The Moulting Behaviour of Palaemonetes varians (Leach) (Decapoda; Palaemonidae)

by

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(with 7 figs.)

Little is known about the number of moults and the length of the intermoult periods in the various Crustacea and yet they are of vital importance to a study of their growth. The following observations were made in the course of a two year study of the biology of the brackish water prawn, *Palaemonetes varians* (LEACH) (*P.v.* var. *microgenitor* (BOAS) of BOAS, 1889; *P.v. occidentalis* (SOLLAUD) of SOLLAUD, 1924) in British estuaries during 1955—57. The moulting histories of over one hundred individual prawns were followed in the laboratory to provide information on the number of moults per year and whether this differed in males and females. As animals do not always behave naturally in aquaria the laboratory data were checked by investigations in the field.

THE ACT OF MOULTING

Observations of the act of moulting in *Palaemonetes varians* show that the process is similar to that described by GURNEY (1923) for *Leander longirostris* (MILNE EDWARDS) and HÖGLAND (1943) for *Leander squilla* (L.). An animal about to moult stands still for one or two minutes with the pereiopods and pleopods extended, the latter being aligned parallel and vertically downwards; a position which they take up only at moulting and when being cleaned by the chelipeds. The eyes and the scales of the second antennae make twitching movements; probably to help release the animal from the

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old exoskeleton. The body then becomes greatly flexed with the carapace and rostrum pointing downwards. After breakage of the cuticle between the carapace and the intercalary sclerite the cephalothorax is gradually drawn out of the old carapace. A pause follows as the antennae are withdrawn, the pereiopods and the whole of the abdomen remaining in the old shell. The moult is completed by a flick of the abdomen which causes the animal to leap upwards. The actual process of moulting takes only 20 seconds. On landing from the liberating leap, the animal falls onto its side as the pereiopods are too pliable for standing. After four to five minutes the newly moulted prawn is able to swim using the pleopods; which it does for long periods. An hour after moulting it is capable of standing and walking. During the soft period the newly moulted animal is liable to attack by other *Palaemonetes* as soon as their antennae touch its body; several were killed in this way. Soft *Palaemonetes* may also be found in the field in a partly eaten condition showing that similar attacks are successful outside the confines of aquaria. Moulting proceeds both during daylight and darkness.

LABORATORY INVESTIGATIONS

Methods

A study of *Palaemonetes varians* in the field (JEFFERIES, 1958) showed that the life cycle is of 2 years duration (Fig. 1). The larvae hatch in June, July and August. Breeding among the larger prawns occurs in the following summer. Females hatching from the late broods, however, do not breed until their third summer; at which time the animals hatched in June are breeding for the second time. Death usually occurs during the third summer after breeding has been completed. The three moulting seasons, 0—6 months, 6—18 months and 18—24 months were studied in 3 groups of animals in the laboratory during the 12 months of 1956 and the early part of 1957. As in JEFFERIES (1958) measurement was made of the carapace plus rostrum of the experimental animals rather than the total length.

Group A (0—6 months): Moulting during the first 6 months of

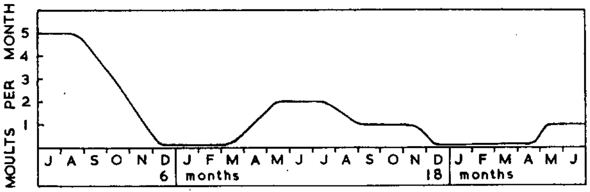

Fig. 1. The complete moulting cycle showing diagrammatically the three moulting seasons which occur during the course of the two-year life cycle.

life was followed in 28 unsexed 1956-hatched animals collected in September 1956. All had a carapace length of less than 6 mm. The early moulting history was obtained from 2 animals which hatched in the laboratory during August 1956.

Group B (6—18 months): Moulting during the first breeding season was followed in 38 female and 33 male, 1955-hatched animals collected at the end of November 1955. The carapace length varied from 6.9 to 14.6 mm in the females and from 7.4 to 12.0 mm in the males; the former grow to be larger than the latter.

Group C (18—24 months): Moulting during the last 6 months of life and the second breeding season was followed in 8 female and 2 male, 1954-hatched animals collected at the end of November 1955. The carapace length varied from 17.4 to 21.1 mm in the females and 14.0 to 15.2 mm in the males.

All the experimental animals were collected from a pool situated alongside the sea wall at Moreton in Cheshire.

Breffit jars were used as aquaria. These were prepared by three-quarters filling them with 50% sea water and 50% matured Liverpool tap water and covering the bases with sand. As far as possible, four *Palaemonetes* were placed in each jar; 2 males and 2 females. The animals for each Breffit were selected on their rostral formula (the rostral armature varies from 2 to 8 teeth dorsally and 1 to 4 teeth ventrally, with a formula of 5/2 the most common) so that each cast exoskeleton could be allotted to a definite animal. They were fed on the green alga, *Ulva*, and Tubificid worms. After preparation the Breffits were placed out in the open to follow the normal winter and summer temperatures of 1956. The water temperature was taken daily at midday so that the mean temperature for each month could be calculated. The jars were examined for cast exoskeletons daily during the summer and on alternate days in the winter. Frequent examination was necessary as the exuvium is often eaten. In this way the moulting history of each individual was noted. The weekly percentage moult (the number of moults in each weak calculated as a percentage of the number of animals starting that week) was also calculated separately for the two sexes. Initiation of moulting appears to occur when the temperature rises above a certain level in the spring (JEFFERIES, 1958). This initiation of moulting at one time causes the appearance of regular peak moulting weeks in which most of the population will moult (Figs. 2 and 3). The usual moulting paths of both sexes of *Palaemonetes* were obtained by counting these peaks and comparing with individual records. By taking the individual animals moulting in the peak week and calculating the mean inter-moult period before their next moult, the mean number of days between the peaks was also found.

Moulting in the three age groups of *Palaemonetes*

Group A: The number of moults during the first six months of life.

