Laboratory Studies on Molting and Growth of the Shore Crab, *Hemigrapsus sanguineus* de Haan, Parasitized by a Rhizocephalan Barnacle

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Abstract. Molting of shore crabs (*Hemigrapsus sanguineus*) parasitized by rhizocephalans (*Sacculina senta*) was observed in the laboratory, and the growth of the molted crabs was compared with that of unparasitized animals. Molting of the host was obstructed by the infestation, but was still possible. After the release of several broods of larvae, the externa (the external reproductive system of the parasite) detached from the host. Subsequent molting occurred within 40 days in about 80% of the animals, but in the remainder, it was delayed for at most 4 months. Soon after molting, a new externa protruded from the abdomen of every crab. Thus, the life-span of the externa and the molting of the host would seem to be closely connected. In the female, the molt frequency was reduced, but the molt increment of the parasitized crabs was not different from that in the unparasitized ones. In the male, however, both the molt frequency and the molt increment were reduced. Thus, the annual growth of parasitized males and females was about half that of unparasitized crabs.

Introduction

Rhizocephala (Crustacea, Cirripedia) are exclusively parasitic on crustaceans, mainly Decapoda. The first larva of a rhizocephalan hatches from the egg as a nauplius. Females of the subsequent larva (cypris) infect the host, and part of the parasite protrudes from the host's abdomen, acting as a saccular reproductive organ (externa). Male cypris larvae migrate through the mantle cavity of the externa into a receptacle where the male larva metamorphoses into a mass of sperm cells (Ichikawa and Yanagimachi, 1958, 1960; Yanagimachi, 1961a, b; Ritchie and Høeg, 1981; Lützen, 1984; Høeg, 1982, 1985a, b, 1987).

The internal part of the rhizocephalan parasite (the interna) branches and thus penetrates various parts of the body of the crustacean host, taking nourishment from its tissues. The effects on the host include difficulty in molting, changes in secondary sexual characteristics, and degeneration of the sexual organs (Reinhard, 1956; Hartnoll, 1967). In particular, sacculinized brachyuran crabs usually cease to molt after the parasite appears external to the host (Veillet, 1945; Reinhard, 1956; Hartnoll, 1967; Lützen, 1984).

Although such pervasive effects might be expected to decrease host survivorship or host reproduction, many local populations of *Hemigrapsus sanguineus* (Decapoda: Grapsidae) are, in fact, heavily infected by *Sacculina senta* (Cirripedia: Rhizocephala). In Amakusa and some other localities in Japan, the prevalence exceeds 70% and is positively correlated with size (Fig. 1, preliminary survey in April 1988). Sacculinized crabs are common among the large size classes, and many of the infected male crabs are feminized in their external form, having a wider abdomen and smaller chelipeds than unparasitized males.

The observed feminization of male crabs presents us with an apparent contradiction, for crustaceans cannot change their external form without molting. Indeed, Reinhard (1956) and Hartnoll (1967) mentioned that all the modifications of male hosts must appear before the externa erupts, since the presence of the externa prevents any further molting of the host.
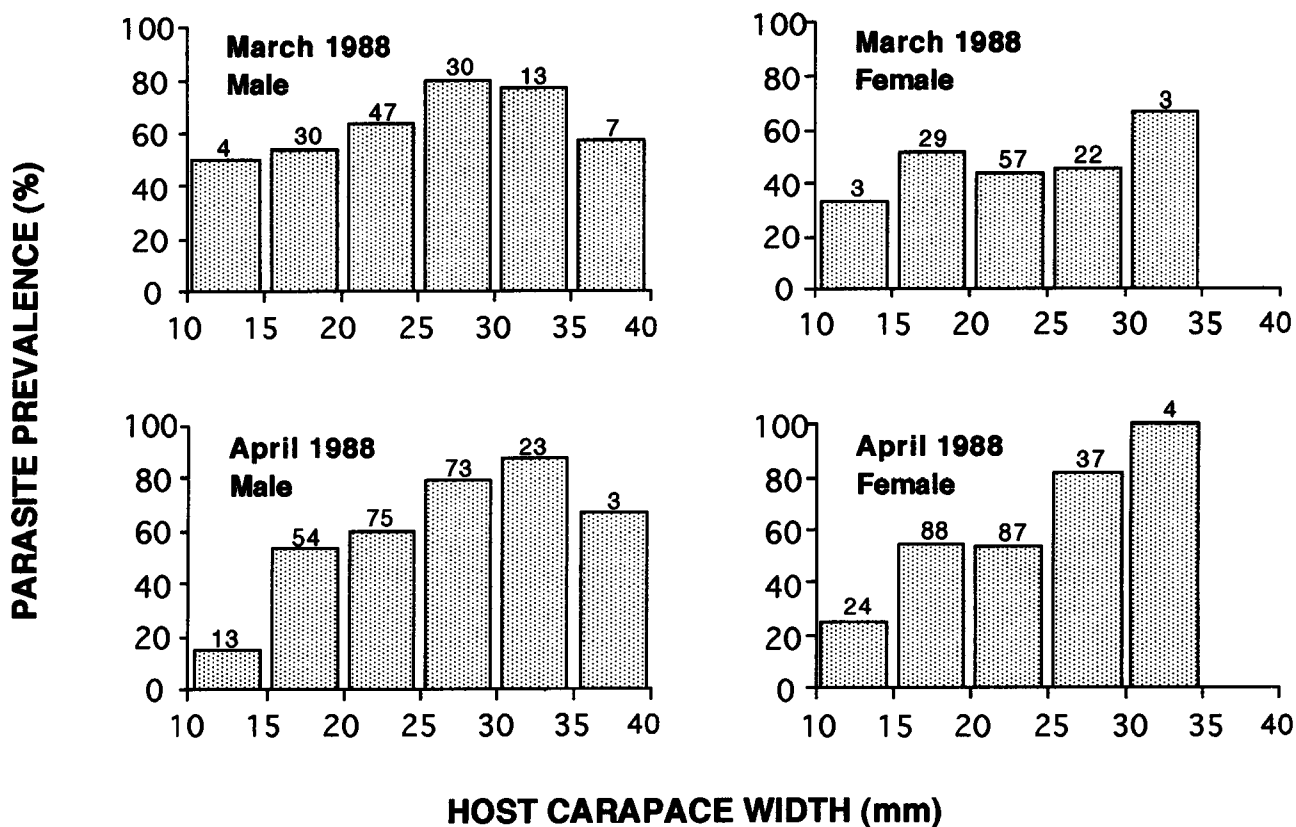
Figure 1. Size-specific prevalence (%) of *Hemigrapsus sanguineus* parasitized by *Sacculina senta*. Animals were adult males and females (>10 mm in carapace width) collected at Inuki Estuary, Amakusa, Japan, in April 1988. Numbers above each column represent the total number of animals collected in each size class.

