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ONTOGENY OF SOCIAL STRUCTURE AND POPULATION DYNAMICS IN THE GIANT FRESHWATER PRAWN, *MACROBRACHIUM ROSENBERGII* (DE MAN)

ABSTRACT

Social organization apparent in adult populations of giant freshwater prawn *Macrobrachium rosenbergii* was analyzed with respect to: a) the weight distribution of a mature population, b) morphological definition of the three male types, and c) growth and maturation characteristics of males and females, including behavioral observations. The ontogeny of social structure was then followed starting from newly metamorphosed postlarvae up to the mature population. We examined various factors influencing growth during juvenile stages by altering environmental conditions and by modifying the established size hierarchy. We then followed and analyzed the consequent changes which occurred in the shape of the weight distribution and in the individual growth rates.

1 INTRODUCTION: SOCIAL DIFFERENTIATION AND CRUSTACEAN BEHAVIOR

Social interaction play a major role in the life history of many animals, in terms of both their probability of individual survival and their reproductive success. In Crustacea, sexual reproduction is the general rule. The two sexes are ordinarily separate, and a marked sexual dimorphism is common. Most species are polygamous, and accordingly, male polymorphism has been observed in several groups of crustaceans. In many instances, different sets of apparently adult males are morphologically distinguishable by the form and dimension of their claws. The several morphotypes present may reach exhibit different behavioral patterns and represent successive phases of development which co-exist in the mature population (Charmiaux-Cotton 1961).

In many polygamous species, the males, as the courting sex, exhibit considerable diversity in role associated behavior and morphology (Wilson 1975). Three hierarchical roles are typical. Dominant single males occupy the social apex. They are followed by a central subordinate of intercompetitive secondary males who are themselves dominant over a population of peripherals. Individuals are not, however, permanently restricted to single, specific roles. Physiological and social changes can occur which permit them to graduate from one social role to another during their lifetimes. On the disappearance of a dominant male, for example, a subdominant one commonly shifts into the vacant niche and develops the appropriate role morphotype (Crook 1970).

Behavior patterns may be fixed genetically (closed system) or they may contain elements modifiable by experience (open system) and hence capable of being adapted to repetitious situations (Mayr 1977). In crustaceans, the development of social-dominance order in males has been observed in the crayfishes *Orconectes virilis* and *Procambarus alleni* (Bovbjerg 1953), as well as in the lobster *Homarus americanus* (Douglass 1946), the hermit crab *Pagurus longicarpus* (Allee & Douglass 1945) and other decapods (Lowe 1956). The formation of a rank order of a social group of crustaceans may be considered to be a training process. The loser in fights between individuals associates the distinguishing traits of its opponent with a punishment comprising the overall stimulus effect of a lost fight. From then on, further encounters with similar traits suffice for the formation of an association, as was shown for *Homarus* and *Carcinus* (Schone 1961).

Crustacean behavior develops during ontogenetic growth. Behavioral patterns affecting modes of movements, feeding, aggressiveness, courtship and mating appear as consequences of periodic maturation of the gonads or other cyclic processes. In some cases (*Uca beebei*, *Procambarus allenl*), young animals may resemble adults morphologically, but the differentiation of behavior lags behind. In other instances (*Ocypode gaudichaudii*, *Orchestia gammerellus*), the differentiation of behavior and morphology derives from a common dominant center, whereupon morphology and ethiology develops in parallel (Schone 1961).

In this chapter we examine some aspects of animal behavior and social organization in the case of the giant freshwater prawn *Macrobrachium rosenbergii*. The choice of this particular organism as a model for this study was based on two main factors: a) the complex social structure apparent in the mature population; and b) the economical value of this organism as a promising candidate for freshwater aquaculture (Ling & Costello 1976, Hanson & Godwin 1977).

2 MACROBRACHIUM ROSENBERGII (DE MAN): THE GIANT FRESH WATER PRAWN

Macrobrachium rosenbergii (Decapoda, Palaemonidae) is the largest of the freshwater prawns (Bhimachar 1965), with a geographical distribution that covers most tropical and subtropical areas of the Indo-Pacific region including the continental margins of southeast Asia, Australia, India, and most of the Indonesian archipelagos, notably Malaysia (Holthius 1950).

Although this species requires brackish waters for spawning and larval development (Fujimura & Okamoto 1970), the postlarval stages have a low tolerance for salinity. Thus, in nature, *M. rosenbergii* larval development occurs in the estuaries, reflecting an obligatory requirement for a salinity of 12-14 ppt, while mature adults inhabit freshwaters such as lakes, reservoirs, paddy fields, and inland streams. The distance between the two habitats may be as much as 500 km (Bardach et al. 1972). The life cycle is established by the downstream migration of sexually matured, berried females and the return upstream of postlarval populations (Raman 1967, Natividad 1980). One may view the river environment as a third, separate habitat, serving as a connection path between the two main biotops.

The simulation of *M. rosenbergii* life cycle in aquaculture includes three main phases (Fig. 1): a) Hatchery - where berried females release newly hatched larvae (2 mm) and larval development continues through to metamorphosis into the postlarval stage (1 cm), b) Nursery - where newly metamorphosed postlarvae are raised to the juvenile stage (34 cm), and c) Growout - where juveniles are raised in earthen ponds to market size (10-15 cm) (Ra'anan & Cohen 1982).

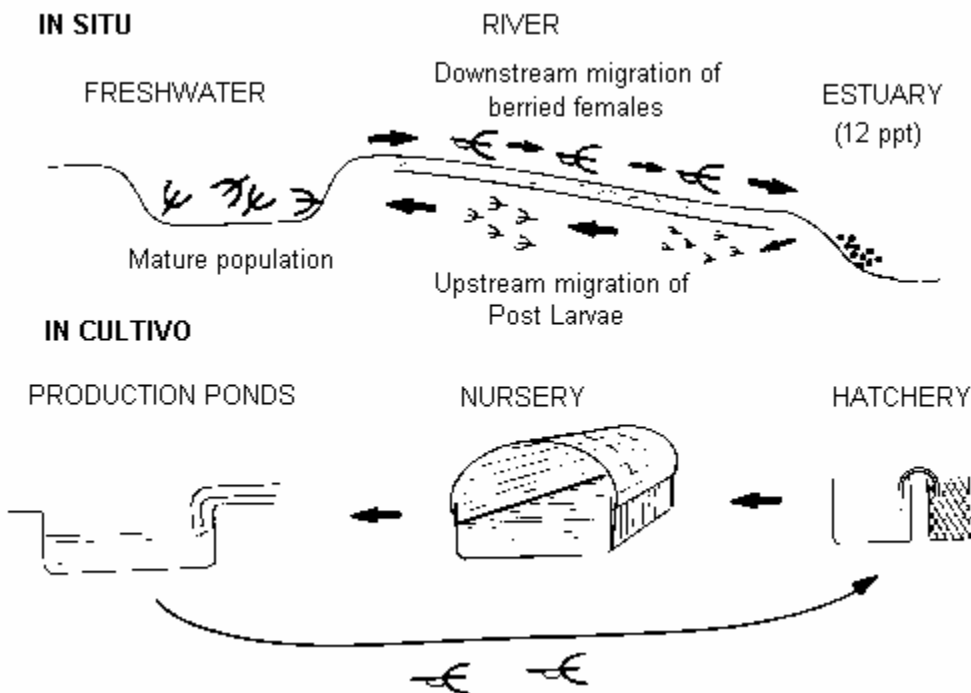


Figure 1. Life cycle of *M. rosenbergii* in nature and its simulation in aquaculture.

3 SOCIAL ORGANIZATION IN ADULT POPULATIONS

M. rosenbergii, being a polygamous species, exhibits sexual dimorphism which becomes apparent after sexual maturation. When sexual selection operates among males in polygamous species, adult males become larger and showier, and their behavior patterns and ecological requirements tend to diverge from those of the females (Wilson 1975).

In decapods, parental care is limited to the period of egg incubation. In *M. rosenbergii* the eggs are attached to the female abdomen prior to her downstream migration towards brackish water. Thus, the reproductive fitness of a male is mainly a function of the number of females it fertilizes. This situation leads to a localized competition among males for mates, resulting in the formation of reproductive-dominance male hierarchies.

In the following sections, we describe some of the characteristic features of a mature population. The data used for population analysis were obtained from field observations, mainly harvests from production ponds, and from laboratory experiments.

3.1 The weight distribution of a mature population

One of the striking properties of adult *M. rosenbergii* populations, as opposed to the juvenile stages, is its characteristic sex associated size distribution. This is observed both in situ (Raman 1967) and in aquaculture ponds (Smith et al. 1978, Cohen et al. 1982). In a typical example, the weight distribution curves of males and females from a population of uniform age are shown in Figure 2, at harvest after six months of growing in an earthen pond.

The weights of females were quite homogeneous (percent coefficient of variation (PCV) = 27.2; skewness (Sk) = 0.057). However, the males, at a nearly 1: 1 ratio with the females in the same population, yielded individual weights which formed a wide positively skewed polymodal distribution, with half the population being considerably larger than the females, and half being quite small (PCV = 71.3; Sk = 1.915).

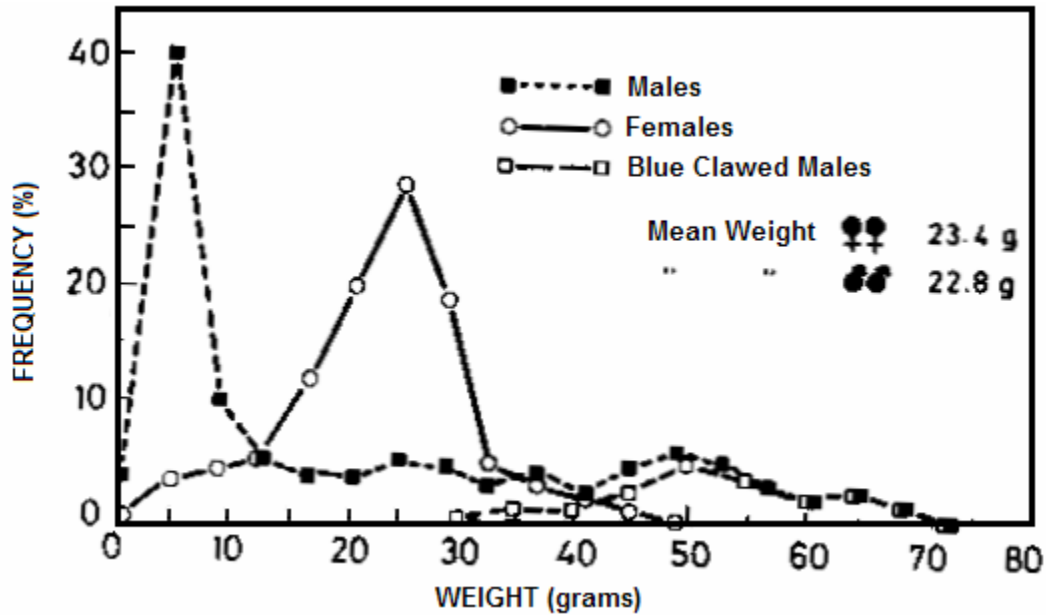


Figure 2. Weight distribution curves of single age *M.rosenbergii* population, six months after release into growout pond (total number = 1065).

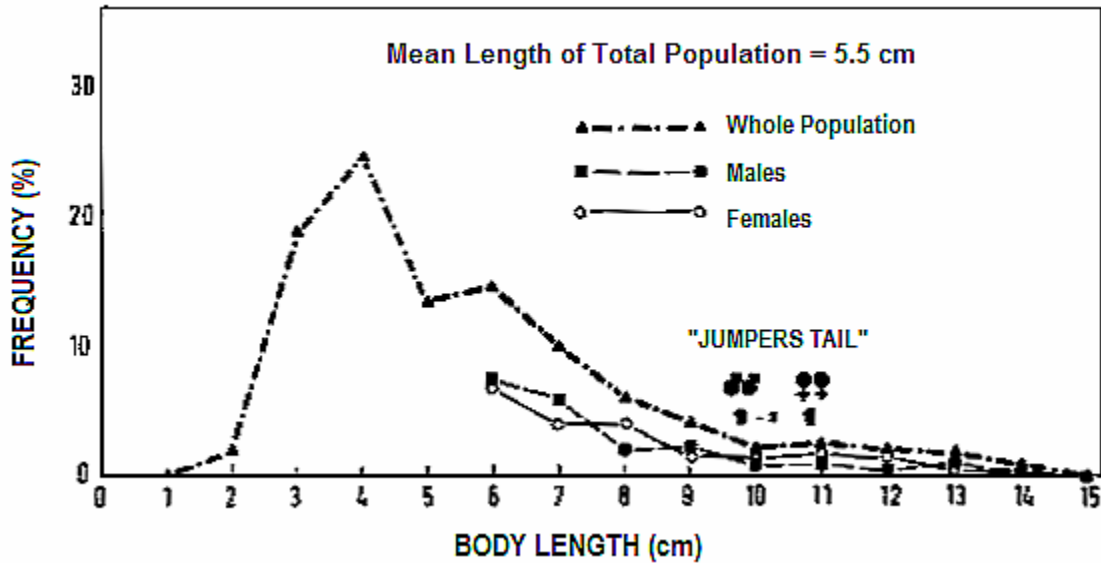


Figure 3. Body length distribution of juveniles, 90 days after metamorphosis.

