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The Social Control of Growth in the Freshwater Prawn, *Macrobrachium Rosenbergii*

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C. ABSTRACT

The development of the agonistic behaviour in the giant freshwater prawn, Macrobrachium rosenbergii was investigated by contrasting one hour long symmetrical contests between males of the three morphotypes. The agonistic ethogram consists of 18 different acts. Contests between male prawns are usually composed of an escalated fighting phase and two additional phases, one prior and one following the fight itself. Differences in agonistic behaviour were found among morphotypes, contest phases, winner and loser. Analyses included also the sequence of acts, during the escalated fighting phase and the prediction of contest winner. The agonistic interactions were also analyzed in mixed groups of the three male morphotypes. Prawns formed a linear dominance hierarchy with the Blue Claw (BC) ranked first, Orange Claw (OC) second and Small Male (SM) last. The stabilization of the hierarchy was evident from the reduction with time in the number of agonistic interactions and their intensity. The effect of size and morphotype on dominance rank was studied in mixed groups composed of large, medium and small prawns of the BC and OC morphotype. BC males were ranked above OC males irrespective of size. Claw length seems to be the most important determinant of dominance. The largest BC male occupying the α position in the dominance hierarchy acquired more food and spent more time in a shelter than the rest of the males. The distribution and behavioural interactions of a small, individually marked, all male group was studied under semi-natural conditions. Aggressive interactions among prawns were brief and of low intensity, reflecting a stable dominance hierarchy. Survival among claw ablated juvenile prawns was twice as high, and the C.V. of their mean weight much smaller, compared to that of juvenile prawns with intact claws. Bi-weekly recording of size and morphotype of individually marked males in large communal cages confirmed the "leap-frogging" hypothesis. This growth pattern is achieved mainly through a delay in the transition from the fast growing OC morphotype to a slow growing BC. Reduction in aggressiveness level of large bull (BC) paired with a runt (SM), by manipulation of its claws (ablation and immobilization), caused a reduction of growth suppression. The major mechanism of growth suppression in runts under our laboratory conditions was a decrease in food conversion efficiency, which was found to be reversible. Metabolic rate of group and isolated individuals was estimated by measuring ventilation rate. Metabolism appears to play a role in the development of heterogeneous individual growth (HIG). Juvenile dominant prawns have a higher resting weight-specific ventilation rate than the less aggressive ones, perhaps indicating that the dominant prawns have a higher anabolic rate which would allow them to grow at faster rates. HIG occurs only in populations where there is a barrier-free animal to animal contact. HIG does not occur in a population of prawns in which individual members are housed in separate compartments, even though free water flow between containers is possible. Water from a free living prawn population could effect the HIG in a "population" of individually housed animals when passed over them indicating that a water borne factor may play a role in the development of HIG. This interdisciplinary study of social behavior, metabolism and growth, addressed one of the most complex problems in aquaculture, namely the variability of growth rate in many species. The knowledge gained will benefit further studies on growth variability in cultured species.

D. OBJECTIVES

- Objective 1: Prawn social behaviour (Israel).
- Objective 2: Relationships among social behaviour, social hierarchy and growth variation (Israel).
- Objective 3: Relationship of competition for food, appetite suppression and food conversion efficiency to growth suppression (Israel, Hawaii).
- Objective 4: Inter-animal cues (Hawaii).

E. RESEARCH ACTIVITIES AND RESULTS

Objective 1: Prawn social behaviour

1.1: Symmetrical Contests between the Three Male Morphotypes of the Giant Freshwater Prawn Macrobrachium rosenbergii (Crustacea, Palaemonidae).

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ABSTRACT

The agonistic behaviour of the giant freshwater prawn, Macrobrachium rosenbergii, was studied in the laboratory. One hour long symmetrical contests between prawns matched to size were carried out with each of the three male morphotypes of this species; small males orange-clawed males and blue-clawed males. The agonistic ethogram consists of 18 different acts which were grouped into indicators of dominance or subordination following the application of cluster analysis. Prawn contests consisted usually of an escalated fighting phase and two additional phases, one prior and one following it. Differences among morphotypes contest phases and winner and loser and their interaction were, analyzed for each agonistic act. The inter and intra-individual sequence of acts of the winner and loser in the escalated fight was analyzed for each morphotype. The ability to predict the outcome of the contest prior to its conclusion, was analyzed for eight different variables. The rapid opening and closing of the dactyllus and the number of nips and their duration were found to be highly significant predictors for winning. The ontogeny of the agonistic behaviour in males is discussed with emphasis on the increase in the damaging potential of the claw and the increase in claw length to body length ratio.

INTRODUCTION

The giant freshwater prawn, Macrobrachium rosenbergii (De Man) has a wide Indo-Pacific distribution ranging from Pakistan in the west to Papua-New Guinea and the Pallau Islands in the east (Holthuis, 1980). It is the largest species within its genus (individuals weighing more than 1/2 kg were captured in rivers), which is composed of over 100 species. This prawn has two pairs of claws; the first small pair is used mainly in cleaning, in capturing small items of food and transporting them to the mouth, and the second pair is mostly used by both sexes in predation and inter and intra-specific aggression and by males protecting females (Peebles, 1979a). These benthic prawns live in fresh to brackish water and are omnivores feeding on a variety of water insects and small fishes, plants and plants seeds as well as dead organisms and organic materials in the sediments (Ling and Mercinan, 1961; Raman, 1967).

Sexually mature populations of this prawn are composed of three male morphotypes which differ in their morphology, physiology and behaviour (Telecky, 1984; Ra'anan and Sagi, 1985; Kuris et al. 1987; Sagi and Ra'anan, 1988). Blue-clawed males

(BC) are large to medium-sized and have a slow growth rate. They possess very long and spinuous chelae often with a blue-colored propodus. Orange clawed males (OC) are large to medium-sized and have a rapid growth rate. They possess medium-sized, non-spinuous claws, often with an orange-colored propodus. Small males (SM) possess short, delicate claws, clear or light-pink colored. They have a very slow-growth rate when raised in groups containing large individuals. All three male morphotypes possess a sexually mature reproductive system and are capable of fertilizing females (Ra'anan and Sagi, 1985). The three male morphotypes are phases in a series of ontogenetic shifts in size, structure and behaviour. Every juvenile male, lacking an appendix masculina transforms when raised in isolation into the slightly larger SM and via OC to BC, all of which possess a fully developed appendix masculina. When raised in groups, only some of the juveniles transform into the large OC and BC morphotype and the rest remain small as SM. All three male morphotypes were found in pond-raised populations which originated from the same spawn of a single female and their frequencies were largely dependent upon density and age (Karplus et al, 1986).

Despite the fact that various aspects of the biology of Macrobrachium rosenbergii were studied in great depth much due to the fact that it is a major species for culture, its social behaviour and agonistic behaviour in particular, have not been studied in detail. In a general description of the reproductive behaviour, competition between males over females and aggressive interactions were mentioned (Rao, 1965). A general account of aggressive group interactions was given by Segal and Roe (1975). In a later study, Peebles (1979b) defined four agonistic acts and provided the only quantitative study on aggressive interactions of this species, demonstrating that relative size, prior residence and length of time rivals have been paired, play important roles in the outcome of a contest over a shelter.

In contrast to the vast research effort devoted to many aspects of the agonistic behaviour of some decapod crustaceans like hermit crabs and fiddler crabs the palaemonid shrimp have recieved relatively little attention. The agonistic behaviour of very few species has been investigated (Hipeau-Jacquotte, 1973; Lee and Fieldler, 1983; Volpato and Hoshino, 1984 and Evans and Shehadi Moakdieh, 1988) and none of them addressed the problem of the ontogeny of the agonistic behaviour.

Differences in the reproductive behaviour of the three male morphotypes have been described. BC males were described to guard soft-shelled females with their claws prior and following mating. Mating occurred following a 180° rotation of the female along her axis by the male (Rao, 1965; Peebles, 1979a). SM males in groups with BC males were observed to fertilize females using an alternative strategy by sneaking between the guarding male and the female and by attaching their spermatophore to the female after crawling below her (Telecky, 1984). OC males paired with a single female mated usually after rotating the female similarly to BC males but did not guard females prior or following fertilization (Frankfurt, pers. comm. 1989). In contrast to some information available on the reproductive behaviour of all three male morphotypes, the agonistic behaviour was only partly described for the large BC morphotype.

The aim of this study was to quantitatively contrast the agonistic behaviour of the three male morphotypes of Macrobrachium rosenbergii in order to allow a better understanding of the ontogeny of the agonistic behaviour in this

species. Symmetrical contests were staged between prawns matched to size in order to reveal the most intensive possible agonistic interactions. This study analyzed for each morphotype the agonistic ethogram, phases of a contest and the behaviour of the winner and loser of a fight.

MATERIALS AND METHODS

Prawn Collection and Maintenance

Prawns were collected during the months October-November 1986-1987 from earthen ponds at the Dor, Fish and Aquaculture Research Station. These ponds contained at harvest sexually mature populations with all three different male morphotypes present. Male prawns sorted to morphotypes (Kuris et al. 1987) were transferred to the Department of Aquaculture at the Volcani Research Center. Each prawn was stocked into a separate aquarium (50x25x40 cm) shielded from all sides except to its top and frontal panel by opaque white plastic sheets. Prawns were thus isolated visually and tactilly prior to testing but not chemically as they all shared the same recirculating water system which consisted of 32 aquaria interconnected to two sedimentation tanks and a biological gravel filter. The level of Amonia and Nitrite tested once every three days was low, not exceeding 0.5 and 0.05 ppm respectively. Water temperature daily recorded, was found to be stable with minor fluctuations ($28 \pm 1^\circ\text{C}$) due to a thermostat controled heater. compressed air was continously supplied to each aquarium via two air stones. oxygen level recorded once a week was always above 4.5 ppm. A double row of four Neon lamps positioned above the aquaria provided light on a balanced schedule of 12L/12D. All prawns were fed on a mixed diet of penaeid feed pellets (40% protein) manufactured by Star (Taiwan) and fish feed pellets (25% protein) provided on alternating days. Occassionaly live food-Daphnia and chironomides or pieces of Tilapia muscle were given in addition to dry pellets. Every two days food leftovers and prawn excretions were removed from the aquaria by a siphon.

The Testing Aquaria

Encounters involving the relative large OC and BC morphotype were carried out in large aquaria (120X50X50 cm.) while those of the SM were carried out in smaller aquaria (70X40X40 cm.) so as to maintain a similar ratio between prawn and aquarium size in all tested morphotypes. A blue wall paper was mounted on to the back and sides of all aquaria in order to eliminate the formation of a mirror image of the prawns. Above each aquarium was installed a wooden frame to which were attached two short 25W Neon lamps which provided the aquaria with a uniform illumination (500 Lux measured at the water surface). Each aquarium was divided into two equal sections by an opaque perspex partition. This partition could be lifted remotely due to a polly system. Each aquarium was surrounded by a "hide" a wooden frame (1.6x1.5x2.0 m) covered with black plastic in order to minimize disturbances. A small window in this hide allowed the filming of the prawn interactions. 24 hours prior to each encounter the water in the aquaria was changed so as to rule out the remaining of any chemical traces of the previous contest. Each testing aquaria was provided with an air stone and a thermostat regulated heater which maintained a uniform temperature ($28 \pm 1^\circ\text{C}$) in these aquaria. All the heating and air supply devices were removed prior to testing.

The Tested Prawns

All encounters were staged between male prawns of the same morphotype. all tested prawns met the following four criteria:

- a) Prawns were isolated at least two weeks prior to testing
- b) Prawns were in stage C of the molt cycle
- c) Prawns were intact, possessing all appendages and lacking any black or white spots (symptoms of two common prawn diseases) or coverage of the exoskeleton by algae.
- d) Every individual was tested only once.

Individuals were matched to size to form a contesting pair. The total length, carapace length, total claw length, propodus length and wet weight were measured (Table 1). On the average there was less than a 5% difference in each of the above parameters in a contesting pair. Molt stage was examined following the method developed for this species (Peebles, 1977) one day prior to a match and following it. The effect of the molt stage on lobster (Cobb and Tamm, 1975; Tam and Cobb, 1978) and on this species behaviour was clearly demonstrated (Peebles, 1978, 1980) and therefore only prawns in the intermolt stage were included in this study. Individual recognition of each contesting prawn was facilitated by a small plastic tag attached to the dorsal part of its carapace with a cyano-acrylic glue that was previously found not to affect prawn behaviour (Sagi and Ra'anan, 1985).

The Contest

Encounters between prawns were filmed only in the morning (05:30-10:30) despite the fact that Macrobrachium rosenbergii is a nocturnal crustacean (Nakamura, 1975; Peebles, 1979a) due to the necessity to obtain high video film quality for subsequent data analysis. Three encounters, with a testing protocol identical to the one pursued during the mornings, were observed at night (20:00-23:00) with the aid of a dim red light which is supposed less to affect prawn activity (Goldsmith and Fernandez, 1968). Although not quantitatively contrasted prawns seemed to behave similarly during day and night encounters. Similar results were also obtained for the crab Cancer magister (Jacoby, 1983). The two prawns participating in a match were transferred at the same time to the testing tank for a period of 15 minutes of acclimatization prior to lifting of the partition which separated them. A JVC GX-N70E video camera with a built in timer was used for filming prawn interactions. Filming of each match lasted for one hour and started with the movement of one prawn towards its opponent. Tests with prawns which did not interact within 20 minutes of the lifting of the partition were terminated without filming and without further testing these prawns.

Data Analysis

Behavioural events during matches were extracted from video tapes with the aid of a National AG-6200 video cassette recorder which allowed forward and backward film inspection at different speeds as well as freezing of frames. Temporal information was usually transcribed at the 1 second time interval level and only seldom at the 0.1 second interval in order to determine the duration of very rapid acts or the inter-individual sequence of acts of two prawns which started their activity during the same second. All data were statistically analysed with the aid of a SAS (1985) computer software package. Details of specific statistical tests used in this study will be presented in the results section.

RESULTS

The Agonistic Ethogram

The description of the agonistic ethogram is based on the examination of over 40 hours of video-taped interactions between the three male morphotypes involving more than 5500 acts. 18 behavioural acts were defined. The body parts and appendages described in the agonistic acts are presented in Fig.2. Acts were classified into the four following categories:

A) Locomotory acts involving movement towards a frontal position:

1) Approach to frontal position (APF)

One prawn moves towards another within a two body length distance, achieving a position of its front directed towards the other prawn. This movement has to be carried out over at least half of a prawns body length.

2) Turn to frontal position (TRF)

A prawn rotates around its own axis, changing its position towards another prawn so that its front instead of its side or rear is directed towards the other prawn.

3) Rush (RSH)

A short (0.7 ± 0.26 sec.) and rapid movement of one prawn towards another within a two body length distance. This act is carried out while the prawn's front is directed towards the other prawn, the pleopods beat rapidly, the body is elevated, the tail fan spread out, the antennae are directed forward and both claws are extended in a forward direction with the dactylus open.

B) Locomotory acts involving movement towards a non frontal position or increase in distance:

4) Move away (MVA)

One prawn moves away from another prawn within a two body length distance. A distance of at least half a body length must be covered.

5) Approach to non frontal position (ANF)

One prawn moves towards another within a two body length distance achieving a position of its front directed away from the other prawn. This movement has to be carried out over at least half of a prawns body length.

6) Abdomen flexing (AFX)

One prawn increases the distance to another prawn by a rapid flexing of its abdomen so as to propel it backwards. During this act (0.36 ± 0.27 sec.) the prawn's abdomen is so arched that its tail fan moves to a forward position, it loses contact with the substrate and its claws are dragged behind its body in a forward extended position.

