Morphological modifications caused by *Sacculina polygenea* in *Hemigrapsus sanguineus* (De Haan) (Brachyura: Grapsidae)

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Abstract. — The morphological modifications caused by *Sacculina polygenea* in the grapsid crab *Hemigrapsus sanguineus* were examined. Parasitized males carrying externa were divided into seven stages of feminization by the degree of reduction of the first and second pleopods and the appearance of biramous pleopods on the third to fifth abdominal segments. All males examined retained first pleopods and most of them were Stage I or II. The development of female-type biramous pleopods rarely occurs. Only 10.1% crabs were in advanced stages of feminization. Enlargement of the abdomen and reduction of chela height in parasitized males were pronounced in small males and less so in larger males. Modification caused by the rhizocephalan parasite likely proceeds from when the host is young and small.

Introduction

It is well known that the sacculinid parasites cause not only the degeneration of the gonads in both sexes of host crabs, but also modification of the secondary sexual characters in the male (Day, 1935). Hartnoll (1967) summarized the morphological modification caused by the infection of sacculinid parasites as follows: reduction in the length of the chela propodus, sometimes to that found in females. The male abdomen is broadened, the marginal setation elongated, and when the abdominal segments are normally fused in males, this fusion disappears. The ster-
Materials and Methods

Morphological studies of *H. sanguineus* were made on the specimens collected in 1992 and 1993 to clarify the local differences in prevalence noted by Yamaguchi et al. (1994). These specimens were collected at 13 sites and preserved in 75% alcohol. A total of 464 males and 298 females bearing externae were examined. The abdominal width (AW) used in the present paper indicates the maximum width of the sixth abdominal segment. In females, the fifth segment is the widest, but, it was more convenient to measure the sixth in both sexes. The maximum carapace width (CW) and chela height (CH) were also measured (Fig. 1). All these measurements were taken using a vernier caliper to the nearest 0.05 mm. Measurements of AW, CW and CH of the normal crabs were conducted on living material. Since crabs that look normal were often infected with the sacculinid and possessed internae, they were dissected after finishing measurements. The data obtained from the infected crabs were excluded. Infected crabs were reared in 1992. Crabs were tagged by a small plastic plate stamped with an individual number, on the carapace then divided into two groups. Each group was held in an aquarium (40 cm × 60 cm × 20 cm H) and fed with sliced fish meat or gold fish pellets everyday. Several hours later food remnants, if any, were removed. Several stones of various sizes were placed in the aquarium to provide shelters for the crabs. A total of 33 males and 21 females were reared between 20 September and 11 December 1992.

Results

Location of externae

A total of 181 males and 187 females were examined. Since there is a possibility that an attached externa together with a scar belongs to the same individual which left the scar, those bearing both scar and externa were excluded. Most of the crabs carried only one externa. The crabs were divided into four groups by the number of externa carried and the distribution of externa on abdominal segments was examined (Fig. 2). The pattern of distribution is similar in the crabs bearing one to three externae. The maximum number of externae attaching to each abdominal segment is 2 (first), 2 (second), 3 (third) and 2 (fourth) in males and 4 (first), 3 (second), 3 (third) and 2 (fourth) in females. In males most of externae were extruded from the first and third segments, while in females externa on the second segment were most common. The distribution of externae is explained by the distance from the base of abdomen and the external surface area of each segment. The second segment is narrow and the strong calcified bridge makes it difficult to extrude more than three externae. In the males with only one externa, about half (49.6%) of the externa were on the first segment. However, in 34 crabs (30.0%) the externa was on the third segment. In females, the much wider second segment without

![Fig. 1. Measurement of abdominal with (AW) and chela height (CH) of the crab, Hemi-grapsus sanguineus.](image-url)
calcified bridge seems to make it easier for the externa to grow on this segment. The number of crabs with an externa on the second segment was the largest; 57 out of 102. There seems to be a tendency to avoid mutual competition among parasites, so that, in the crabs parasitized with more than two parasites, externae were tended to distribute evenly among the segments.

*Stages categorized by the condition of pleopods*

The infected males were divided into seven stages as defined below by the reduction of the first and second pleopods and the appearance of biramous pleopods on the second to fifth abdominal segments (Fig. 3).

Stage I: Minor reduction of the length of the first pleopod or no apparent morphological change.

Stage II: Detaching of the second pleopod from the first pleopod.

Stage III: The second pleopods replaced by female-type biramous pleopods. Further reduction of the first pleopod.

Stage IV: Appearance of female-type biramous pleopods on the third segment.