O'Brien (1984) showed that the majid crab *Pugettia producta*, when parasitized by the sacculinid *Heterosaccus californicus*, undergoes a reduced number of molts preceding the allometric molt of puberty. The externa of the parasite emerges after this molt of puberty, which then becomes the terminal molt of *P. producta*. Such precocious maturity among parasitized crabs results in a negative relationship between size and prevalence; *i.e.*, the prevalence decreases with the host size. O'Brien and Van Wyk (1985) emphasized that this host-parasite relationship is characteristic of sacculinid infections.

However, the positive size-prevalence pattern of *Hemigrapsus sanguineus*, as shown in Figure 1, does not conform to that of *P. producta*. It indicates that host-sacculinid relationships do not share a single mechanism. The natural molt format of *H. sanguineus* is different from that of *P. producta:* the pubertal molt of *H. sanguineus* is not a terminal molt. Although many brachyurans do not stop molting after the molt of puberty, host-sacculinid relationships of such groups are little known, except that parasitized *Carcinus maenas* may resume molting if the externa of the *Sacculina carcini* is detached (Day, 1935; Veillet, 1945; Lützen, 1981).

This study demonstrates that parasitized shore crabs, *Hemigrapsus sanguineus*, do not stop molting or growing. We have investigated their molting processes and compared the growth of parasitized and unparasitized crabs. Finally, we infer the causal factor leading to the positive size-prevalence pattern of *H. sanguineus*.

Materials and Methods

Sacculinized crabs were collected from the pebbled intertidal zone of Inuki Coast (32°25' N, 130°25' E), Amakusa, Kyushu, Japan, where their prevalence had been found to be about 70% (Fig. 1). Unparasitized crabs were collected from Tomoe Cove (32°32' N, 130°02' E), Tomioka, Amakusa, where the prevalence of parasitized animals is below 1%.