7) Turning aside (TSD)

A prawn from a position with its front directed towards another prawn, rotates around its own axis so that its side or rear are directed towards the other prawn. This act is usually accompanied by the lowering of the prawn's claws and body to the substrate.

C) Behavioral acts based on claw position and movement without a contact:

8) Cheliped extending (CEX)

Extending of the claw of one prawn towards another without contact. This movement is based on the enlargement of the

angle between propodus to carapus and carapus to merus untill these segments are located on an almost straight line. Extending may be carried out with one or both claws (Fig.3 & 4), sometimes accompanied with rapid opening and closing of the dactyllus.

9) Meral spread (MSP)

The body is in an elevated position with both claws lifted above the substrate and parallel to it. The ischium and merus are perpendicular to the body axis. The ischium is lifted up to a 45° above the horizontal plane. The merus is positioned at the same angle as the ischium or parallel to the horizontal plane. The carpus forms an angle of 90° - 135° with the merus and the propodus a 90° - 180° angle with the carpus (Fig.4).

10) Strike (STR)

A very rapid (0.15 ± 0.06 sec.) parallel forward extending of both claws towards another prawn. This act is usually accompanied by the closing of the dactyllus (Fig.4).

11) Complete lifting (CLF)

The lifting of the claws and the anterior part of the body in the direction of another prawn. The body is in a very elevated position, the carapace forming an angle of 45° - 90° with the horizontal plane. The abdomen is extended, the tail fan opens and closes while the pleopods beat vigorously. The claws are lifted upwards at an angle of 45° - 90° to the horizontal plane (Fig.3). CLF is occasionally carried out while rapidly opening and closing the dactyllus.

12) Incomplete lifting (ILF)

An act similar to CLF except that the two claws are not lifted upwards but remain in the horizontal plane (Fig.3).

13) Scissoring (SCR)

A very rapid (0.15 ± 0.12 sec) bringing together of the two claws from a spread position in a scissoring motion above the body of another prawn without touching it. During this act the angle between the propodus and carapace changes simultaneously in the two claws from a very wide angle to close to 90° (Fig.3).

14) Thrust (THR)

A very rapid (0.2 ± 0.07 sec.) simultaneous opening of the two claws in the direction of another prawn. This act starts from a position of the two claws lifted in the horizontal plane. This movement involves usually several segments of the claw but it may also be carried out only with the propodus (Fig.4).

15) Cheliped shaking (CSH)

Very rapid movements of opening and partly closing of the dactyllus while the claw is beeing partly extended in the direction of another prawn. These rapid dactyllus movements result in a shaking effect of the entire claw which is most pronounced at its end (Fig.4).

D) Behavioral acts involving contact with the claws:

16) Embrace (EMB)

One prawn embraces another with its claws. This act is carried out from behind or the side usually while the embracing prawn is higher relative to the other. During this act contact is usually made between the claws of the embracing prawn and the appendages or body of the embraced one (Fig.3). EMB is occasionally carried out while rapidly opening and closing the dactyllus.

17) Nip (NIP)

"An aggressive act where one animal closes down the tips of its chela on the body part of another animal" (Peebles, 1979b).

18) Push (PSH)

An aggressive act where one animal pushes one of its chelae against the body of another animal" (Peebles, 1979b). This act is carried out with the exterior side of the propodus through the extension of the claw similar to CEX except that a contact is made.

Bout - An agonistic exchange between two animals. a bout starts with the approach of two animals within a two body length. The bout terminates with either the increase in the distance between the two prawns to a two body length, or the lack of movement of both prawns for at least a 60 sec period. From this situation the next bout starts with the performance of any agonistic act by one of the prawns except to the act of moving away. 83% of all bouts were defined following approach and moving away and only 17% following resumption of activity by two previously motionless prawns.

The Frequency of the Behavioral Acts and Their Grading as Indicators of Dominance and subordination

A total of 5551 acts were recorded during all symmetrical contests with a similar contribution of the three morphotypes (31%, 34% and 35% for BC, OC and SM respectively). The frequency of the different acts comprising the agonistic ethogram is presented in Fig.5. Moving away (MVA) and approaching (APF and ANF) were by far the most common acts (22.7% and 19.4% respectively), their relative frequency similar in the three morphotypes. There were three rare acts : PSH, THR and CSH, each of which contributed less than 1% to the total observed acts. The frequency of locomotory acts involving body movements (categories A&B) vs. acts based mainly on claw position and movement (categories C&D) was similar in the three morphotypes (averaging 58% and 42% respectively). These results reflect the importance of claws in the agonistic behavior of the three male morphotypes.

Agonistic acts were graded as indicators for dominance-subordination with the aid of cluster analysis. We assumed that acts which characterized a dominant or submissive animal will occur asymmetrically in the two contesting opponents when the dominance relationship has been established. The level of asymmetry may be expressed by the index: $(f_A - f_B) / (f_A + f_B)$, where f_A and f_B represent the frequency of a specific act performed by individuals A and B, respectively (Schielder, 1988). The values of this index range from +1 to -1, its absolute value representing the level of the asymmetry and its sign the direction of the asymmetry. The asymmetry indexes were calculated for each act in every contest of each morphotype. These data were analysed using Ward's Minimum Variance Cluster Analysis. Only acts which comprised at least 1% of the total acts of each morphotype were included in the analysis. The clustering of the acts into three dendrograms, one for each morphotype, is presented in Fig.6. There is a clear division of the behavioral acts into two main groups. One consisting of ANF, TSD, MVA and AFX belonging to categorie B, acts involving movement towards a non frontal position or increase in distance. It seems that this group is typical of a submissive individual. The second group, comprises the other acts including clearly aggressive acts like

nip seems to be typical for the more dominant animal. The only exception are CLF and CSH which appear in the first group in BC and in the second in OC. The classification of the acts with the aid of cluster analysis enabled the reorganization of the initial tables of asymmetry. The direction of the index was not determined by the arbitrary assigning to one animal role A and the other role B but by determining their role in such a way that the asymmetrie index was positive for most dominant acts and negative for most submissive acts. Table no.2 represents the mean values of the asymmetry index of each act for the three morphotypes.

The second phase of the analysis was the grading of all acts along a symmetrical scale (Barlow and Balin, 1976; Aspey, 1977) according to their ability to serve as indicators for dominance or submission with respective positive and negative values. Due to the similarity in the dendrograms of the three morphotypes a single scale was prepared (Fig.7). The three following points were considered when ascribing a specific value to an act: 1) The position of this act in the dendrograms. 2) The mean value of asymmetrie index of the act. 3) The consistency of 1 and 2 in the three morphotypes. The order of the acts does not necessarily reflect their level of aggression. Both CLF and SCR reflect attack but are not good indicators for dominance since these acts are displayed simultaenously by both prawns before the determination of winning or losing.

Phases in the Contest and the Determination of Winner and Loser

Table 3 summarises some general information concerning prawn contests. There were no significant differences among the male morphotypes in number of acts and bouts per contest ($P > 0.3$) when contrasted by a one way ANOVA carried out on log transformed data. However, there were significant differences with regard to the total duration of interaction time ($P = 0.0016$) which was about twice as long in the BC males compared to SM and OC. The time interval until first interaction was significantly ($P < 0.03$) longer for the SM than the other male morphotypes. All contrasted parameters of the contest, showed relative high variability as evident from the high values of the standard deviation presented in table 3.

During a one hour contest two prawns unknown to each other met and usually established a dominance-subordinance relationship. During this proccess several changes occurred in their behaviour which can be useful to split the contest into several biological meaningful phases. Contest data can be pooled according to these phases rather than using an arbitrary time or bout number scale. Prawn contests in our study usually included a phase of one or two escalated fighting bouts which differed from the agonistic bouts which came before and after it. Therefore a contest could be subdivided into three phases:

- Phase I - pre-escalated fighting
- Phase II- escalated fighting
- Phase III- post-escalated fighting

Table 4 summarises several parameters of the different phases of the three morphotypes. A two-way ANOVA contrasting these parameters with regard to contest phase and morphotype revealed significant differences between phases with regard to number of bouts, number of acts per bout and length of bout ($P < 0.05$).

Contrasting the phases (Duncan's multiple range test, $\alpha=0.05$) revealed that only phase 2 differed from the rest. No differences were found between morphotype or interaction between morphotype and phase ($P>0.05$) in all tested parameters. No differences were found between phases or morphotypes in time interval between bouts.

The escalated fighting phase consists usually of only one bout as compared to several bouts of either phase I or phase III. Phase II includes about three times more acts per bout than phases I and III and its bout duration is much longer. Phase II also includes several acts like CLF and ILF at a much higher frequency in the two contesting prawns as in any other phase. Therefore the subdivision of the contest into three phases is justified and will be incorporated in the quantitative comparisons among the fighting behaviour of the three male morphotypes.

The determination of the winner of a contest was based on the differential frequency of submissive acts given by the two prawns (Rowell, 1974). TSD was previously found to be the best indicator for submission but due to its low frequency, another element, MVA- the most common act was added and applied to the contests where TSD did not occur. Since the contest was subdivided into phases, the winning prawn was determined according to the lower frequency of TSD or MVA in phase III following the escalated fight. In contests which did not include phase II no winner or loser were determined.

The Effect of Morphotype, Contest Phase and Winner/Loser and their Interaction on Prawn Fighting Behavior

The effects of morphotype, contest phase and winner/loser on prawn fighting behavior were analysed with a three way ANOVA carried out on the mean frequency per bout of each act. All contests where a winner/loser could be determined, totaling 31, were included in the analysis. When a significant ($\alpha = 0.05$) effect was found for either a main variable or interaction between variables. Multiple comparisons were carried out with the aid of T-tests (contrasted by least square means).

Comparison of Morphotypes

Table 5 presents the mean frequency of each act in the three morphotypes. For some acts (CEX, CSH and ANF) significant differences were only found between morphotypes (table 6). In other acts (SCR, ILF, CLF and MSP) significant differences were found both between morphotypes and interaction between morphotype and contest phase. Finally for some acts (NIP and AFX) significant differences were only found for the interaction between morphotype and contest phase. When contrasting the different morphotypes for the acts where only the main effect was significant, the following results were obtained:

ANF: SM < OC = BC ; CEX and CSH: SM = BC < OC

In all other acts where a significant interaction between morphotype and contest phase were found the difference between morphotypes were only found in phase 2 (the escalated fighting phase) with the following results:

SCR and MSP : BC > OC > SM (Fig.8).
CLF : BC=OC > SM (Fig.8).
ILF : BC < OC = SM (Fig.8).
NIP : BC < OC = SM (Fig.8).
AFX : BC = SM < OC (Fig.8).

In all the above acts, except to AFX, the trend of the difference is from BC to SM with the OC occupying an intermediate position, sometimes similar to BC, sometimes to SM and with regard to some acts all three morphotypes differed. The acts CLF, SCR and MSP occur in a relative high frequency in BC and not in SM. The acts NIP and ILF show the reverse trend occurring relatively seldom in BC and often in SM.

Comparison of Contest Phases

Table 5 also presents the mean frequency of each act for every phase of the contest. In all acts where a difference was found it resulted from a higher frequency in phase 2 relative to phases 1 and 3 which were similar. In all acts that differed in the frequency in the different phases a significant interaction was found either with morphotype or with winner\loser. The first interaction reflects the difference among morphotypes with regard to changes in act frequency with the contest phase.

CLF, SCR and AFX : differences only in BC and OC (Fig.8).

ILF and NIP : differences only in SM and OC (Fig.8).

MSP : differences only in BC (Fig.8).

The second interaction reflects the differences between the performance of specific acts by winner and loser in phases 1 and 3 (details in next section).

Comparison between Winner and Loser

Table 5 also presents the mean frequency of each act for the winner and loser. Since winner and loser were defined following the frequency of TSD and MVA, these acts were not discussed due to evident circularity and were only analysed with regard to differences between morphotypes and phases of the contest.

The acts CEX and RSH differed only in the main factor and both of them were displayed at a higher frequency by the winner. In the rest of the acts a significant interaction between winner\loser and contest phase was found. The acts APF and EMB were displayed at a higher frequency by the winner in phases 2 and 3 but not in 1 (Fig. 9). The acts MSP and TRF were displayed at a higher frequency by the winner only in phase 3 but not in phase 1 and 2 (Fig. 9). The submissive act ANF was displayed at a higher frequency by the winner in phase 2 but significantly less in phase 3. In phase 3, this act was more often displayed by the loser ($P=0.057$). No significant interaction was found between winner\loser and morphotype indicating that behaviour of winner and loser do not differ among morphotypes.

The Behaviour Sequence

Analysis of the sequence of agonistic acts was carried out on phase 2 since the escalated fighting provides the key to the entire contest. Each bout was analyzed separately. The sequence of acts involving both intra and inter-individual transitions of winner and loser was analyzed simultaneously on a temporal basis and is presented in three kinematic charts, one for each morphotype (Fig. 10).

The BC morphotype: The similarity in the frequency and sequence of acts of the winner and loser is most evident in the acts CLF - CSR - AFX. These acts are performed in the above sequence by both contesting prawns often simultaneously and are therefore both represented in the intra and inter individual sequence of the prawns. The transition from SCR to AFX is mostly

intra-individual due to the short duration of both these acts and the interval between them. The major differences in the sequence of the winner and loser acts are:

- a. The occurrence of APF only in the sequence of the winner.
- b. The occurrence of TSD only in the sequence of the loser.
- c. MVA occurs only in the loser as part of the inter individual sequence namely following the aggressive act - MSP by the winner.

The typical escalated fighting sequence consists of the frontal approach by the winner with its claws in the MSP position. The loser lifts its carapace and claws - CLF, as does also the winner and both perform several times the sequence of claw-lifting, scissoring and abdomen flexing. Finally, the loser terminates the bout by moving away (MVA) or directing its side to - the winner.

The OC morphotype: The typical escalated fight of the OC morphotype is similar to that of the BC by also incorporating, although at a lower frequency (not pictured in the kinematic chart) the typical sequence CLF - CSR - AFX. However, the relative importance of ILF and NIP is much higher and both these acts are often followed by AFX. Nip occurs at a similar frequency in the sequence of the loser and winner while the acts CEX, APF and EMB are more common in the sequence of the winner and MVA in that of the loser.

The SM morphotype: The escalated fight of the SM is more similar to that of the OC than the BC. The relative importance of NIP and ILF increases further as these acts compose the two major components of the winner and loser escalated fighting sequence. The acts CLF and SCR disappear completely. The typical escalated fighting sequence consists of the approach by one prawn followed by incomplete lifting (ILF) and abdomen flexing (AFX) by both prawns or alternatively NIP followed by AFX. The bout is terminated by the loser moving away.

The prediction of winning the escalated fight

A bout of escalated fighting may include two levels of intensity. The first level consists of the aggressive displays CLF and ILF displayed simultaneously by both contesting prawns at most with slight physical contacts between the prawns. The second level, always preceded by the first, consists of massive physical contacts of nipping. The possibility to predict which prawn will win an escalated fighting bout before its termination was examined by testing the following behavioural events as possible predictors of the outcome of the fight:

- 1) The initiator of the bout - the first prawn to approach its opponent.
- 2) The initiator of the first level of escalation - the first prawn to perform ILF or CLF.
- 3) The number of "loops" - rapid intra-individual sequences of CLF - SCR - AFX displayed by the BC and OC morphotype and ILF - AFX by the OC and SM morphotype.
- 4) The rapid opening and closing of the dactyllus during CLF and ILF.
- 5) The initiator of the second level of escalation - the first prawn to nip.
- 6) Number of nips.
- 7) Time spent nipping.
- 8) Victory in the previous escalated bout.