The weekly percentage moult in the 28 animals is shown in Fig. 2. Examination of individual moulting records showed that the number of moults in this age group could not be obtained by counting the peaks. This was because the young animals were moulting too frequently for this type of analysis. A typical history is given for one animal in Table I. Some animals ended the season's moulting in late November (As No. 1 and No. 3 in Table I) whilst others moulted again in early December. The former animals were able to moult again in early January, probably due to the mild winter of 1956—57 (Fig. 4); the latter, however, did not moult again until the start of the following season (mid-February). The number of moults in the second season (6-18 months) can be followed easily from the final part of Fig. 2, the moults and their peaks being well separated. The final part of Fig. 2, of course, is equivalent to the first section of Fig. 3; in Fig. 2, however, the sexes are not separated.

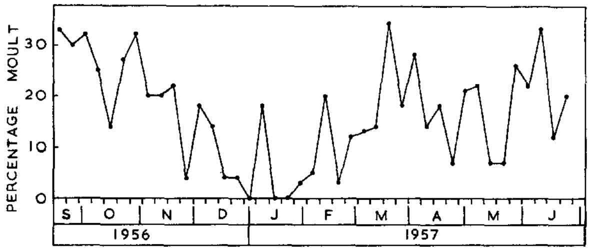

Fig. 2. The weekly percentage moult of 1956-hatched (Group A) animals (the number of moults per week expressed as a percentage of the number of animals entering that week). The period shown covers the last few months of the first moulting season and the first few months of the second. The sexes are not separated.

The early moulting history was obtained from 2 animals which were reared from a brood which hatched in the laboratory during the night of 3—4 August 1956. After the sixth larval moult one became post-larval on 10 September (38 days) and the other on 15 September (43 days). (There are normally 6 larval stages and thus 6 moults before the post-larval stage is reached (GURNEY, 1924).) Their moulting histories and intermoult periods are shown in Table I. These show that an animal hatched in early August moults 15 times (counting the larval moults) before the end of the season; a period of only 5 months. At first the intermoult periods are very short

TABLE I.

Moulting histories of three 1956-*hatched (Group A) animals from September* 1956 *to January* 1957.

Moult	Hatched in laboratory 3—4 Aug. 1956		Hatched in field 1956 No. 3)
	No. 1) Post larval Sept. 10	No. 2) Post larval Sept. 15	
6	Sept. 10 (3 days)		
7	Sept. 13 (4 days)	Sept. 15 (5 days)	
8	Sept. 17 (5 days)	Sept. 20 (5 days)	
9	Sept. 22 (7 days)	Sept. 25 (5 days)	Sept. 21 (6 days)
10	Sept. 29 (7 days)	Sept. 30 (7 days)	Sept. 27 (9 days)
11	Oct. 6 (7 days)	Oct. 7 (7 days)	Oct. 6 (16 days)
12	Oct. 13 (10 days)	Oct. 14	
13	Oct. 23 (13 days)	died	Oct. 22 (8 days)
14	Nov. 5 (26 days)		Oct. 30 (31 days)
15	Dec. 1		Nov. 30
	Jan. 9		Jan. 9

(3—7 days). Later as autumn progresses the periods lengthen. The animals caught at Moreton had similar moulting dates and numbers of moults per month (Table I), although probably not of the same age as the laboratory reared animals. It is probable that during these first few months of life, the number of moults per month is governed more by the temperature during that month than by age. As Table I shows, there are about 5 moults in each of the warmer months, this means that any animals hatching in early July would probably complete at least 20 moults before the end of the season. Similarly those hatching in early June would complete at least twenty five. Thus during the first six months of life there may be from 15 to 25 moults according to the date of hatching.

Group B: The number of moults during the period 6 to 18 months; the first breeding season.

Moulting in the Females:

In the Caridea the developing eggs are attached by "cement" to ovigerous setae on the pleopods (YONGE, 1937). These setae only appear on the integument at the moult preceding copulation and egg-laying. The long egg-carrying or berried intermoult interrupts moulting in the female in summer as moulting cannot be accomplished until the eggs have hatched. The ovigerous setae are lost at the moult after hatching; the next intermoult being normal. The modified integument, or breeding dress of *Palaemonetes varians* (Jefferies, 1958) is very similar to that described for *Leander squilla* (Högland, 1943).

Twenty five females in this age group became berried during the course of 1956. The dates at which berrying occurred were: early May, 7; late May, 13; early June, 1; late June, 2; early July, 2. Only 3 females berried twice in the season. Thirteen of the smaller females did not become berried; probably because they were immature. Dividing the berried females into size groups (Table II) shows that the larger females tended to become berried before the smaller. The weekly percentage moult is shown in Fig. 3. This was constructed from the moulting data of all the females present; it reflects the moulting path of the majority rather than of the several minorities. Individual records follow this path closely but occasional moults are missing; presumably due to exuviae being eaten before being noted.

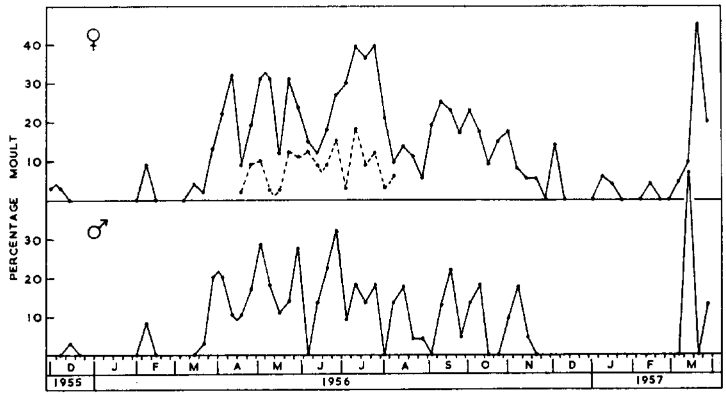

Fig. 3. The weekly percentage moult of 1955-hatched (Group B) animals covering the second moulting season and the first month of the third. The lower broken line in the graph for females represents the females not berrying during 1956 (the number of moults per week in these 13 females is expressed as a percentage of the total number of females in the experiment).