Stage V: Appearance of female-type

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**Fig. 2.** Frequency distribution of externa on each abdominal segment (AS) of *H. sanguineus*. E: number of externae attached, NE: total number of externae, N: sample size.
Fig. 3. Diagrammatic illustrations of abdomens of normal male, normal female and parasitized individuals (stages I–VI) of *H. sanguineus*. Stage I and II are shown by two illustrations.

Fig. 4. Frequency distribution of the males of *H. sanguineus* infected with *Sacculina* classified into seven stages by the modification of pleopods.

biramous pleopods on the fourth segment.

Stage VI: Appearance of female-type biramous pleopods on the fifth segment.

Stage VII: Female-type biramous pleopods completed on the second to fifth abdominal segments. First pleopods absent.

The frequency of each stage is presented in Fig. 4. The number of crabs and the percentage of each stage were as follows: Stage I (146, 31.5%), Stage II (271, 58.4%), Stage III (26, 5.6%), Stage IV (12, 2.6%), Stage V (4, 0.9%), Stage VI (5, 1.1%), Stage VII (0). Nearly 90% of the males were in Stage I and II. The total number
of the crabs of Stage III to VI was only 47 (10.1%). The development of female-type biramous pleopods occurs in a few crabs. All infected males retained first pleopods which, however, became short and slender. None of the infected males attained the last stage. The males were divided into four groups by the number of externae carried, and the frequency of each stage in each group is presented in Fig. 5. In the males carrying one externa, the percentage of Stage I is high compared with the crabs of other groups. However, there is no clear relationship between the number of externae and the stage of feminization; all males carrying four or more externae were in Stage I and II, but this may be a consequence of the small sample.

**Broadening of abdomen**

The broadening of abdomen and reduction in size of chelipeds are very characteristic modifications of the infected males of *H. sanguineus*. The AF-index is calculated from the size difference of AW between male and female. The

![Fig. 5. Frequency distribution of the infected males of *H. sanguineus* into six stages, according to the number of externae attached.](image)

![Fig. 6. Diagram showing the procedure of calculation of AW- (A) and CH- (B) indices. The letter a or a' indicate the difference of the value between the two sexes. The letter b or b' show the difference of the value between the infected male and the normal male or normal female. NM: normal male, NF: normal female.](image)
Fig. 7. The relationship between the abdominal width and the carapace width of normal males and females of *H. sanguineus*. NM: normal males, NF1: immature normal females, NF2: mature normal females.

AW of a normal female is defined as 1.0 and that of a normal male as 0.0. The FA-index is represented by the ratio of AW against the size difference between normal female and male. In Fig. 6-A, the procedure of calculation is illustrated. The bar a is the size difference between the normal female and male, and the bar b is the size difference between an infected male and the normal male. The ratio b/a is the FA-index.

To calculate the index, regression lines relating AW to CW were obtained by measuring 699 normal females and 580 normal males (Fig. 7). In females, there is a considerable difference in the shape of abdomen before and after the pubertal moult. The size of maturity is about 16 mm CW. Two equations, in immature normal females (NF-1) and in mature normal females (NF-2), are presented.

A total of 464 infected males were examined and divided into 12 groups by their FA-index, and the frequency distribution of each group is illustrated in Fig. 8. Only 15 males (3.2%) had a complete or almost complete female-sized abdomen (FA-index, > 0.9), while 55 males (11.9%) still possessed a complete or almost complete male-type abdomen (FA-index, < 0.1). The males with intermediate values, 0.3 to 0.7, occupy 55.4%. In order to know the relationship between the pleopod
condition and the broadening of the abdomen, the frequency distributions of FA-index groups in Stage I to VI are presented in Fig. 9. In Stage I, except for one individual showing the index of 1.05, the FA-index is below 0.6 in all crabs. A very clear shift of distribution is observed between Stage I and II. In the latter stage the center of distribution comes to 0.5–0.6, and the crabs showing an index larger than 0.6 make up 34.7% of all crabs examined. In the males of Stage III and IV, the percentage of the crabs showing a higher FA-index increased. A few crabs, however, show a value less than 0.6.

Fig. 10 shows the relationship between male size and the FA-index in each stage. It might be reasonable to expect that the large-sized males would show higher FA-indices if the infection occurs when crabs are young. The large-sized crabs should show more morphological modification caused by the parasites than in small-sized males. However, there occurs not an increase but a decrease in the FA-index.

In the males of Stage I and II, none of the males more than 35 mm CW showed an FA-index larger than 0.5. In medium or small-sized individuals, the crabs showing the index over 0.5 are common. This result indicates that the broadening of the abdomen probably proceeds when crabs are young and is halted or delayed in the larger crabs. The relationship between the number of externae carried and the FA-index is presented in Fig. 11. There is no clear increase of the FA-index value resulting from increased numbers of externae. None of the eight crabs carrying four or more externae had an FA-value of more than 0.7.