In the juvenile stages prior to sexual maturation, prawns of both sexes were equally represented over the whole size range (Fig.3). As they matured, however, the growth patterns of males and females differentiated from one another, eventually producing the distinctly bimodal distribution which characterizes the mature population.

This typical shape of the size distribution curve occurred over a wide range of environmental growth conditions, as is demonstrated by the analysis of three separate populations reared at different stocking densities (Fig.4; Table 1). In all instances, the distribution curves of males and females are clearly distinguishable, demonstrating sex-characteristic growth patterns (Cohen et al. 1982).

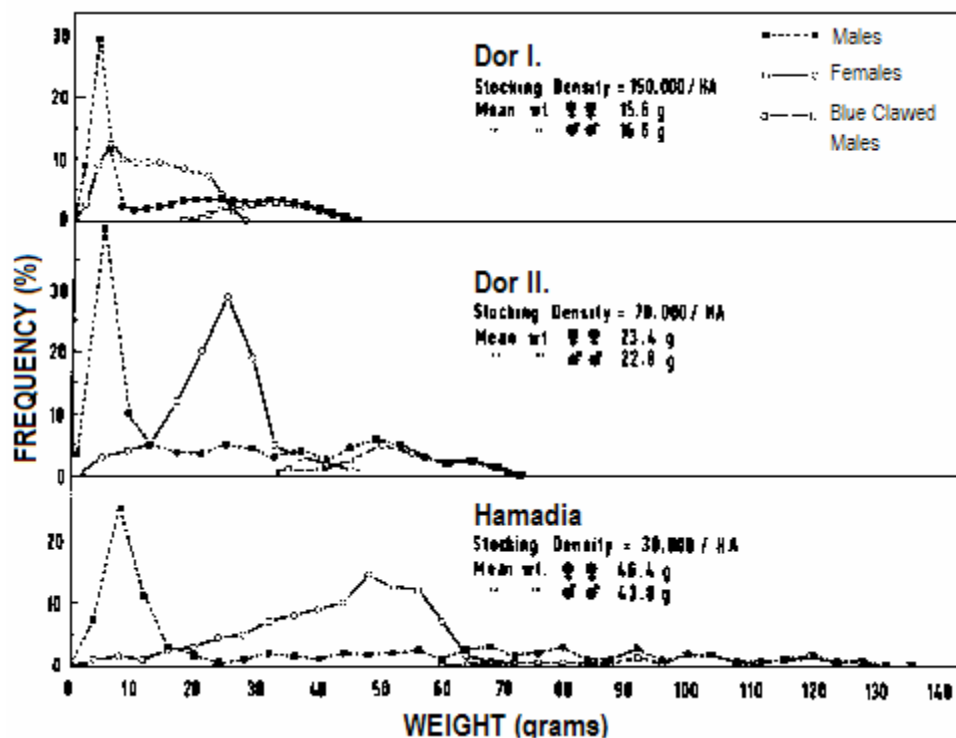


Figure 4. Size distribution curves of adult populations from three different growout ponds, stocked at different densities, 180 days after release of juveniles.

Table 1. Characteristics of *M.rosenbergii* populations raised in growout ponds at three different stocking densities, a - Sample size from each pond was 1 000 individually measured animals. b - Frequency.

A. Stocking and growout information:

Location	Pond area (ha)	Stocking density (prawns * ha ⁻¹)	Stocking size (g)	Stocking size (days)	Growout period
Dor I	0.04	150 000	0.010	180	
Dor II	0.04	70 000	0.010	180	
Hamadia	0.18	30 000	0.015	180	

B. Harvest – general information:

Location	Final density (ha ⁻¹)	Biomass (kg ha ⁻¹)	Mean weight (g)
Dor I	122 600	1 974	16.1
Dor II	38 800	908	23.4
Hamadia	18 100	726	40.1

C. Harvest – breakdown by morphotypes:^a

Location	Males			Females						
	Small males	Orange claw	Blue claw	With eggs			Without eggs			
F ^b	Av. wt.	F	Av. wt.	F	Av. wt.	F	Av. wt.	F	Av. wt.	
(%)	(g)	(%)	(g)	(g)	(%)	(g)	(%)	(g)	(%)	
Dor I	21.8	4.13	21.6	25.5	6.5	28.9	15.0	17.0	35.0	14.9
Dor II	25.3	6.50	19.7	34.4	5.0	61.3	20.1	26.0	29.9	21.4
Hamadia	25.4	6.00	18.2	71.9	6.4	111.8	22.1	50.4	27.9	25.4

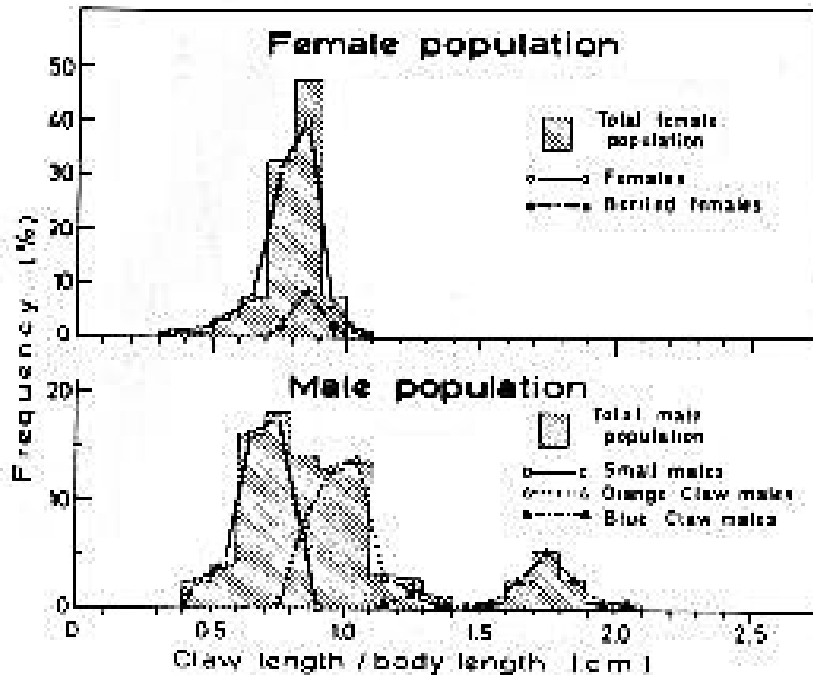


Figure 5. Frequency distributions, by relative claw length, of females (above) and of three male morphotypes (below) in mature population.

3.2 Morphological definition of the three male types

The male population can be divided into three distinct morphotypes based upon a) the individual's position within the population size distribution, b) its claw color, and c) the ratio of its claw length to body length (relative claw length).

When the male population was divided with respect to claw color, and when this criterion was superimposed on the frequency distribution of the relative claw length (Fig.5), three distinct male categories emerged that were not obvious on the basis of body weight alone. Small males (SM), represented in the peak of the male weight distribution, are characterized by clear or light pink claws with a relative claw length of 0.4-0.9. Orange Claw (OC) males are larger, characterized by the orange color of their claws and by a relative claw length of 0.8-1.4. Blue Claw (BC) males, which are the largest of the male population, are characterized by thick, dark-blue claws and have a relative claw length of 1.4-2.0.

The relative proportions of SM, OC and BC males are nearly 5 :4: 1, respectively, and are rather constant for populations reared under various environmental conditions (Brody et al. 1980, Cohen et al. 1982).

3.3 Growth and maturation characteristics of males and females

The typical sex associated weight distribution apparent in an adult *M.rosenbergii* population indicates that males and females possess different patterns of growth and sexual maturation. The following is a description of growth dynamics of both males and females with regard to environmental and social factors which affect the onset of sexual maturation.

In general, maturation time can be considered as an adaptive balance between increased fecundity associated with further growth, and decreasing survival probability with time (Smith et al. 1978, Law 1979). In the case of *M.rosenbergii*, the slight negative asymmetry observed in the female weight distribution curves (Fig.4) may result from the inhibition of

further growth which occurs once a female begins reproduction. Under all population densities examined, berried females were the largest of the females, although the size of the berried females decreased markedly when density increased (Table 1). We also observed (unpublished) that berried females were found earlier in densely populated ponds where growth rates were relatively low. Thus, the smaller size of the mature females in densely populated ponds is the result of a combination of lower growth rate and earlier maturation. The reduction in growth rate at high density is most likely caused by a competition for resources, mainly food. Early maturation can be considered as an adjustment to the intensity of competition for resources.

The size distribution of males becomes increasingly positively skewed with time and is strongly affected by population density. Although the range and positive asymmetry of the male size distribution are inversely related to density (Fig.4), neither the proportions, nor the relative positions of the three male morphotypes were affected by any of the densities examined. Nevertheless, although the mean weights of both QC and BC males were also inversely related to density, the mean weight of the SM morphotype males was hardly affected at all (Table 1). The reason may be that both QC and BC males are strictly bottom dwellers (Peebles 1979) and are, therefore, more susceptible to competition as density increases. Moreover, at high densities in which female maturation occurs early, it is reasonable to expect males also to mature early and at a relatively small size.

Another possible explanation for early male maturation at high densities is associated with the male reproductive-dominance hierarchy. This is based on an analysis by Mertz (1971) in which he infers that early maturation may be a favorable trait in a growing population intrinsically characterized by a high ratio of juveniles to adults; whereas, declining population contain many adults and fewer juveniles. In a study dealing with socially induced inhibition of male maturation in the platyfish *Xiphophorus maculatus*, Sohn (1971a) suggested that a juvenile can presumably 'determine' the growth rate of its local conspecific population by its own social interactions with adults and juveniles. If most of the interactions are with juveniles smaller than itself, it is in a growing population and maturation is soon initiated. In a declining population most interactions involve adults or larger individuals, and maturity is delayed. Consequently, as we found, juvenile prawns raised in successively increasing densities reacted as if to progressively growing populations and resulted in males maturing respectively at smaller sizes.

3.4 Behavioral characteristics and growth dynamics of the three male morphotypes

Each of the three male morphotypes is associated with a particular social position. The BC male is dominant, territorial, and sexually active. It defends a territory against other males (Ramam 1967). The territory probably combines some shelter and feeding area with the availability of females. Females which are ready to mate evidently seek males that can protect them during their vulnerable period just before and after molting (Peebles 1979). The long chelae and the distinctive blue color of the BC male attracts females and aids in defending the territory. At most, eight to ten females are associated with a single BC male. The average fitness of BC males, evaluated as the average number of females fertilized per BC, is constant as long as the fraction of BC among all males is less than about 10%. If the fraction of BC males increases, their fitness decreases because there are fewer females available per male. The BC male is the climax of the male development pathway. It is irreversible (i.e., BC males cannot change back to QC males), and growth is almost completely

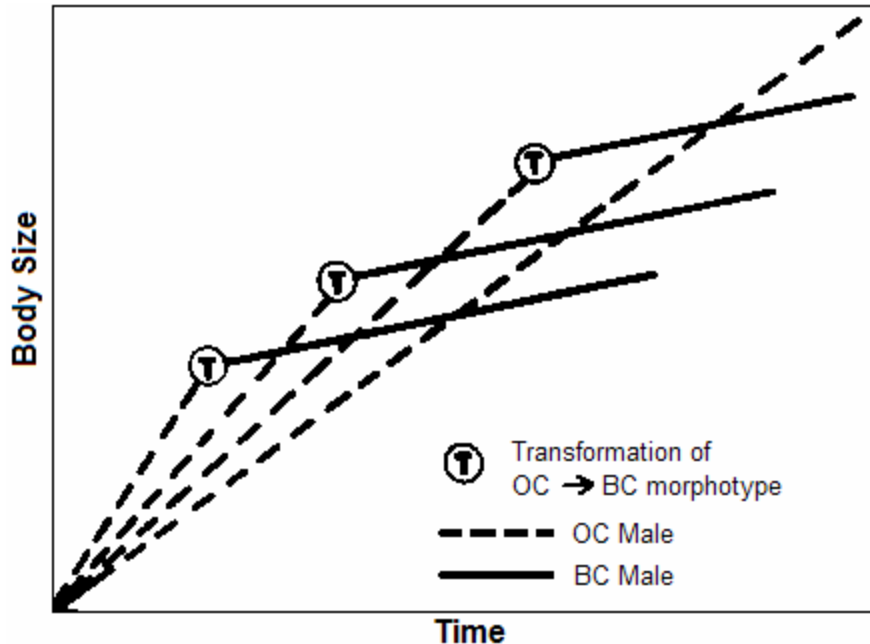


Figure 6. 'Leap frogging' pattern of growth and maturation of orange-clawed (QC) and blue-clawed (BC) males in mature population.

stopped. Body coverage by epibionts is a useful indicator of the time elapsed since the last molt (Smith et al. 1979). When a number of BC males from a population of uniform age is examined, it can be seen that the amount of algae colonizing the animals' claws and carapaces is inversely related to the size of the animal, demonstrating that the earliest BC males to appear in the population were smaller than those which appeared later on, and that growth and molting frequencies of BC males are strongly inhibited.