From 1 February 1989 to 30 June 1990 (17 months), 40 adult crabs (>15 mm in carapace width) were kept in the laboratory (Aitsu Marine Biological Station, Kumamoto University). When one crab died, another specimen would be supplied, so that 64 crabs (36 sacculinized and 28 unparasitized) were reared during this study. As some of the sacculinized crabs carried multiple externae, a total
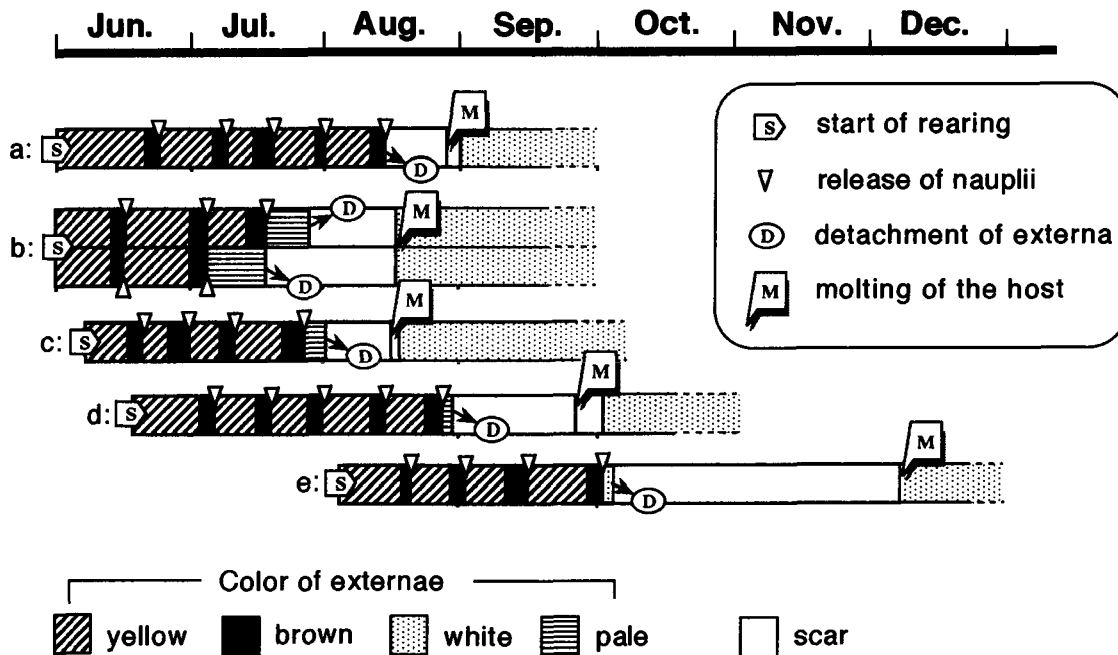
Figure 2. Examples of successive reproduction of the parasites and subsequent molting of the hosts. a–e: Six externae on five hosts changed their color along with the development of their incubated eggs. b: The host had two externae.

of 47 externae were attached on the 36 sacculinized crabs at the beginning of rearing. The crabs, kept individually in small plastic boxes with several holes (about 1.0 cm in diameter) in the bottom, were reared in running seawater that had been passed through a sand filter system to prevent any additional invasion by the cypris or nauplius larvae of *Sacculina*.

The mussel *Musculus senhousia* (Bivalvia, Mytilidae) and the green alga *Ulva pertusa* were kept in these plastic cases as nonpolluting living foods that could be eaten by the crabs at any time. In addition, at 1–3 day intervals, the crabs were fed artificial pellets that are ordinarily used for Kuruma prawn culture (Higashimaru Co., Ltd.). The quantity of food was controlled individually at each observation time, so there was always a little left over.

The color of the externae changed as the incubated eggs of the parasite developed, so the externae of the parasites were classified into four categories according to color (see Results). Before and after the molting of the host, the carapace width (CW) of the host was measured, with a hand caliper, to the nearest 0.05 mm.

Any increase in size at ecdysis was determined as the relative molt increment [100 (CW of postmolt − CW of premolt)/CW of premolt].

The various terms and abbreviations used in this paper are as follows:

Unparasitized crab (U): defined on the basis of its external appearance (no externa or scar, and not castrated);

crabs with an internal infestation could not be completely excluded.

Sacculinized crab: parasitized crabs displaying one or more externae of *Sacculina senta*.

Parasitized crab (P): externally parasitized crabs ("sacculinized crabs") plus internally infected crabs that are not yet carrying externae or that have already lost their externae.

Results

Detachment of externae and subsequent molting of the host

The newly erupted externae are distinguishable because they are colorless, lack a mantle opening, and are less than 3 mm in diameter. They are virgin females; if a male cypris invades the receptacle, the externa begins to grow and change color. The color first gradually changes to yellow, then becomes brown when the externa contains embryos with eyes.

Thus, the color of externae can be classified into four categories: (1) white (virgin externa; maximum diameter is less than 3 mm); (2) yellow (normal type externa, with male cells in the receptacles); (3) brown (externa packed with mature embryos with eyes); and (4) pale (empty externa).

Some examples of the changes in the externae are shown in Figure 2. These externae dropped off the host after

several spawnings of nauplii. The other externae, which could not be drawn in Figure 2, showed similar succession patterns. The interval between two spawnings varied according to the temperature of the seawater. For instance, the interval was about 12 days in August when the average seawater temperature was 26.7°C; in November (18.3°C) it was 24 days. There was considerable individual variation.

While the eggs of a sacculinid were being incubated, its next brood was already being prepared. After the release of several broods of larvae, the externa detached, leaving a scar on the abdomen of the host. Only then was the host able to molt (Fig. 2).

Table I shows the number of days required for the host crab to molt after the externa had fallen off, and the number of days from the time of molting to the appearance of a new externa during the year from May 1989 to April 1990. The temporal distribution of the molt with respect to the detachment of the externae is shown in Table II. The unparasitized control crabs most frequently molted in July, whereas the parasitized animals had a broader molting period—from July to September. Although the parasites released larvae throughout the year, most of the detachment of externae occurred between June and October. Following detachment, most parasitized crabs molted within about 1 month. For instance, of the eight sacculinized crabs that lost their externae in June 1989, one specimen molted in June and the other seven molted before the end of July. In 21 of the 31 examples (67.7%), molting resumed within 30 days; in 25 examples (80.6%), it occurred within 40 days (Tables I and II).