Moulting path of females berried in late May: The majority of the breeding females followed this path. Fig. 3 shows 9 peaks between the beginning of April and the end of November; each peak corresponding to a moult. No animals moulted in January but four females moulted in the week of 5—11 February 1956. However, the previous week was very cold and a rapid increase in water temperature from — 1°C to 8°C in 3 days appears to have been the moulting stimulus. This moult was very unlikely to have taken place in the field owing to the larger amount of water involved and the fact

TABLE II.

Breeding of 1955-hatched (Group B) females in 1956; the effect of size of female on date of berrying (B indicates a second berried moult).

Carapace size-group	Date of berried moult					
	E.May	L.May	E.June	L.June	E.July	L.July
14—16 mm.	2	1	—	—	1	—
12—14 mm.	5	5	1	1	1 + B	B
10—12 mm.	—	7	—	1	—	B

that the warm period lasted only 3 days. The normal moulting season appears to start in March. Only 2 females moulted in mid March, the main body moulting for the first time for the season in very late March and early April with a peak in the week of 8—14 April. After a mean intermoult period of 26 days the next moult occurred in early May. There was then a shorter intermoult period of 21 days before the berried moult when these females mated. The berried intermoult lasted for an average of 43 days in the animals berrying in the peak week of 20—26 May; the moult after hatching occurring in early July. Moults then took place in late July and early August, September, October and November with intermoult periods of 15, 17, 27, 27 and 35 days respectively. An intermoult period of 140 days followed the moult of early November. A few females moulted in December, January and February. These, however, were all animals which did not moult until late in October and thus missed the usual moult of early November. The long intermoult period after the November moult shows that this was normally the last moult of the second season in 1956. Moulting started earlier in 1957 with the first peak in the week of 17 to 23 March; three weeks earlier than in 1956. The above moulting path is summarised in Table III. It shows that in females berrying in late May there are 9 moults in the season from late March to November.

The moulting paths of females berrying at dates other than late May were found by examination of individual moulting records. These follow a set pattern similar to the one described above.

Moulting path of females berried in early May: Seven females berried during early May. The moulting record of the following individual is typical of the seven. Moults occurred on 6 April, 10 May, berried until 22 June, 7 July, 18 July, 1 August, 12 September

TABLE III.

Possible moulting paths of Group B females during the period 6 *to* 18 *months; the first breeding season.* (M indicates a normal moult, B a berried moult and an arrow, the berried intermoult period).

Month	1. Usual path: Berry Late May	2. Berry Early May	3. Berry Early June	4. Berry Late June	5. Berry Early July	6. Berry twice: 1st time early May	7. Berry twice: 1st time late May	8. Not Berried
Apr. Early	M	M	M	M	M	M	M	M
Late	—	—	—	—	—	—	—	—
May Early	M	B	M	M	M	B	M	M
Late	B	|	M	M	M	|	B	M
June Early	|	↓	B	M	M	↓	|	M
Late	↓	M	| ↓	B	M	M	↓	M
July Early	M	M	M	| ↓	B	B	M	M
Late	M	M	M	M	|	|	B	M
Aug. Early	M	M	M	M	↓	↓	|	M
Late	—	—	—	—	M	M	↓	—
Sept. Early	M	M	M	M	M	M	M	M
Late	—	—	—	—	—	—	—	—
Oct. Early	M	M	M	M	M	M	M	M
Late	—	—	—	—	—	—	—	—
Nov. Early	M	M	M	M	M	M	M	M
Late	—	—	—	—	—	—	—	—
No of moults	9	9	10	10	10	8	8	11

and 6 October. It is possible that the moult of early November was missed in this animal as others of the seven moulted at this time. Thus as before there are 9 moults in the season (Table III). As seven females followed this path it is shown to be the second commonest path in the experiment. It has an effect on the outline of Fig. 3. The moult at which these females berried, of course, is shown by the second peak. The projection on the left hand side of the large double peak of July is caused by the finish of the above berried intermoult; the moult after hatching occurring in the last week of June.

Moulting path of females berried in early June: Only one of the females berried in early June. Its record shows which moults are undertaken by animals berrying at this time of year. Moults occurred on 4 April, 1 May, 18 May, 9 June, berried until 15 July, 27 July, 7 August and 24 September. This moulting path is summarised in Table III. There are probably 10 moults in the season; moults of October and November being missing in the above record.

Moulting path of females berried in late June: Two females berried during late June. Unfortunately their moulting record is rather incomplete. One of them berried on 16 June and moulted again on the 23 July; the other berried on 23 June and finished its berried intermoult on 31 July. The data from individuals berrying in early July, below, show that it is probable that these animals moulted twice in June. Their moulting paths would then be as summarised in Table III with 10 moults in the season.

Moulting path of females berried in early July: Two females berried during early July. The record of the following individual is typical, with moults occurring on 3 May, 23 May, 2 June, 22 June, 11 July, berried until 18 August, 13 September and 9 October. There are probably 10 moults in the season, the moults of early April and early November being missing is the above record (Table III).

Females berrying twice; first time in early May: Three of the females berried twice in the season. One of these berried for the first time in early May and two in late May. It is probable that there is not enough of the summer left for a second berrying if the first is later than late May. The female which berried for the first time in early May moulted as follows. First on 2 April then 7 May when it was berried until 25 June. It then moulted again on 11 July when it was berried until 22 August. Moults then occurred on 13 September and 15 October. There are probably only 8 moults in the season in this case, the one for early November being missing from the above record (Table III).