The QC males are subdominant, non-territorial, and sexually incomplete. Aquarium observations reveal that in the absence of BC males a newly molted female is often approached and hurt by QC males. QC males were never observed protecting females. However, in a few instances, mating occurred, and fertile eggs appeared (Ra'anan 1982). This suggests that QC males may physiologically be capable of mating and fertilizing, but may lack some behavioral patterns associated with sexual maturation.

It is likely that under natural conditions, QC males never have a chance to mate. They continue to grow, however, and eventually transform into BC males. Such a transformation would occur when an QC male succeeds in occupying a territory containing females, either by displacing a smaller or weakened BC male or when a BC male dies. QC males continuously explore the area and frequently engage in a threat display contest with the BC male dominant in the territory. This pattern of replacement of BC by QC would result in a 'leap frogging' pattern of growth and maturation of males as illustrated schematically in Figure 6.

Sohn (1977b) described a similar phenomenon for the growth and maturation pattern of *Gambusia manni* (Pisces: Poeciliidae) males. The males stop growing or grow very little when they mature, and the presence of adult males delays the maturation of juvenile males until they are larger than the adults. Krurnholtz (1963) suggested that the basis for this effect is social interactions, and that in natural populations the delay is related to the

frequency of encounter with mature males. Thus, if there are many mature males in the population and/or mature males remain in the population for a long time, the size of juvenile males at maturity should increase. Borowsky (1969) showed that in *Xiphophorus* various male dominance, coloration, and position in size hierarchy are related to maturity. In observations in sibs, he demonstrated that the first male sib to mature was smaller and less brightly colored than the second. The third male sib to mature was larger than the second and so forth. In general, the longer the delay preceding maturation, the larger and more brightly colored the fish. In later works, Borowsky (1973a,b) reported that the presence of mature male delays maturation of juveniles, but not their growth. He concluded that maturation is under social control, although he did not specify how such control was exerted.

The fitness of an *M.rosenbergii* OC male in terms of reproductive potential resides primarily on its probability of survival prior to becoming a BC and its chances of obtaining a territory. Since the chances of obtaining a territory depend very much on the size of the OC as compared to the nearby BC, only the largest OC males normally transform into the BC morphotype. However, absolute size is not a prerequisite for the transition, since it can occur at different sizes (Fig.6). OC in aquaria went through morphotypic transformations more frequently in the absence of BC than they did in their presence. Moreover, several events of aggressiveness on the part of a BC towards another recently molted male were recorded. That these combined behavioral aspects may maintain fixed ratios of BC to OC in mature populations is supported by observations in a number of pond studies (Cohen et al. 1982), showing that the proportions of the various morphotypes in mature populations were constant.

The small males (SM) are not territorial, and do not attempt to occupy a benthic territory. They avoid competition by retreating into the water column and by hanging onto non-benthic substrates such as rocks and vegetation (Peebles 1980). Being small and highly mobile, SM can find food on the bottom before being chased away by larger prawns, males or females (Harpaz 1980). SM were observed to be strongly attracted to premating molted females and occasionally succeeded in copulating with a female by sneaking in between it and its BC male. In several events females were successfully fertilized when only SM were present indicating that SM are capable of sexual competence. The reproduction potential of the SM morphotype has two modes: a) staying small and achieving a sneak fertilization at a low probability, or b) growing, becoming an OC male, and eventually transforming into a BC male. The fitness of the first mode decreases as a function of the relative frequency of SM. The fitness of the second mode decreases as a function of the relative frequency of OC males. Thus, at an evolutionary stable strategy (ESS) we may expect the relative frequencies of SM and OC males to be such that the fitness of the SM in the respective modes are equal (Maynard Smith 1978). Since the probability of a successful sneak copulation under natural conditions is presently unknown, it is impossible at this stage to make any testable predictions. However, the hypothesis is consistent with the existing observations of a constant frequency distribution of the three male morphotypes over a wide range of population densities and ecological conditions in the ponds (Cohen et al. 1982).

4 FACTORS INFLUENCING GROWTH IN JUVENILE POPULATIONS

Since one of the most direct indications of the social organization and state of maturation of *M.rosenbergii* populations is revealed by the shape of the weight distribution curve, we

have followed and analyzed the changes occurring in such distributions, starting from newly metamorphosed postlarvae. In the following sections we describe this development, examining the rate of change and the shape of the weight distribution curves in juvenile populations.

4.1 *Characterization of changes in the weight distribution of juvenile populations with time*

The weights of newly metamorphosed postlarvae average $9 \times 10^{-3} \pm 2.4 \times 10^{-3}$ g, N = 400. With time, the distribution changes gradually, as variance and skewness increase (Sandifer & Smith 1975, Malecha et al. 1977). A 'leading tail' is formed that represents individuals which are larger than the bulk of the population. Fast growing individuals, henceforth termed 'jumpers', can grow as much as 15 times larger than the population mode within a period of 60 days from metamorphosis (Willis & Berrigan 1977, Ra'anan & Cohen 1983).

Heterogeneous growth in aquatic species has been associated with a) intrinsic factors, such as genetic differences, hatching order, or age at metamorphosis (Newkirk et al. 1977, Sandifer & Smith 1979), b) environmental factors, giving rise to competition for limited resources such as space and food (Magnuson 1962), and c) social factors, such as position within the size hierarchy (Brown 1946), social status, and territoriality (Symons 1972).

Growth of body weight can be described (Brown 1946, Ricker 1958, Wilbur & Collins 1973) by the exponential function,

$$W_T = W_t e^{R(T-t)}$$

in which W_T and W_t represent body weights at times T and t ($T > t$), respectively, e is the

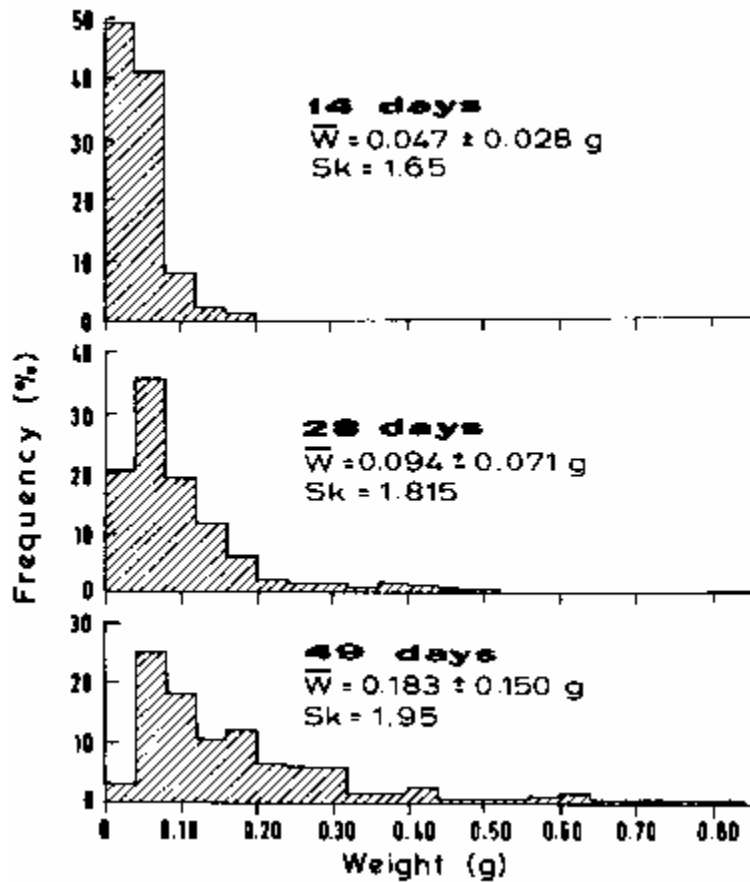


Figure 7. Frequency histograms of body weights of juveniles sampled at three times after metamorphosis.

base of the natural logarithm, and R is the exponential relative growth rate. Ostensibly then, a population of individuals growing at a uniform exponential R value would have an expanded variance in size distribution at maturity as a result of differing initial weights at metamorphosis. Alternatively, a leading tail of individuals which are much larger than the bulk of the population may be a result of a significantly higher R value possessed by these, the jumpers, as compared to the R of the remaining population. In order to distinguish between the two possibilities, weights were transformed on a natural logarithm base ($\ln W$), the changes of the \ln -transformed weight distribution with time was examined. An increase in the variance of the logarithmic function would indicate variability of the growth rates among individuals within the population.

Frequency histograms of body weights of juveniles stocked at a density of 0.5/liter, at three time points after metamorphosis are given in Figure 7, and shown as their m -transforms in Figure 8. The change in the \ln -transformed weight distribution curve with time (Fig. 8) showed an increase in both skewness and percent coefficient of variation, indicating that the jumpers' leading tail in the linear size distribution (Fig.7) results from specific variations in the relative growth rates of individuals within the population. It is the jumpers, which may or may not be the largest animals at the time of metamorphosis, which are characterized by relatively enhanced growth rates.

Larvae from a single brood may transform into the postlarval stage in three to seven days (Ra'anan & Cohen 1982). Sandifer & Smith (1979) reported that early metamorphosis confers to growth or development advantage, nor late metamorphosis any disadvantage, in *M.rosenbergii* postlarval populations. The initial stimulus for the enhanced relative growth rate exhibited by the jumpers is not yet clear. However, once a size hierarchy is formed

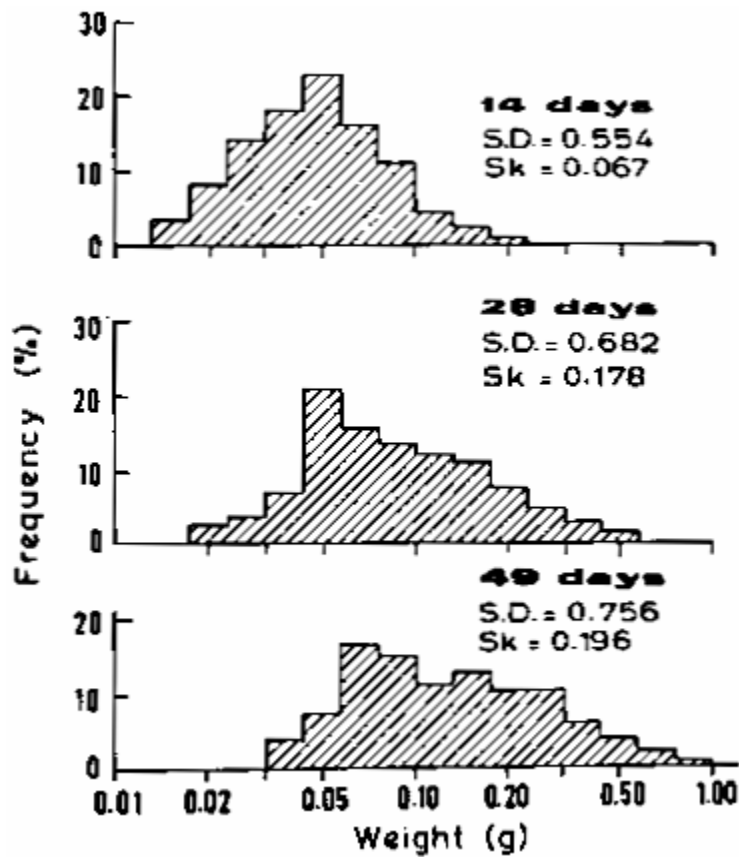


Figure 8. Frequency histograms in (Natural logarithm) transformed body weights of juveniles sampled at three times after metamorphosis.

