

Developmental Pathways of Male Morphotypes of *Macrobrachium rosenbergii* in Natural Habitat

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The probable transformation pathways of male morphotypes in natural habitat were investigated using the distance function analysis and size characterization of morphotypes. The relative distance between different male morphotypes suggested the possibility of transformation of morphotypes following three developmental pathways. The normal pathway was SM -WOC -SOC -t-SOC -WBC -SBC -OBC, while the two bypass transformation pathways were SM -WOC -WBC -SBC -OBC and SM -WOC -t-SOC -WBC -SBC -OBC. The mechanism underlying transformation of morphotypes following normal and bypass developmental pathways is discussed.

Key words: *Macrobrachium rosenbergii*, male morphotypes, developmental pathways

Sexually matured male population of *Macrobrachium rosenbergii* inhabiting both grow out and natural habitats are differentiated into three morphologically distinguishable forms, small males (SM), orange clawed males (OC) and blue clawed males (BC), based on differential growth pattern, reproductive behaviour, relative body size, second cheliped characteristics and social hierarchical dominance (Cohen *et al.*, 1981; Sagi, 1984; Ra'anan & Cohen, 1985; Harikrishnan & Kurup, 1997). These morphotypes represent three developmental stages of male maturation process and are presumed to undergo transformation from SM to OC to BC (Kuris *et al.*, 1987). The transitional stages of OC males viz, weak orange clawed (WOC) and pre-transforming orange clawed (t-SOC) have also been recognized, the former, transitional between SM and OC (Kuris *et al.*, 1987) and the latter, transitional between strong orange clawed (SOC) and BC male (Sagi & Ra'anan, 1988). In the present study, an attempt is made to elucidate the probable transformation pathways undergone by the male morphotypes in the natural habitat by resorting to

distance function analysis and size characterisation.

Materials and Methods

The exploited male population of *M. rosenbergii* in Vembanad lake (on the south-west coast of India) was examined every month from March 1994 to February 1995. The morphotypes viz. SM, SOC and SBC and their transitional stages such as WOC, t-SOC, WBC and OBC were identified (Harikrishnan & Kurup, 1997), primarily based on morphological characteristics of second cheliped podomeres such as colouration, spineation, stoutness etc., and also on the basis of relative differences in the body size. Of the total samples of morphotypes examined during the present study, morphometric measurements were recorded for 454 males in the size range 71-354 mm. The measurements recorded for distance function analysis were total length, carapace length, rostral length, second cheliped length, and lengths of podomeres of second cheliped (ischium II, merus II, carpus II, propodus II and dactylus II). All measurements were taken to the nearest millimetre. Total length was mea-

sured with a ruler from tip of the rostrum to the tip of the telson while the carapace length was measured with a vernier caliper from the posterior margin of the right orbit to the posterior margin of the carapace at the mid line. Total cheliped length was measured along the extended cheliped with a ruler, from the proximal basis of the ischium to the distal tip of propodus along the ventro lateral surface. Measurements of each podomere were taken following Kuris *et al.* (1987) and total weight was recorded to 0.1 g using a top loader scale. For size characterization, length and weight frequency distributions were prepared following 20 mm and 10 g intervals respectively. The number of male morphotypes belonging to various length and weight classes was enumerated on a monthly basis and average frequencies were arrived at. Statistical analysis of the data was done following Snedecor & Cochran (1967).

Results and Discussion

The variance-co-variance matrices of pair-wise analysis between various male morphotypes were worked out and the D_9^2 values were statistically tested. All D_9^2 values derived from various combinations except that of WOC - t-SOC and SOC - t-SOC were found to be significantly different at 1% level (Table 1). Square root of D_9^2 values between pairs of morphotypes indicated approximate distance between them and mutual relationship of such morphotypes are depicted in Fig.1. Highest distance was found between SM and OBC, as they occupied the initial and terminal positions respectively in the transformation pathway (Ra'anan & Cohen, 1985). The positions of transition stages of orange clawed males (WOC, SOC and t-SOC) were relatively nearer to SM while those of WBC, SBC and OBC were relatively farther from SM. Among OC males, WOC and t-SOC occupied positions closer to SM, when compared with