The new externae sometimes appeared within 1–2 days after molting, when the carapace of the host was still soft; but others appeared later, after the host's new shell had become hard (Table I). One crab molted twice, and the new externa appeared after the second molting. Consequently, among 31 parasitized hosts, externae reappeared in all but one host, which failed in molting and died (Table I).

Effects on growth of the host

The growth rate of crustaceans generally varies with the water temperature and is also affected by reproductive conditions. Because the temperature of the seawater is not stable and molting is seasonal, growth rates in different months could not be compared. Furthermore, because adult crabs (CW > 15 mm) molt only two or three times a year, only the relative growths of crabs that lived through a certain half or one-year period were compared (Table III). The half-year periods that were compared were between 1 April 1989 and 30 September 1989 (Section I), and between 1 October 1989 and 31 March 1990 (Section II). The one-year period was defined as extending from

Table I

Time between the detachment of the externa and the next molt, and between that molt and the appearance of a new externa

Date of detachment of externa	Time to next molt (days)	Water temperature; from detachment to next molt (mean, range)	Time from molt to new externa (days)
31 May 1989	30	21.8, 20.9–22.5	7
2 June	18	21.6, 20.9–22.0	1
3 June	33	21.9, 20.9–22.5	3
5 June	32	21.9, 20.9–22.7	0
25 June	8 + 35*	22.4, 22.1–22.5 24.2, 22.1–25.9	9**
25 June	9	22.4, 22.1–22.5	17
25 June	8	22.4, 22.1–22.5	43
27 June	10	22.5, 22.1–22.7	0
30 June	23	23.6, 22.1–24.9	0
11 July	23	24.6, 23.8–25.7	1
16 July	16	25.1, 24.6–25.7	2
21 July	12	25.4, 24.9–25.7	3
22 July	29	26.4, 25.7–27.0	0
28 July	31	26.7, 26.5–27.0	0
10 August	9	26.8, 26.6–27.0	6
13 August	14	26.8, 26.5–26.7	4
21 August	51	24.9, 19.9–27.1	3
25 August	15	26.4, 25.7–27.1	2
27 August	112	21.6, 15.0–27.1	0
27 August	31	25.9, 24.6–27.1	***
31 August	28	25.7, 24.6–26.9	2
2 September	23	25.6, 24.6–25.9	0
3 September	6	25.8, 25.7–25.9	1
5 September	28	25.5, 24.6–26.2	1
12 September	13	25.5, 24.6–25.9	2
27 September	124	18.0, 9.8–24.9	2
2 October	117	18.0, 9.8–24.9	5
5 October	29	22.0, 19.9–24.6	3
6 October	72	19.4, 15.0–24.6	4
26 October	9	21.2, 20.8–21.5	0
9 January 1990	101	13.3, 9.8–16.2	13

* Molted twice (8 days to first molt and 43 days to second molt.
** Days from second molt.
*** Died (failed to molt).

15 April 1989 to 14 April 1990 because the number of crabs that lived a full year was greatest during that time.

In both sexes, the mean annual relative growth of parasitized crabs was about half that of unparasitized crabs. But the discrepancy between the growth of unparasitized and parasitized female crabs appears to have a different basis from that in males. Throughout Sections I and II, relative growths and relative molt increments of the parasitized males were clearly smaller than those of the unparasitized males. The molt frequency (number of molts) of the parasitized males was significantly smaller than that of the unparasitized males during the one-year period, though the difference was not significant during Section I or Section II. None of the parasitized female crabs molted during Section II. During Section I, all of the seven un-

Table II

Distribution of the detachment of externae and subsequent molts in each month (May 1989–April 1990)

Months when crabs lost externae	Number of crabs that lost externae	Month when parasitized crabs next molted [number of crabs (Days, or range, between loss of externa and molt)]											
		May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr
May	1		1 (30)										
June	8		1 (18)	7 (8–35)									
July	5				5 (12–31)								
Aug	7				2 (9, 14)	3 (15–31)	1 (51)		1 (112)				
Sep	5					3 (6–23)	1 (28)			1 (124)			
Oct	4							2 (9, 29)	1 (72)	1 (117)			
Nov	0												
Dec	0												
Jan	1												1 (101)
Feb	0												
Mar	0												
Apr	0												
Total molts per month	P	0	2	7	7	6	2	2	2	2	0	0	1 (Sample 31)
	U	1	1	10	2	0	4	3	3	1	1	0	2 (Sample 28)

P = parasitized; U = unparasitized controls.

parasitized females listed in Table I were ovigerous once, and their molt frequency, relative growth, and relative molt increments were not significantly different from those of the parasitized crabs ($P > 0.05$, Student's t test). Therefore, the difference between the annual growth of unparasitized and parasitized female hosts was mainly due to a difference in the molt frequency during Section II, whereas that of the males was due to a difference in both the molt frequency and the relative molt increment.