Reduction of chela height

The CH-index is obtained from the size difference of chela height (CH) between the two sexes. In *H. sanguineus* the male cheliped is larger and thicker than in the female. In the infected males, morphological changes occur in the cheliped. The CH-index represents the ratio of chela
height to the size difference between normal males and females. The chela height of the normal male is defined as 1.0 and that of the normal female with the same carapace width is 0.0. In Fig. 6-B, the procedure of calculation is illustrated. The bar \(a'\) is the size difference between the normal male and female, and the bar \(b'\) is the size difference between an infected male and a normal female. The ratio \(b'/a'\) is the CH-index. In Fig. 12, the relationship between CH and CW in normal males and females is illustrated. No specific difference was observed between immature and mature males and females.

A total of 464 infected males were examined. Six crabs which lost either or both of the chelipeds were excluded. With the progress of feminization, the chela height of an infected male decreases. Therefore the CH-index of a male with completely feminized chelipeds is 0.0 and that of the male with no morphological changes is 1.0. The crabs examined were divided into 12 groups by their CH-indices, and the frequency distribution of each group was illustrated (Fig. 13). Most males were in an intermediate condition. The total number of crabs showing CH-index of 0.7 to 0.3 is 301 (65.7%), while the males with complete or nearly complete female-type chelipeds and male-type che-
Fig. 10. The relationship between the abdominal width (AW) and the carapace width (CW) in the infected males of *H. sanguineus* divided into six groups by the stage. Left: distribution of the abdominal width. Solid line = linear regression for normal male. Dotted line = linear regression for normal female. Right: distribution of FA-index.

Chelipeds (CH-index of less than 0.1 or above 0.9) are 11 (2.4%) and 36 (7.9%) respectively. The frequency of each CH-index group in the crabs of Stage I to VI is shown in Fig. 14. A clear difference in the frequency distribution is found between Stage I and II. In Stage I, many of the males still retained the male-type cheliped and the CH-index is high and only 5.5% of the males had the index below 0.4, while in the crabs of Stage II such individuals reached to 39.5%. Fig. 15 shows
the relationship between crab size and CH-index in each stage. No clear relationship between crab size and CH-index is recognized in the crabs of Stage II and VI. Moreover, there is no distinct tendency of a decrease in the index resulting from an increase in crab size. In Stage I, the large-sized crabs showed a higher value than small-sized crabs; in some crabs the index is larger than 1.0. This tendency indicates that in the large-sized crabs, the reduction of chela height does not proceed so much as in the small-sized crabs.

**The relationship between AW- and CH-indices**

The broadening of the abdomen and the reduction in chela height are major morphological modifications in the parasitized males. In Fig. 16, the relationship between the two indices is illustrated. With the increase in the FA-index, the CH-index decreases. The $R^2$ value shows that the two modifications are significantly correlated with each other. However, there is a considerable scattering of points. It is apparent that these morphological changes do not always progress in
parallel. In some crabs, the broadening of the abdomen proceeds far more rapidly than the shortening of chela height and vice versa.

Morphological changes in infected females

The relationship between the abdominal width and the carapace width of the parasitized females is presented together with those of immature and mature normal females and normal males in Fig. 17. The two regression lines show a marked overlap. In Fig. 18, the relationship between the chela height and the carapace width of the infected females is illustrated together with that of normal females. The regression lines overlap almost completely, a fact suggesting that no morphological changes occur in the abdomen and the cheliped in the parasitized females.

Morphological changes following moult ing

The changes in abdominal width and chela height in eight crabs (five males and three females) following moult ing are illustrated in Fig. 19. In the all males not only the carapace width but also abdominal width and chela height increased. How-
ever, there is no distinct increase in the FA and CH indices. In females, the abdominal width and chela height (of the females) were almost the same as those of normal females before and after moulting.

Discussion

According to Okada & Miyashita (1935) who studied sacculinization in the Japanese mitten crab, Eriocheir japonica, externae of the parasite, Sacculina gregaria are small and gregarious; 20–40 externae can be found on a single crab. The total number of externae they found on five crabs was 154 and their distribution on abdominal segments is as follows: 39 (first), 32 (second), 39 (third), 27 (fourth), 15 (fifth) and 2 (sixth). The externae are mainly on the first to third segments, and are less numerous on the second segment. The distribution pattern accords well with that of H. sanguineus, especially crabs carrying more than four externae.