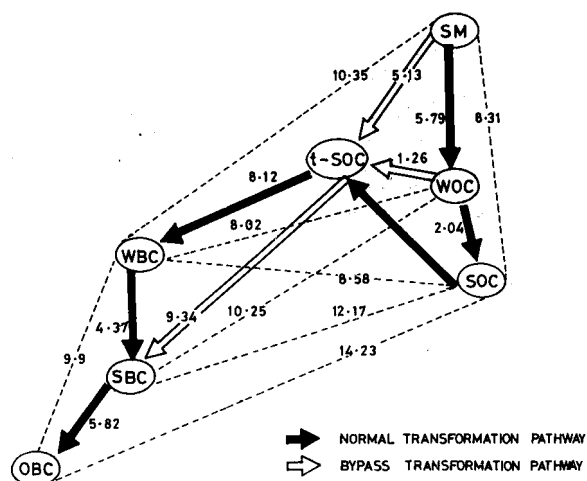


Fig. 1. Mutual relationship of various male morphotypes and the probable transformation pathways in *Macrobrachium rosenbergii* (de man) arrived at on the basis of D-square analysis.

length and weight frequency distribution of various male morphotypes. Their transitional stages are shown in Fig.2. Among the three male morphotypes, SM, SOC and SBC exhibited perceptible differences with regard to both length and weight profiles. SM, SBC and OBC appeared in distinctly different length groups whereas in the case of WOC, SOC, t-SOC and WBC such differences could not be seen. There was significant overlapping among them. Weight frequency distributions also showed a similar pattern. It could be seen that weight frequency distribution pattern of the morphotypes and their transitional stages provided more precise characterization. WOC, t-SOC and WBC predominantly belonged to lower weight groups (30 - 150 g), and SOC, SBC and OBC, to the higher weight groups. Minimum and maximum of total length and weight of various morphotypes studied and their modal values are given in Table 2. SM were represented in the lowest size group, ranging from 71 - 125 mm in total length and 6 - 18 g in weight. A gradual increase in length and weight ranges could be observed from SM to SOC whereas t-SOC and WBC showed

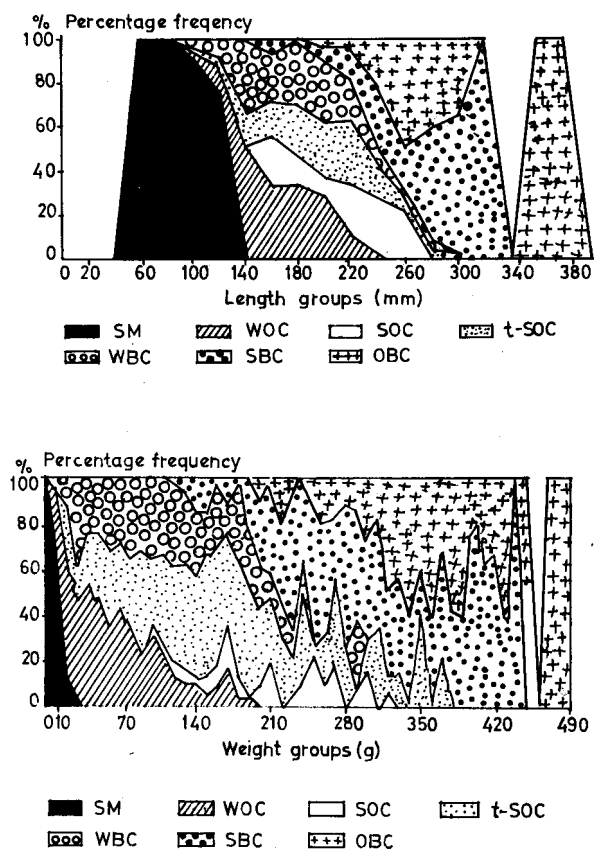


Fig. 2. Length (top) and weight (bottom) frequency distributions of male morphotypes of *Macrobrachium rosenbergii* (de man).

very wide length and weight ranges. Both t-SOC and WBC included individuals having size less than that of SOC. Minimum length and weight of t-SOC were 131 mm and 22 g respectively while the same for WBC was 105 mm and 12 g respectively. Similarly, OBC group was also characterized with a length less than 204 mm and weight of 86 g and this, in comparison with its preceding morphotypes (SBC) was far less. A gradual increase in modal values of length and weight from SM to SOC and from WBC to OBC could also be observed. However, both in t-SOC and WBC, modal lengths and weights were found to be lower than that of SOC. 88% of WOC morphotypes were similar to SOC in length. WOC were distinctly smaller than SOC, when weights

of the two groups were compared. The three probable transformation pathways traced from the length characterization of morphotypes are depicted in Fig. 3.