In Figure 3A, every relative molt increment of the male crabs is plotted against the premolt carapace width. The relative molt increments of the unparasitized control males tended to decrease with increasing crab size, and this fact should be noted when considering the male groups of this experiment: *i.e.*, the average premolt carapace width of the parasitized males used in this study [22.38 mm ± 3.55 (SD) (n = 16)] was significantly larger than that of the unparasitized males [19.10 mm ± 3.95 (SD) (n = 14)] ($P < 0.05$, t test). On the other hand, there was no significant difference between the average premolt carapace width of parasitized females [19.23 ± 2.50 (SD) (n = 15)] and that of unparasitized females [19.92 ± 2.85 (SD)] ($P = 0.49$, t test).

The regression line showing the correlation between the relative molt increment and carapace width for unparasitized control males was

$$Y = 31.95 - 0.88X, r = 0.61,$$

comparable to that reported for this species by Kurata (1962)

$$Y = 28.61 - 0.69X, r = 0.86,$$

(recalculated by us for animals larger than 15 mm) ($P > 0.05$, ANCOVA). To eliminate this size effect, the regression line for parasitized males

$$Y = 21.24 - 0.57X, r = 0.44$$

was compared with that for the unparasitized males used in this experiment and with that from Kurata (1962). The intercept of parasitized males was significantly smaller than that of the unparasitized males, both in this experiment and in that of Kurata (1962) ($P < 0.05$, ANCOVA). But the regression line calculated for parasitized males lacks any significant reliability ($P > 0.05$, F test). Then, translating the Y axis of Figure 3A into real postmolt carapace width, the regression lines of parasitized and unparasitized males were redrawn in Figure 3B (the so-called Hiatt's growth diagram; Hiatt, 1948). The regression lines that were recalculated are as follows:

U: $Y = 3.51 + 0.97X$ ($r = 0.95$, $P < 0.01$, F test)

P: $Y = 2.42 + 0.97X$ ($r = 0.97$, $P < 0.01$, F test).

These two regression lines are parallel, but the intercept of parasitized males was significantly smaller than that of unparasitized males ($P < 0.05$, ANCOVA). Consequently,

Table III

Molt frequency, relative growth, and relative molt increments of crabs that lived through two half-year periods or that lived longer than one year

Period	Number of crabs		Number of molts in period (mean)	Relative growth (%)[a]: [means (SD)]	Relative molt increment (%)[b]: [means (SD)]
1 April 1989–30 September 1990 (Section I)	U ♂	7	10 (1.43)	21.31 (9.45)	14.34 (4.04)
	P ♂	5	4 (0.80)	5.95 (5.46)**	7.44 (4.99)**
	U ♀	7	10 (1.43)	19.20 (8.74)	12.95 (3.53)
	P ♀	4	6 (1.50)	19.84 (12.29)	12.59 (4.05)
1 October 1989–31 March 1990 (Section II)	U ♂	8	6 (0.75)	12.16 (12.20)	15.79 (3.27)
	P ♂	14	5 (0.36)	3.51 (5.55)*	9.84 (4.73)*
	U ♀	9	7 (0.78)	8.84 (5.88)	11.37 (3.54)
	P ♀	11	0*	0***	—
15 April 1989–14 April 1990 (One year)	U ♂	7	12 (1.71)	26.69 (15.25)	14.73 (8.78)
	P ♂	9	10 (1.11)*	10.26 (6.39)*	9.22 (4.72)*
	U ♀	6	11 (1.83)	25.79 (7.32)	13.33 (4.89)
	P ♀	5	4 (0.80)*	12.21 (13.13)*	14.85 (6.35)

Values are means ± SD; P = parasitized crabs; U = unparasitized.

[a] Relative growth (%) = 100 (CW_e − CW_b)/CW_b, where CW_e is carapace width at the end of the period, and CW_b is carapace width at the beginning.
[b] Relative molt increment (%) = 100 (CW_{post} − CW_{pre})/CW_{pre}, where *post* and *pre* refer to molt.

* Value for parasitized crabs is significantly smaller than that for unparasitized crabs. Mann Whitney *U* test was used for number of molts, and Student's *t* test was used for relative growth and relative molt increment: (***), $P < 0.001$; (**), $P < 0.01$; (*), $P < 0.05$.

the relative molt increments of parasitized males are smaller than those of unparasitized males.

The relative growths over 365 days are given in Table III. The average molt frequencies of male and female unparasitized crabs were 1.71 and 1.83 respectively, whereas those of parasitized crabs were 1.11 and 0.80 respectively. Therefore, after the loss of their externae, parasitized crabs had smaller relative growths than did unparasitized crabs, in both sexes.

Mortality of the host

The annual survival rates of unparasitized and parasitized crabs were 63.4% and 64.3% respectively—virtually indistinguishable values.