Females berrying twice; first time in late May: Two females followed this path. One of these moulted as follows. First on 3 May, then on 26 May when it was berried until 9 July. It moulted again on 27 July when it was berried until 10 September. Moults then occurred on 1 October and 3 November to finish the season. The other female moulted and berried as above but moulted first on 6 April. It would thus appear that in the first female the first moult was overlooked and 8 moults take place in the season (Table III). It will be seen that in all three females berrying twice there was only one normal intermoult period between the two berried intermoults. During this normal intermoult the integument does not carry the ovigerous setae of the female "breeding dress". A completely new set of setae is derived at the moult before the second berrying.

Moulting path of females not berrying during the 1956 season: Thirteen small, immature females did not become berried during the experiment. Although their moulting data had already been integrated in Fig. 3, a separate weekly percentage moult was calculated for these animals. The number of moults was calculated as a percentage of the total number of females in the experiment so that the resulting graph could be incorporated in Fig. 3 (broken line). The results clearly show that these small animals moult twice in May, June and July and thus complete 11 moults in the season. The mean durations of the five consecutive intermoult periods between the moults of early May and late July were 22, 18, 19, 14 and 15 days. A summarised path is given in Table III.

Moulting in the Males:

As in the females, the second moulting season began in March (Fig. 3). The first moult, however, was earlier in the males than it was in the females. This would seem to be the usual occurrence as the same thing happened in 1957. The first peak moults in 1956 and 1957 were, respectively, 25 March—7 April and 10—16 March in the males and 8—14 April and 17—23 March in the females. This first peak is followed by nine others between March and November; each representing a moult. The second moult followed 28 days after the first in late April—early May. Moults then occurred in late May—early June, late June, early and late July, mid August, late September and early October and November with mean intermoult periods of 23, 21, 24, 15, 20, 24, 21 and 31 days, respectively. A mean intermoult period of 127 days followed the last moult of the season in early November. Thus the males of 6—18 months moult 10 times in the season.

Group C: The number of moults during the last six months of life; the second breeding season.

The moulting histories of the eight females are given in Table IV. It shows that most of these animals berried at the moult occurring during the period of late April—early May as did the largest females in Group B (Table II). In four instances this was the first moult of the season. Of 34 two-year-old females which became berried in laboratory conditions in other experiments all did so on their first moult. Thus it is likely that the initial moult of the two-year-old females occurs at the time of the second moult of the younger animals; this first moult also being the berried moult. This theory is supported by the fact that when the 1955-hatched (Group B) females had reached the age of nearly two years in the spring of 1957, they first moulted and became berried in March (Fig. 3); this being the time of the second moult of the 1956-hatched animals (Fig. 2). A few females do, however, complete the earlier moult, as is shown by Table IV.

TABLE IV.

Moulting histories of eight Group C females during the period 18—24 *months; the second breeding season* (M indicates a normal moult, B a berried moult and an arrow, the berried intermoult period).

Month		Length of Carapace in mm.							
		1. 17.9	2. 17.4	3. 19.7	4. 19.9	5. 19.8	6. 19.1	7. 21.1	8. 17.4
Apr.	Early	M	M	—	—	—	—	—	—
	Late	—	—	—	—	—	B	M	—
May	Early	B	B	B	B	B	↓	—	M
	Late	│	│	│	│	│	Died	B	M
June	Early	↓	↓	↓	↓	↓		│	M
	Late	M	Died	M	M	M		↓	M
July	Early	—		M	M	M		M	B
	Late	M		M	M	M		Died	│
Aug.	Early	Died		—	M	—			↓
	Late			—	—	M			M
Sept.				Died	Died	Died			Died

The moulting records given in Table IV show that moulting continued in these females after the hatching of the larvae. Where this occurred it followed the pattern of the younger females which also berried at this date (Table III). It is unlikely, however, that moulting continues in the field. Histograms from field samples at Moreton (JEFFERIES, 1958) show that the majority of these females died after finishing the berried intermoult period. It is probable then that there are usually only two, or occasionally three, moults in the final moulting season of the females. The laboratory females may have survived breeding because of the uniform conditions in captivity; the salinity, for instance, was constant throughout the year.

Unfortunately, the two males died before the start of the moulting season so accurate moulting histories for the two-year-old males are lacking. However, comparison of Figs. 2 and 3 shows that, as in the females, the time of the first moult of the two-year-old males coincides with that of the second of the one-year-old animals.

MOULTING AND TEMPERATURE

In *Palaemonetes varians* initiation of moulting in the spring has been found to be actuated by the rise in water temperature (JEFFERIES, 1958). The level of the temperature required seems to be universal in all the animals of one sex as is shown by the appearance of regular peak moulting weeks (Fig. 3) in which most of the population moult. The fact that the males moult before the females in the spring may be because they have a slightly lower initiating temperature. Results from the above laboratory experiment suggest that this is about 9—10°C. In 1956, this temperature was not reached in the Breffits until mid-March; examination of Fig. 3 shows that this was the time when the first cast exoskeletons were found (discounting the isolated moults occurring during February which were due to a sudden 9°C rise in temperature). In 1957, the winter and spring were much warmer and a temperature of 10°C was first reached at the end of January (though the temperature decreased slightly for a short period afterwards). Fig. 2 shows that the second season's moulting started much earlier in 1957 than in 1956, in fact, at the beginning of February.