Potts (1910) noted resegmentation of the abdomen in sacculinized males of Carcinus maenas. Day (1935) classified the infected males of Portunus holsatus (=Liocarcinus holsatus) into three categories according to modification of the abdomen: Group I: no redivision of the abdominal segments; Group II: partial redivision of the third, fourth, and fifth abdominal segments; Group III: complete redivision of these segments. The males of Group III had the abdomen broader than those of Group I and II, but narrower than that of normal females. Weng (1987) divided males of Portunus pelagicus infected with Sacculina granifera into four groups, M1 to M4, according to the advance of morphological modifications of abdomen and noted that the males of M4 had a resegmented, broadened abdomen. Reinhard (1950) examined the effect of the sacculinid Loxothylacus texanus to the host crab Callinectes sapidus and found that complete resegmentation of the abdomen occurs in the male. He reported that neither the size of the externa nor the number of externae per
host was related to the amount of morphological deviation. The most striking modification in the male is that the abdomen becomes proportionally as broad as, or even broader than that of normal females. Hochberg et al. (1992) also studied the effect of *Loxothylacus texanus* on *Callinectes sapidus* and confirmed that the abdominal width in both male and female parasitized crabs is significantly wider than that of normal ovigerous females. They thought such change facilitates the parasite's life cycle.

In *H. sanguineus*, normal males have a perfect segmentation on the abdomen so that no resegmentation can be caused by infection. As shown in Figs. 17 and 18 no morphological changes occur in the parasitized females; no excess enlargement of the abdomen takes place as in *C. sapidus*. There is no specific advance of abdominal broadening or FA-index resulting from increase in the number of externae. This evidence agrees with that of Reinhard

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Fig. 14. Frequency distribution of the value of CH-index in the infected males of *H. sanguineus* divided into six groups by their stages.
Fig. 15. The relationship between the chela height (CH) and the carapace width (CW) in infected males of *H. sanguineus* divided into six groups by the stages. Left: distribution of chela height. Solid line = linear regression for normal male. Dotted line = linear regression for normal female. Right: distribution of CH-index.

(1950) who found in *C. sapidus* no specific relationship between the number of externae and the amount of deviation from the normal.

The reduction of chela size, broadening of the abdomen, degeneration of pleopods and the appearance of female-type biramous pleopods are the most characteristic morphological modifications in male crabs caused by the rhizocephalan para-
site. These modifications occur also in anoumuran crabs. Okada & Okasawa (1939), examining the porcelain crab *Petrolisthes japonicus* infected by *Lernaeodiscus cornatus*, noted that the broadening of the abdomen and the development of extra female appendages proceeded in the infected males. In females, abdominal appendages received modification but male-type appendages never appeared on the first segment. Brinkmann (1936) studied the morphological modification of the galatheid *Munida sarsi* infected with two rhizocephalan parasites, *Triangulus munidae* and *Lernaeodiscus ingolfi*. The size reduction and morphological modification of pleopods take place in the male's abdomen and there are species differences in the modification. However, no specific cheliped modification was observed. Hoggarth (1990) examined the lithodid crab, *Paralomis granulosa* infected with the rhizocephalan, *Briarosaccus callosus*. The parasitized males had smaller chelae and broadened abdomen.

Smith (1910), examining the males of *Inachus mauritianicus (= I. thoracicus)* infected with *Sacculina neglecta (= Drepanorchis neglecta)*, noted that the males showed every degree of modification towards the female type: in crabs of an advanced stage, the abdomen is distinctively broadened and one or two additional appendages are developed; the most advanced forms were found usually among smaller and medium-sized individuals, the chelae and abdomen of which almost represented the adult female form. The only male feature retained was the first pleopods, which, however, was sometimes reduced to a minute knob. Hartnoll (1962) examined the morphological modification in *Macropodia longirostris* caused by *Drepanorchis neglecta* and found broadened abdomen, elongations of fringing setae of the abdomen, reduced genital papillae, modified pleopods and reduced cheliped size. Hartnoll (1967) also examined morphological modification in Jamaican *Geograpsus lividus* that was caused by *Sacculina hartonolii*. There was an increase in the width of the abdomen, but no appreciable difference occurred in the length of chela propodus, and the decrease in the length of the first pleopod was small. In the spider crab *Microphrys bicornis*, parasitized by *Sacculina bicuspidata*, the abdomen was broadened and the length of chela propodus was reduced. In most of infected males, however, the pleopods were normal.