(within two weeks after metamorphosis), larger postlarvae will continue to grow at an accelerated rate (Ra'anon & Cohen 1983). Similar phenomena have previously been observed and were termed 'heterogeneous individual growth' (Nakamura & Kasahara 1955); that is, individuals in a given population show a higher relative growth rate than the smaller individuals, a tendency that generates an increasing asymmetry in the size distribution curve with time. The possible role of competition for limited resources, such as space and food, as the basis for this phenomenon in the case of *M. rosenbergii* postlarvae can be evaluated by examining the effect of population density on the dynamics of the size-distribution curve.

4.2 The effect of initial stocking density on growth of postlarvae

Newly metamorphosed postlarvae (PL) swim freely in the water column and gradually shift their behavior until they come to settle on the available benthic surface (Ling & Merican 1961). We therefore examined the effect of population density on postlarval growth by modifying stocking densities per volume as well as on a surface area basis. PL from a single brood, averaging 0.009 g, were stocked in four replicates each at 1/liter, 5/liter, and 10/liter. At each density, two of the four replicates included identical amounts of added

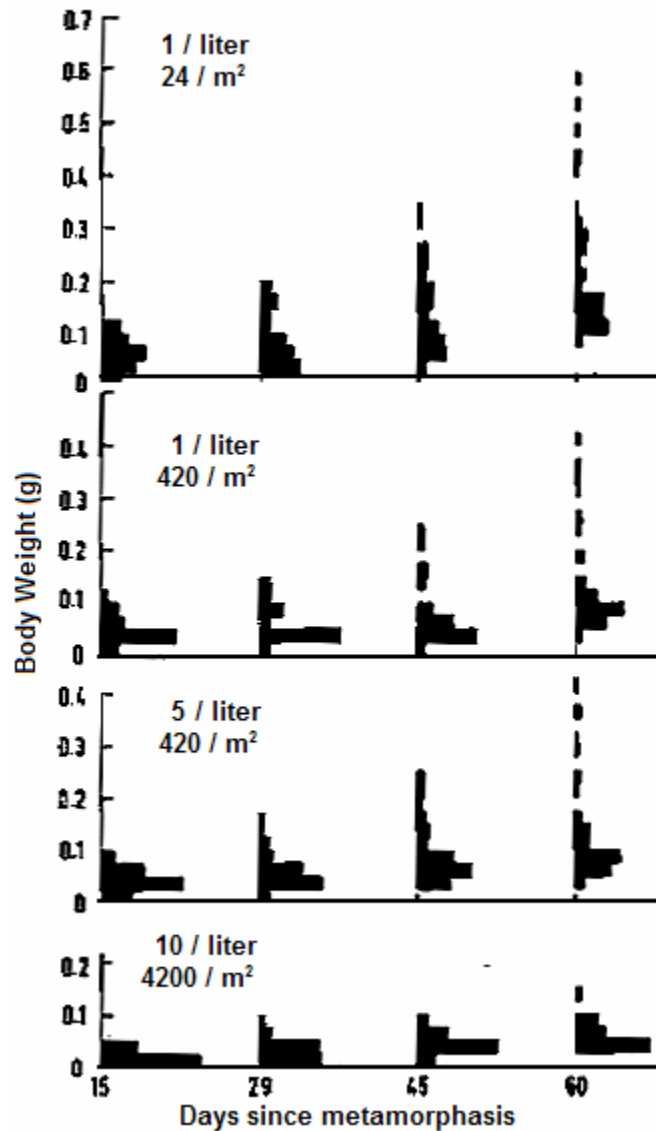


Figure 9. Frequency histograms of body weights of juveniles stocked at various densities, sampled at selected times after metamorphosis. Note development of skewness and rapid overall growth at lower densities.

submerged substrates. Haphazard samples of at least 100 PL, were individually weighted weekly, during a period of 60 days. In the relative frequency histograms of body weights of juveniles sampled at selected times after the start of the experiment (Fig. 9), it can be seen that each of the final curves obtained under the higher densities corresponds to an intermediate stage of the size distribution curves at the various time intervals for the lowest density. This suggests that the same process of size differentiation occurred at all densities examined but at different rates. Increased stocking densities affected the dynamics of the size distribution of a juvenile population in several ways. Average growth rate and degree of size variation decreased as density increased, and, significantly, skewness of the distribution also decreased with increasing density.

Wilbur & Collins (1973) describe similar effects of stocking density on the development of size variation in larval *Rana sylvatica* reared under various initial densities. Median body size and percent coefficient of variation were both inversely related to the initial stocking density. However, when they examined the effect of stocking density on skewness, they found that skewness increased as a function of increasing density, a result that was interpreted as evidence for competition. Initial small differences between individuals are magnified during the course of competition, suppressing the growth of smaller individuals while increasing the relative growth advantage of larger ones. Similar phenomena were described by Wohlfarth (1977) in a review of the 'shooting phenomenon' apparent in various types of fish such as the common carp, sunfish hybrids, and catfish. In all cases, the increased asymmetry was more pronounced under restricting growth conditions, but generally disappeared under improved conditions. This, too, was interpreted as an effect of competition.

In contrast to the preceding studies in *M. rosenbergii* experimental populations is inversely related to density. In other words, the positive asymmetry becomes more pronounced in less competitive situations. The possibility of competition for food in the present study was obviated to the extent that all tanks were fed with excess live *Daphnia* which remained alive and suspended in the entire body of water throughout the whole experiment. These findings suggest that the appearance of jumpers is not primarily a result of competition, if at all, but of factors intrinsically associated with population development.

The next step was to evaluate the relative contributions of genetic and social factors to the wide variations in growth rates of *M. rosenbergii* juveniles.

4.3 *The effect of interactions among individuals on the development of size variation*

We have seen, then, that unlike the situation in other aquatic organisms, the advent of *M. rosenbergii* jumpers becomes more pronounced when the competition for space and food is reduced. Apart from competition, heterogeneous growth in aquatic species has been associated with intrinsic factors (Newkirk et al. 1977) and social factors (Brown 1946, Symons 1972). With regard to *M. rosenbergii*, Sandifer & Smith (1975) suggested that the observed wide variation in growth rates may be caused primarily by genetic rather than environmental factors. On the other hand, Malecha et al. (1977) felt that size variance was due more to social interactions than to the segregation and independent assortment of genes controlling growth.

One way to differentiate between the relative contribution of genetic and social factors is the observed heterogeneous growth is to compare the change in the logarithmic variance of weight with time in postlarval populations reared communally to the corresponding

change in those raised individually. An increase in variance of the In-transformed weight would indicate the heterogeneity of the individuals' relative growth rates. If intrinsic factors are directly responsible for the variation in growth rates, one would expect the logarithmic variance to increase in a similar manner in both the individual and the communal rearing systems. However, if interactions among individuals, whether through direct physical contact or mediated by the communal growth medium, are responsible for the observed growth heterogeneity, the logarithmic variance in weight should differ between the two culture regimes, since that of juveniles reared individually should tend to remain constant with time.

In order to examine these questions, newly metamorphosed postlarvae were divided into two groups. One group was reared in individual aquaria without water connections, while the other group was reared in a communal aquarium. Stocking densities per volume and per surface area were equivalent in both groups. All prawns were individually weighed once a week during a period of 63 days. Data were analyzed on two levels. First we estimated the changes occurring in the variance of the In-transformed weights in order to assess the degree of growth variation in both the individually and communally reared juveniles. Next we calculated the individual relative growth rates, R , for all the juveniles in both populations. Comparative estimates of the R value distributions of communally and individually reared juveniles would permit a direct evaluation of the respective growth heterogeneities.

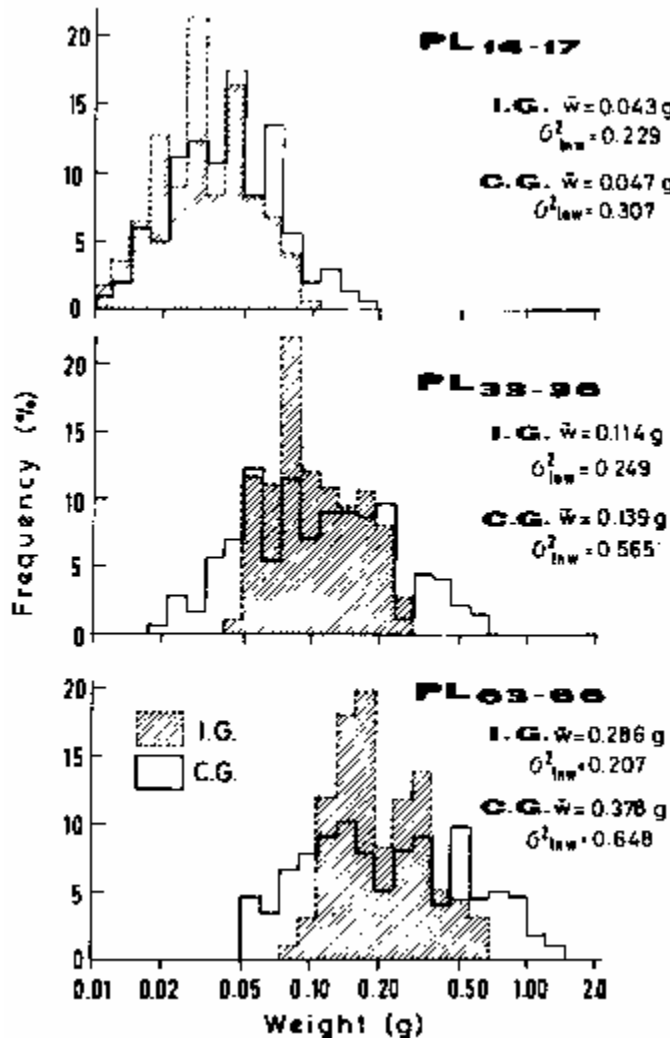


Figure 10. Frequency histograms of body weights of postlarvae reared under individual (I.G., N = 120) and communal (C.G., N = 180) growth conditions, at three times after metamorphosis.

Table 2. The effect of three stocking densities, with and without the addition of substrates, on population size distribution 60 days after metamorphosis. Figures denoted by different superscripts are significantly different at the $\alpha=0.01$ level: figures bearing the same superscript within the same parameter are not statistically different (ANOVA, ONEWAY-RANGES, LSD-test, Nie et al. 1971). * SD - Standard Deviation; PCV - Percent Coefficient of Variation; Sk - Skewness.

Group no.	No of animals stocked	Stocking density Volume (l ⁻¹)	Surface (m ⁻¹)	Body weight distribution. Mean (g)	SD (g)	PCV %	Sk	Survival (%)
No added substrate:								
1	100	1	420			0.124c	0.089c	71.6c
2	500	5	2100			0.090b	0.050b	55.5b
3	1000	10	4200			0.064a	0.023a	35.6a
With added substrate:								
4	100	1	84			0.290d	0.226d	77.95d
5	500	5	420			0.127c	0.093c	73.1 c
6	1000	10	840			0.103b	0.054b	53.1b

4.3.1 *The development of size variation*

The frequency histograms of body weights for the individually reared postlarvae (Fig. 10) and their statistical analyses (Table 2) approximated a log normal distribution. While the average weight increased with time, the logarithmic variance remained relatively constant throughout the experiment. Under communal growth conditions, however, both the average weight and the logarithmic variance continued to increase with time, and the initial normal distribution became positively skewed. The degree of skewness increased until the fifth week and then decreased slightly. The rate of the average weight increase in both groups was similar until the sixth week (Fig.11). Afterwards, weight increase in the com-

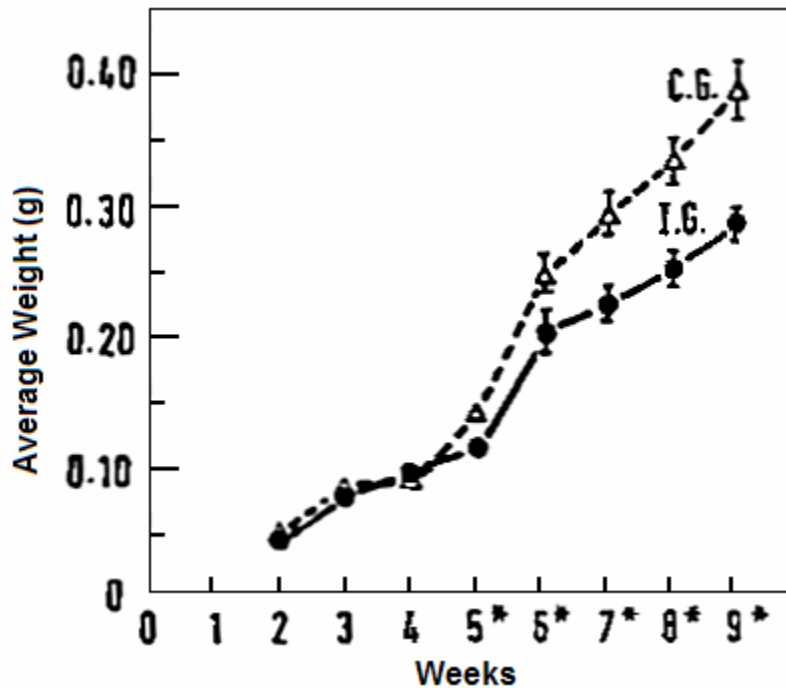


Table 3. Changes with time in the mean weight (W), standard deviation (SD) and skewness (Sk) of the In-transformed weight distribution curves of juveniles reared under individual and under communal growth conditions*. Differences between mean weights are statistically significant (t - test, Q = 0.05).