Once the moulting cycle has been initiated it follows the temperature cycle fairly closely (Fig. 4). In 1956 moulting ended for the majority of the population at the end of November; at which time the mean monthly temperature had again dropped to 9.9°C. However, occasional moults occur in individual animals during the winter months, as is shown by Fig. 3. These moults are largely occasioned by rapid increases in temperature over a few days. Moults may occur

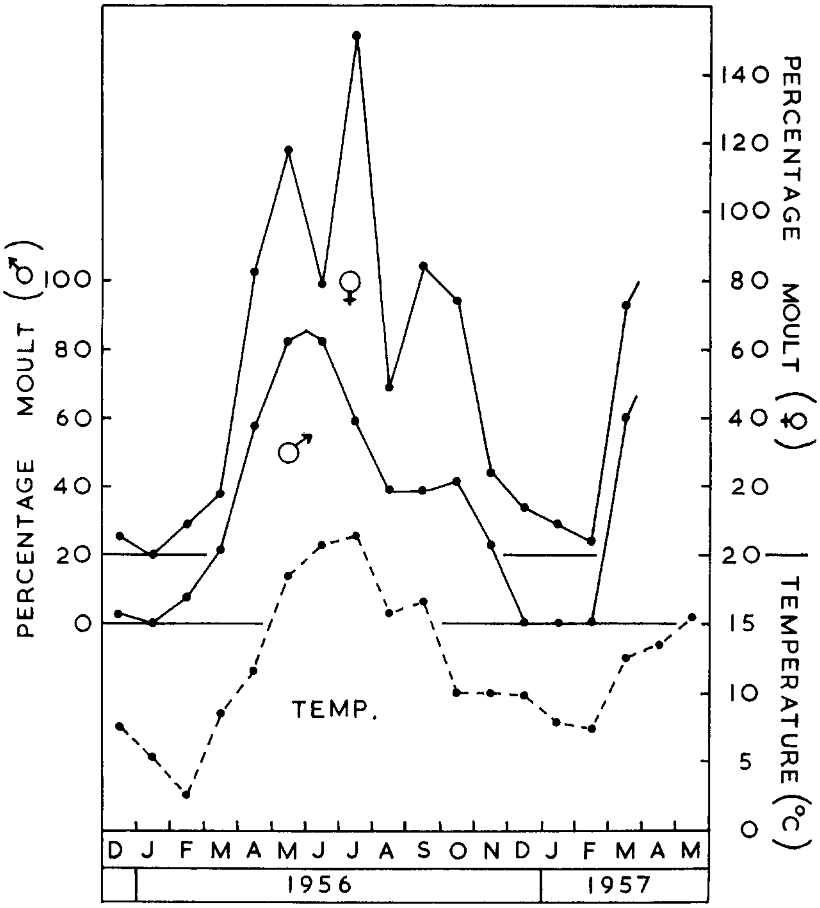

Fig. 4. The monthly percentage moult of 1955-hatched (Group B) animals (the number of moults per month expressed as a percentage of the number of animals alive at the start of that month). The monthly means of the daily water temperature readings are also shown for purposes of comparison (broken line).

in this way at temperatures several degrees below the usual moulting temperature of the majority of the population.

The Intermoult period

The mean of the individual intermoult periods after moults occurring in each month was calculated for both sexes of Group B (Table V). The results clearly show the effect of temperature. There is a reduction in the period with the increase in temperature as the summer progresses; the shortest interval between moults occurring in July, the warmest month of the summer (Fig. 4). The variations

TABLE V.

Mean intermoult periods of 1955-*hatched (Group B) animals after moults occurring in each month of* 1956. *Minimum and maximum intervals given in brackets.*

Month	Mean intermoult period after a moult occurring in that month (in days)	
	Females	Males
1955		
December	111.0 (111)	—
1956		
February	56.3 (49—63)	—
March	29.7 (25—39)	25.0 (20—28)
April	27.1 (13—44)	24.8 (17—31)
May: Normal	20.7 (10—35)	22.5 (13—35)
Berried	43.3 (38—49)	
June: Normal	18.5 (14—31)	21.0 (14—29)
Berried	38.2 (36—42)	
July: Normal	14.6 (11—21)	16.7 (11—20)
Berried	42.0 (38—45)	
August	24.2 (15—33)	20.0 (13—26)
September	26.2 (17—39)	24.1 (18—38)
October	36.1 (29—45)	31.2 (29—33)
November	133.2 (123—140)	124.5 (122—127)

in the intermoult period with temperature are greater in the females than they are in the males. In the females the period varies from 30 days in March to 15 days in July and back to 36 days in October. Whereas in the males these periods are 25, 17 and 31 days respectively. Thus, compared with the males, the females have a longer intermoult period when the water is cold and a shorter one when it is warm. The result is that there is little difference between the sexes in the number of moults in the year.

THE BERRIED INTERMOULT PERIOD

During the berried intermoult periods the developing eggs were examined daily in order to determine the durations of the various stages of embryonic development. This information enables one to estimate the number of days which have elapsed since the previous moult of a female bearing eggs. Thus it is useful for correlation with data obtained on the moulting in the field.

The four stages into which the berried females were divided were:

B 1: This stage extends from the time when the eggs are first laid to the time when the eyes of the embryo first become pigmented.

B 2: This stage continues from the point at which the eyes have begun to be pigmented until the embryo is so large that the yolk does not take up more than a quarter of the volume of the egg.

B 3: This stage comprises the last stage of development up to and including hatching.

B 4: The "cemented" stage. This stage lasts the few days between the act of hatching and the moulting of the breeding dress.

The first period is the longest of the four and covers over half of the embryonic development. The start of the second stage and the appearance of the eyes can easily be observed with the naked eye without the possible harm to the animals caused by removal from the water and examination under a microscope. During this second stage the egg retains the dark olive green colour of the yolk; the start of the third stage being apparent when the egg and embryo have become almost completely transparent. The eyes of the third stage are clearly seen as circular black spots; in the second stage they are merely black lines. The last stage is usually very short, lasting only a few days.

The mean duration of these stages after berried moults occurring in early and late May, June and July are given in Table VI (the table also includes the data on two females maintained in similar conditions but in an unrelated experiment). The intervals given in Table VI are the numbers of days elapsing from the berried moult to the end of each of the four stages of the intermoult. It will be seen that as the summer progresses the embryonic development periods get shorter; after June, however, the periods lengthen. At first sight it may be thought that the length of the development period does not follow the temperature cycle; the shortest periods following berried moults occurring in June and not July. It must be remembered, however, that females berrying in June have the embryonic development period extending over July whereas females berrying in July, although they berry in the warmest month of the year, have the development period extending over August. In 1956 August was much cooler than the preceding month. Note that in the animals berrying in July, the early part of development, stage B 1, was shorter than the corresponding period of animals berrying in June. This, of course, is due to the fact that this period was spent in July in the July breeding animals and in June in their June breeding counterparts. The embryonic development period thus follows the temperature cycle very closely; the higher the temperature the shorter the period.