For each of the above variables the winner or loser of each fight received the score 1 if this variable could be directly applied to it (e.g. prawn to initiate bout) or it obtained a higher value of this variable (e.g. nipped its opponent more times than it was nipped by it). The other prawn received the score 0 in these cases. The results of the escalated bouts of all morphotypes were pooled due to their small number and were tested by a Chi-square test, applied separately to each variable (Table 7). The tested variables could be grouped into three categories:

- Group 1 -Highly significant predictors ($P < 0.01$) closing and opening of the dactyllus, number and duration of nips.
- Group 2 -Significant predictors ($P < 0.05$) initiator of the bout and victory in the previous bout.
- Group 3 -Non-significant predictors ($P > 0.05$) initiator of the first level of escalation, number of "loops" and initiator of the second level of escalation.

The frequency of escalated contests which include the second level of intensity, namely nips increases with the transition from the BC via OC to the SM morphotype (Fig.11). On the other hand, the frequency of contests where rapid closing and opening of the dactyllus were performed showed the reverse trend increasing from the SM via OC to the BC morphotype (Fig.11). Nip number and duration and the opening and closing of the dactyllus, the most reliable predictors of winning a contest are differently displayed by the different morphotypes. In the BC morphotype with its extremely large and powerful claws, the winner can often be predicted at the first level of contest intensity on the basis of rapidly opening and closing the dactylus. In the OC and particularly the SM with its delicate small claws, opening and closing of the dactyllus are performed only seldom and the winning of a contest can be predicted mainly following massive physical contacts of nipping.

DISCUSSION

The Phases of the Contest

In the initial quantitative studies on crustacean aggressive interactions all the recorded data was usually pooled together and treated as one unit for sequence or information analysis while disregarding stationarity which is an essential assumption underlying these two quantitative analyses (Bekoff, 1977; Oden, 1977). Several investigators have subsequently demonstrated the lack of stationarity during a contest when they split it into several segments and analyzed each segment separately. The splitting of stomatopod contests into segments on an arbitrary time basis revealed significant differences in the sequence of acts and the amount of information transmitted (Dingle 1969, 1972). In other studies, contests were split and pooled on the basis of serial act number (Hazlett and Estabrook, 1974; Rubenstein and Hazlett, 1974). Salmon and Hyatt (1983) analyzed fiddler crabs contests following their subdivision on the basis of a biological meaningful event namely the point of surrender of one of the contestants. In our study we proceeded in that direction demonstrating that one hour long symmetrical contests between two Macrobrachium rosenbergii males are complex dynamically changing processes which may be subdivided into several biological meaningful phases. The contest may include an escalated fighting phase and two additional phases, one prior and

the other following it. The three phases differed not only in the frequency of the different acts but in their performance by the winner and loser during the different phases of the contest. Detailed analysis of long contests in other species will possibly reveal similar processes which should lead to a better understanding of crustacean fighting behavior and even to more cautiousness when pooling together data.

The componets of the agonistic act

The three major componets of Macrobrachium rosenbergii agonistic acts are the claw position and movement, the body elevation and its orientation towards the opponent. In numerous species of crustaceans of different groups, the claws were described as the main componet of several agonistic displays (Dingle, 1983). The comunicative value of claw position and coloration have been demonstrated in several experimental studies (Hazlett, 1972a,b; 1975, 1979; Caldwell and Dingle, 1976 Dunham, 1978a, b, 1981).

Body elevation has been less investigated although mentioned in many studies as a componet of agonistic acts. In some studies, a low and high body position were defined as discrete behavioural acts of the agonistic ethogram (Jachowski, 1974; Hazlett and Estabrook, 1974). Hazlett (1975) has demonstrated with models that three different levels of body elevation had a different effect on two species of xanthid crabs. In our study, Macrobrachium rosenbergii was found to change its body elevation during the contest. At the start of the contest both prawns meet in the MSP position with elevated body. During the esclated fight, the frequency of CLF and ILF increases in the opponents thus the anterior part of their body is now directed diagonally upwards to the horizontal plane. Following the point of decision of who wins the contest, the winner is again in the elevated MSP position or EMB position while the loser is very low, as in the TSD position. At the beginning of a contest, the body elevation may serve as a cue for the evaluation of relative size but following the decision of who wins the contest, it probably reflects dominance-subordinance relationship.

Crustacean body orientation during agonistic interactions was so far not studied in detail. In Callinectes sapidus, orientation during contests was analyzed but without reference to winning or loosing the contest (Jachowski, 1974). In our study, "Approach" was subdivided into APF and ANF (differing only in orientation). The very different position od these acts in the dendrograms of the cluster analysis and their different frequencies in the behaviour of the winner and looser confirm the notion that these acts are indeed different. Similarly to the body elevation, also the body orientation of the two interacting prawns changes during the contest. An escalated fight starts only when the two prawns face one another, this is particularly evident when they display simultaenously CLF or ILF. The exact point in an escalated fight when the decision is reached to who wins a contest is marked by a change in the oriantation of the loser to a non-frontal position by TSD or MVA. This orientation is later maintained during the contest and is particularly evident when the winner performs EMB with its front directed towards the loser which turns away directing its rear or side towards the winner. Thus body orientation at this stage of the fight seems like body elevation to reflect the dominance-subordinance relationship.

The antenna and antenullae are certainly important elements in Macrobrachium rosenbergii agonistic behaviour. Lee and

Fieldler (1983) included in the agonistic ethogram of a related species M. australiense, two acts which focused on these structures: antennae pointing and antennules whipping. We did not include the prawn's antennae and antennulae in our study due to the inability to analyze precisely and consistently from video films their position, movement and contact with the other prawn.

The Ontogeny of the Agonistic Behaviour

The three male morphotypes are phases in a series of ontogenetic shifts in size and structure (Kuris et al. 1987). In all three morphotypes the claws are similarly important as evident from the lack of a difference in the relative frequency of total number of acts involving the claws. However, in the SM morphotype there are fewer discrete acts which include claw position and movement as compared to the BC and OC morphotype. The differences in the agonistic behaviour of the three morphotypes are most pronounced during the escalated fight. A higher level of lifting (CLF), meral spread (MSP), scissoring (SCR) and rapid opening and closing of the dactylus versus a lower frequency of incomplete lifting (ILF) and nipping (NIP) were evident when comparing the BC with the SM morphotype. The OC is occupying an intermediate position between the SM and BC morphotype with regard to the above acts. In addition to the observed differences in the frequency of the different acts among morphotypes, there is a tendency for longer total interaction time with the transition to the BC from the SM with the OC again occupying an intermediate position. The SM is also different from the other two by often lacking the pre-escalated fighting phase in its contest. The tendency to shift from shorter interactions involving more physical contacts towards longer interactions with less contact, reflects the increased ritualization with a reduction in the possibility of physical damage. The longer and the stronger the claws, the larger is the risk of their actual usage in the contest and therefore, we see a tendency for settlement of conflicts by displays only, without the involvement of physical contact (Maynard Smith and Parker, 1976).

The claws of the three morphotypes, differ also in the length ratio between claw to body. This ratio probably affects the spatial position of the claw incorporated in the agonistic acts of the three male morphotypes. The BC performs acts with its very long claws not completely extended in the horizontal plane but rather flexed in the MSP or lifted diagonally to the horizontal plane in CLF. The OC with its much shorter claw has an increased tendency to display in the horizontal plane during CEX and ILF and less in the MSP position. In the SM with its short and light claws, the MSP is not displayed at all and only ILF is performed. The differences in the claw weight and length in the three morphotypes which affects the claw momentum, may underly the above mentioned differences.

Although few studies have been devoted to the ontogenetic changes in crustacean agonistic behaviour, some of the emerging trends are similar to those found in our study. Hazlett and Provenzano (1965) have reported that in agonistic interactions of juveniles, fewer displays are included and more physical contact is employed than by adults. Juvenile Cancer magister were reported to interact in a more variable sequence and in a less controlled intensity as compared to adults (Jacoby, 1983).

Transmission of Information during the Contest

The function of agonistic displays carried out by two fighting animals following the classical ethological view, was thought to be the transmission of information concerning the tendencies to attack or retreat (Lorenz, 1981). An alternative view based mainly on game theory predicts that natural selection will favor individuals that during a contest will not reveal any information concerning their tendencies to give up the fight (Maynard Smith, 1974, 1982; Caryl, 1979).

The differences in the behaviour of the winner and loser in male Macrobrachium rosenbergii contests described in our study, fit better the game theory approach since the two prawns behaved similarly until a late phase of the contest. Even the two behaviour elements which were found to be the most significant predictors of victory, namely opening and closing of the dactylus and number and duration of nips are both often occurring at a late phase of the contest and close to the point of decision of who wins the contest. A similar result, similarity in behaviour of winner and loser was also reported by Glass and Huntingford (1988) for the swimming crabs, Liocarcinus depurator.

The similarity in the behaviour of two contestants was suggested to reflect the need not to reveal any information concerning their intentions. Displays of contestants should transmit information only concerning the resource holding potential (RHP) following game theory applied to animal contests (Parker, 1974). The behavioural displays performed by fighting Macrobrachium rosenbergii, are structured to transmit information concerning size (MSP, ILF and CLF) and strength as well (opening and closing of the dactylus, NIP and SCR) both of which are the major components of the RHP.

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Table 1

The means and standard deviations of several morphometric parameters of the three morphotypes included in this study.

BC - Blue Claw, OC - Orange Claw, SM - Small Males

	SM (n=24)	OC (n=32)	BC (n=26)
Total length (cm)	7.8 ± 0.7	12.3 ± 0.9	12.4 ± 0.8
Claw length (cm)	6.6 ± 0.6	14.9 ± 1.9	21.7 ± 2.9
Carapace length (mm)	24.5 ± 2.3	42.2 ± 3.6	43.7 ± 3.0
Propodus length (mm)	22.8 ± 2.8	63.8 ± 9.7	95.1 ± 14.6
Weight (gr)	10.7 ± 2.5	52.9 ± 13.4	64.5 ± 13.6

Table 2.

The means of the asymmetry indexes calculated for each agonistic act from all contests of each morphotype. (* = category of act)

BC - Blue Claw, OC - Orange Claw, SM - Small Males

BC					OC					SM				
act	mean assy. index	n	%	*	act	mean assy. index	n	%	*	act	mean assy. index	n	%	*
CEX	0.61	89	5.3	c	NIP	0.60	105	5.2	d	EMB	0.79	223	11.3	d
EMB	0.52	132	7.8	d	CEX	0.57	194	9.6	c	STR	0.68	46	2.3	c
PSH	0.49	18	1.1	d	EMB	0.43	141	7.0	d	CEX	0.55	93	4.7	c
NIP	0.43	44	2.6	d	TRF	0.37	101	5.0	a	APF	0.53	334	17.0	a
ILF	0.42	23	1.4	c	MSP	0.35	65	3.2	c	RSH	0.51	45	2.3	a
APF	0.38	191	11.3	a	APF	0.33	209	10.4	a	NIP	0.50	123	6.3	d
TRF	0.37	113	6.7	a	RSH	0.29	29	1.4	a	TRF	0.33	159	8.1	a
MSP	0.29	166	9.8	c	STR	0.27	25	1.2	c	ILF	0.27	300	15.2	c
CSH	0.15	17	1.0	c	CSH	0.25	24	1.2	c	MSP	0.17	11	0.6	c
RSH	0.08	11	0.6	a	PSH	0.22	20	1.0	d	CLF	0.08	1	0.0	c
CLF	0.03	168	9.9	c	SCR	0.22	18	0.9	c	PSH	0.08	2	0.1	d
SCR	0.01	51	3.0	c	ILF	0.14	90	4.5	c	SCR	0	0	0	c
STR	0.00	6	0.4	c	CLF	0.11	97	4.8	c	CSH	0	0	0	c
THR	-0.08	4	0.2	c	THR	0.06	9	0.4	c	THR	0	0	0	c
AFX	-0.11	109	6.4	b	ANF	-0.03	144	7.2	b	AFX	-0.12	57	2.9	b
MVA	-0.17	383	22.6	b	AFX	-0.29	158	7.9	b	MVA	-0.45	454	23.1	b
ANF	-0.20	126	7.4	b	MVA	-0.35	425	21.1	b	ANF	-0.69	75	3.8	b
TSD	-0.25	43	2.5	b	TSD	-0.59	48	2.4	b	TSD	-0.72	32	1.6	b
Total:		1694					1902					1955		

Table 3.

Means and standard deviations of several parameters of the contest of the three morphotypes. BC - Blue Claw, OC - Orange Claw, SM - Small Males

Morphotype	No. of acts	No. of bouts	Interaction Time (min.)	Time until first Interaction (min.)
BC	143 ± 70	15.4± 5.0	23:10 ±6:10	2:35 ±2:54
OC	124 ± 85	12.3± 6.1	14:51 ±6:59	4:22 ±3:00
SM	164 ±126	18.3±13.6	11:53 ±7:35	8:12 ±5:00

Table 4

The mean values of several parameters of contest phases calculated for each of the three male morphotypes.

BC - Blue Claw, OC - Orange Claw, SM - Small Males

Phase:	Mean bout duration (sec.)			Mean interval length (sec.)			Mean number of bouts			Mean number of acts per bout		
	1	2	3	1	2	3	1	2	3	1	2	3
BC	82	158	81	106	78	140	8.5	1.4	4.7	6.3	21.9	6.8
OC	76	226	74	349	189	239	6.2	1.1	6.2	7.8	31.1	8.6
SM	34	65	39	107	43	144	4.6	1.1	12.2	4.8	19.3	8.6

Table 5

The mean frequency of the agonistic acts (per bout) according to morphotype, contest phase, and contest winner/loser.

	MORPHOTYPE			PHASE			W/L	
	BC	OC	SM	1	2	3	Winner	Loser
APF	1.05	1.25	1.44	1.11	1.36	1.15	0.83	0.40
TRF	0.82	0.53	0.65	0.49	0.97	0.52	0.40	0.28
RSH	0.07	0.11	0.27	0.05	0.14	0.20	0.10	0.04
ANF	0.62	0.78	0.20	0.76	0.58	0.42	0.32	0.25
MVA	2.29	2.52	1.77	1.94	2.67	2.02	0.84	1.39
AFX	1.14	3.00	1.07	0.17	4.48	0.19	0.81	0.96
TSD	0.36	0.37	0.22	0.20	0.60	0.15	0.10	0.23
CEX	0.49	1.16	0.44	0.53	0.93	0.62	0.50	0.21
MSP	0.98	0.60	0.04	0.48	0.96	0.36	0.33	0.28
CLF	1.66	1.61	0	0.16	2.99	0.22	0.62	0.61
ILF	0.38	1.30	2.92	0.12	3.14	0.38	0.71	0.62
SCR	0.48	0.25	0	0.01	0.72	0.03	0.16	0.13
STR	0.05	0.12	0.11	0.05	0.12	0.08	0.06	0.03
THR	0.11	0.11	0	0.11	0.13	0.01	0.05	0.03
CSH	0.07	0.26	0	0.09	0.13	0.12	0.08	0.03
EMB	0.80	0.82	0.92	0.54	0.94	0.94	0.63	0.20
NIP	0.59	1.35	2.34	0.16	2.98	0.40	0.74	0.54
PSH	0.05	0.11	0	0.08	0.06	0.04	0.03	0.03

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Table 6

Results of the Three Way Analysis of Variance (P-values) performed on each agonistic act, testing the effect of morphotype, contest phase, and contest winner/looser and their interaction. Bold numbers represent significant P-values ($P < 0.05$).