Days after Metamorphosis (g)	Individual growth (N = 120)			Communal growth. (N = 180);		
	W (lnW)	SD	Sk	W (g)	SD (lnW)	Sk
14	0.043	0.478	-0.024	0.047	0.554	0.067
21	0.077	0.470	-0.032	0.077	0.647	0.107
28	0.096	0.464	0.079	0.094	0.682	0.178
35*	0.114	0.499	0.047	0.139	0.751	0.196
42*	0.212	0.482	0.120	0.241	0.770	0.242
49*	0.221	0.470	0.099	0.287	0.780	0.221
56*	0.250	0.471	0.045	0.327	0.788	0.184
63*	0.286	0.455	0.052	0.378	0.805	0.154

in the communally reared population exceeded that of the experimental group. A comparison of the growth of the largest 10%, smallest 10%, and the median body weight individuals of both populations (Table 3), shows that the highest average growth rate is attained by the largest communally reared juveniles. Growth of the smallest communally grown animals began to lag about four weeks after metamorphosis, while the median individuals in both populations grew at similar rates. Clearly, growth heterogeneity in juvenile populations, as evaluated b) the increased variance of the In-transformed weight distributions with time, is much higher for communally reared juveniles than for those reared as individuals.

Communally raised carps also had larger size variance than those reared individually (Yamagishi 1962). The isolated carp, however, grew at rates similar to those exhibited by the fastest growing individuals under communal growth conditions. This result was explained by the absence of the competition which had apparently inhibited growth of the smaller group reared fish. In contrast, the excess in average weight of the communally reared *M. rosenbergii* juveniles relative to that of the individually grown animals (Fig.11) indicates that the jumpers' superior growth rate results from the presence of some stimulus which is lacking under conditions of individual isolation. This is supported by the observation that the 10% largest individuals in the communal growth group reached an average weight of 1.19 g while the 10% largest isolated individuals reached an average weight of only 0.57 g during the same interval (Table 3). Lee & Fielder (1983) reported the identical phenomenon in the prawn *Mastraliense*, 'Under laboratory conditions, group held juveniles produce more biomass than equivalent numbers of individually held prawns kept for the same time. However, the individually held prawns had a more uniform growth as shown by smaller standard errors in their mean sizes. . .', without reference to the social stimulation of growth that is the basis of the distribution patterns they observed. Growth stimulation was also described by Uematsu (1971a,b) in the guppy *Poecilia reticulata* Peters where the social facilitation of growth observed in the communal rearing system was associated with changes in feeding behavior and rates of respiration. In the Himekaka (*Oryzias latipes*), social facilitation of growth, exerted by a companion, was recognized and termed 'the presence recognition effect' (Uematsu & Takamor 1976).

Sastry & French (1977) and Aiken & Waddy (1977) found a strong correlation between the size of the container and the growth rate of the housed subject (*Homarus americanus*).

Van Olst & Calberg (1979) estimated that in order to avoid reduction in growth rate, the area of the container must be approximately the square of three times the body length of the lobster, or $(3BL)^2$. The maximum body length we observed in this experiment was: 5 cm, which, in terms of the above formula, would dictate a surface area of 56 cm². Nevertheless, in order to ascertain that the growth of the largest individuals-in the separated was not inhibited by the size of the container or some other variable correlated with it, another experiment was conducted in which both individuals and groups were raised in identical aquaria. The results were consistent with the previous experiment. Communally reared jumpers grew significantly faster than the fastest individually housed juveniles, even though the space available for the former this time was much less than that available for the latter. Thus, the possibility that container size adversely affected the wth of the largest individually reared prawns is ruled out.

In addition to growth facilitation and the appearance of jumpers, the 10 % smallest individuals demonstrated an opposite phenomenon, a growth lag. From frequency histograms of body weights at various times (Fig.10), it seems that the jumpers' stimulated growth preceeded the growth lag of the smallest individuals. The later appearance of the growth in small individuals was also correlated with the decrease in skewness of the distribution curve starting from the fifth week (Table 2). Such retarded growth might due to the cumulative suppressive effect borne by the small individuals in the presence of jumpers.

In summary, interactions among individuals play a major role in the development of the size distributions observed in juvenile populations. Two consequent processes can be observed: a) growth stimulation results in the occurrence of jumpers, and b) the presence of jumpers is associated with the growth suppression of 'laggards' within the population. Neither jumpers nor laggards were evident under individual growth conditions. These data

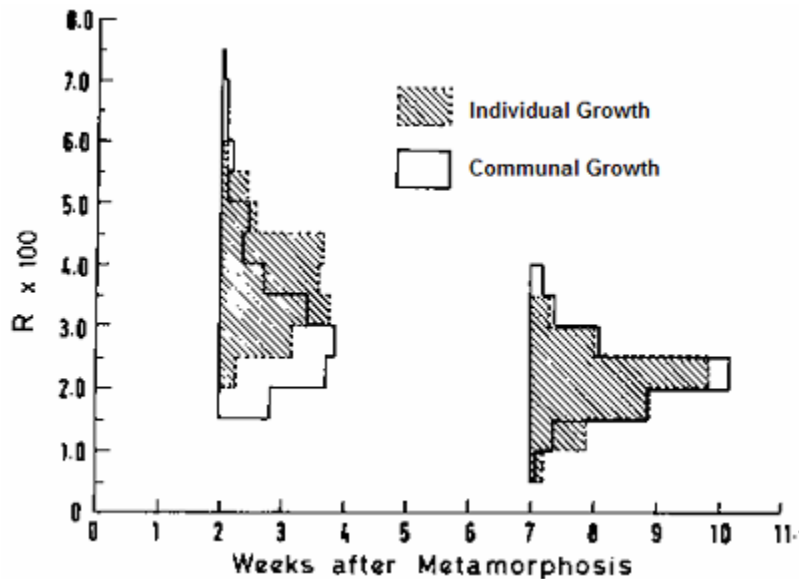


Figure 12. Frequency distribution of relative growth rates (R) in individually and communally reared juvenile populations, two and seven weeks after metamorphosis.

support the notion that social rather than genetic factors control size variation in *M.rosenbergii* juvenile populations.

4.3.2 *The distribution of relative growth rates*

So far we found that the logarithmic variance of body weights of juveniles reared in groups increased with time, while that of individually housed prawns remained constant. This suggests that some interactions among juveniles are responsible for the observed wide size variation.

We then calculated individual relative growth rates in both systems in order to measure directly the variation of R values in each case, as well as to learn about the changes of R value with time in isolated versus communally grown prawns. In the communal culture we noticed that several marked individuals maintained their relative size ranking, on which basis we inferred that such a stability is fairly general. Variance of 1.12 and 0.72 of communally and individually reared populations, respectively, two weeks after metamorphosis, decreased to 0.34 and 0.23, respectively, by the seventh week. The R distribution of the communal population was wider, and was positively skewed at the initial growth period as compared with a narrower, more normal distribution attained by the individually reared juveniles (Fig.12). Respective R values were plotted against initial body weights of juvenile prawns reared communally between 14 to 21 and 56 to 63 days after metamorphosis (Fig. 13). Dividing the population into deciles in order of increasing weight, we found that R was positively correlated with the initial body weight in both periods, and that this correlation was more pronounced during the first interval, when animals were smaller.

R ordinarily decreases with age and size (Brown 1946, Yamagishi 1962), and, indeed, the growth rate of all the individuals in this experiment decreased with time as their weight increased, under both culture conditions. The R value variance at the initial growth period was more pronounced for the communally than for the individually reared populations, but with time it, too, decreased.

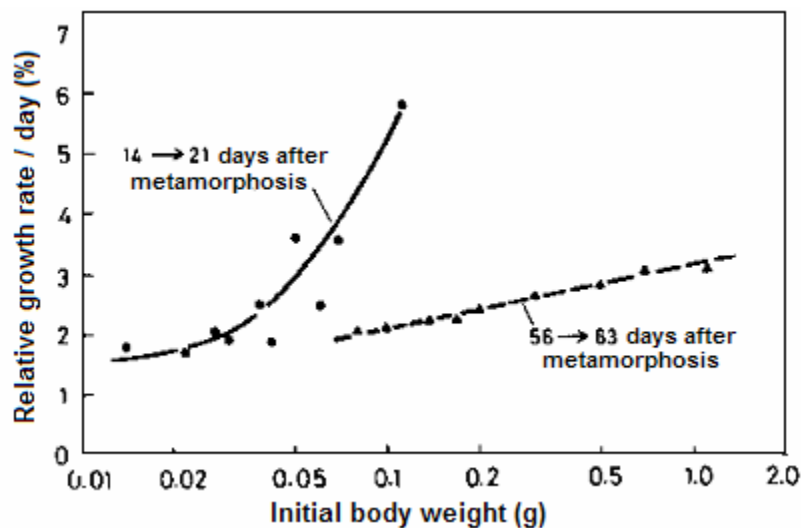


Figure 13. Relation between initial body weight and relative growth rate of juvenile prawns communally reared, at two time intervals after metamorphosis.

Koyama & Kira (1956) proposed four types of size frequency distributions which were obtained mathematically, assuming an exponential growth by individual plants in a population. They refer to the condition in which initial weight (W_0) and R have normal distributions, and in which R is positively correlated with size, as the N-N correspondent type. Just such a positive correlation was obtained between initial body weight and relative growth rates of our juveniles throughout the eight week period after metamorphosis. The marked increase in the positive asymmetry of the juvenile weight distribution observed under communal growth conditions can be attributed to the high growth rate shown by the larger juveniles, and especially the largest juveniles. Yamagishi (1962), examining frequency distribution of larval length during the post embryonic growth of three marine fishes, found an opposite kind of N-N correspondent type distribution in which it was the slow growth of the smallest individuals which skewed the length distribution negatively. Brown (1946) had reported that individual relative growth rates in trout fry were usually higher for larger individuals. Thus, the order of descending weight was also an order of decreasing relative growth rate for the group. The correlation of R values with the individual's position in its population's size ranking may be fairly general phenomenon.

The next step in our study was to investigate the nature of the relationship between the relative growth rate and size ranking in *M.rosenbergii* juvenile populations.

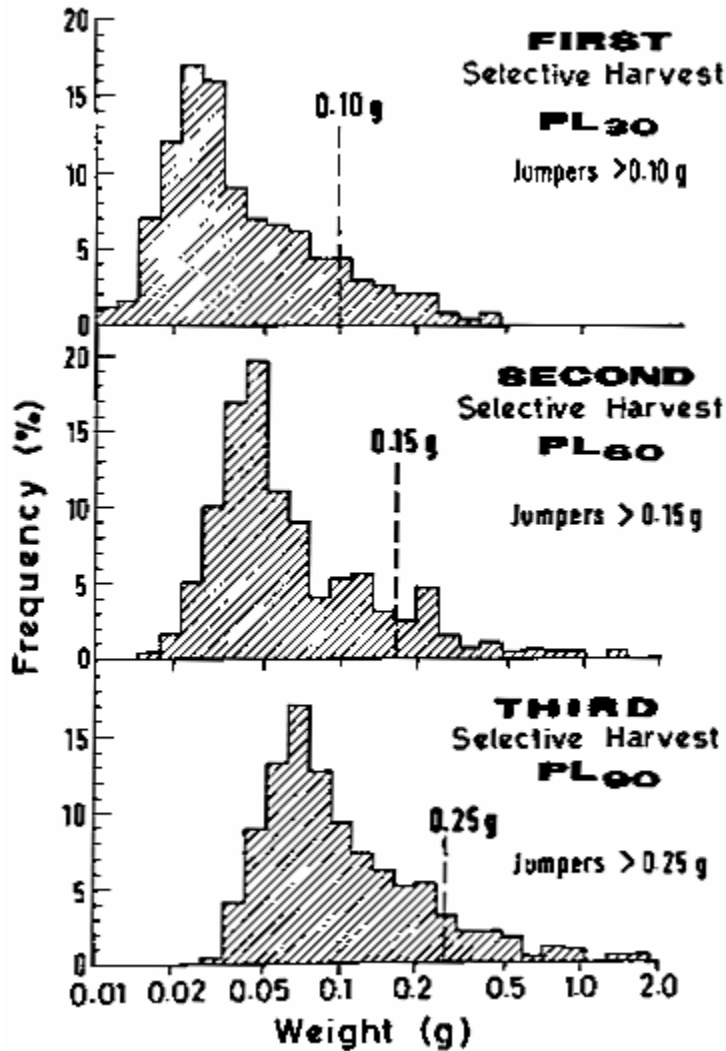


Figure 14. Frequency histograms of juveniles' body weight. Jumpers were defined for each population as shown, and selectively removed at 30 (PL₃₀), 60 (PL₆₀) and 90 (PL₉₀) days after metamorphosis.