TABLE VI.

The mean durations of the four stages of the berried intermoult period after breeding moults occurring in May June and July. Data from 1954 and 1955-hatched females maintained in aquaria during 1956. Figures in brackets refer to the minimum and maximum intervals and also the number from which the mean was calculated.

When Berried	Mean number of days from the berried moult until the end of stages:				
	B. 1. No. of days until embryos eyed	B. 2. No. of days until embryos transparent	B. 3. No. of days until hatching	B. 4 No. of days until moulting	Period between hatch & moult
Early May	24.7 (21-27)(4)	32.4 (30-35)(5)	41.6 (37-45)(5)	45.4 (43-49)(5)	3.8 (2-6)(5)
Late May	26.1 (24-27)(7)	33.3 (32-35)(3)	39.5 (36-41)(10)	41.9 (38-45)(12)	2.6 (1-5)(11)
Early June	24.7 (21-27)(3)	31.0 (28-35)(3)	36.0 (33-40)(3)	39.0 (36-42)(3)	3.0 (2-4)(3)
Late June	21.0 (21) (1)	28.0 (28) (1)	35.0 (35) (1)	37.0 (37) (1)	2.0 (2) (1)
Early July	20.0 (20) (2)	—	37.0 (36-38)(2)	40.7 (38-42)(3)	5.0 (4-6)(2)
Late July	23.0 (22-24)(2)	26.0 (26) (1)	39.0 (37-41)(2)	44.0 (43-45)(2)	5.0 (4-6)(2)

In some instances females lost the eggs after becoming berried. This took place in two ways. In some animals the eggs were dropped within an hour of their release from the ovary. These eggs never became cemented to the ovigerous setae; as soon as the brood chamber, formed by the pleopods, was disturbed, all the eggs dropped out. Examination of the eggs showed that they lacked the outer membrane of cement and the twisted strands of cement which usually tie the eggs together in the brood chamber. Thus in these animals no cement was produced by the tegumental glands of the pleopods. In other animals, the eggs remained cemented to the ovigerous setae for some days after berrying. They then began to drop out until after about a week there were none left. In these cases cement was produced but was apparently deficient in some factor. It was probably too brittle and the eggs were lost when the tying strands were broken by pleopod movements. The eggs were quickly eaten when lost but I have never seen a female remove eggs from the pleopods for the purposes of food. The second method of losing eggs was found to be by far the commonest.

A few mature females were maintained in 50% sea water without the presence of males. It was found that when the females moulted into the breeding dress, although copulation had not occurred, the eggs were always released within 24 hours of moulting. This fact was also noted by HÖGLAND (1943) for *Leander squilla.* As in the latter animal these unfertilised eggs rolled out of the brood chamber as soon as the female moved after egg laying. There was no production of cement in either *Palaemonetes* or *L. squilla.* In the above reported cases in which the eggs were lost immediately after laying, it is probable then that no copulation took place. Only in two such instances was the intermoult period determined. The interval after an unsuccessful berried moult in late May was 22 days in one case and 17 days in the other. Thus the intermoult period is normal (short) in females which lose their eggs quickly due to lack of cement production.

In the second group of females which lost their eggs after bearing them cemented for a few days, the eggs were always infertile. Any eggs remaining after about five days were always pale yellow in colour instead of the deep green of the well cemented and fertile eggs. Attempts at copulation with several of these females after their moults into the breeding dress were definitely observed. However, in none of these attempts did I see a spermatophore being passed to the female or observe a spermatophore between the last pair of pereiopods after the attempts had ceased. In these females the berried intermoult was still as long as when the eggs are retained until hatching. It was even shortened in females having the intermoult period over July compared with those having it over June. Thus in successful berried intermoults occurring after a berried moult in May, the mean intermoult period was 42.9 days (38—49 days; 17 results) and after a berried moult in June, 38.5 days (36—42 days; 4 results). In unsuccessful berried intermoults where the eggs were lost after a few days, these periods were: May, 43.2 days (43—44; 5 results) and June, 38 days (1 result).

FIELD INVESTIGATIONS

As animals do not always behave naturally in aquaria, some check on moulting in the field was necessary to gauge the accuracy of the laboratory results. Although determination of the moulting rate in the field is difficult, it is possible to obtain the outline of the moulting cycle by using a method based on the appearance of calcareous concretions at the time of moulting. It has been known for a long time that calcium is removed from the exoskeleton before moulting. CHANTRAN (1874a and b) noticed the gastroliths of the larger crustacea and came to the conclusion that they were reserves of calcium removed prior to moulting and used to consolidate the new exoskeleton in the first few days after exuviation. HUSSON (1952), working on *Astacus* and *Cambarus*, killed animals at increasing intervals from their date of moulting and weighed both animals and gastroliths. His results supported CHANTRAN's theory as the gastroliths were found to decrease in size with the elapse of time from the date of moulting.

I have not found any gastroliths in *Palaemonetes;* there are, however, small spots which appear on the body at the time of moulting and which probably have the same function. Dissection of the rostrum, where these spots are at their largest, showed that they were formed of hard sub-spherical bodies situated in the lumen of the rostrum close to the cuticle (Fig. 5). When crushed they were found to be composed of a crystalline material which dissolved in concentrated hydrochloric acid. They are only noticeable in the dead specimens preserved in formalin; when alive the transparency of the body and nodules renders them difficult to see. The spots become most numerous just after moulting when they are found on many parts of the exoskeleton (rostrum, scales of second antennae, carapace, abdominal epimera, pereiopods and uropods); they then decrease in number over the following weeks. The first to go are those on the pereiopods, carapace and epimera; these not lasting more than a few days. Those on the scales and uropods last much longer but eventually go leaving just a few on the rostrum which may still be present a month after moulting. This sequence of events was discovered by examining the berried females (both 1954 and 1955-hatched) in a sample of *Palaemonetes* caught at Moreton in June 1956. The berried stage, as has already been explained, is easily split into 4 sub-stages, the durations of which were found during laboratory experiments. After division of the field sample into these

TABLE VII.