	<u>Source of variation</u>						
	Morph	Stage	W/L	Morph- Stage	Morph- W/L	Stage- W/L	Morph- Stage- W/L
APF	0.23	0.68	0.0001	0.9	0.14	0.01	0.43
TRF	0.17	0.01	0.06	0.05	0.68	0.01	0.28
RSH	0.16	0.19	0.03	0.8	0.15	0.1	0.26
MVA	0.24	0.17	0.0007	0.18	0.79	0.02	0.55
ANF	0.04	0.2	0.63	0.18	0.05	0.002	0.21
AFX	0.12	0.0001	0.66	0.0009	0.85	0.9	0.98
TSD	0.24	0.0001	0.006	0.72	0.92	0.001	0.42
CEX	0.0003	0.07	0.0005	0.39	0.39	0.09	0.39
MSP	0.009	0.01	0.72	0.01	0.96	0.03	0.55
CLF	0.007	0.0001	0.98	0.0001	0.98	0.84	0.99
ILF	0.04	0.0001	0.57	0.0001	0.72	0.8	0.99
SCR	0.04	0.0001	0.62	0.0001	0.87	0.85	0.99
STR	0.4	0.91	0.2	0.21	0.1	0.23	0.35
THR	0.64	0.45	0.54	0.14	0.82	0.77	0.76
CSH	0.006	0.92	0.23	0.91	0.25	0.8	0.89
NIP	0.38	0.0001	0.36	0.01	0.96	0.85	0.98
PSH	0.09	0.76	0.86	0.14	0.49	0.14	0.53
EMB	0.96	0.1	0.0001	0.20	0.44	0.007	0.62

Table 7

The distribution of eight behavioural events of the escalated fighting bout, and their significance as predictors of bout outcome.

a= initiator of bout. b= initiator of escalation. c= more "loops". d= more opening & closing of dactyllus. e= nip first. f= more nips g= longer nip duration. h= winner of previous bout.

	a	b	c	d	e	f	g	h
Winner	39	35	21	24	17	15	21	21
Looser	26	30	14	9	15	6	7	12
Total	65	65	35	33	32	21	28	33
χ^2_1	5.20	0.77	2.80	0.25	13.64	7.71	4.91	14.00
P	<0.05	>>0.05	>0.05	<<0.01	>>0.05	<0.01	<<0.01	>0.05

Fig 1. The three male morphotypes of the giant freshwater prawn, Macrobrachium rosenbergii. BC-blue claw; OC-orange claw; SM-small male.

Fig 2. Appendages and body parts of Macrobrachium rosenbergii.

CLF - Complete Lifting

ILF - Incomplete Lifting

NIP

SCR - Scissoring

CEX - Cheliped Extending

TSD - Turning Aside

EMB - Embrace

Fig 3. Agonistic acts of the giant freshwater prawn, Macrobrachium rosenbergii (arrows indicate direction of movement).

Fig 4. Agonistic acts of the giant freshwater prawn, Macrobrachium rosenbergii (arrows indicate direction of movement).

Fig 5. The frequency of performance of the different agonistic acts by the three male morphotypes in symmetrical contests.

BLUE CLAW MALES

ORANGE CLAW MALES

SMALL MALES

Fig 6. The clustering of prawn agonistic acts on the basis of similarity in the asymmetrie index, presented separately for each morphotype. Only acts which consisted of more than 1% of the total sum of acts of each morphotype, were included in the analysis.

Fig 7. Ranking of the agonistic acts of Macrobrachium rosenbergii along a dominance-subordinance scale.

Fig 11. The left histogram represents the frequency of escalated fighting bouts which included massive physical contact (NIP) in the three morphotypes. The right histogram represents the frequency of the escalated contests which included the rapid opening and closing of the dactyllus (DCT) during CLF and ILF. BC-blue claw; OC-orange claw; SM-small males.

Fig 8. Mean frequency of agonistic acts performed by each morphotype during the different phases of the contest. points sharing the same letter do not differ significantly ($\alpha = 0.05$).

Fig 9. Mean frequency of agonistic acts performed by the winner and loser during the different phases of the contest. Points sharing the same letter do not differ significantly ($\alpha = 0.05$).

Fig 10. Kinematic graphs describing the inter and intra individual sequences of the winner and loser in an escalated fighting bout in the three male morphotypes. Only transitions of at least 1.5% of all sequences of each morphotype were included in the analysis. The size of the circle represents the frequency of each act. Full arrows represent a transition initiated by the winner. Broken arrows represent a transition initiated by the loser. The width of the arrow is proportional to the relative transition frequency. The value at its beginning represents the probability of that transition.

1.2: The Formation of Dominance Hierarchies in Mixed Groups of the Three Male Morphotypes of the Giant Freshwater Prawn Macrobrachium rosenbergii (Crustacea, Palaemonidae).

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ABSTRACT

The agonistic interactions in ten groups, each composed of six Macrobrachium rosenbergii males, were studied in circular arenas over a period of three days. Each group consisted of two blue claw (BC) males and two orange claw (OC) males matched to size and two much smaller, small males (SM). Male prawns formed a linear dominance hierarchy with the BC ranked first, OC second and SM last. The stabilization of the hierarchy was evident from the reduction in the number of agonistic interactions and their intensity with time. The character of the mixed morphotype hierarchy was evaluated by investigating the extent to which the different morphotypes were involved in agonistic interactions and the nature of these interactions.

INTRODUCTION

Dominance and territoriality in group living animals are functionally interpreted as two social mechanisms for optimal utilization of limited resources (Wilson, 1975). These mechanisms are of different nature with regard to the dispersion of individuals. While territoriality is site related and space is divided by the individuals, dominance hierarchy exists among space sharing individuals (Brown, 1975).

Although the nature of dispersion in natural populations of Macrobrachium rosenbergii is not known, some information from prawn fishery (Raman, 1967; George, 1969), suggests that these animals are found in groups. Peebles (1979) studied the dispersion of prawns in commercial ponds and found that they are clustered in groups. This finding was recently confirmed by Karplus and Harpaz (1990) who followed an individually marked group consisting of 25 adult males in a clear water earthen pond. At the same time, they did not observe any territorial behaviour among group members. On the basis of the above information

Macrobrachium rosenbergii is expected to form a dominance hierarchy in groups, by which the need for continuous intraspecific aggression is reduced. Out of the limited number of studies on dominance hierarchies in crustaceans, size related hierarchies were commonly described (e.g. Bovbjerg, 1953, 1956 and Lowe, 1956 in crayfish; Fielder, 1965 in spiny lobsters; Hazlett, 1966 in hermit crabs; Lee and Fielder, 1983 in Macrobrachium australiense). Adult populations of the freshwater prawn Macrobrachium rosenbergii are characterized by a wide range of size distribution (Fujimura and Okamoto, 1972; Smith et al, 1978) which is mainly the result of the coexistence of 3 male morphotypes: "Blue Claw Males" (BC) - medium to large males whose chelipeds are long relative to the body, "Orange Claw Males" (OC) - medium to large males whose chelipeds are short relative to the body and "Small Males" (SM) - males with small chelipeds

(Ra'anani and Cohen, 1985). Provided a dominance hierarchy is formed, we expect the SM morphotype to occupy a low position in the male dominance hierarchy due to its small size and the larger BC and OC males to occupy a higher rank.

The development of the male morphotypes in a population is socially controlled by male agonistic interactions (Ra'anani and Cohen, 1985; Karplus et al, in prep.). Therefore, exploring the social organization of the three morphotypes will contribute to the understanding of growth processes in prawn populations and the biological significance of these male morphotypes.

The aims of this study were 1) to examine whether male prawns in groups establish dominance hierarchies. 2) To establish which of the three types of hierarchy: linear, non-linear or despotic (Bekoff, 1977) is formed and the position occupied by the different morphotypes. 3) To investigate the process of hierarchy formation. 4) To contrast intra and inter morphotypic agonistic interactions.

MATERIALS AND METHODS

The source of animals and their maintenance in the laboratory, as well as the video system used for data collection, were the same as described in a previous study (Barkai et al, in prep., a).

The testing arena

Observations were carried out in two round arenas, 150 cm. in diameter and approx. 25 cm. deep. The bottom of each arena was divided into 16 sub-areas as shown in Figure 1. Each arena was surrounded by a black screen, slit in the front to allow video camera photography. In order to maintain optimal water conditions, the following means were used: 1) An external filter (EHEIM 2017) for continuous circulation and filtration of water. 2) A 2000 watts heater, controlled by a thermostat, kept water temperature at $28 \pm 2^\circ\text{C}$. 3) An air pump for additional aeration of water. Water quality (ammonium & nitrite) and temperature were daily recorded after data collection.

The tested prawns

There were 10 different test groups, each containing six adult males of the same age, two size-matched prawns of each morphotype. All prawns which were included in this study met the following criteria: 1) Prawns in molt stage C. 2) Prawns were kept in isolation for at least two weeks prior to the experiment. 3) Only healthy and undamaged prawns were used. One day before the experiment, the individuals of the test group were measured, weighed, and their molt stage determined (Peebles, 1977). Prawns were marked by glueing small colour bands on their carapace. The BC and OC males were matched to body and carapace length while the SM were, by definition, smaller (Table 1).

The testing procedure

Observations were made between 20:30-23:00 hours, in minimal light levels necessary for video photography (30 lux measured during the experiment, as compared with 250 lux measured during the day). Each group was observed for one hour during three successive nights. Every night two groups were observed. After each set of three nights when the two observed groups were replaced, the water in the arenas was changed as well. The prawns were first put into a device made of 6 opaque cylinders located in the center of the arena, allowing for adaptation of 10 minutes without any possibility of visual or tactile contact. After 10 minutes this device was removed.

Video photography was made from above and lasted one hour, using the Focal Animal method (Altman, 1974), by which the camera focused on each individual for 10 minutes, recording all interactions of this individual with all the others. Individuals were picked at random, by casting a dice. On the first day recording began after removing the adaptation device, but not before agonistic interactions between individuals were observed. On the second and third days the air pump and the external filter were disconnected 15 minutes before video photography started, in order to keep the water surface smooth. After the end of each observation period, prawns were fed with commercial pellets - 40% protein (Star, Taiwan), and during the day the arena was cleaned of uneaten food and prawn excreta. After the third day all individuals of the group were removed from the arena and their molt stage was reexamined to make sure no individual had entered the premolt stage.

Data recording and analysis

Data was transcribed from the video films, processed using Lotus-123 on a PC, and analysed with SAS (1985) on a main computer. An interaction was defined as the occurrence of an agonistic act between two individuals located within a range of one body length (of the larger individual). All agonistic acts were sequentially recorded with respect to the sender and the receiver. Most agonistic acts analysed in this study have been described in details in a previous study (Barki et al, in prep., a). Due to the video filming of the prawns in the arena from an elevated position of the camera, the act "Meral Spread" was excluded since it was unrecognisable. "Complete Lifting" and "Incomplete Lifting" were combined into a single behaviour pattern - "Lifting" (LFT), since they were undistinguishable.

The mobility of each focal male was recorded. One mobility unit was defined as a shift from one section to the next. The small sections 1a, 1d, 4a, 4d (Fig. 1) were excluded from this calculation. Determination of an interaction's winner and loser was based on all agonistic acts performed during the interaction. For each individual a "Dominance Index" (D.I.) was calculated weighing the frequency of all agonistic acts in the interaction, and their weight, as indicators of dominance/subordination (Barki et al, in prep., a) by the following formula:

$$D.I. = \frac{\sum (ACT'S \text{ FREQUENCY} \times ACT'S \text{ WEIGHT})}{\sum (ACT'S \text{ FREQUENCY})}$$

The winner of an interaction was the individual with the higher D.I. Group members were arranged in rank order following the method described by Brown (1975). By this method individuals are arranged in the dominance matrix in a rank order which minimizes the number of interactions below the diagonal (reversals). The degree of linearity of the dominance hierarchy was calculated following the method described by Appleby (1983) which is based on Kendall's index of linearity, K. However, values obtained in the calculations could not be used for testing the significance of linearity (Appleby, 1983), due to the irrelevance to ranking of the order by which the two prawns of the same morphotype were ranked. This fact increased the probability of obtaining linearity by chance. Linearity is said to be strong if K value ≥ 0.9 , as arbitrarily defined by Chase (1974) for Landau's index h, which is identical to K for odd group size and is nearly identical for even group size.

We were interested in the effect of two factors on behavioral variability: the morphotype and time factors. In order to pool data from all groups, both individuals from each morphotype were assigned number 1 or 2 according to their relative rank (1 for the higher rank, 2 for the lower rank), thus a third factor, the relative rank, was added.

Each of the following 10 behavioral variables were analysed with a three-way ANOVA: number of interactions, rate of mobility (log transformed values), and eight agonistic acts (frequency per interaction) each of which constituted more than 3% of the total acts (Fig. 2). Since the agonistic acts were used to determine the rank order, they were not tested for the effect of relative rank but for the interaction of this factor with the morphotype factor. In order to further explore differences between the different levels of factors which were found significant (when number of levels > 2) Duncan's Multiple Range Test ($\alpha=0.05$) was used. Mobility was used as the covariate in the analysis of covariance which tested the effect of time on the number of interactions. The rationale of this was that a decrease in the mobility may be the cause for the decrease in the number of interactions, rather than the effect of the time factor.

To portray the directions (addresses) of agonistic acts between dyads we followed the format presented by Myrberg (1972) and Barlow and Ballin (1976). In each figure representing a different agonistic act the six individuals of the group were arranged according to their rank, the dominant at the top. The arrows represent the directions of the behaviour in the dyadic relationship and their width is proportional to the frequency which is marked above them (values are the number of occurrences per 10 interactions).

RESULTS

Dominance rank

Dominance matrices were initially constructed for each day separately. However, due to the small number of agonistic interactions, mainly on the second and third days, we had to pool the data of all three days.

In two out of ten test groups the number of dyads (out of 15 possible dyads in a group of six) with missing relationship was too high (6 and 7 dyads) to permit ranking. In the other eight groups the number of missing relationships did not exceed four, a fact which enabled the construction of a rank order. Table 2 is a summary of rank orders in eight groups, based on their dominance matrices. In only one group (no. 8) a circular relationship occurred in a triad of two OC and one SM which were ranked 3, 4, and 5, respectively. The degree of linearity in this group was very low ($K=0.28$). In six groups one tie occurred where none of the two adjacent individuals dominated the other and their relationship with all other individuals were identical. In half of these cases the tie was within morphotype. In only two groups linearity was found to be strong ($K \geq 0.90$). Although the significance of linearity couldn't be tested, the high consistency of the dominance rank in all groups was very pronounced. BC males were consistently ranked at the top of the hierarchy, followed by the OC, and the SM were always ranked at the bottom.

Components of behavioural variability

Results of the analysis of variance carried out on behavioural variables are presented in Table 3. All interactions

between factors, except one which is discussed below, were not significant and, therefore, are not listed in Table 3.

After eliminating the effect of mobility (by analysis of covariance), the effect of time on the number of interactions was still very significant ($p < 0.001$), with a much higher value on the first day than in the second and third days (Fig. 3). The effect of the morphotype factor was also significant ($p < 0.001$). However, a significant interaction between days and morphotypes (the only significant interaction, $p < 0.05$) reveals that the difference in the number of interactions between the morphotypes changed across the days. On the first day: $BC = OC > SM$, on the second day: $BC > OC = SM$, and no difference between the morphotypes was found on the third day (Fig. 3). There was a significant difference among days in the mobility ($p < 0.001$), with a much higher value on the first day, as compared to the two other days, but no significant difference among morphotypes ($p > 0.05$).