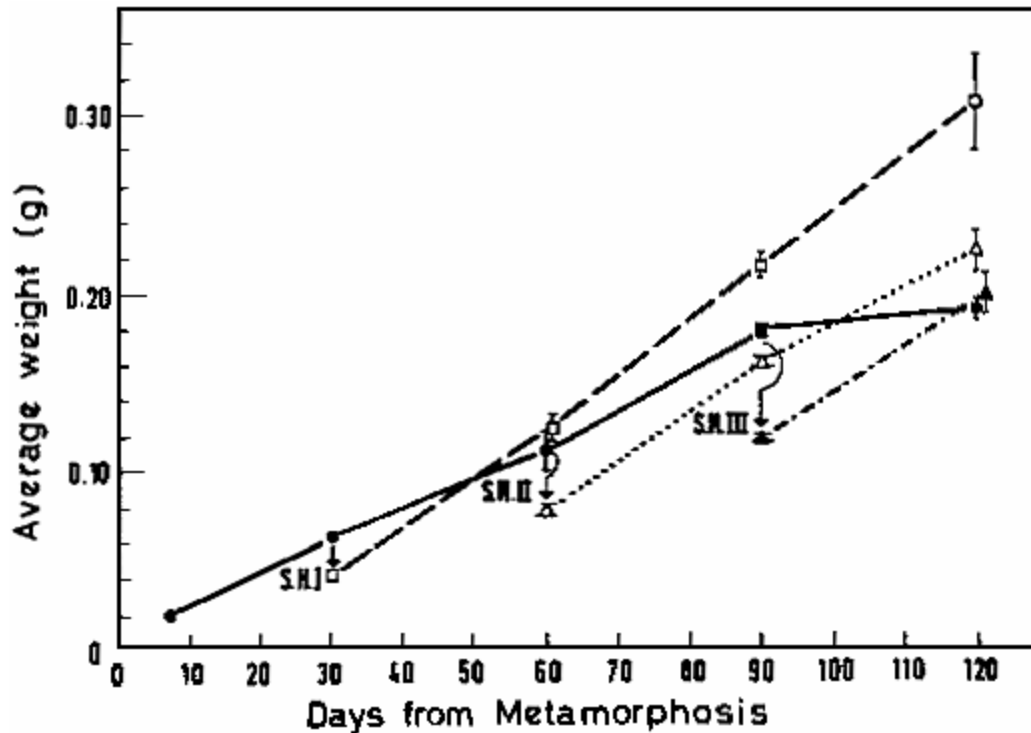


Figure 15. Average weight of juvenile populations following selective removal of jumpers. (—) control, whole population; (---) 1st selective harvest (S.H.I), (...) 2nd selective harvest (S.H.II), (-.-) 3rd selective harvest

4.4 The effect of selective removal of jumpers on growth of the remaining population

In sections 4.2 and 4.3 we showed how skewed size distributions of postlarval populations developed with time, suggesting that the presence of jumpers brings about a suppression of growth in the remaining population. In order to validate this view, we investigated the effect of selective removal of the first occurring jumpers on subsequent growth of the remaining population.

Newly metamorphosed PL were divided into three groups with two replicates each. In each of the three replicate groups, jumpers, defined heuristically by the shape of the logarithmic weight distribution curve, in this instance about 15 % of the population, were harvested selectively, at 30, 60 and 90 days post-metamorphosis, for groups I, II, and III, respectively (Fig. 14).

Soon after any removal of jumpers, a rapid increase in average weight of the remaining prawns was observed, especially obvious when compared to the normal average growth of the unharvested control population (Fig. 15). For example, following the first selective harvest, 30 days after metamorphosis, the average weight of the residual animals was 0.042 g, as compared to 0.064 g in the unharvested population. Thirty days later, the average weight of the selectively harvested population increased to 0.123 g, $R = 3.58$, while the average weight in the control unharvested population increased to 0.111 g, $R = 1.83$. This is remarkable, because the growth rate of the control population is expected to be positively biased by the rapid growth of the original jumpers which were not removed. The phenomenon was not time dependent. A similar pattern was found when jumpers were removed 60 and 90 days after metamorphosis. The gradual increase of both the standard deviation and the skewness of the size distribution curve after the selective removal

of jumpers gives expression to the gradual regeneration of the positively skewed distribution curve as new jumpers emerge.

Selective removal of large individuals, or size grading, is routinely practiced in fish hatcheries on the assumption that small fish will grow better when larger contemporaries are removed, probably because of the diminution of competition and the disruption of the social hierarchy. Gunnes (1976) examined the effect of the stage of development of salmon fry at the time of selective harvest of larger fry on subsequent growth performance. The best mean growth occurred when the fish were graded at six months, before the weight distribution had departed from normal, that is, before a social hierarchy had developed. Although we, too, observed increased growth rates of small individuals after the removal of large ones, the compensatory growth of *M. rosenbergii* juveniles occurred continuously throughout the juvenile period. The regeneration of the jumpers' leading-tail indicates that non-jumpers are actually manifesting heterogeneous individual growth after the removal of jumpers, and new jumpers consequently evolve. This again indicates that non-jumpers retain an inherent capacity for compensatory growth: their growth rate does not depend individually on genetic factors, a result which is consistent with the view expressed by Malecha et al. (1981).

4.5 *The effect of size ranking on growth rate of juveniles*

Interactions among individuals play a major role, as we have seen, in generating the wide size variation that is apparent in juvenile populations. We demonstrated that juveniles in a group can be affected in different ways. Their growth is either stimulated or inhibited as a function of social position, defined by rank within the group's size hierarchy. A strong association between relative size and social rank was also reported by Bovbjerg (1953) in a study of the dominance order in the crayfish *Orconectes viridis*, in which he reported that size is an important factor in determining the dominance order, wherein individuals can lose or regain their dominance according to their relative size within the group. By shifting the group associations of *M. rosenbergii* juveniles to reposition their rank by weight, we asked whether the growth characteristics of individual prawns would be retained or adjusted to accord with the imposed changes in social position.

4.5.1 *Size ranking and the individual's growth rate*

In a given population, prawns of different social positions may vary in age as well as in body weight. We have generally used an animal's weight as the criterion determining its size ranking, our key to categorizing its social position. Now, we should like to differentiate between the effect of the prawn's absolute weight-dependent growth characteristics and those aspects which are influenced by its own weight relative to that of other prawns in its immediate group. In order to clarify the direct association between size ranking and growth performance, we established a situation in which juveniles of the same age and size were placed in several defined social situations and measured the effects on their subsequent growth.

PL from a single brood were stocked at a density of 3/liter in a 120 liter aquarium equipped with a built-in biofilter. Ninety days after metamorphosis, all juveniles were collected and individually weighed. At this stage, elected juveniles (81) were obtained from a narrow weight range ($0.33 \text{ g} < \text{SJ} < 0.35 \text{ g}$) at the middle of the wide size distribution of the whole population.

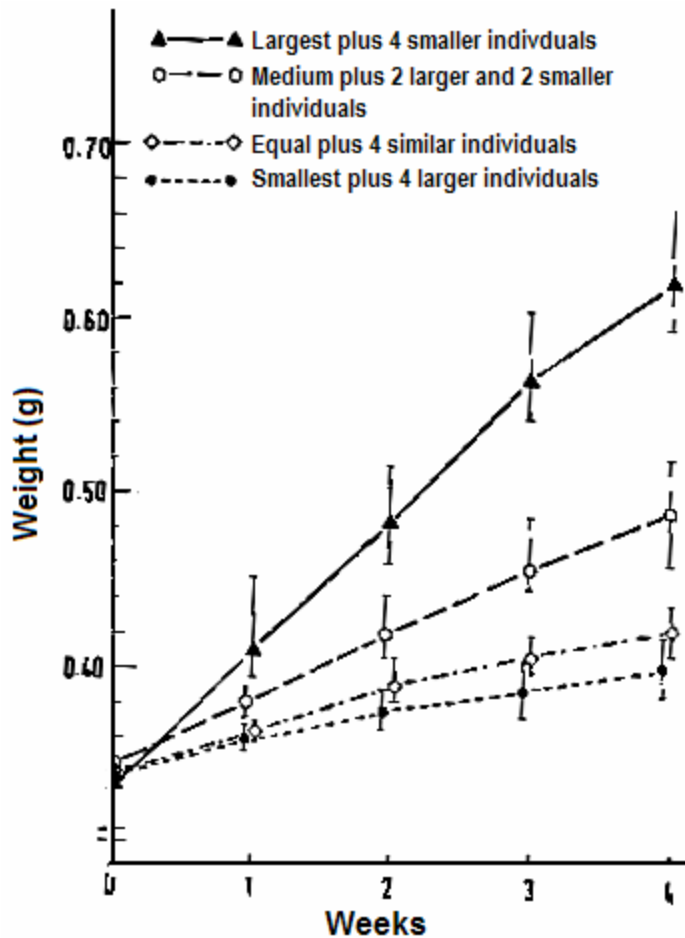


Figure 16. Effect of social position, as measured by size ranking within population, on average weight of juvenile prawns.

Each SJ, marked by clipping off the right tip of its telson fin, was restocked together with four other individuals taken from the same population. In each of four categories of social position, six replicates were established in which the SJ was: a) Largest - SJ plus four prawns <0.25 g (SJ >4), b) Medium - SJ with two <0.25 g and two >0.50 g individuals (2)SJ >2), c) Equal - SJ and four others of 0.33 to 0.35 g (SJ = 4), and d) Smallest - SJ and four prawns >0.50 g (4)SJ). In order to minimize the competition for food, juveniles were fed daily with an excess of live *Daphnia* and ground fresh fish. The selected juveniles were weighed individually for four weeks. R values were calculated accordingly.

The observed growth rates were directly related to the individual's size ranking (Fig. 16). Juveniles in the presence of smaller individuals increased in weight at a faster rate than those stocked together with larger individuals, and those stocked in the Medium position (2) SJ > 2) grew at a faster rate than those stocked in the Equal position (SJ = 4). The mean relative growth rate over four weeks was significantly higher for juveniles in the Largest position, 2.22 ± 0.53 , compared to the Medium position, 1.23 ± 0.22 , or the Smallest position, 0.51 ± 0.06 . The relative growth rate of juveniles in the Equal position, 0.76 ± 0.26 , was slightly higher than that of the juveniles in the smallest position, although not statistically different at the level of $\alpha = 0.05$. It is evident that exposure of juveniles to a change of position within the size hierarchy resulted in strong immediate effects on their growth performance as those individuals' relative growth rate adjusted in relation to the size of the other individuals present. Since all the selected juveniles were originally

obtained from the same population, had the same size and therefore the same R, as well as the same age, the observed differences in their growth rates can only be associated with the experimentally imposed change in their size ranking.

4.5.2 Lasting effect of size ranking on growth

Having found that juveniles of identical original social position underwent drastic growth rate modifications upon transfer to alternative positions of size rank, we tested whether animals of equal size and age, occupying different positions within their particular populations would retain their growth characteristics after being separated from their original populations.

Drawing on our previous observation, section 4.2, that average weight in the population is strongly affected by the population stocking density, we raised two groups of single age postlarvae under different stocking densities, 10/liter and 1/liter. We obtained two populations (Fig. 17), in which jumpers from a high-density group I) were equal in size to the non-jumpers from the low-density group (11). At this stage, jumpers, marked by clipped right telson fins, from Group I, and non-jumpers from Group 11, all weighing between 0.12 and 0.22 g, were withdrawn and restocked in two replicates each, in three different combinations: a) jumpers alone, b) non-jumpers alone, and c) mixed population of 50 % jumpers and 50% non-jumpers. Stocking density in 120 liter tanks, was uniformly set to 0.5 juveniles per liter, and every animal was weighed individually once a week for an additional growth period of 70 days.