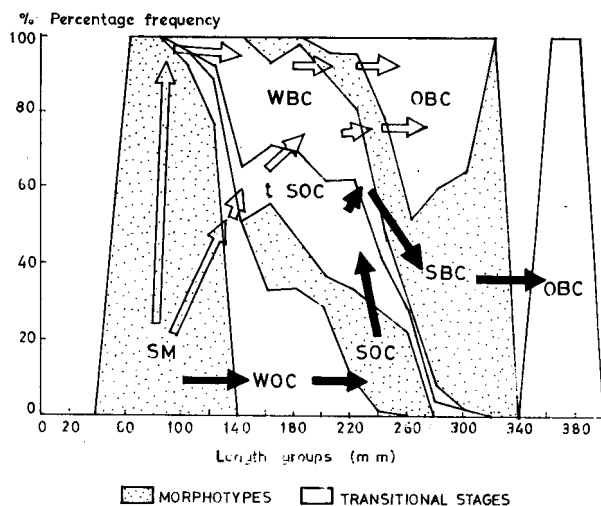


Fig. 3. Developmental pathways in *Macrobrachium rosenbergii* (de man) traced on the basis of length frequency of male morphotypes.

The morphotypes of *M. rosenbergii* represent various stages in the developmental pathway and may transform from SM to BC in an irreversible manner (Cohen *et al.*, 1981; Kuris *et al.*, 1987). The results of D_9^2 analysis in the present study also support this hypothesis. The relative distance between the male morphotypes as reflected in the distance function analysis suggests the possibility of transformation following three different pathways in the natural habitat. SOC was far distant from SM than t-SOC, which would suggest that they followed leapfrog growth pattern since BC males have already established their dominance. Their transformation to SBC through t-SOC would take place only after they grow bigger than the BC males. Results of present study also support the view that male morphotypes of *M. rosenbergii* from a natural population exhibit clear size heterogeneity similar to that of a pond population.

Table 1. Differences between mean values of various measurements of male morphotypes and transitional stages of *Macrobrachium rosenbergii*

Pair	Dp	Df1	Df2	F
MALE MORPHOTYPES				
SM X WOC	33.4902	54	9	51.65*
SM X SOC	69.0883	43	9	78.89*
SM X t-SOC	26.3558	30	9	22.19*
SM X WBC	107.1101	54	9	165.20*
SM X SBC	223.3955	58	9	370.82*
SM X OBC	451.8774	52	9	668.15*
WOC X SOC	4.1703	39	9	4.47*
WOC X t-SOC	1.5764	42	9	1.87
WOC X WBC	64.3263	50	9	92.42*
WOC X SBC	105.0481	54	9	162.02*
WOC X OBC	259.5109	48	9	357.95*
SOC X t-SOC	1.3320	31	9	1.20
SOC X WBC	73.5573	39	9	78.89
SOC X SBC	148.1200	43	9	169.13
SOC X OBC	202.5405	37	9	209.45*
t-SOC X WBC	65.8594	42	9	78.02*
t-SOC X SBC	87.2806	46	9	110.35*
t-SOC X OBC	197.9840	40	9	225.85*
WBC X SBC	19.1056	54	9	29.47*
WBC X OBC	97.3818	48	9	134.32*
SBC X OBC	33.8703	52	9	50.08*

Significant at 1% level

SM - small male, WOC - weak orange clawed male,

SOC - strong orange clawed male

t-SOC - transforming strong orange clawed male,

WBC - weak blue clawed male

OBC - old blue clawed male

The rate of transformation from one morphotype to another is controlled by social organisational set up prevalent in their habitat (Karplus *et al.*, 1991). The growth of SM was found to be suppressed by the presence of BC males with strong second chelipeds in their vicinity and the removal of these large individuals stimulates SM to grow at a faster rate to become OC and eventually to BC males (Ra'anan & Cohen, 1985; Karplus *et al.*, 1992). As per normal developmental pathway, SM transforms to SOC through WOC and SOC transforms to