For a better understanding of the differences among morphotypes we checked with whom each individual interacted by calculating the proportion of interactions for each dyad in the group. Since the day and morphotype factors had a significant interaction ($p < 0.05$), this calculation was made separately for each of the three days. The mean values of all groups are shown in Table 4. Special attention should be paid to the following trends: a) The proportion of interactions of the BC-BC dyad is the highest on all three days of the experiment. b) The percentage of the intra-morphotypic interactions of BC and OC is higher than the percentage of their inter-morphotypic interactions with the morphotypes they dominate. c) The percentage of interactions of the BC morphotype with the OC morphotype, which is closer in rank, is higher than that with the lowest ranking SM morphotype. d) The percentage of the intra-morphotypic interactions of SM is also higher than the percentage of the inter-morphotypic interactions with OC and BC, on the second and third days.

The frequency of only two agonistic acts, move-away (**MVA**) and lifting (**LFT**), differed significantly across days ($p < 0.01$ and $p < 0.05$ respectively, Table 3) with a lower value on the third day as compared to the first two days (Table 5). It is revealed from Table 3 that the effect of the morphotypes on behavioural variability is stronger than the effect of time. In six out of eight agonistic acts this effect was statistically significant: In the dominant behaviour patterns Approach and Turn to frontal position (**APF** and **TRF**) and Embrace (**EMB**) the frequency decreased from BC to SM ($BC > OC = SM$) and the submissive behaviour pattern move away (**MVA**) showed the opposite trend ($SM > OC = BC$). Another submissive behaviour pattern, Approach to non-frontal position (**ANF**) showed a different trend than **MVA** ($OC > BC = SM$) (Table 5). The frequency of Lifting (**LFT**), which is not an indicator of dominance or submission, changed across morphotypes by the following order: $BC > SM > OC$. This behaviour pattern is occasionally performed simultaneously by the two opponents. A total of 25 such interactions between or within morphotypes were recorded. Twenty cases of simultaneous lifting (80%) occurred between BC males, two (8%) between SM, and three (12%) between BC and OC. Twenty cases of simultaneous lifting (80%) occurred on the first day, and five (20%) on the second day, while none occurred on the third day.

The analysis of differences between prawns was based on the mean value obtained from five different dyads for each individual. In order to understand the behavioural characteristics

of the hierarchy at the dyadic level, the frequency of agonistic acts addressed in each dyadic relationship was calculated. Since dominance rank is based on data pooled over days, calculations were performed accordingly. The results of all agonistic acts are portrayed in Figure 4. Acts are not directed similarly to the different individuals. Differences in characteristics of the intra- and inter-morphotypic interactions are often evident. A few points should be pointed out: Approach to frontal position (APF) and move-away (MVA), each differently directed, characterize both intra and inter-morphotypic interactions with no substantial difference. The agonistic acts which characterize a dominant individual: embrace (EMB), turn to frontal position (TRF) and nip (NIP) mainly characterize BC in the inter-morphotypic interactions with OC. Furthermore, EMB and TRF characterize the dominant individual in the intra-morphotypic interactions of the three morphotypes, whereas NIP characterizes the dominant individual in the intra-morphotypic interactions of SM only. Lifting (LFT) characterizes intra-morphotypic interactions, but while it is performed by the two individuals in the BC interactions, it is rather a characteristic of the dominant individual in OC and SM intra-morphotypic interactions.

DISCUSSION

The major finding of this study is the formation of a dominance hierarchy by Macrobrachium rosenbergii males where the BC is dominant over OC, which in turn is dominant over SM.

The linear order of the morphotypes in the hierarchy may be related to their relative size. However, size differences in the case of the BC and OC morphotypes when matched to size is expressed mainly in the chelipeds, which are larger in the BC males. Cheliped size appears to be an important factor in the determination of dominance order. This point was further analysed in a study on the effect of size and morphotype on the formation of dominance hierarchies in mixed groups of BC and OC (Barki et al, in prep., b).

The changes in the agonistic interactions among group members over three days revealed that a dominance hierarchy was stabilized within this period. The establishment of dominance relationship between the individuals was reflected in a significant decline, after the first day, in the frequency of interactions and mobility. Besides their frequency, there was also a change in interactions characteristic. This change was reflected in the significant decline in the frequency of the behaviour patterns Move away (MVA) and Lifting (LFT), mainly on the third day, which suggests that the process of hierarchy stabilization extended beyond the first day. The significance of the decline in MVA is that, following an interaction, a subordinate need not retreat from a dominant, since his close proximity is tolerated by the dominant after the relationship has been established. The decline in simultaneous LFT reflects the decline in the number of intense agonistic interactions (zero on the third day), which is a further evidence for hierarchy stabilization. A similar pattern of decrease in the frequency and intensity of agonistic interactions (Bovbjerg, 1953; Lowe, 1956; Hazlett, 1969; Jacobson, 1977; Sastry and Heinger, 1980; Lee and Fielder, 1983) was described during hierarchy formation in other crustaceans.

The behavioural nature of the mixed morphotype hierarchy can be evaluated by considering the extent to which the different

morphotypes are involved in interactions and the nature of these interactions. A high proportion of interactions are intra-morphotypic interactions of the BC morphotype, in which the most dominant individual is involved. It is more likely that an individual would rather interact with his rank-neighbour (i.e. of his own morphotype) than with a morphotype it dominates, and the greater the social disparity is, the less likely an interaction will occur. In a system which includes the three morphotypes, this fact confers a certain advantage to a subordinate morphotype being less exposed to the dominant's aggression, and a certain cost to the dominant in terms of energy spent in aggressive interactions. Lowe (1956) presented data on the crayfish Cambarellus shufeldtii which indicated that the dominant individual in a group of 4 was involved in more interactions than the other three. Winston and Jacobson (1978) found no such difference between 4 group members of the hermit crab Pagurus longicarpus. However, the dominant crab initiated more interactions than the subordinate one.

Intra and inter-morphotypic interactions differ not only by their frequency but also by their nature. Escalation in the interaction which is expressed by a simultaneous "Lifting" of the opponents (Barki et al., in prep., a) occurred mostly between the dominant and subdominant BC males. On the other hand, "Nip" was mostly addressed by the dominant BC towards the lower ranked OC males. "Nip", unlike the "Lifting" display, is a behaviour pattern which involves physical contact and therefore can be considered as a more aggressive one. This leads to the conclusion that despite the fact that most interactions of the dominant BC are intra-morphotypic, these interactions are of a less aggressive nature than its inter-morphotypic interactions. These findings corroborate two theoretical predictions on animal conflict, derived from game theory (Maynard Smith and Parker, 1976; Parker and Rubenstein, 1981): 1) Aggressive interactions would more likely occur between closely matched individuals. 2) The greater the probability of injury, the smaller the risk an animal will take of incurring that injury. Thus the dominant will not as readily escalate to a highly aggressive behaviour when interacting with a close ranked individual as with a lower ranked individual.

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Table 1

The means and standard deviations of several morphometric parameters of the three morphotypes included in this study.
BC - Blue Claw, OC - Orange Claw, SM - Small Males

	SM (n=20)	OC (n=20)	BC (n=20)
Total length (cm)	6.1 ± 1.2	12.0 ± 0.3	12.0 ± 0.4
Claw length (cm)	4.8 ± 0.8	13.5 ± 1.1	22.7 ± 1.3
Carapace length (mm)	18.9 ± 1.8	41.2 ± 1.5	42.2 ± 1.4
Propodus length (mm)	15.7 ± 2.9	56.7 ± 5.0	98.1 ± 7.1
Weight (gr)	5.6 ± 1.4	46.7 ± 5.0	60.0 ± 5.5

Table 2

Rank order, number of ties and circular triads, and the degree of linearity of the hierarchy (K) in eight test groups (A tie between two individuals is marked by - * -). BC - Blue Claw, OC - Orange Claw, SM - Small Males

Group no.	1	2	Rank				No. of circular triads	K
3	BC1	BC2	OC1	* OC2	SM1	SM2	1	0.97
4	BC1	BC2	OC1	OC2	* SM1	SM2		0.72
5	BC1	BC2	OC1	OC2	SM1	SM2		0.84
6	BC1	BC2	* OC1	OC2	SM1	SM2		0.97
7	BC1	BC2	OC1	OC2	SM1	* SM2		0.50
8	BC1	BC2	OC1	OC2	SM1	* SM2		0.28
9	BC1	BC2	OC1	OC2	* SM1	SM2		0.72
10	BC1	BC2	OC1	OC2	SM1	SM2		0.47

Table 3

Results of a three-way ANOVA of male morphotype (Morph), relative rank (Rank), and time (Day) on several behavioural variables.

ANF= Approach to non-frontal position. **APF**= Approach to frontal position.

CEX= Cheliped extending. **EMB**= Embrace. **LFT**= Lifting. **MVA**= Move away.

NIP= Nip. **TRF**= Turn to frontal position.

Variables	Source of variation			
	Morph	Rank	Day	
Interactions	***	ns	***	
Mobility	ns	ns	***	
Behavior:				
ANF	*		ns	ns - not significant
APF	***		ns	* - P<0.05
CEX	ns		ns	** - P<0.01
EMB	***		ns	*** - P<0.001
LFT	***		*	
MVA	***		**	
NIP	ns		ns	
TRF	***		ns	

Table 4

The percentage of the different intra and inter-morphotypic interactions in each of three successive days.

DYADS		Day 1		Day 2		Day 3	
		%	mean %	%	mean %	%	mean %
<u>Intra-morph.</u>							
	BC1xBC2	18.2		24.8		22.3	
	OC1xOC2	9.5		5.8		7.6	
	SM1xSM2	4.4		8.8		9.4	
<u>Inter-morph.</u>							
BCxOC	BC1xOC1	10.3		16.4		9.3	
	BC2xOC1	8.6	8.90	1.2	8.83	7.3	10.15
	BC1xOC2	9.2		14.2		17.0	
	BC2xOC2	7.5		3.6		7.0	
BCxSM	BC1xSM1	0.7		5.7		2.5	
	BC2xSM1	2.7	3.22	3.1	4.37	2.5	3.12
	BC1xSM2	4.6		3.0		6.2	
	BC2xSM2	4.9		5.7		1.3	
OCxSM	OC1xSM1	3.4		0.8		1.3	
	OC2xSM1	2.9	4.77	3.1	1.85	1.3	1.90
	OC1xSM2	4.4		3.5		2.5	
	OC2xSM2	8.4		0.0		2.5	

Table 5

The frequency of agonistic acts (per individual per interaction) by morphotype (Morph) and by day. **ANF**= Approach to non-frontal position. **APF**= Approach to frontal position. **CEX**= Cheliped extending. **EMB**= Embrace. **LFT**= Lifting. **MVA**= Move away. **NIP**= Nip. **TRF**= Turn to frontal position.

	MORPH			DAY		
	BC	OC	SM	1	2	3
ANF	0.02	0.10	0.02	0.04	0.07	0.03
APF	0.32	0.11	0.14	0.27	0.16	0.13
CEX	0.23	0.24	0.15	0.19	0.26	0.17
EMB	0.17	0.04	0.03	0.08	0.10	0.07
LFT	0.16	0.02	0.07	0.11	0.12	0.00
MVA	0.28	0.38	0.58	0.54	0.42	0.20
NIP	0.05	0.01	0.04	0.03	0.04	0.02
TRF	0.19	0.05	0.07	0.13	0.12	0.05

Fig 1.
Scheme of the arena used for hierarchy experiments

Fig. 2

Frequency of performance of agonistic acts by mixed groups of the three male morphotypes.

Fig. 3

The number of interactions per hour (on a logarithmic scale) for each morphotype across 3 days. Points sharing a common subscript are not significantly different (Duncan's Multiple Range Test, $P < 0.05$)

Fig. 4

The addresses of behaviour patterns among the six prawns of the three male morphotypes: BC - Blue Claw, OC - Orange Claw, SM - Small Males. The individuals are ordered by their rank (dominant on top). Values are mean number of addresses per 10 interactions in the direction of the arrow, and arrow width is proportional to this value.

ANF= Approach to non-frontal position. APF= Approach to frontal position. CEX= Cheliped extending. EMB= Embrace. LFT= Lifting. MVA= Move away. NIP= Nip. TRF= Turn to frontal position.

1.3: Effect of Size and Morphotype on Dominance Hierarchies in Mixed Groups of Blue and Orange Clawed Males of the Giant Freshwater Prawn Macrobrachium rosenbergii (Crustacea, Palaemonidae).

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ABSTRACT

The agonistic interactions among twelve groups, each composed of six Macrobrachium rosenbergii males, were studied in circular arenas over a period of three days. The effect of size and morphotype on dominance rank was studied with large, medium and small prawns of the BC and OC morphotypes. A linear dominance hierarchy was formed. BC males were ranked above OC males irrespective of size. Claw length seems to be the most important determinant of dominance in Macrobrachium rosenbergii. The largest BC, occupying the α -position in the male dominance hierarchy acquired more food and occupied more time a shelter than the rest of the males. The relevance of male dominance hierarchies to the understanding of the "leap frogging" growth pattern is discussed.

INTRODUCTION

Sexually mature populations of the giant freshwater prawn Macrobrachium rosenbergii are composed of females and three male morphotypes which differ in their morphology, physiology and behaviour (Telecky, 1984; Kuris et al. 1987; Sagi and Ra'anani, 1988.). Blue claw (BC) males are large to medium in size and possess long claws with a spinuous and often blue colored propodus. Orange clawed (OC) males are large to medium in size and possess medium sized claws with a non spinuous propodus often orange colored. Small males (SM) possess small delicate claws with a transparent or pink colored propodus.

Agonistic interactions among Macrobrachium rosenbergii male prawns were studied in the laboratory in groups of six individuals, two representing each morphotype. Males were organized in a linear dominance hierarchy, with the BC males ranked first and second, OC males were ranked third and fourth and the two lowest ranks were occupied by the SM males. Although matched in total length the tested BC and OC males differed markedly in claw length and consequently in their wet weight. (Barki et al. in prep. b.) One may generalize with regard to the inferior position of the SM due to its consistent small size relative to the other morphotypes. However, the situation is more complex with regard to the BC and OC males. These two morphotypes overlap over a wide size range (Karplus et al 1986)., and therefore their relative rank is uncertain.

The understanding of the dominance hierarchy among OC and BC males of different sizes is of particular interest due to the "leap frogging" growth pattern described in this species. This growth pattern was first suggested by Ra'anani and Cohen (1985), and later confirmed by bi-weekly monitoring of individually marked prawns in large cages (Karplus et al in prep.) According

to the "leap frogging" growth pattern the fast growing and short clawed OC metamorphoses into the slow growing and long clawed BC only when becoming larger than the largest BC in its vicinity.

The aim of this study was to analyze the effect of size and morphotype on male dominance rank. Emphasis was given to the formation of the hierarchies, the ranking of males, the variation in the performance of specific agonistic acts and their direction towards specific opponents. The relationship between dominance rank and priority of access to resources food, shelter and receptive females were investigated independently aiming to clarify the function of the "leap frogging" growth pattern.

MATERIALS AND METHODS

Prawn Collection and Maintenance

Prawns were collected during October 1986 from earthen ponds at the Dor, Fish and Aquaculture Research Station. Each prawn was maintained in a separate aquarium, isolated visually and tactilly but not chemically due to the sharing of the same recirculating water system. Details of the system for maintaining prawns as well as the feeds and feeding regime have been described in detail in a previous study (Barki et al. in prep. a.)