Discussion

Detachment of the externae, subsequent molting of the host, and regeneration of new externae

Parasitized *Hemigrapsus sanguineus* resume molting, and molt rather frequently, once the externa falls off. This resembles the response of a portunid host, *Carcinus maenas*, which molted after the externa of *Sacculina carcini* dropped off (Veillet, 1945; Lützen, 1981).

Heath (1971) and Lützen (1981) noted that a new externa of *S. carcini* appeared after the parasitized *C. maenas* molted. Lützen, however, concluded that regeneration of

the externa did not play a significant part in the life cycle of the parasite. In the present study, new externae always appeared soon after molting in the infected crabs examined. Thus, the new externa had probably been prepared inside the host. Of 31 instances of molting, 21 appeared within 30 days of the molt, and 25 appeared within 40 days. Therefore, the life span of the externa and the molting of the host are closely related. This is schematically illustrated in Figure 4, a modification of Heath's model (Heath, 1971) with the resumption of molting replacing seasonality. Although detachment of the externa and molting of the host occurred frequently between June and October, the parasite reproduced continually throughout the year; thus the persistent reproduction of the parasite overshadowed the seasonality of the host.

Although the secondary eruption of externae is called *regeneration*, there is no direct evidence that a secondary externa sprouts from the same root as its antecedent. Indirect evidence suggests that regeneration may occur. For instance, Day (1935) found, in serial sections, a live main root trunk in a number of scarred or strongly feminized swimming crabs. But one cannot completely rule out the possibility that some of the new externa come from multiple infections.

Effects on host growth

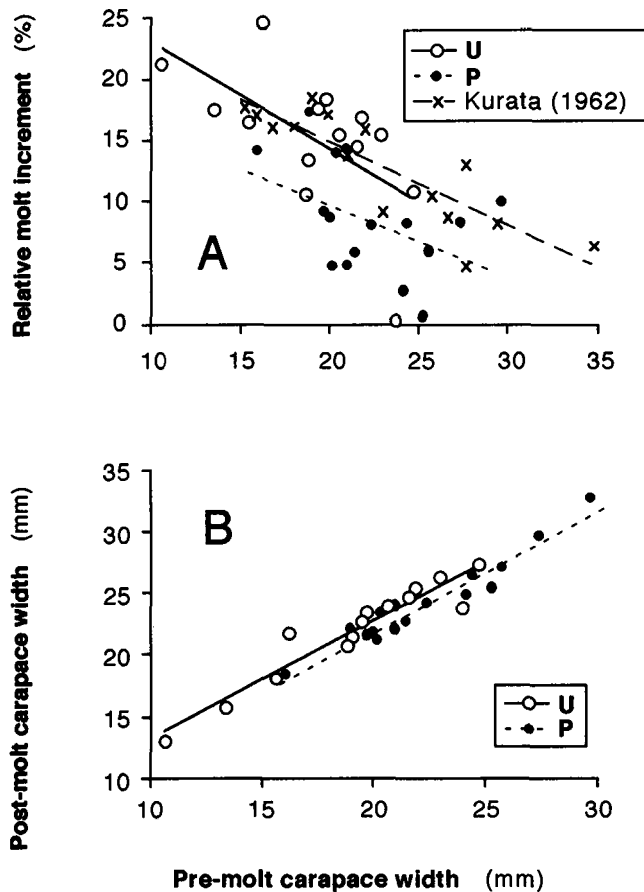The annual growth of both parasitized males and females was about half that of unparasitized crabs, but this

Figure 3. Premolt and postmolt relationships of parasitized and unparasitized male *Hemigrapsus sanguineus*. A: relationship between premolt carapace width and relative molt increment. B: Hiatt's growth diagram for male hosts.

discrepancy did not have the same basis in the two sexes. In the male, both the molt frequency and the molt increment of parasitized crabs were smaller than in the unparasitized crabs; but in the female, the discrepancy was mainly due to a difference in the molt frequency. During Section II (October–March) in particular, none of the parasitized females molted. During Section I, all seven unparasitized females recorded in Table III were ovigerous once, and this might have been a handicap to molting. The molting state of sacculinized crabs is similar to that of ovigerous females.

No study on the growth of sacculinized brachyuran hosts is comparable to the present study. But even if we examine the studies on the effects of rhizocephalans from a different family, the results are similar to those obtained in the present study. Hawkes *et al.* (1987) examined the growth of Alaskan blue king crabs, *Paralithodes platypus* (Decapoda, Anomura), parasitized by *Briarosaccus callosus*. There was no significant difference in the molt frequency between parasitized and unparasitized crabs, in

either sex. The molt increment of parasitized males was significantly smaller than that of unparasitized males, and that of parasitized females was also smaller than that of unparasitized females, although not significantly.

