production of redclaw crayfish, *Cherax quadricarinatus* (von Martens) (Decapoda: Parastacidae), cultured under earthen pond conditions. Aquaculture 189, 63–71.

Jones, C.M., Ruscoe, I.M., 2001. Assessment of five shelter types in the production of redclaw crayfish, *Cherax quadricarinatus* (Decapoda: Parastacidae) under earthen pond conditions. J. World Aquac. Soc. 32, 41–52.

Jussila, J., 1997. Physiological responses of Astacid and Parastacid crayfishes (Crustacea: Decapoda) to conditions of intensive culture, Doctoral dissertation, University of Kuopio, Finland.

Karplus, I., 2005. Social control of growth in *Macrobrachium rosenbergii* (De Man): a review and prospects for future research. Aquac. Res. 36, 238–254.

Karplus, I., Barki, A., 2004. Social control of growth in the redclaw crayfish, *Cherax quadricarinatus*: testing the sensory modalities involved. Aquaculture 242, 321–333.

Karplus, I., Malecha, S.R., Sagi, A., 2000. The biology and management of size variation. In: New, M.B., Valenti, W.C. (Eds.), Freshwater Prawn Culture. The Farming of *Macrobrachium rosenbergii*. Blackwell Science, Oxford, pp. 259–289.

Lowery, R.S., 1988. Growth, moulting and reproduction. In: Holdich, D.M., Lowery, R.S. (Eds.), Freshwater Crayfish. Biology, Management and Exploitation. Croom Helm, London, pp. 83–113.

Manor, R., Segev, R., Leibovitz, M.P., Aflalo, E.D., Sagi, A., 2002. Intensification of redclaw crayfish *Cherax quadricarinatus* culture II. Growout in a separate cell system. Aquac. Eng. 26, 263–276.

McLay, C.L., 1985. Moulting and growth in *Pagurus traversi* and *P. novizealandiae* (Decapoda: Anomura: Paguridae): the effects of neighbours. N.Z. J. Mar. Freshw. Res. 19, 327–337.

Mills, B.J., McCloud, P.I., 1983. Effects of stocking and feeding rates on experimental pond production of the crayfish *Cherax destructor* Clark (Decapoda: Parastacidae). Aquaculture 34, 51–72.

Morrissy, N.M., 1992. Density-dependent pond growout of single year-class cohorts of a freshwater crayfish *Cherax tenuimanus* (Smith) to two years of age. J. World Aquac. Soc. 23, 154–168.

Morrissy, N.M., 2002. Culturing the marvelous marron in Western Australia: 1967–1997. Freshwater Crayfish 13, 13–38.

Morrissy, N.M., Bird, C., Cassells, G., 1995. Density-dependent growth of cultured marron, *Cherax tenuimanus* (Smith 1912). Freshwater Crayfish 10, 560–568.

Naranjo-Páramo, J., Hernandez-Llamas, A., Villarreal, H., 2004. Effect of stocking density on growth, survival and yield of juvenile redclaw crayfish *Cherax quadricarinatus* (Decapoda: Parastacidae) in gravel-lined commercial nursery ponds. Aquaculture 242, 197–206.

Pinto, G.F., Rouse, D.B., 1996. Growth and survival of the Australian red claw crayfish *Cherax quadricarinatus* at three densities in earthen ponds. J. World Aquac. Soc. 27, 187–193.

Ra'anan, Z., Cohen, D., 1985. Ontogeny of social structure and population dynamics in the giant freshwater prawn, *Macrobrachium rosenbergii* (de Man). In: Wenner, A., Schram, F.R. (Eds.), Crustacean Issues, Growth, vol. 2. A.A. Balkema, Rotterdam, pp. 277–311.

Rodriguez-Canto, A., Arredondo-Figueroa, J.L., Ponce-Palafox, J.T., Rouse, D.B., 2002. Growth characteristics of the Australian redclaw crayfish, *Cherax quadricarinatus*, cultured in an indoor recirculating system. J. Appl. Aquac. 12, 59–64.

SAS, 2003. JMP 5.1. SAS Institute, Cary, NC.

Segal, E., Roe, A., 1975. Growth and behavior of post-juvenile *Macrobrachium rosenbergii* (de Man) in close confinement. Proc. World Maric. Soc. 6, 67–88.

van Olst, J.C., Carlberg, J.M., 1978. The effects of container size and transparency on growth and survival of lobsters cultured individually. Proc. Annu. Meet.-World Maric. Soc. 9, 469–479.

van Olst, J.C., Carlberg, J.M., Hughes, J.T., 1980. Aquaculture. In: Cobb, J.S., Phillips, B.F. (Eds.), The Biology and Management of Lobsters, Ecology and Management, vol. 2. Academic Press, New York, pp. 333–384.

Verhoef, G.D., Austin, C.M., 1998. Combined effects of temperature and density on the growth and survival of juveniles of the Australian freshwater crayfish, *Cherax destructor* Clark, Part 1. Aquaculture 170, 37–47.

Verhoef, G.D., Austin, C.M., 1998. Combined effects of shelter and density on the growth and survival of juveniles of the Australian freshwater crayfish, *Cherax destructor* Clark, Part 2. Aquaculture 170, 49–57.