The effect of social milieu on individual growth performance is clearly revealed by comparing the weights achieved by jumpers and non-jumpers stocked separately and in the mixed population. While jumpers alone attained an average weight of 1.075 g, R = 2.64, in the mixed population they rose to an average weight of 1.275 g, R = 2.85. Non-jumpers alone had an average weight of 0.655 g, R = 1.99, but in the presence of jumpers had an

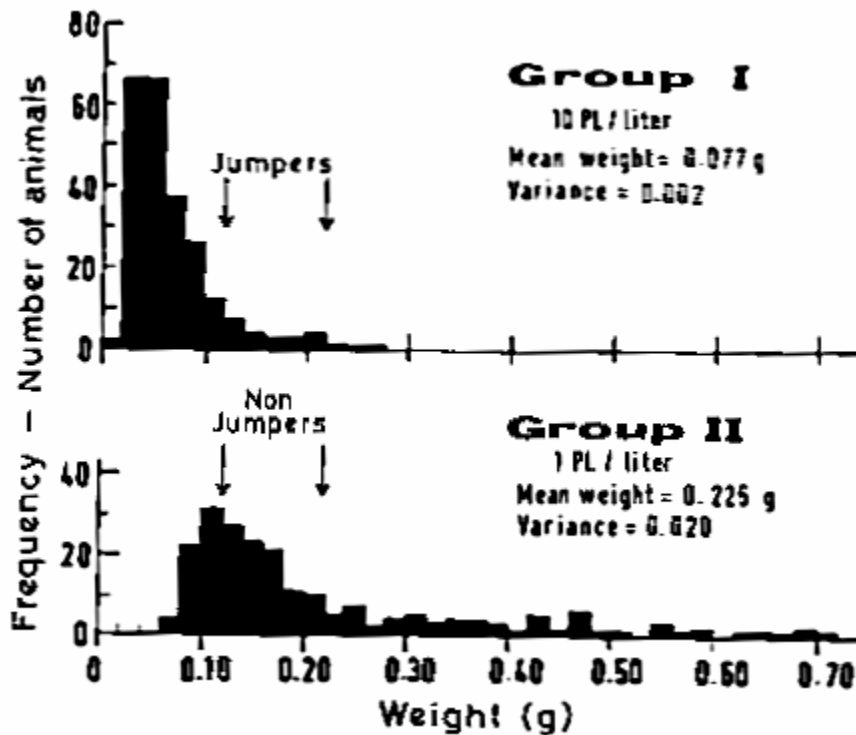


Figure 17. Frequency histogram of body weights of post larvae (PL), reared under two different densities, 60 days after metamorphosis.

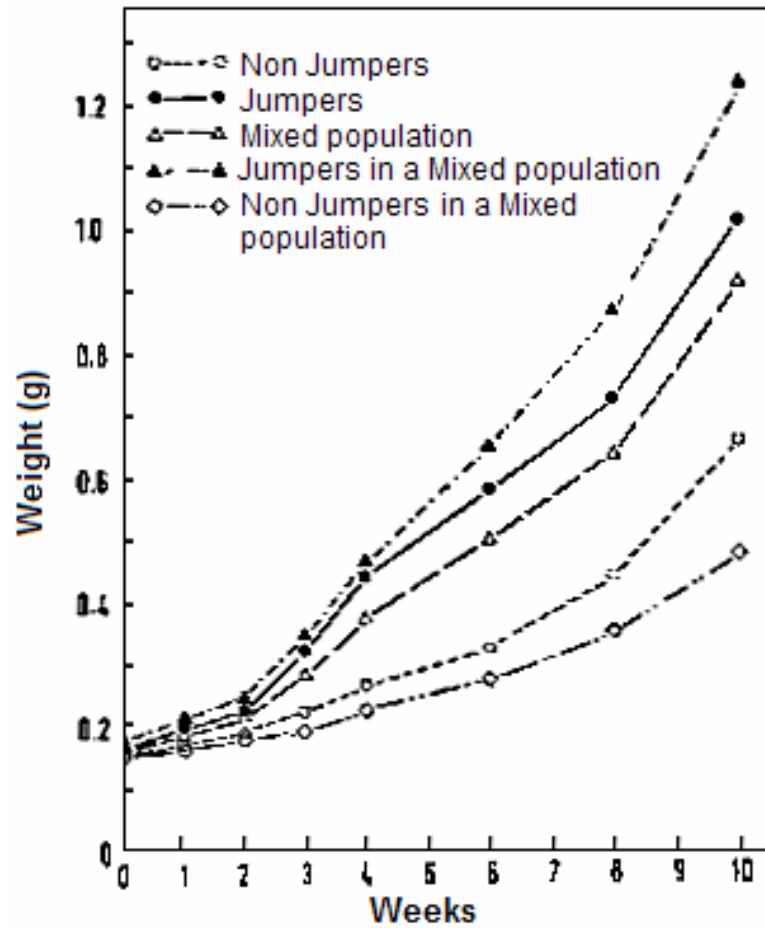


Figure 18. The effect of previous social position on further growth of juveniles selected from two distinct subpopulations, restocked in three combinations: jumpers alone, non-jumpers alone, and a mixed population.

average weight no greater than 0.475 g, $R = 1.84$. R values for both classes were statistically different at the level of $\alpha = 0.05$. In short, jumpers had augmented growth in the presence of non-jumpers, while the non-jumpers' growth was retarded in the mixed social setting (Fig.18).

The observation that jumpers had a higher growth rate than non-jumpers of similar size and age when all were stocked together indicated that the effect of social rank on growth is retained, even after size differences were neutralized. Moreover, the differential growth rates of jumpers and non-jumpers in pure and mixed groups corresponded directly to the growth stimulation of jumpers and the growth suppression of non-jumpers previously observed under communal growth conditions (section 4.3).

The last two experiments indicate that social position and the growth characteristics accompanying it are not a function of the animal's absolute size or age alone.

Breaking the associations of jumpers and non-jumpers away from their original populations revealed that social positions are more than merely differences in size ranking within a population. A juvenile social position and associated relative growth rate are based, therefore, on environmental, apparently social, stimuli and on factors intrinsic to the individual which were presumably acquired during early postlarval development when the initial size hierarchy evolved.

4.6 *Size ranking and the individual molt cycle*

Growth in crustaceans occurs as a balance between sequential molting events and molting frequency. Thus, an investigation of the molt cycle becomes a key point in the attempt to gain further insight into the growth dynamics of *M.rosenbergii*. We therefore followed the molt cycle of individuals which vary in their social positions in terms of size ranking, when grown individually and in pairs. Since there were indications of intrinsic differences between jumpers and non-jumpers, other than those of size ranking and body weight, we compared molting frequency and percent added weight between two sequential molting events. This was done in isolation or together with one other juvenile, either a jumper or a non-jumper.

Newly metamorphosed postlarvae from a single brood were divided into two groups. Group I was held at a stocking density of 10/liter and Group II at 1/liter. Under the effect of stocking density, Group I had an average weight of 0.08 g. 60 days after metamorphosis, while Group II reached an average weight of 0.24 g. during the same growth period (Fig. 19).

Jumpers of Group I were defined as individuals above 0.20 g. and non-jumpers as those below 0.16 g. Jumpers in Group II were defined as individuals above 0.48 g. and non-jumpers as individuals below 0.30 g. Jumpers in both groups were larger than one standard deviation above the mean weight. Between 0.20 and 0.30 g. there was a weight overlap between jumpers of Group I and non-jumpers of Group I and non-jumpers of Group II.

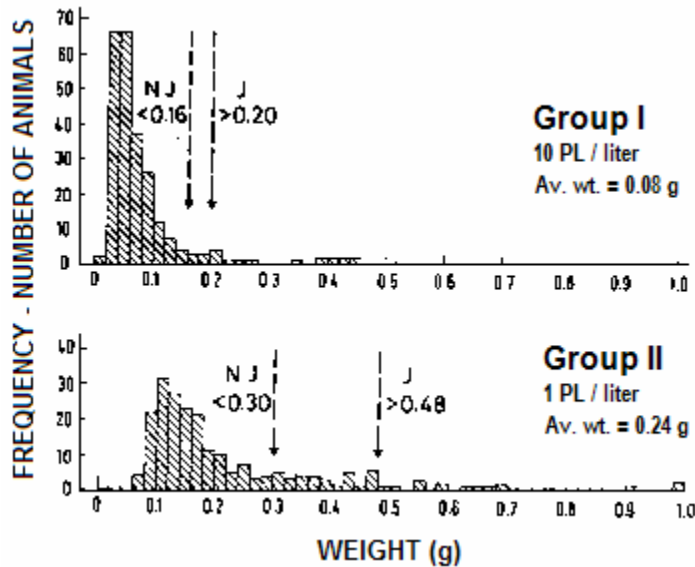


Figure 19. Frequency histograms of body weights of juveniles nursed under two different stocking densities, 60 days after metamorphosis. J – jumpers, NJ – non-jumpers.

Table 4. Increase in average weights (g) of the largest (upper 10 %), smallest (lowest 10%) and the median body weight experimental subjects reared under individual (IG) vs. communal (CG) growth conditions. *: Differences between means are statistically significant (t - test, α - 0.05).

Days after Metamorphosis (N = 10-12)	10 % Largest (N = 16-18)		Median		10 %Smallest (N = 16-18)	
	IG	CG	IG	CG	IG	CG
14	0.08*	0.15	0.031	0.041	0.017	0.018
21	0.16*	0.25	0.066	0.063	0.031	0.027
28	0.20*	0.39	0.080	0.073	0.042	0.031
35	0.28*	0.47	0.109	0.103	0.061*	0.037
42	0.38*	0.72	0.152	0.160	0.083*	0.062
49	0.48*	0.87	0.177	0.191	0.097*	0.073
56	0.55*	0.99	0.208	0.223	0.114*	0.081
63	0.57*	1.19	0.227	0.252	0.138*	0.084

At this stage, individuals chosen from each group were placed into three or four replicate 8-liter aquaria in the following combinations:

Stocking combinations	Group I	Group II
a) A jumper alone	J>0.20 g	J>0.48 g
b) A non-jumper alone	NJ<0.16 g	NJ<0.30 g
c) Two jumpers		
d) Two non-jumpers		
e) A jumper and a non-jumper		

Individuals were marked by a clipped tip of either right or left telson fin, and a similar clipping procedure was followed for individually reared juveniles in order to simulate possible stress effects. During a period of 90 days, aquaria were checked twice daily for molts, which were removed whenever they were found. Molting cycle duration and percent weight increase per cycle were calculated.

4.6.1 *The relationship between animal size and molting frequency*

In isolation, molting cycle duration was always positively correlated with the animal's weight (Table 5). In Group I, jumpers averaging 0.35 g and non-jumpers averaging 0.12 g went through an intermolt period of 28.0 ± 0.8 and 9.1 ± 1.2 days, respectively. In Group II, jumpers averaging 0.75 g and non-jumpers averaging 0.24 g demonstrated an intermolt period of 31.4 ± 1.4 and 7.7 ± 1.7 days, respectively. These observations correspond well with the general phenomenon described for other crustacean decapods (the crabs - *Carcinus maenas*, Breteler 1975, *Cancer anthonyi*, Anderson & Ford 1976, *Rithropanopeus harrisi*, Hartnoll 1977, and the lobster *Homarus americanus*, Mauchline 1977).

4.6.2 *The relationship between animal size and molt increment*

Many investigators of crustacean growth have reported that both weight and length increment per molt decrease with the absolute size of the animal. Thus, the molt increment was higher in small specimens than in larger ones (in crabs - *Paralithodes camtschatica*, Kajita & Nakagawa 1933, Sato 1958, *Cancer magister*, MacKay & Weymouth 1935;

Table 5. Intermolt period and percent weight increment per cycle of juvenile prawns held in various stocking combinations. Index letters indicate statistical significance of differences between treatments within each column. The values bearing the same index letter within each treatment do not show a significant difference at the level of $\alpha = 0.05$ (ANOVA, ONEWAY-RANGES, LSD-test).