The Testing Arena

The study of the social interactions in groups of males were carried out in circular arenas (150 cm diameter). A detailed description of the arena, its protection from disturbances as well as the maintenance of water quality during the study have been described in detail in a previous study (Barki et al. in prep., b.)

The Tested Prawns

Out of thousands of harvested prawns, males of the OC and BC morphotype (Kuris et al. 1987) were carefully selected following the measurment of the total length. All tested prawns met the following criteria:

- a) Prawns were isolated at least two weeks prior to testing.
- b) Prawns were in stage C of the molt cycle.
- c) Prawns were intact, possessing all appendages and lacking any black or white spots, or coverage of the exoskeleton by algae.
- d) Every prawn was only tested once. Prawns were individually marked as described in detail in a previous study (Barki et al prep.a)

The Hierarchy Study

Each tested group consisted of six males. Large medium and small size were each represented by two prawns of each morphotype matched to size (Table 1). Observations were carried out during three successive days. Every day the behavior of four groups was monitored between 7:00 - 13:00. The manner the prawns were introduced into the arena via opaque cylinders, the sequence of monitoring their behavior with the aid of a JVC GX-N70E video camera following the focal animal procedure (Altman, 1974) have been described in detail in a previous study (Barki et al. in prep. b). As different from that study this time, the arena was covered with a net to prevent the prawns from jumping out of the water. 20 minutes before the monitoring of behavior the net was removed as well as the air stone and heater. A total of twelve

replicate groups were run.

Resource Competition.

Competition for resources was studied during three days in continuation to the three days of monitoring the social interaction among prawns. Competition for food, a receptive female and shelter were tested during half an hour. Competition for only one resource was tested per day and the order of testing was randomly determined following the casting of a dice.

About one hundred females were maintained in four large plastic containers (600 l.) to provide the receptive females necessary for our study. Receptive females were identified using the method described by Sagi and Ra'anan (1985). Into each container was introduced a large BC male with its gonopores plugged with a cyano-acrylic glue to prevent the extrusion of a spermatophore. This male is not able to fertilize females but on the other hand it protect them with its second large pair of claws. The receptive females in our study were selected on the basis of three criteria: a) being guarded by the male, b) the molt of the soft female is located in close proximity of the pair, c) the female possesses a fully developed gonad. Following half an hour of recording the response of the males to the receptive female, the female was removed and examined for the presence of spermatophores. In case no spermatophore was attached to the female's sternum, the female was re-examined for receptivity by introducing her to an isolated BC male.

Competition for food was tested among prawns starved for 48 hours. Penaeid shrimp feed pellets (40% protein) manufactured by Star (Taiwan) were used. 60 feed pellets were introduced into the arena with the aid of a small vessel attached to a long pole in order not to disturb the prawns. The pellets were placed within a distance of about 40 cm from the spot where most prawns concentrated.

Half a flower pot with its bottom removed served as a shelter. The shelter was introduced into the arena at a distance of about 40 cm from the spot where most prawns concentrated, within a 30 cm from the wall of the arena.

Competition for any resource was recorded on video by filming the resource and the area surrounding it during 1/2 hour since its presentation. Since there were no responses to shelters within this period of time observations were extended over a period of 4 hours. At 10 minutes intervals, the prawns occupying the shelter were recorded.

Data Analysis

Data were analyzed as described in detail in a previous study devoted to the dominance hierarchies of the three male morphotypes of Macrobrachium rosenbergii (Barki et al prep.b).

RESULTS

Rank in the Dominance Hierarchy

The ranking of the prawns within the male dominance hierarchy was carried out separately for the first day and jointly for the second and third day. Table No 2 summarizes the ranking of the prawns in all arenas. Not included in this analyses were arena 7 for the entire period and arena 3 + 4 for day two and three due to insufficient data which did not allow the ranking of prawns (missing of information concerning the relationship between more than four pairs).

There was a marked difference in the ranking of the prawns on day one as compared to day two and three. In only two groups (No 8 + No 11) was the ranking the same. Ranking on the first day was generally more variable. Only the position of the largest BC was already well established in 10 out of the 11 arenas. Concerning the morphotype there was some tendency for the occurrence of the BC morphotype above the OC (in 8 groups of 11 a BC was ranked second and in 7 groups out of 11 as third). The effect of size was less pronounced except to the fact, that the largest BC occupied the α -position. The largest OC was ranked in 7 out of 11 groups before the medium and small ones. However, the medium and small prawns of both morphotypes were ranked a similar number of times one before the other.

The ranking of the prawns on day two and three was more consistent in the different arenas. In all groups where individuals were ranked (9 groups) the largest BC occupied the α -position. Concerning the morphotype, the BC was consistently dominant over the OC, occupying number two position in all arenas and in 8 out of 9 arenas also rank number three. Concerning the effect of size in the BC morphotype, the largest BC was indeed ranked before the medium and the small, however the smallest BC was unexpectedly ranked in 7 out of 9 arenas before the medium one. In the OC morphotype the effect of size was more consistent. In 7 out of 9 arenas the large OC was ranked before the medium and small ones and similarly the medium OC was ranked before the small OC as number five.

The greater consistency in the rank of the prawns on day two and three VS. day one, could be evaluated by contrasting the standard deviation of the rank (Barlow and Balin, 1976) at these two time intervals. (Fig. 1) In all ranks the variability was higher on day one as compared to day two and three which reflects the stabilizitation of the dominance hierarchy. The fact that the lowest variability was found for the largest BC on both time intervals reflects the early establishment of the α -position relative to the rest.

On the basis of the ranking of the prawns in all arenas during day two and three which reflects a more stable hierarchy one may generalize that ranking of prawns differing in size and morphotype follows the order: LBC > SBC > MBC > SOC > MOC > SOC.

Differences in the rank of individuals in the prawn dominance hierarchy on day one VS. day two and three were also evident from the number of circular relationships and number of equality of ranks (Table 2) which except to one case all occurred on day one. These differences are also reflected in the K index of linearity. This index was in all groups, except to one higher on day two and three as compared to day one. In only 3 out of 9 groups (27%) its value on day one was higher than 0.9, the critical value for linearity to be considered strong (Chase, 1974). In 7 out of 9 groups (78%) on day two and three the index of linearity was higher than 0.9 out of which 4 arenas actually attained significance ($P < 0.05$) of linearity (Table 18).

Variation in Agonistic Behavior

The effect of three major variables, morphotype, size and time on prawn agonistic behavior was investigated. 11 components of the agonistic behavior were examined with a three way ANOVA. These components included the number of agonistic interactions, prawn mobility and 9 behavioral acts each of which comprised more than 3% of the total number of recorded acts (Fig. 2). Table No 3 + 4 presents the results of the analyses. Only the

interaction between morphotype and size was presented in Table 4 since all other interactions were found to be non significant.

The Number of Agonistic Acts and Mobility

There was a significant difference in prawn mobility among days ($P < 0.001$). Prawn mobility was higher on day one as compared to the other days. No significant difference in mobility was found among the different tested individuals (Table 4). Since prawns moving around have a higher chance to interact the number of agonistic interactions among days were compared following the application of an analysis of covariance to rule out a possible bias due to differences in prawn mobility (the covariate). Following this adjustment the number of agonistic interactions was still much higher on day one as compared to the second and third days which did not differ between themselves. A significant difference in number of agonistic interactions was found among morphotypes and in the interaction between morphotype and size. This resulted from the much higher number of agonistic interactions involving the BC as compared to all the rest of the prawns (Fig.3).

Table No 5. summarizes the mean percentage of the agonistic interactions between specific prawns out of the total number of interactions. There was a tendency towards more inter-morphotype interactions in the BC morphotype during each of the three days. There was no consistent tendency within this morphotype for interaction involving certain sizes. However, in the OC morphotype, more interactions were recorded between the small and medium sized prawns as compared to interaction involving the large orange claw male.

Variation in Agonistic Acts

The frequency of the different agonistic acts are presented in Fig. 2. There was a relative high frequency of acts which did not involve physical contact. The effect of morphotype, size and day and their interaction on the agonistic acts were analyzed with a three way ANOVA (Table 3+4).

Significant differences among days were obtained only for approach to frontal position - APF ($P < 0.001$), move away - MVA ($P < 0.005$) and push - PSH ($P < 0.01$). In all these comparisons a higher value was obtained on day one as compared to the second and third day.

The effects of morphotype and size were more pronounced than that of time. As expected, acts that differed between morphotypes and characterized a dominant individual (TRF, PSH, NIP, EMB and APF) occurred at a higher frequency in the BC morphotype and those that characterize a submissive individual - MVA occurred more often in the OC (Table 3). LFT which does not characterize neither dominant nor submissive individuals were performed more often by the BC. Concerning the effect of size, those acts which characterize dominance (PSH NIP and APF) were more frequently displayed by large individuals while those that characterize subordination (ANF and MVA) were less frequent displayed by it as well as LFT. For three acts MVA, NIP and PSH a significant interaction between morphotype and size was found. NIP was displayed at a much higher frequency by the large BC compared to all the rest of the prawns which did not differ among themselves (Fig. 4). The differences in the performance of the acts MVA and PSH by the different prawns were gradual, reflecting their relative rank (Fig. 4)

The Direction of Agonistic Acts

Analysis of the number of acts performed by the different prawns ignored the important question to which individual they were directed. This analysis were carried out in detail separately for day one and day two and three for four acts which represent different categories of acts. (Fig.5).

Move away (MVA), a typical submissive act was directed most commonly towards higher ranking individuals in a similar pattern on day one and day two and three. The acts NIP and EMB typical for a dominant individual were on both days mainly directed towards lower ranking. NIP which was directed by the large BC on day one mainly to the subdominant small BC was directed on day two and three often towards lower ranking individuals of the orange morphotype. The act LFT which was more often recorded for the BC morphotype was performed mostly in intra-morphotypic interactions with no marked differences between days (Fig. 5). The large BC did not often direct this act towards the OC males. However the medium and small BC engaged more often in such activities. This phenomenon is also evident from the incidents of simultaneous display of LFT by both interacting prawns (Table 6). Out of 12 cases of simultaneous inter-morphotype display of LFT the large BC was involved only in one case.

Competition for Resources

Food: Competition for food among prawns starved for 48 hours, was relative to other resources, rapid and intense. Mean time for the first prawn to start feeding since the introduction of food was 2.5 min. and that was also the mean time for the consumption of all the food. Table No 7 presents the mean time spent in proximity of the food and mean number of pellets consumed by each prawn. In two out of the twelve trials there was no response towards the food within half an hour since its introduction. The large BC consumed at least three times more pellets than any other prawn, it also spent at least twice as much time in proximity of the food. These differences were significant ($P < 0.05$). The rest of the prawns did not differ among themselves with regard to these aspects. All interactions in proximity of the food within a single square (40x40cm) marked on the arena floor were recorded and pooled due to their low number. The loser of an interaction was considered the individual which moved for at least one body length away from its opponent (Table 8). The superiority of the large BC was very pronounced. This individual was involved in 61% of all agonistic interactions and it won 96% of all those that it was involved in.

Receptive Females: In eight out of the twelve trials the female was fertilized. The following prawns mated with the female: large BC - twice, large OC - once, Medium OC - three times and small OC - twice. There was no correlation between rank of the prawn and its success in fertilizing females in our arenas. The space around the female and the agonistic interactions among males were defined as in the section dealing with competition for food. A total of twelve agonistic interactions were recorded. In nine was the large BC involved and it won eight of them. Many more agonistic acts were observed with the introduction of the female among males that were not in her close proximity and were therefore not recorded by the video camera.

Shelter: Entrance into the shelter was not recorded within half an hour of its introduction which occasionally caused the

withdrawal of the prawns. In 7 out of the twelve arenas was the shelter occupied at least for some time within a four hour period since its introduction. The number of arenas where a specific prawn was recorded within the shelter during a 4 hour period is presented in Table 9. There was a tendency to record more individuals in the shelter with time, this was particularly marked between the first and second hour. Most often was the large BC observed in the shelter. The two lowest ranking prawns the Medium OC and small OC were not observed even once in the shelter.

DISCUSSION

The Formation of the Dominance Hierarchy

Analysis of the agonistic interactions in groups of male prawns over a period of three consequential days allowed the understanding of the formation of dominance hierarchies. The difference in the number of agonistic interactions and frequency of specific acts changed from day one to day two and three which did not differ between themselves in these respects. Thus already following the first day the dominance hierarchy has undergone changes not occurring between day two and three which reflect increased stability. Similar results were also obtained from the higher level of linearity attained on day two and three and the lower standard deviation of the prawn's ranking at these time intervals.

One of the earliest phases in the formation of the male prawn dominance hierarchy involved the establishment of the α position. This position occupied by the largest BC was already well established on day one and changed relatively little on subsequent days. In dominance hierarchies of the despot type this is probably the end of the process of the hierarchy formation. In hierarchies of the linear type like in the freshwater prawns the establishment of the α position is only the first simple and straight forward step to be followed by the more complex grading of the rest of the prawns.

The formation of dominance hierarchies was described in several other species of decapods including Homarus americanus (Jacobson, 1977; Sastry and Ehinger, 1980), Cambarellus shufelditi (Lowe, 1956) and Orconectes virilis (Bovbjerg, 1953, 1956). Although the linearity of the hierarchies was not calculated in these species the establishment of the hierarchies was also found to occur within a relative short time interval reflected in a reduction in the number of agonistic interactions and their intensity. Also in these studies the α position of the hierarchy was the first to be established.

The Determinant of Dominance

Size in crustaceans appears to be a consistent predictor of contest victory and of superior hierarchial position (Hyatt, 1983). The effect of size on dominance rank was found both in species lacking claws (Fielder, 1965) and those possessing developed claws (Bovbjerg, 1953, 1956; Lowe 1956; Lee and Fielder 1983). As different from the above species where claw and body size were correlated, in large Macrobrachium rosenbergii due to the existence of orange and blue clawed males, claw and body size are not necessarily matched. The BC males in our study were always ranked above the OC in the male hierarchy. Even the smallest of the BC males which was by far inferior to the OC with regard to wet weight possessed a claw that was longer than that

of OC. In some cases a 10% advantage in claw length overid a 70% disadvantage in wet weight, thus it seems that claw length and not wet weight is the most important determinant of dominance in Macrobrachium rosenbergii. Agonistic encounters between BC and OC males with the latter having a longer claw would be instructive to whether it was the longer claw in our study that determined the higher rank of the BC males or there are some other non morphological traits which contributes to the superior hierarchial position of the BC morphotype.

Size is expected to be the major determinant of rank among M. rosenbergii of the same morphotype since within each morphotype body and claw size are correlated. Male dominance rank within the OC morphotype fully followed these expectations, but only partly in the BC morphotype. The largest BC occupied the α position but the smallest BC occupied consistently a higher rank than the medium sized one. We have no, explanation to this result.

The Advantage of beeing Dominant

The advantage of the α - male in the prawn dominance hierarchy with regard to priority to limited resources was most evident with respect to food acquisition (i.e.-food pellets). In the natural habitat it is likely that the α -male defends from its conspecifics with equal success a limited and concentrated resource like a dead fish.

Priority in shelter occupation and successful eviction of intruders was also found for the α -male. However, the attraction towards a shelter occurred only following a period of partial withdrawel of the prawns from the relative large and newly introduced flower pot. Our results on competition among groups of males over a shelter confirm earlier findings on competition between pairs of prawns over a shelter carried out by Peebls (1979 b) who demonstrated the importance of size which overuled with time the advantage of prior shelter occupation.