Positive size-prevalence pattern

Inverse size-prevalence patterns are found in *Pugettia producta* parasitized by the sacculinid *Heterosaccus californicus* and in the mud crab *Rhithropanopeus harrisii* parasitized by *Loxothylacus panopei* (O'Brien, 1984; O'Brien and Van Wyk, 1985; O'Brien and Skinner, 1990). The authors of these reports describe the inverse size-prevalence pattern as typical of sacculinid-host associations. Contrary to these reports, we observed that the prevalence of *H. sanguineus* increased with the size of the host (Fig. 1). This pattern is rather similar to that of the peltogastrid rhizocephalan-host relationship (O'Brien and Van Wyk, 1985). These authors suggested that enhanced growth of parasitized hosts might be one factor determining the positive size-prevalence pattern, but such enhanced growth has not been documented in laboratory studies.

In the present study, *H. sanguineus* showed a positive size-prevalence pattern with suppressed host growth. The mechanisms that cause the size-prevalence pattern are not very clear, but we can suggest three reasonable factors.

1. *H. sanguineus* does not stop molting after the molt of puberty, whereas the molt of *P. producta* is a terminal molt.
2. Parasitized *H. sanguineus* can molt and grow even after the externae of the host have emerged.
3. The parasite does not have a lethal effect on the host.

Consequently, the parasite probably lives on after the detachment of the externa and then regenerates a new externa. Therefore, the high prevalence of parasitism among the large size classes may simply reflect the fact that the large host has been repeatedly exposed to infections, as suggested by Day (1935).
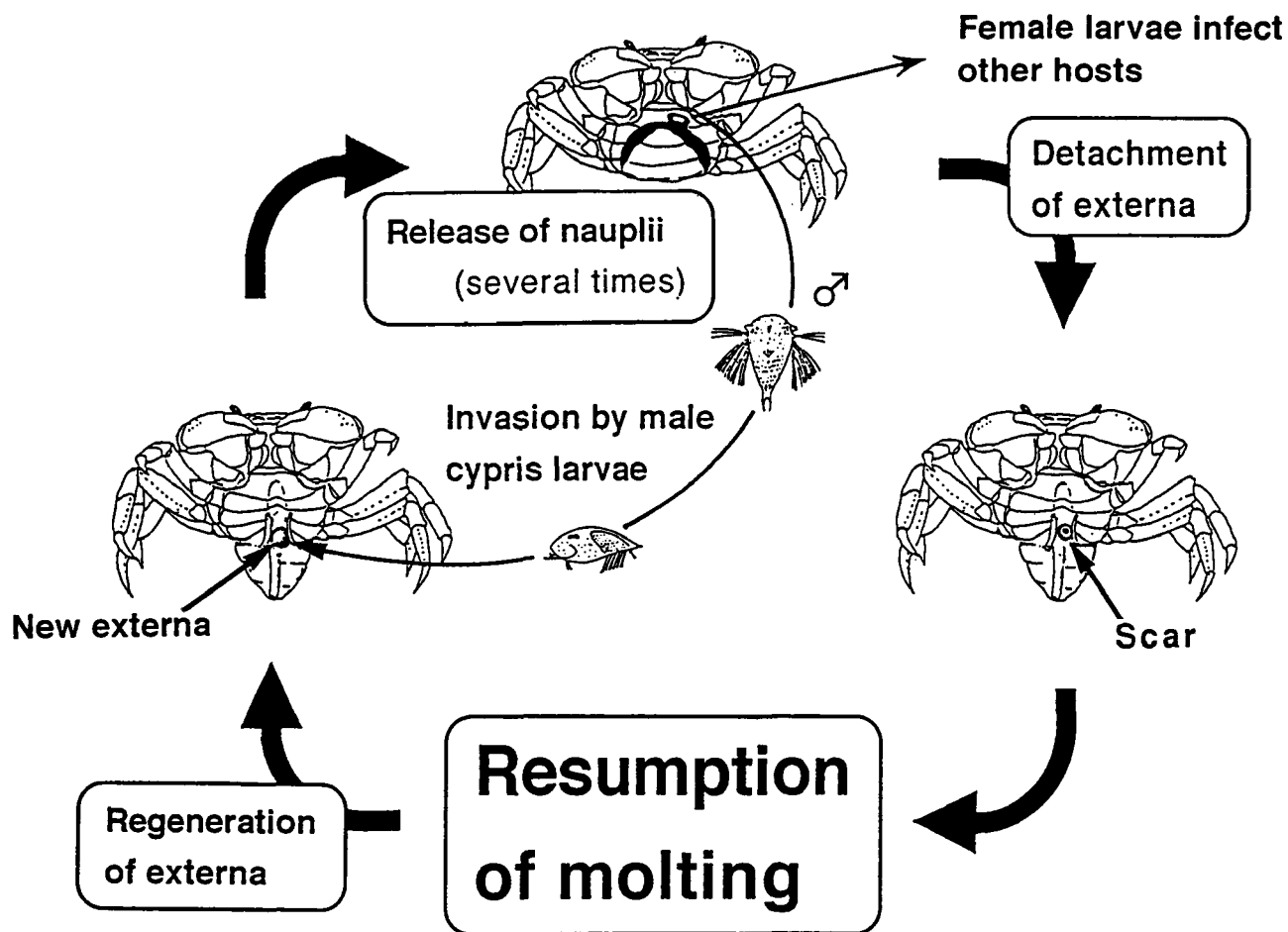
Figure 4. Relationship between the reproductive cycle of *Sacculina senta* and the molting of the host.