Occurrence of moulting spots or nodules in the four stages of the berried intermoult period of females caught at Moreton on 21st June 1956. The durations of the stages shown in the final column are the means of the results for May and June appearing in Table VI. In the second column figures in brackets refer to the number of animals examined.

Group	Percentage of Group bearing spots	Mean Number of spots on rostrum (Min-Max limits)	Percentage of group bearing spots on pereiopods	Mean number of rostral spots in these animals	Number of days between moulting and end of stage
B1.	75.0 (144)	3.30 (1-14)	10.4	7.00	25
B2.	44.8 (87)	2.51 (1-7)	0	—	32
B3.	4.2 (120)	2.40 (1-4)	0	—	39
B4.	3.8 (26)	1.00 (1)	0	—	42

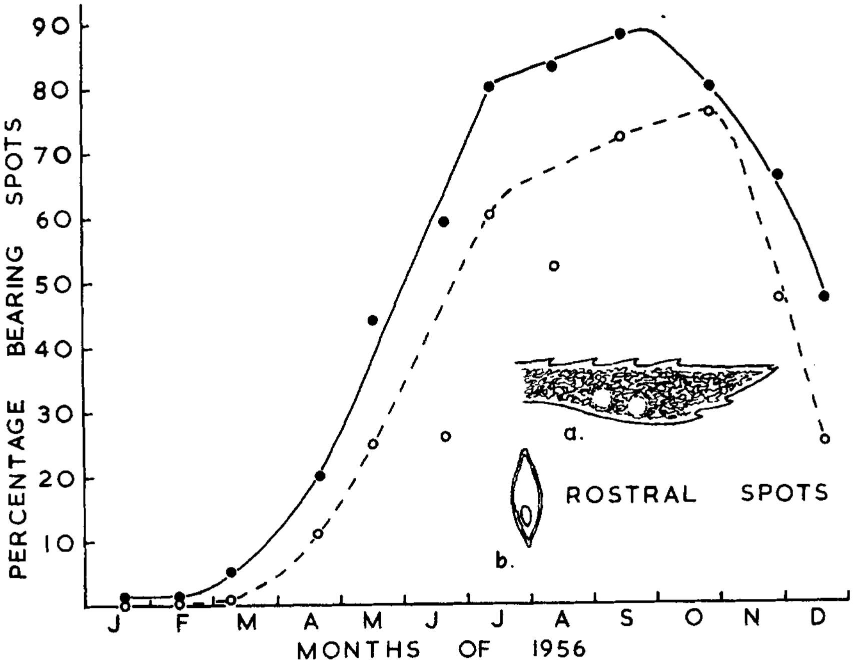

Fig. 5. Percentage of 1955-hatched animals bearing moulting spots or nodules in monthly samples caught at Moreton in 1956 (Broken line: Males; Continuous line: Females). Inset: Rostrum showing two spots (a: lateral view; b: transverse section).

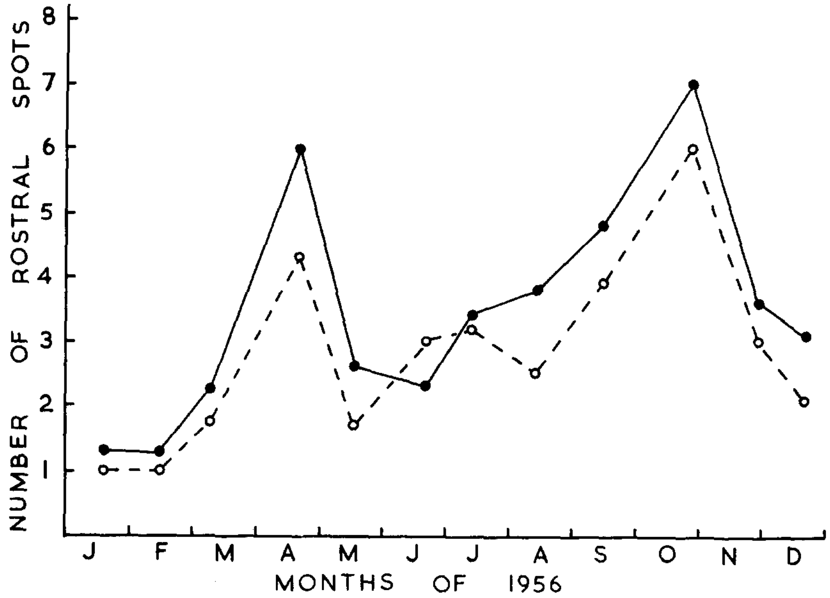

Fig. 6: Mean number of rostral spots in 1955-hatched animals caught at Moreton in 1956 (Broken line: Males; Continuous line: Females).

categories each group of animals was analysed with respect to the percentage bearing spots, the mean number of spots on the rostrum and the percentage bearing spots on the pereiopods. The results (Table VII) clearly show the reduction in the number of spots with the elapse of time from the date of moulting. The form of the nodules or spots and their connection with moulting would suggest that they were formed of calcium and performed the same function as the gastroliths of the larger crustacea. In *Palaemonetes* removal of calcium must be completed in a very short period prior to moulting as in the berried intermoult stage B 4, very few animals bear spots and none do so on the pereiopods or in the numbers found in the first few days after moulting. Replacement occurs more slowly; in some animals all spots have gone within 25 days of moulting, in others spots are still present at 42 days.