As different from the priority of accesss to food and shelter the α -male did not show any advantage with regard to fertilization of receptive females. The guarding of the receptive female prior to her pre-mating molt by the BC male has been described (Rao,1965; Telecky,1984; Sagi and Ra'anani 1985). The active selection of the BC male by the female prawn (prior to the pre-mating molt) when simultaenously presented with the three male morphotype has been documented (Frankfurt, S.pers comm). The artificial situation of a receptive female (following the pre-mating molt), moving freely around in an arena with several sexually mature males (due to removal from her guarding male) possibly underlies the lack of a correlation between male dominance rank and reproductive success. Probably female choice prior to the pre-mating molt plays also an important role in the reproductive success of the α male.

"Leap-frogging" growth pattern and male dominance hierarchies

A "leap-frogging" growth pattern for the transition from the OC male morphotype to the BC morphotype of Macrobrachium rosenbergii was suggested on the basis of differential epibiont coverage (Ra'anani and Cohen, 1985). According to this hypothesis, the short-clawed OC metamorphoses into the long-clawed BC only after becoming larger than the largest BC in its vicinity. This results in a series of differently sized BC males, who's size is negatively correlated with the time of their metamorphosis. Bi-weekly recording of size and morphotype of individually marked M. rosenbergii raised in large communal cages, confirmed the "leap-

frogging" hypothesis. This growth pattern is achieved mainly through a delay in the transition from the fast-growing OC morphotype into the slow-growing BC one. This delay may be due to social interactions among males as it was not observed in males isolated in small cages (Karplus et al. In prep.). The understanding of the social organization of groups of males of the OC and BC morphotype can provide some insight into the function of the "leap-frogging" growth pattern. The prawn that reaches the BC morphotype while being larger than any other BC in its vicinity following the "leap-frogging" growth pattern, obtained for at least some time the α position in the male dominance hierarchy with priority of access to limited resources.

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Table 1

Means and standard deviations of several morphometric parameters of the Orange Claw and Blue Claw males included in this study. OC - Orange Claw, BC - Blue Claw

	SMALL		MEDIUM		LARGE	
	OC	BC	OC	BC	OC	BC
Total length (cm)	10.8±0.3	10.6±0.3	11.7±0.2	11.8±0.2	13.0±0.3	13.0±0.2
Carapace length (mm)	36.4±1.1	37.1±1.2	40.1±1.1	42.1±1.3	46.1±1.4	46.8±1.0
Cheliped length (cm)	11.3±0.8	19.2±1.1	14.0±1.0	21.8±1.2	16.5±0.8	25.7±0.9
Propodus length (mm)	44.4±4.0	82.2±4.3	59.2±4.7	94.9±6.9	70.2±3.5	112.1±4.4
Weight (gr)	32.3±2.7	40.7±4.1	44.4±3.0	56.7±4.6	64.4±5.3	81.4±3.3

Table 2

Rank order, number of ties and circular triads, the degree of linearity of the hierarchy (K), and the significance of linearity (P) in twelve test groups (a tie between two individuals is marked by - * -).

Group #	RANK ORDER												NO. OF		INDEX OF		P	
	day 1						day 2+3						CIRCULAR TRIADS		LINEARITY - K		P	
	6	5	4	3	2	1	6	5	4	3	2	1	day 1	day 2+3	day 1	day 2+3	day 1	day 2+3
1	SOC	LOC	SBC	MBC	LOC	LBC	SOC	MOC	LOC	SBC	MBC	LBC			0.62	1	>>0.1	<0.05
2	SBC*	SOC	LBC	MBC	MOC	LOC	SOC	MOC	LOC	MBC	SBC	LBC		1	0.69	0.50	>0.1	>>0.1
3	SOC	SBC	LOC	MOC	MBC	LBC							1		0.66	--	>>0.1	--
4	MBC	SBC	LOC	MOC	LOC	LBC							1		0.16	--	>>0.1	--
5	MOC	SOC	LOC*	SBC	MBC	LBC	SOC	MOC	LOC	MBC	SBC	LBC			0.60	0.91	>>0.1	0.051
6	SOC	MOC	MBC	LOC	SBC*	LBC	SOC	MOC	LOC	MBC	SBC	LBC	1		0.69	0.84	>0.1	>0.1
8	SOC*	LOC	MOC	SBC*	MBC	LBC	LOC	SOC	MOC	MBC	SBC	LBC			0.94	1	0.051	<0.05
9	MOC	LOC	SOC	MBC	SBC	LBC	LOC	SOC	MOC	MBC	SBC	LBC	1		0.48	0.91	>>0.1	0.051
10	MOC	LOC*	MBC	SOC	SBC	LBC	MOC	SOC	LOC	MBC	SBC	LBC			0.91	1	0.051	<0.05
11	MOC	SOC	LOC	MBC	SBC	LBC	MOC	SOC	LOC	MBC	SBC	LBC	1		0.41	0.91	>>0.1	0.051
12	MOC	SOC*	LOC	SBC	MBC	LBC	SOC	MOC	SBC	LOC	MBC	LBC			0.97	1	0.051	<0.05

LBC- Large BC LOC- Large OC
MBC- Medium BC MOC- Medium OC
SBC- Small BC SOC- Small OC

Table 3

The frequency of acts (per individual per interaction) performed by Macrobrachium rosenbergii males of the Blue and Orange Claw morphotypes according to day, size and morphotype.

ANF= Approach to non-frontal position. **APF**= Approach to frontal position.
CEX= Cheliped extending. **EMB**= Embrace. **LFT**= Lifting. **MVA**= Move away. **NIP**=
Nip. **PSH**= Push. **TRF**= Turn to frontal position.

	DAY			SIZE			MORPH	
	1	2	3	Large	Medium	Small	BC	OC
ANF	0.06	0.06	0.04	0.03	0.06	0.07	0.05	0.05
APF	0.20	0.08	0.11	0.16	0.13	0.11	0.18	0.08
CEX	0.27	0.28	0.30	0.32	0.29	0.24	0.29	0.28
EMB	0.09	0.15	0.13	0.15	0.13	0.10	0.20	0.05
LFT	0.08	0.05	0.08	0.04	0.08	0.09	0.10	0.04
MVA	0.40	0.29	0.33	0.20	0.39	0.43	0.22	0.47
NIP	0.04	0.03	0.04	0.06	0.02	0.02	0.05	0.02
PSH	0.05	0.02	0.02	0.05	0.01	0.02	0.05	0.01
TRF	0.10	0.11	0.08	0.11	0.09	0.08	0.14	0.05

Table 4

Results of a three way ANOVA testing the effect of morphotype (Morph), size, day and interaction between morphotype and size, on several behavioural variables of Macrobrachium rosenbergii males of the Blue and Orange Claw morphotypes (abbreviations as in Table 3)

Variables	Source of variation			
	Morph	Size	Day	Morph-Size
Interactions	*	ns	**	*
Mobility	ns	ns	***	ns
ACTS :				
ANF	ns	*	ns	ns
APF	***	*	***	ns
CEX	ns	ns	ns	ns
EMB	***	ns	ns	ns
LFT	***	*	ns	ns
MVA	***	***	*	***
NIP	**	**	ns	***
PSH	***	*	**	*
TRF	***	ns	ns	ns

ns - not significant

* - $P < 0.05$

** - $P < 0.01$

*** - $P < 0.001$

Table 5

The percentage of the different intra and inter-morphotypic interactions in each of the three days. (abbreviations as in Table 2)

DYADS		Day 1		Day 2		Day 3	
		%	mean %	%	mean %	%	mean %
<u>Intra-morph.</u>							
BC	LBCxMBC	7.3		8.5		14.7	
	LBCxSBC	11.5	8.63	7.2	8.35	8.8	10.13
	MBCxSBC	7.1		9.3		6.9	
OC	LOCxMOC	5.5		4.3		3.4	
	LOCxSOC	5.4	6.37	6.3	6.91	3.7	4.93
	MOCxSOC	8.2		10.2		7.7	
<u>Inter-morph.</u>							
	LBCxLOC	9.8		6.1		8.9	
	MBCxLOC	4.9		4.1		5.8	
	SBCxLOC	5.2		5.1		5.5	
	LBCxMOC	5.7		8.2		5.6	
	MBCxMOC	3.9	6.11	7.2	6.02	4.7	6.09
	SBCxMOC	4.8		6.9		4.2	
	LBCxSOC	8.1		7.7		7.7	
	MBCxSOC	5.7		3.6		5.2	
	SBCxSOC	6.8		5.3		7.2	

Table 6.

Number of interactions with simultaneous performance of "Lifting" by two contesting prawns. (abbreviations as in Table 2)

	SBC	MBC	LOC	MOC	SOC
LBC	21	22	0	0	1
SBC		5	3	0	0
MBC			3	4	1
LOC				2	1
MOC					8

Table 7.

Mean time spent in proximity of food and amount of food ingested by prawns. (abbreviations as in Table 2)

	LBC		MBC		SBC		LOC		MOC		SOC	
	$\bar{x}$	s.d	$\bar{x}$	s.d	$\bar{x}$	s.d	$\bar{x}$	s.d	$\bar{x}$	s.d	$\bar{x}$	s.d
No. of pellets (n=8)	34.9±16.8		9.9±14.9		3.0± 5.4		4.7±4.0		5.9± 5.3		9.4±10.0	
Time (sec) (n=10)	71.1±44.4		28.7±49.2		17.9±30.4		9.8±9.6		12.5±10.9		13.4±14.3	

Table 8.

Dominance matrix of male prawns based on agonistic interactions during competition over food. (abbreviations as in Table 2)

		Loser							
		LBC	SBC	MBC	LOC	MOC	SOC	wins	losses
Winner	LBC	--	6	12	6	11	10	45	2
	SBC	1	--	4		1	2	8	8
	MBC		1	--	1	5	3	10	16
	LOC	1			--	3	2	6	8
	MOC				1	--	5	6	21
	SOC		1			1	--	2	22

Table 9.

Number of groups where different prawns were observed inside the shelter in each of the four hours of observation (abbreviations as in Table 2).

	LBC	MBC	SBC	LOC	MOC	SOC	Total
hour I	1	1					2
hour II	2	2	1	1			6
hour III	3	1	1	1			6
hour IV	5	1	1				7
Total	11	5	3	2	0	0

Fig. 1. The standard deviation of the dominance rank of Macrobrachium rosenbergii males during day one and day two and three.

LBC- large blue claw LOC- large orange claw
MBC- medium blue claw MOC- medium orange claw
SBC- small blue claw SOC- small orange claw

Fig. 2.
Frequency of agonistic acts performed by groups of Macrobrachium rosenbergii males of the orange and blue clawed morphotype.

Fig. 3. Mean number of agonistic interactions per hour performed by Macrobrachium rosenbergii males of the orange and blue clawed morphotype. Prawns sharing common superscript are not significantly different (Duncan's Multiple Range Test, $P < 0.05$). Abbreviations as in Fig. 1.

Fig. 4. The frequency per interaction of performance of agonistic acts by Macrobrachium rosenbergii males of the blue and orange clawed morphotype. Prawns sharing a common superscript are not significantly different. (Duncan's Multiple Range Test, $P < 0.05$). Abbreviations as in Fig. 1.

day 1

- 69 -

day 2+3

Fig. 5. The addressing of agonistic acts towards specific individuals by *Macrobrachium rosenbergii* males of the orange and blue clawed morphotype during day one and day two and three. The six prawns composing each group are presented according to their rank in the male dominance hierarchy. The numbers and thickness of the arrow represent the mean value per ten interactions (abbreviations as in Fig.1.).

1.4: Preliminary observations on behavioral interactions and distribution patterns of freshwater prawns Macrobrachium rosenbergii under seminatural conditions.

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ABSTRACT

The distribution and social interactions of a small, individually marked, all-male group of Macrobrachium rosenbergii prawns were studied. A round shape earthen pond, with an observation tower located at its center, was constructed for this purpose. The single most important environmental cue affecting prawn distribution was the level of illumination. Prawns, all in the intermolt stage, exhibited a tendency to cluster together within a limited space. The prawns did not exhibit territoriality, as evident from the lack of exclusion of other individuals from within fixed areas. Aggressive interactions were brief and of low intensity, reflecting a stable dominance hierarchy.

INTRODUCTION

Macrobrachium rosenbergii is a large clawed fresh water prawn. The major distribution areas of this crustacean are the lakes and river systems of South East Asia (Ling, 1969). Research on it's biology in the natural habitat has relied mainly on information gathered from the fisheries industry (Raman, 1966; Rao, 1967).

Our knowledge of M. rosenbergii's social behavior is very limited. The first descriptions of prawn behavior were given by Ling & Merican (1961) and Ling (1969), and were of a general descriptive character. Rao (1965) provided a description of the behavioral interactions between males and females prior to and during mating. A general account of aggressive group interactions was given by Segal & Roe (1975). In a later study Peebles (1979b) provided the only quantitative study of aggressive interactions for this species, demonstrating that relative size, prior residence and length of time rivals had been paired, play important roles in the outcome of a contest. Other studies were devoted to particular aspects of prawn behavior such as shelter occupancy (Smith & Sandifer, 1979) and response to food stimuli (Moller, 1978; Harpaz et al. 1987). All these behavioral studies were carried out in the laboratory, while prawns were kept in aquaria/containers. The social interactions of this relatively large prawn are rather difficult to interpret since the behavior might be strongly influenced by the restricting laboratory conditions.

One of the only attempts to reveal the behavioral patterns of M. rosenbergii under "field" conditions was carried out by Peebles (1979a) who utilized densely populated commercial ponds. In his study, Peebles made use of rather heavy radio tagging devices weighing around 10 gms that were attached to the prawn's back. In the present study, in order to prevent possible restrictions to the prawn's movements, only small light plastic tags were stuck to the prawn's back. The specific molt stage which is occupied by each prawn is of utmost importance to its

behavioral performance (Peebles, 1978; Harpaz et al., 1987). Therefore all prawns selected for the experimental observations were in the intermolt phase.

Under natural conditions, during certain seasons of the year the mature females migrate to the estuaries leaving the "stage" to the males alone (Raman, 1966). Females were, therefore, not introduced to the experimental pond since we were interested in establishing a male behavioral base line to which, at a later stage, one could compare behavioral interactions evoked by the presence of females.

The aim of the present study was to elucidate the relationship between prawn distribution and the behavioral mechanisms governing it, under "field" conditions. Hence the use of a specially designed observation pond, which enabled us to closely follow the non constrained behavioral interactions taking place among the prawns in a large area under semi-natural conditions.

MATERIALS AND METHODS

Animals

Twenty seven adult Macrobrachium rosenbergii male prawns were used in this study. Each prawn was carefully measured. Carapace and propodus lengths and weights are listed in Table 1. Male prawns were selected from a population reared in a production pond and classified into three distinct morphotypes. For a complete description of the various morphotypes see Kuris et al. (1987). Seven Blue Clawed (BC), ten Orange Clawed (OC) and ten Small Males (SM) were used. All the prawns were in stage C (intermolt) of the molt cycle. Molt staging was done according to Peebles (1977). The experimental prawns were each individually marked using the following method: The carapace was thoroughly dried and small thin flexible strips (2 cm X 0.4 cm) of white or yellow plastic were adhered to the dorsal side of the carapace with the aid of the fast drying LOCTITE super glue-3. One to five white strips represented animals # 1 to #5, while one to five yellow strips represented animals #6 to #10. Preliminary tests showed that the strips did not fall off during prolonged contact with water, nor were the prawns able to "clean them off". They were clearly visible and distinguishable in the water even when the prawns occupied the deepest area of the pond.