Okada & Miyashita (1935) classified the infected males of *Eriocheir japonica* into five categories. Type I: Appendages on the second abdominal segment were rudimentary or slightly enlarged; first pleopods slender. Type II: The second abdominal appendages assumed the form of biramous female ones; first pleopods were slender and reduced; Type III: Two pairs of female appendages developed; first pleopods were reduced. Type IV: Three or four pairs of biramous appendages developed; first pleopods were reduced or rudimentary; Type V: Four pairs

![Image](image-url)
of complete female appendages appeared; first pleopods entirely absent. Matsumoto (1952) examined a total of 302 (135 males and 167 females) Charybdis japonica parasitized by sacculinids. All the males had a broadened abdomen to the same degree as a normal female. Their abdomens were completely segmented. No intermediate stages were observed. In C. japonica the degeneration of pleopods also occurs in females, and in the most advanced condition, only traces of them remain. Therefore, both the parasitized male and female change to the intermediate degenerate condition closely resembling each other. However, we did not find any degeneration of pleopods in the parasitized females in H. sanguineus.

Day (1935) examined males of Portunus holsatus (= Liocarcinus holsatus) infected with a sacculinid and mentioned that the smaller the crab the greater the degree of modification. Foxon (1940) studied the life history of Sacculina carcini and
Fig. 18. The relationship between the chela height (CH) and the carapace width (CW) of parasitized females of *H. sanguineus*. Solid line = infected females (PF). Dotted lines = normal females (NF) and normal males (NM).

reported that the degree of modification of the host crab does not depend on its size; the larger the host the less liable it is to modification, and the smaller the host, the greater the modification is. In the present study we also found that the larger the crab is, the less progressive is the morphological modification. Weng (1987) found that some small males have developed the M4 shape abdomen, while some large males had the M2 abdomen. He suggested that the difference in the effects of some chemical substance which causes feminization might be a cause of the difference in the degree of modification.

In Fig. 20 the relationship between crab size and the FA- and CH-indices of *H. sanguineus* is presented. Parasitized males were divided into four size groups: immature (below 16 mm CW), small (16–20 mm CW), medium (20–30 mm CW) and large (above 30 mm CW). The percentage distribution of the FA-index is signifi-
Fig. 19. Growth of infected males (PM) and females (PF) of H. sanguineus following moulting. Each mark (solid circle, open circle etc.) represents an individual. The marks presented at left side show the values before moulting and the same mark in upper right indicate the values after moulting. N = sample size. Note: After moulting the values of carapace width, abdominal width and chela height increased.

Significantly different between the immature and large groups. In the immature group none of the crabs had an index below 0.4, while in the large group all crabs had an index below 0.8. The difference of CH-index between the two groups is less apparent. In the large group the percentage of the crabs with the index of more than 0.6 is high compared with those of the medium and small-sized crabs. This fact indicates that the percentage of males having less modified cheliped is higher in the large-sized males.

Day (1935) who considered the internal development of S. carcini lasts 9 months explained the liability of small crabs to modification as follows: if a crab is infected when young, it will be able to cast its shell more often, during the nine months prior to the appearance of the externa, than will an older crab during the same period. At the time when the externa appears and prevents further moulting, it is probable that the recently
acquired shell of its young host will be modified. In the case of an older crab it is possible that no ecdysis may have taken place during the period following infection, and there will be no external modification at all.

As is well known sacculinized brachyuran crabs do not moult, as a rule, after the parasite has become external. Morphological alterations induced by parasitism can only occur at the ecdysis which takes place while the crab is harboring the sacculinid as an endoparasite. The number of moults which the infected host undergoes prior to the emergence of the parasite undoubtedly plays a part in determining the degree of modification to which it attains. In *H. sanguineus*, the parasitized crab does not moult when it is affected by an externa. However, the crab can moult after detaching of the externa. Takahashi & Matsuura (1994) studied the molting and growth of *H. sanguineus* parasitized with the present sacculinid parasite (they erroneously identified the species as *Sacculina senta*) and reported

Fig. 20. Frequency distribution of the FA- and CH-indices in the males of *H. sanguineus* which are divided into four groups by their carapace width (CW).
that the infected crab could moult after detaching of externa, and that the annual relative growth of parasitized crabs was about half that of unparasitized crabs. They attributed the difference to the difference in moult frequency. However, Sumpton et al. (1994) reported that in *Portunus pelagicus* infected with *Sacculina granifera* there was no large difference in the size distribution between the normal and infected crabs. In the present study we examined the morphological modification following moultling and found that there was no distinct progress in the modified feature such as enlargement of the abdomen and reduction of the chela height. It is very likely that the modification caused by the rhizocephalan parasites proceeds when the host crab is young, and in crabs, which are infected after attaining a larger size, no considerable external modifications occur.

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