Stocking combination	Weight	No. of range at stocking (g)	No. of animals	Percent weight molting cycles	Intermolt increase per cycle (% \pm SD)	period (days \pm SD)
Group I						
Individual growth:						
- Jumpers	0.20 - 0.40	4	4	60.00 \pm 2.43 ^a	28.0 \pm 0.8 ^a	
- Non-jumpers	0.06 - 0.15	4	18	21.46 \pm 0.98 ^b	9.1 \pm 1.2 ^b	
Growth in pairs:						
11) Two jumpers	0.22 - 0.45	6	28	20.17 \pm 4.82 ^b	9.4 \pm 1.3 ^b	
b) Two non-jumpers	0.06 - 0.16	6	23	20.39 \pm 5.94 ^b	7.1 \pm 1.1 ^b	
c) Jumper and non-jumper						
- Jumper	0.20 - 0.42	3	12	43.55 \pm 11.59 ^c	13.7 \pm 1.2 ^c	
- Non-jumper	0.08 - 0.14	3	9	38.67 \pm 13.33	16.9 \pm 2.2 ^d	
Group II						
Individual growth:						
- Jumpers	0.60 - 0.80	4	5	40.32 \pm 3.52 ^a	31.4 \pm 1.1 ^a	
- Non-jumpers	0.15 - 0.30	4	20	11.05 \pm 3.48 ^b	7.7 \pm 1.7 ^b	
Growth in pairs:						
a) Two jumpers	0.58 - 0.79	6	35	14.73 \pm 5.45 ^c	9.5 \pm 1.7 ^b	
b) Two non-jumpers	0.16 - 0.30	6	22	17.57 \pm 3.60 ^d	9.0 \pm 2.0 ^b	
c) Jumper and non-jumper						
- Jumper	0.60 - 0.83	3	11		20.03 \pm 7.25 ^d	
- Non-jumper	0.15 - 0.32	3	5	52.70 \pm 9.71 ^e	15.7 \pm 2.7 ^c	
					31.6 \pm 2.1 ^a	

in lobsters - *Homarus americanus*, MacKay 1929, Templeman 1936, Panulirus argus Latereille, Travis, 1954). However, Kurata (1962) in a general review stated that "... , the connection between ecdysis and growth is by no means simple, and very little is known about mechanisms by which the growth at molting is controlled". More recent works have demonstrated a strong influence of environmental factors such as temperature and salinity on weight increment per molt (Hartnoll 1977, Hartnoll & Dalley 1981).

Although *M. rosenbergii* juveniles in this experiment were kept under similar environmental conditions, jumpers, notwithstanding their larger absolute size, had proportionally greater weight increments per molt cycle than non-jumpers. Weight increase in Group I was 60 % per cycle for jumpers, 21.5 % for non-jumpers, and, likewise, jumpers of Group II increased by 40.3 % per cycle while the non-jumpers trailed with only 11.05 % (Table 5). Moreover, although of similar weight when removed from their respective native populations, jumpers of Group I showed a much higher weight increase per cycle (60 %) than non-jumpers of Group II (11.05 %). Thus, the molt increment attained by the animals in this experiment was associated with the specific growth patterns typical of the individual social position as determined during the incipient stages in the ontogeny of the native social structure, and not with the juvenile's current absolute weight.

It should be noted, however, that within a given size rank category, the rule of reciprocity of

molt increment and size remains valid: a) jumpers originally weighing 0.40 g (Group I) and 0.75 g (Group 11), gained 50.0 and 40.3 % per cycle, respectively, and b) non-jumpers separated at an average weight of 0.15 g (Group I) and 0.24 g (Group 11), gained 21.4 and 11.0 % per molt cycle, respectively.

4.6.3 *The effect of pairing individuals on their respective molting frequencies*

When two individuals were placed together in one aquarium, the intermolt period of each animal was markedly different from that observed for similar animals raised in isolation (Table 5). We found that the interval between molts of a jumper was shortened by 50 % when it was paired with a non-jumper, as compared to the intermolt period in isolation. Conversely, non-jumpers had an intermolt period 50 % longer in the presence of a jumper than they had as solitary individuals.

Since most of the studies on crustacean molting cycles were performed on animals in isolation, very little information exists with regard to the effect of interactions between individuals on their molting frequency. Still, Cobb & Tamm (1974) found that when juvenile lobsters were held in pairs, the time interval between molts generally increased. They also reported that the subordinate animal molted less frequently than the dominant animal, an observation which agrees with our finding that a non-jumper's molting is less frequent in the presence of a jumper.

Neither the mechanism nor the adaptive value of these phenomena are clear. Since food and space for our pairs were not limiting factors, the possibility of competition is largely reduced. Moreover, the 8 liter volume in which either one or two juveniles were raised was not of a magnitude small enough to induce growth inhibition. The striking differences between responses of jumpers and non-jumpers to pairwise culture are dependent on the relative size ranking of each individual within its native population; these differences are not a simple function of the animal's present size or age. Jumpers and non-jumpers represent physiologically diverse sub-populations which respond differently to similar sets of cues. The social situation of pairing individuals evidently triggers physiological signals to which the 'dominant' jumpers respond by increasing molting frequency, while the response of the 'subordinate' non-jumpers is to decrease theirs.

5 SUMMARY

The population structure of *M. rosenbergii* adult prawns is characterized by the coexistence of three male types differentiated with respect to morphology, growth dynamics, and their respective social roles in the prawn population. We have shown how the weight distribution of a mature prawn population of uniform age is associated with its typical social structure. The changes which occur in the population size distribution, starting from newly metamorphosed postlarvae through the juvenile stages up to the mature population are also described.

The main findings presented in this work are:

1. Newly metamorphosed postlarvae have a log-normal size distribution which becomes positively skewed with time.
2. Individuals within the size distribution's leading-tail, jumpers, exhibit a higher growth rate than the bulk of the population.
3. The advent of the leading-tail is enhanced under low initial stocking densities. This suggests that the appearance of jumpers is not primarily a result of competition.

4. Interactions among individuals, present in the case of communal growth, play a major role in the development of the size distribution observed in juvenile populations. Two consequent processes were observed: a) social stimulation, resulting in the enhanced growth rate of jumpers, and b) growth suppression, resulting in a lag of growth, as evidenced by the later emergence, in the presence of jumpers, of slow growing individuals, laggard. Neither the jumpers nor laggards were apparent under solitary growth conditions, proving the lack of genetic predetermination of an individual's growth rate.

5. Following the selective removal of jumpers, smaller juveniles increased their growth rate, some acquired jumper's attributes, and, eventually, the jumpers' leading-tail regenerated in the size distribution curve.

6. The exposure of juveniles to various social conditions resulted in strong immediate effects on their growth performance. We suggest that the relative growth rate of juveniles is correlated with, and readjusted to changes in, the prawn's relative social position within the population.

7. Juveniles of equal size and age, but differing in their social position within their particular populations, retained their original position and associated growth characteristics when separated from their native populations.

8. Isolated jumpers differed from each other in regard to intermolt period and intermolt weight increment. In these respects they also differed in their responses to the ambient social milieu when reared in pairs.

9. During early juvenile stages, the jumpers' leading-tail wasn't associated with either male or female growth characteristics and included an equal ratio of males to females.

10. Different male and female growth patterns became apparent at about three months after metamorphosis. Males exhibited an increasing positively skewed size distribution, while female growth became homogeneous.

11. At the onset of sexual maturation, three distinguishable male morphotypes develop: a) large dominant blue-clawed males (BC); b) large sub-dominant orange-clawed males (OC); and c) small undifferentiated clear-clawed males (SM).

12. BC is dominant, territorial and sexually active. The BC role is the irreversible climax of the male development pathway, and growth at this stage is almost completely stopped.

13. OC is sub-dominant. It is not territorial and is sexually incompetent. OC continues to grow and may eventually transform into BC males. The reproductive potential of an OC depends on its probability of survival until it becomes a BC and its chances of obtaining a territory.

14. The replacement of OC by BC conforms to a 'leap frogging' pattern of growth and maturation.

15. SM are not territorial. It is likely that they are capable of sexual competence and have a small probability of achieving successful fertilization of females. Being small and highly mobile they sometimes manage to sneak between a BC male and a female and apparently succeed in copulating. The reproductive potential of SM has two modes: a) staying small and achieving a 'sneak copulation' with a low probability, and b) growing to become an OC, eventually becoming a BC.

16. The coexistence of the three male morphotypes is consistent with an evolutionary stable strategy (ESS) since a constant frequency distribution of the three male morphotypes was observed over a wide range of population densities and ecological conditions.

The field observations and laboratory experiments described were made under conditions which differ considerably from those prevailing in the natural habitat of *M. rosenbergii*.

Although we believe that these findings represent the fundamental processes governing the ontogeny of the organism, it would be desirable to verify them in the natural habitat, or a closer facsimile thereof.

6 APPLICATION TO AQUACULTURE

The tropical freshwater prawn, *M. rosenbergii*, requires a temperature of 25-30°C for optimal growth and development (Raman 1967). The temperature in Israel drops below that, which is lethal for these organisms during the six month period of November to May. On the other hand, the six month summer season is not long enough for the development of economic yields of prawns when the entire production cycle, hatchery included, is carried out within this interval. Thus, economic feasibility dictates the extension of the growth period into the winter in this and other temperate zone areas. Larval development in the hatchery lasts for about one month. Since growout performance is markedly improved when nursed juveniles rather than postlarvae are stocked in production ponds (Smith & Sandifer 1980, Willis & Berrigan 1977, Ra'anan & Cohen 1982), the introduction of a nursery phase, in which postlarvae are accumulated and stored, has been recognized to be significantly beneficial.

The major economic constraint on the winter activities of the hatchery and the nursery is the need to conduct operations under cover and to apply and preserve heat in order to maintain suitable water temperatures. On the other hand, the flushing and exchange of the growth medium necessitates high production efficiency in order to justify the cost.

6.1 Intensification of nursery

Economic efficiency in the nursery stage is strongly dependent on the stocking density of the postlarvae (PL). Density may be increased as long as it allows for growth in body weight and ensures high survival probabilities of the nursed juveniles, without exerting a negative effect on the juveniles' growth potential upon their release into the grow out ponds. During the course of this study, we found that in early postlarval stages stocking density per unit of surface area was more significant than density per unit volume. The introduction of submerged substrates into the nursing facilities, for example, increased the carrying capacity of the system by 10 fold. It was a common belief, initially, that a density of 1 PL/liter is the maximum capacity of a commercial nursery. Today, some nurseries in Israel practice stocking densities of up to 10 PL/liter while still maintaining high survival rates and high growth potential (Ra'anan & Cohen 1982). Usable substrates are as variable as plastic egg trays, fruit crates and palm leaves. The common denominator is that about 60-70 % of the water body should contain substrates, and that these should be characterized by complexed surfaces in order to multiply hiding places for small and newly molted animals.

Experiments aimed at increasing densities showed that the final mean weight of nursed juveniles is inversely related to stocking density. Although maintenance of optimal temperature for juvenile growth, 26°C, resulted in better growth, it enhanced development of wide size variation which could lead to reduced survival by way of cannibalism. Laboratory experiments, however, confirmed that the selective removal of jumpers at various times

during the nursing period increased the growth of the remaining bulk of the population, until a new jumpers' leading-tail was established. The application of such selective harvest to commercial nurseries led the achievement of high final mean weight, reducing in the size distribution range and significantly improved survival rates.

6.2 *Improved production in the growout phase*

Since the growout period in the temperature zones is temperature restricted, the main objective of the farmer is to achieve the maximal number of marketable prawns at the end of a limited growout period of about six months. Physical contact among the animals leads to the establishment of a size hierarchy, especially within the male population and strongly effects both individual growth rate and relative social position. One way to approach this problem is to decrease stocking rates in the growout ponds in order to reduce the contact among the individual prawns to a minimum. Stocking the ponds at extremely low densities, 2,000-10,000/ha. is highly feasible in polyculture systems which include various types of fish, and where prawns are a marginal element. In such systems, yield of 300-500 kg/ha of large size prawns are highly profitable as an addition to the routine fish crops (Cohen et al. 1983, Cohen & Ra'anan 1983).

Another approach to the problem of a limited growout period is presently being examined in intensive prawn monoculture systems. The idea is to stock the ponds initially at high rate (70,000-100,000/ha) with fast growing juveniles. Separation of sub-populations by size is easily done by seining the nursery ponds with specific mesh-size nets. This permits selective stocking of the ponds, which is beneficial since it leads to size homogeneity of the juveniles at stocking and at the same time eliminates the growth suppression effect on smaller juveniles engendered by the presence of jumpers. Preliminary field experiments, conducted at the Ginossar experimental station, gave positive indications to this approach, mainly with respect to the percentage of marketable prawns at the end of the growout period, including the final average weight and the final survival rate (Ra'anan & Cohen 1983).

Significant improvement of intensive prawn monoculture was also achieved by periodic selective removal of the largest individuals, starting at the onset of sexual maturation as determined by the appearance of the first BC males. It was found that maturation time and body size maturation are inversely related to stocking density. After sexual maturation, moreover, both males and females diverted most of their energy to processes associated with reproduction at the expense of further growth. By then, the establishment of a social hierarchy, especially within the male population, resulted in about half of the males remaining small. Thus, the practice of periodic removal of the largest individuals, mainly BC and large OC males would result in: a) harvest of large males which have mostly reached a terminal stage with respect to further growth, b) reduced reproductive activity among females, and c) interruption of the steady state in the frequency distribution of the three male morphotypes, thereby promoting enhanced growth of small males under their tendency to regenerate the natural optimal frequency of BC and OC males. The selective harvest strategy is already being applied at several aquafarms in Israel, resulting in overall yield improvements which make the monoculture system economically feasible even under conditions which restrict the growout period.

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