Literature Cited

Day, J. H. 1935. The life-history of *Sacculina*. *Q. J. Microsc. Sci.* **77**: 549–583.

Hartnoll, R. G. 1967. The effects of sacculinid parasites on two Jamaican crabs. *J. Linn. Soc. (Zool.)* **46**: 275–295.

Hawkes, C. R., T. R. Meyers, and T. C. Shirley. 1987. Growth of Alaskan blue king crabs, *Paralithodes platypus* (Brandt), parasitized by the rhizocephalan *Briarosaccus callosus* Boschma. *Crustaceana* **52**: 78–84.

Heath, J. R. 1971. Seasonal changes in a population of *Sacculina carcini* Thompson (Crustacea: Rhizocephala) in Scotland. *J. Exp. Mar. Biol. Ecol.* **6**: 15–22.

Hiatt, R. W. 1948. The biology of the lined shore crab, *Pachygrapsus crassipes* Randall. *Pac. Sci.* **2**: 135–213.

Høeg, J. T. 1982. The anatomy and development of the rhizocephalan barnacle *Clistosaccus paguri* Lillgeborg and relation to its host *Pagurus bernhardus* (L.). *J. Exp. Mar. Biol. Ecol.* **58**: 87–125.

Høeg, J. T. 1985a. Cypris settlement, kentrogon formation and host invasion in the parasitic barnacle *Lernaeodiscus porcellanae* (Müller) (Crustacea: Cirripedia: Rhizocephala). *Acta Zool., Stockh.* **66**: 1–45.

Høeg, J. T. 1985b. Male cypris settlement in *Clistosaccus paguri* Lillgeborg (Crustacea: Cirripedia: Rhizocephala). *J. Exp. Mar. Biol. Ecol.* **89**: 221–235.

Høeg, J. T. 1987. Male cypris metamorphosis and a new male larval form, the trichogon, in the parasitic barnacle *Sacculina carcina* (Crystacea: Rhizocephala). *Phil. Trans. R. Soc. London B.* **317**: 47–63.

Ichikawa, A., and R. Yanagimachi. 1958. Studies on the sexual organization of the Rhizocephala. I. The nature of the 'testis' of *Peltogasterella socialis* Kruger. *Annot. Zool. Japn.* **31**: 82–96.

Ichikawa, A., and R. Yanagimachi. 1960. Studies on the sexual organization of the Rhizocephala. II. The reproductive function of the larval (Cypris) males of *Peltogaster* and *Sacculina. Annot. Zool. Japn.* **33**: 42–56.

Kurata, H. 1962. Studies on the age and growth of Crustacea. *Bull. Hokkaido Reg. Fish. Res. Lab.* **24**: 1–115.

Lützen, J. 1981. Field studies on regeneration in *Sacculina carcini* Thompson (Crustacea: Rhizocephala) in the Isefjord, Denmark. *J. Exp. Mar. Biol. Ecol.* **53**: 241–249.

Lützen, J. 1984. Growth, reproduction and life span in *Sacculina carcini* Thompson (Cirripedia: Rhizocephala) in the Isefjord, Denmark. *Sarsia* **69**: 91–105.

O'Brien, J. 1984. Precocious maturity of the majid crab, *Pugettia producta*, parasitized by the rhizocephalan barnacle, *Heterosaccus califonicus. Biol. Bull.* **166**: 384–395.

O'Brien, J., and D. M. Skinner. 1990. Overriding of the molt-inducing stimulus of multiple limb autotomy in the mud crab *Rhithropanopeus*

harrisii by parasitization with a rhizocephalan. *J. Crust. Biol.* **10**: 440–445.

O'Brien, J., and P. Van Wyk. 1985. Effects of crustacean parasitic castrators (epicaridean isopods and rhizocephalan barnacles) on growth of crustacean hosts. Pp. 191–218 in *Crustacean Issues Vol. 3*, A. M. Wenner, ed. A. A. Balkema, Rotterdam.

Reinhard, E. G. 1956. Parasitic castration of Crustacea. *Exp. Parasitol.* **5**: 79–107.

Ritchie, L. E., and J. T. Høeg. 1981. The life history of *Lernaeodiscus*

porcellanae (Cirripedia: Rhizocephala) and co-evolution with its porcellanid host. *J. Crust. Biol.* **1**: 334–347.

Veillet, A. 1945. Recherches sur le parasitisme des crabs et des Galathées par les Rhizocéphales et les Epicarides. *Ann. Inst. Océanogr.* **22**: 193–341.

Yanagimachi, R. 1961a. Studies on the sexual organization of the Rhizocephala. III. The mode of sex determination in *Peltogasterella*. *Biol. Bull.* **120**: 272–283.

Yanagimachi, R. 1961b. The life cycle of *Peltogasterella* (Cirripedia: Rhizocephala). *Crustaceana* **2**: 183–186.