Pond and Observation Tower

An earthen round pond (12m diameter) was constructed. Water depth was 1 m in the center and tapered off towards the banks which were fortified with rocks and pebbles (Fig 1). A criss-cross network of black nylon strings was pulled above the water level, at 1 m spacing thus forming an easily visible grid of 1m² squares identifiable by numbers and alphabetical letters placed on the pond banks.

A metal observation tower was erected from the center of the pond extending to a height of 3 m above the water level. The base of the tower was anchored in concrete. A steady bridge stretching above the water across from the bank enabled easy access to the observation platform.

The pond was filled with well water. Water temperature was 23±2 °C. Simazin (at 0.5 gr/m³) was applied in order to reduce unicellular algal growth. Prawns were introduced 2 days later and allowed to "settle in" for 3 days. One day prior to the beginning of the observation period, the prawns were fed, and about two thirds of the water volume was emptied and replaced with fresh

well water. This was done after the pond water was observed to be in the initial stages of turning green/murky, in order to obtain water clarity throughout the observation period.

Experimental protocol

Observations began a short while after dawn (when prawns were clearly visible and distinguishable) and were carried out by two independent observers. One recorded the exact location of all visible prawns every 10 mins. The second observer, with the aid of binoculars and a tape recorder, continuously noted agonistic encounters taking place, their exact location, time and sequence of acts involved. This procedure was carried out throughout the light hours of the day until close to dusk, when the animals were no longer identifiable. The results presented are based on a total of 122 location observations carried out in the above described manner, during two sessions in October.

The following agonistic acts were recorded during the course of this study: "Approach"- movement of one prawn towards another within the range of one body length. "Rush" - a rapid movement towards the opponent. "Extend"- cheliped extending towards the opponent without physical contact. "Push"- pushing motion performed with the aid of the claws. "Embrace"- using both chelipeds in order to embrace the opponent prawn. "Nip"-the closing of the dactylus on the body or appendage of another prawn. "Retreat"- movement of one prawn away from another within the range of one body length. The description of the agonistic acts is based on that of Peebles (1979b) and Barki (1989).

RESULTS

Of the total number of prawns introduced into the experimental observation pond only 50% were actually spotted during the course of the observation period. At any given time approximately six or seven were roaming around. The frequency at which each prawn was spotted throughout the observation period is presented in Table 1. A larger number of prawns was observed during early morning and towards sun set in comparison with noon time. Some of the "missing" prawns were seen entering crevices in the rocky banks or burrows at the base of the observation tower.

The prawns preferred the shaded areas of the pond, and adjusted their position according to the sun's position (see Fig 2). The point at which the sand reached the rocks comprising the tower base, was preferred over the sandy area of the pond. Animals were very rarely seen to occupy the shallow rocky periphery of the pond. The prawns spent roughly 90% of the time in the area surrounding the tower base which comprised only 10% of the pond area available to them. Both BC and OC morphotypes did not exhibit particular preference within the limited occupied area. Only 2 of the small males participating in this experiment were spotted during the entire observation period. Furthermore, these prawns were seen mainly in the rocky shallow water region of the pond.

The number of prawns co-occupying the same 1 m² areas was higher than the values expected while assuming random distribution (Fig. 3). This behavior was especially pronounced around noon time. In order to analyse the distribution pattern of individual prawns we recorded the incidences of co-occupation of the same square by the 5 prawns predominantly spotted throughout the experimental observation period (Table 2). Four prawns (OC₁, OC₉, OC₅ and BC₂) behaved similarly with regard to

co-occupation of the same square with other prawns, and differed from BC₁ with which the same square was less often shared (see appendix 1). The experimental prawns were actually clustered together in a relatively small patch within the 12m square area occupied by them. This is in spite of the fact that the total preferred (shaded) area available to them was much larger. Prawns were often seen sitting in a position in which one prawn's claws were resting on top of another's back for long periods at a time.

Agonistic interactions between prawns were brief, usually consisting of a single aggressive act performed by one prawn (82.9%) followed by the retreat of the opponent. Only one sixth of the total 158 agonistic encounters observed, consisted of 2-3 aggressive acts of both participants. The most common aggressive act was the "approach" of one prawn to another (72.2% out of 176 aggressive acts). The second most common was "push" (14.2%) followed by "extend" (7.4%). The rest of the aggressive acts namely "embrace", "nip" and "rush" were all rare comprising less than 3% of the recorded acts.

The supplanting of one individual (loser) by another (winner) was selected as a criterion for the construction of a dominance matrix, since the overwhelming majority of all encounters were terminated with the retreat of one prawn. The dominance hierarchy of the five predominantly appearing prawns is presented in Table 3. A clear dominance pattern is evident in which blue clawed males are positioned above orange clawed ones. The percentage of aggressive encounters initiated by a specific prawn was correlated with its rank. The highest ranking prawn (BC₂) initiated 41.4% of all aggressive interactions, followed by 28.3% of the second ranking (BC₁), 18.4% by OC₁, 7.9% by OC₂ and 3.9% by OC₃.

The majority (60%) of all aggressive interactions occurred during the early hours of the day, at the western shaded side of the tower base. Interactions took place when prawns moved towards those areas, or rearranged their position. Similar position changes, in accordance with the shaded areas during noon and afternoon involved fewer aggressive interactions (21.5%).

DISCUSSION

A single most important environmental cue affecting prawn spatial distribution in our study was the level of illumination. Throughout the day prawns rearranged their position closely following the shaded areas of the clear-water pond. A similar result- preference of dimly illuminated areas was obtained in a laboratory study with juvenile Macrobrachium rosenbergii (Smith & Sandifer 1979). This phototactic negative response is in accordance with the nocturnal nature of M. rosenbergii (Nakamura, 1975). Levels of light intensity were also found to affect the general motor activity since prawns were more active at sunset and again early in the morning. This confirms earlier findings in this species observed in ponds (Peebles, 1979a) as well as in laboratory studies (Nakamura, 1975). The transparent pond provides an excellent opportunity to clearly observe individually marked prawns and monitor their social behavior. However, one must bear in mind the fact that the high level of illumination does not necessarily resemble natural conditions, and greatly influences the spatial distribution of the prawns in the pond.

Prawns in our study did not exhibit territoriality when a territory is defined as a "fixed exclusive area with the presence

of defence that keeps out rivals" (Brown & Orians, 1970). In the present study male prawns were often clustered together sharing the same area. Aggressive interactions were carried out not in order to exclude individuals from within a certain fixed area, but rather when individuals approached each other to within close range. Occasionally aggressive interactions took place in order to gain access to preferred areas. As soon as the previous area holder was supplanted, all aggressive interactions ceased. A dominance hierarchy seems to regulate the priority of access to preferred areas in our small group of Macrobrachium rosenbergii males overlapping in their distribution. The fact that a single aggressive act of low intensity (i.e. approaching) was mostly involved in agonistic interactions, and that the encounters overwhelmingly led to the immediate supplanting, are both indicative of the stability of this hierarchy. However, the intensity of aggressive interactions also reflects the value of the contested resource. Introduction of receptive female or food, after a period of starvation would probably raise the level of agonistic interactions as compared to that witnessed when prawns contest over a preferred area near a rock.

The prawn morphotype seemed to affect its position in the male dominance hierarchy. Blue clawed males were positioned above orange clawed males irrespective of their size. Although the results are based on a single group of prawns they are in accord with a large multi replicate laboratory study. In this laboratory study the position of a prawn in the dominance hierarchy within each morphotype was largely based on its size (Barki 1989). The results of the pond study are less conclusive in this regard probably due to the fact that the largest blue-clawed prawn participating in the study had one claw shorter than the other, as well as an incomplete dactylus. This prawn was positioned below a smaller blue clawed male in which both claws were complete and equal.

The transparent pond with its observation tower and individually marked prawns provided us with a tool to investigate prawn social behavior under semi-natural conditions alleviating the constraints encountered in the aquaria.

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APPENDIX

Statistical analysis of spatial prawn distribution

The number of concurrences i.e. the number of times each pair of prawns occurred together in a given square out of the 122 observations was analysed using "likelihood ratio tests" (Kendall & Stuart 1961).

Three models were specified concerning probabilities P_{ij} of concurrences of the prawn pairs i and j $i \neq j = 1, 2, \dots, 5$.

1. The general model M_3 : $P_{ij} = p_i p_j$ $i \neq j = 1, 2, \dots, 5$.
2. The two valued model M_2 : $P_{ij} = \begin{cases} p_1 p_2 & \text{for } i=1 \text{ } j=2, 3, 4, 5 \\ p_2 p_2 & \text{for } i \neq j = 2, 3, 4, 5. \end{cases}$

where prawn number 1 is BC_1 .

3. The one valued model M_1 : $P_{ij} = p_0^2$ $i \neq j = 1, 2, \dots, 5$.

The likelihoods were maximized given the data of Table 2 under each of the three models giving L_3, L_2 and L_1 respectively, using an iterative procedure. Model M_2 was tested against M_1 by the asymptotic test of $-2\log(L_2/L_1)$ and found highly significant ($P < 0.001$). This means that the data indicates that BC_1 has significantly less inclination to concurrence than the other prawns.

Model M_3 was also tested against M_2 and found that it does not give significant improvement beyond that of M_2 . Thus, the hypothesis of no difference between BC_2, OC_1, OC_3 and OC_5 in their probability of concurrence can be accepted.

Table 1

Description of Macrobrachium rosenbergii males stocked in the experimental pond.

Morphotype	Carpace (mm)	Propodus (mm)	Weight (gms)	% Observed
BC 1	51.3	113.3	84.7	100.0
BC 2	44.4	93.6	65.3	100.0
BC 3	40.6	70.0	49.3	0
BC 4	38.2	81.3	46.0	6.7
BC 5	32.3	62.1	26.5	0
BC 6	31.3	68.0	25.4	0
BC 7	29.8	69.8	22.9	2.5
OC 1	49.3	61.3	75.8	100.0
OC 2	45.6	67.4	62.8	0
OC 3	43.7	63.5	54.6	46.2
OC 4	40.7	71.2	48.6	0
OC 5	40.8	59.8	46.8	100.0
OC 6	41.5	55.3	46.1	3.4
OC 7	40.6	54.4	43.6	13.4
OC 8	40.2	62.8	43.4	5.0
OC 9	39.3	46.6	39.8	98.3
OC 10	36.8	33.7	33.7	0
SM 1	28.1	28.5	14.3	0
SM 2	24.0	24.0	10.9	8.4
SM 3	25.0	21.0	10.3	2.5
SM 4	22.6	24.2	9.4	0
SM 5	22.4	21.0	8.4	0
SM 6	23.0	17.0	8.2	0
SM 7	20.4	17.0	6.9	0
SM 8	18.0	12.2	6.5	0
SM 9	18.5	20.0	6.1	0
SM 1	18.6	16.5	5.3	0

Table 2

Number of incidences when specific Macrobrachium rosenbergii males were spotted co-occupying the same 1 m² squares of the experimental pond.

	BC ₂	BC ₁	OC ₁	OC ₉	OC ₅
BC ₂		25	51	59	51
BC ₁			26	17	18
OC ₁				49	53
OC ₉					56

Table 3

Dominance matrix of Macrobrachium rosenbergii males based on social interactions in an experimental pond.

		Losing Prawn						
		BC ₂	BC ₁	OC ₁	OC ₉	OC ₅	total wins	total loses
winning prawn	BC ₂	-	21	21	6	9	57	4
	BC ₁	2	-	12	7	8	29	21
	OC ₁	2	-	-	3	11	16	33
	OC ₉	-	-	-	-	4	4	17
	OC ₅	-	-	-	1	-	1	32

Figure 1

Structure of experimental pond with its observation tower.
 A. Side-view.
 B. Bird's eye view with the criss-cross network of 1 m
 equally distributed grid.

Figure 2

Total number of prawns observed at the base of the observation tower during the different hours of the day throughout the entire observation period. Darkened areas represent shaded areas in the pond according to noted times.

Figure 3

The spatial distribution of *Macrobrachium rosenbergii* male prawns in the experimental pond. Expected values expressed as percentage were computed by simulation using a random number generator.

F. DESCRIPTION OF COOPERATION

The research carried out in Israel and Hawaii complemented one another in the understanding of the behavioural-metabolic mechanisms regulating social growth control. Cooperation between the Israeli and Hawaiian research groups was mainly through written and verbal communication regarding the experimental design of the respective experiments that were to be conducted in each country. The overlapping nature of the science conducted by both the Israeli and Hawaiian research groups dictated close cooperation.

G. EVALUATION OF RESEARCH ACHIEVEMENTS

1. This research provided a detailed knowledge of social behaviour and social organization of Macrobrachium rosenbergii which is a prerequisite for any future problem oriented research with a component of behaviour.
2. In this study we contributed to the understanding of the mechanism of growth suppression in Macrobrachium rosenbergii which is one of the major obstacles to increase profitability in the culture of this species. The growth of runts is inhibited via a low food conversion efficiency due to aggressive interactions with large individuals. Reduction of growth suppression is not likely to be achieved by addition of extra food but by reduction of actual physical contact between individuals by the addition of shelters or suspended partitions.
3. The large claws of this species were found to constitute the major structure involved in growth suppression both in juveniles and adults. Juveniles with ablated claws enjoyed both high survival and a uniform growth pattern. Large adults with ablated claws did not inhibit the growth of runts. These results stress the great potential of a short clawed or clawless strain.
4. This interdisciplinary study of social behaviour, metabolism and growth, addressed one of the most complex problems in aquaculture, namely the variability of growth rate in many species. The knowledge gained will benefit further studies on growth variability in cultured species.

H. LIST OF PUBLICATIONS

The following publications were published or are in preparation as a result of this study:

- Barki, A. , I. Karplus and M. Goren. Symmetrical contests between the three male morphotypes of the giant freshwater prawn Macrobrachium rosenbergii (Crustacea, Palaemonidae). In prep.
- Barki, A. , I. Karplus and M. Goren. The formation of dominance hierarchies in mixed groups of the three male morphotypes of the giant freshwater prawn Macrobrachium rosenbergii (Crustacea, Palaemonidae). In prep.
- Barki, A. , I. Karplus and M. Goren. The effect of size and morphotype on dominance hierarchies in mixed groups of blue and orange clawed males of the giant freshwater prawn Macrobrachium rosenbergii (Crustacea, Palaemonidae). In prep.
- D'Abramo, Louis R. , Malecha, Spencer R. , Fuller, Marty J. , Daniels, William H., and Heinen, John M. Reassessment of the prospects for freshwater prawn culture in the United States: Complementary research efforts in Hawaii and Mississippi.
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- Malecha, S. R. , L. E. Barck, E. R. MacMichael, S. Masuno, G. Webber, and D. Zacarias. Biology and management of growth variation in the freshwater prawn, Macrobrachium rosenbergii. 2. Compensatory growth potential of individual runt juveniles. In prep.

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- Malecha, S. R. , L. E. Barck, E. R. MacMichael, S. Masuno and D. Zacarias. Biology and management of growth variation in growth. In prep.
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- Zacarias, D. , S. R. Malecha, L. E. Barck, E. R. MacMichael, S. Masuno, P. Ha- Tamaru, and D. Hedgecock. Biology and management of growth variation in the freshwater prawn, Macrobrachium rosenbergii. 1. Relationship between larval, juvenile and adult growth using allozymes as genetic tags. In prep.