BC through t-SOC (Kuris *et al.*, 1987; Sagi & Ra'anan, 1988). Sagi & Ra'anan (1988) recognized t-SOC animals as individuals with SOC morphology but showing first appearance of blue colouration as in BC animals. The carapace length and weight ranges of t-SOC identified by them were higher than that of SOC. However, in addition to such t-SOC morphotypes, some individuals (2.99%) with morphology and size ranges similar to WOC, but for the appearance of blue colouration on propodus of second chelipeds, could also be encountered in the present study. Similar heterogeneity was also observed in BC population where some WBC morphotypes (8%) showed morphology similar to WOC except for the blue coloured second pereopods. These observations indicate the possibility of by-pass transformation, besides the existence of normal developmental pathway. Sureshkumar & Kurup (1996) reported that SM showed changes in colouration similar to that of BC when it was maintained with female in the absence of a dominant BC male.

Harikrishnan (1997) reported that there was a predominance of WOC, SOC and t-SOC in the exploited stock of *M. rosenbergii* from the Vembanad lake during January to August while during September to December, a predominance of WBC, SBC and OBC could be observed. The appearance of some of the intermediary morphotypes in the lake does not show full conformity with the expected sequence of developmental pathway and therefore, the heterogeneous nature of morphotypic composition was attributed to the by-pass transformation. Biochemical characterization of male morphotypes of *M. rosenbergii* has also shown the possibility of normal as well as alternative developmental pathways from SM to WBC (Sureshkumar & Kurup, 1998). Ra'anan (1982) observed that some individuals of *M. rosenbergii* reach BC status in the early stages of morphotypic

Table 2. Minimum, maximum and modal values of length and weight of various male morphotypes and transitional stages of *Macrobrachium rosenbergii*

Morphotype	Total number observed	Length			Weight		
		Minimum (mm)	Maximum (mm)	Mode	Minimum (mm)	Maximum (mm)	Mode
SM	38	71	125	102	6	18	6.86
WOC	280	107	246	193	8	192	56.47
SOC	47	186	284	256	48	320	176.00
t-SOC	412	131	310	221	22	378	93.57
WBC	317	105	289	199	12	292	84.14
SBC	157	238	308	255	200	442	235.38
OBC	73	204	393	270	86	510	325.83

Abbreviations as in Table 1

differentiation at a smaller body size. The urge for acquiring hierarchical dominance might make some SM morphotypes to transform to BC status by bypassing SOC stage through SM- WOC- WBC- SBC- OBC- or SM- WOC- t-SOC- WBC- SBC-OBC pathways during early stages of population development. It is now known that BC males show clear dominance over OC males irrespective of their size. But once such dominating BC are formed, rest of the WOC may follow normal transformation pathway through SOC since SOC represents a stage of high somatic growth (Sagi & Ra'anan, 1988). The largest BC becomes the most dominant, occupying the α position and having a clear advantage in access to resources (Barki, 1989) and this is achieved through a "leap frog" growth pattern (Ra'anan & Cohen, 1985) in which an OC will metamorphose into a BC only after it has become larger than the largest BC in its vicinity.

In the "leap frog" pattern of growth, a wide heterogeneity among morphotypes with regard to size is caused by delayed transition from fast growing OC morphotype to the slow growing BC (Kurup, 1997). This might be the reason for the wide range of size groups in t-SOC and WBC. Large sized

individuals of these morphotypes might have formed by transition from SOC stage, following the normal transformation pathway. The disparity in length and weight between WOC and SOC, as observed in the present study, indicates differences in somatic growth in terms of stoutness. There is not much difference in lengths of WOC and SOC while perceptible variation could be observed in weight gain during transformation to SOC. The growth rate of WOC is reported to be rapid in a grow out system (Ra'anan & Cohen, 1985; Kuris *et al.*, 1987). Kuris *et al.* (1987) reported that animals intermediate between WOC and SOC may also be present. This may explain the presence of large sized WOC prawns resembling SOC, except for claw characteristics, in the natural population. The complex nature of population profile development in *M. rosenbergii* is well reflected in the size frequency distribution of male morphotypes.

From the results of the present study, it may be inferred that in natural population, morphotypic transformation may not be taking place by strictly adhering to normal SM- WOC- SOC- t-SOC- WBC- SBC- OBC pathway. Appearance of WBC having a size lower than that of the smallest WOC

(Harikrishnan, 1997) also supports the above inference. If the transformation had taken place only by abiding the normal developmental pathway, t-SOC and WBC must have had sizes much higher than SOC. However, the results of the size characterization are at variance with the above.

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