The above results, besides supporting the work of HUSSON, suggest a method of investigating the moulting cycle in the field by analysis of the usual samples. An investigation on these lines was attempted with samples obtained from Moreton in 1956. On analysis the percentage of animals bearing spots, the mean number of rostral spots and the percentage of animals bearing spots on the pereiopods was calculated for each monthly sample; the results being separated into males and females and 1954, '55 and '56 age groups. Examination

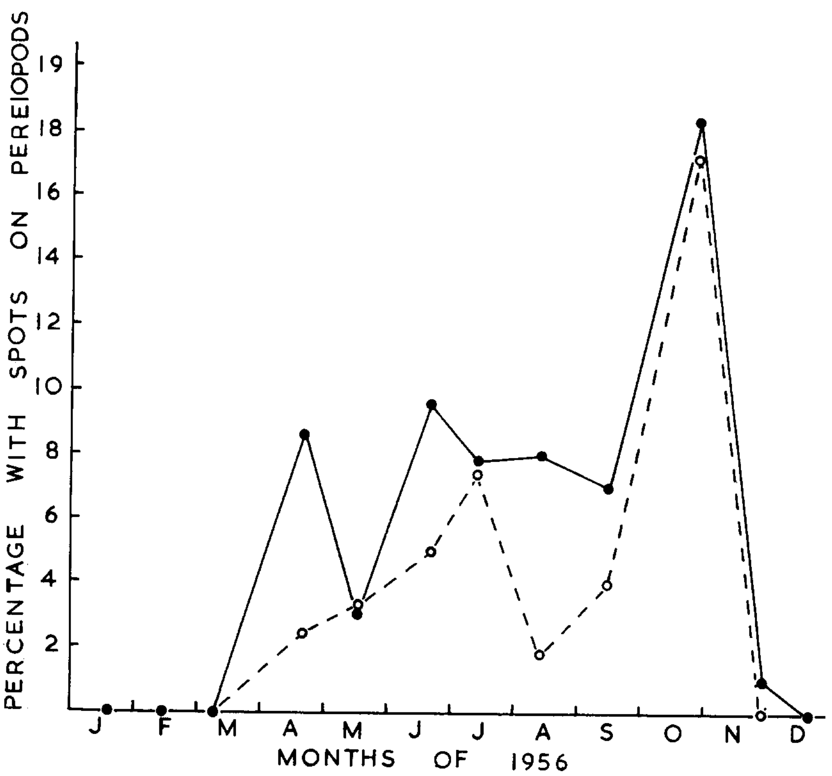

Fig. 7. Percentage of 1955-hatched animals bearing spots on the pereiopods in monthly samples caught at Moreton in 1956 (Broken line: Males; Continuous line: Females).

of the results for the monthly percentage of 1955-hatched animals bearing spots (Fig. 5 — based on a total of 4,379 males and 5,285 females) shows that moulting starts in March; this being corroborated by the discovery of exuviae floating in the water for the first time when the March sample was being collected. The percentage of animals in the population bearing rostral spots then increases rapidly, the slope of the graph being very steep up to the month of July. After July the percentage increases more slowly until October when it begins to fall to the winter level.

As might be expected, the mean number of rostral spots (Fig. 6) and the percentage bearing spots on the pereiopods (Fig. 7) varies greatly due to variation in time elapsed since the previous moult. The samples of April and October were obviously collected very shortly after moulting had occurred in many animals of the population; 42% of the females bearing spots in April and 21% of the males, also had spots on the limbs. In October these percentages were 23% and 22% respectively. Despite the variations, however, Fig. 6 shows that the number of spots on the rostrum first rises above the winter level in March and then increases as the summer progresses until October, after which the number decreases.

The explanation for the results in Figures 5 and 6 is probably to be found in the fact that the intermoult period decreases as the temperature increases in the summer, reaching a minimum in July and then lengthening again in the autumn (Table V). The above figures show that the first moults occur in March when both the percentage bearing spots and the mean number of rostral spots rises from the low winter level. During the long intermoult period following this moult the nodules are slowly reabsorbed and may disappear completely in some cases before the next moult occurs. As the intermoult periods get shorter the percentage of animals bearing spots and also the number of spots carried will increase rapidly because most of the animals never have time to reabsorb all the calcium from the previous intermoult before moulting again. This is seen on examination of Table VII. It takes 45% of the berried females 25—32 days to reduce the number of rostral spots from 7.0 to 2.5 in May and June and normal intermoult periods at this time of year are about 18 to 22 days (Table V). The high rate of increase is continued up to the month of July after which the rate decreases. This could be due to the intermoult period being at its shortest in July in the field and after this month the animals begin to catch up on their reserve calcium. After October the intermoult period has become lengthened to such an extent that most of the animals are able to remove the nodules completely before the next moult thus the percentage bearing spots and the number of spots both begin to decrease. Moulting would appear to end by December because very few animals in the population bear spots in January and February and the number of spots borne is very small. Also, after November no animals were found bearing spots on the limbs. However, some animals retained spots throughout the winter. These probably moulted in December and with the low metabolic rate of the cold months the reabsorption of calcium most likely came to a standstill; thus the spots would remain until the spring. The fact that the percentage of animals bearing spots and the mean number of rostral spots are consistently higher in females than in males (Figs. 5 and 6) does not necessarily mean that the former moult more often than the latter. As females are larger than males at any given age they may conceivably remove more calcium and so bear more spots.

The field data for the 1956-hatched animals (Table VIII) shows that the moulting rate was very high in August but decreased in

TABLE VIII.

Occurrence of moulting spots or nodules in 1956*-hatched animals caught at Moreton in* 1956 (*figures in brackets refer to the numbers of animals examined*).

Date of sample	Sex	Percentage of animals bearing spots	Mean number of spots on rostrum	Percentage of animals bearing spots on pereiopods
Aug. 13	Unknown	76.0 (25)	10.95	56.0
Sept. 14	Unknown	36.7 (248)	2.84	9.7
	Males	50.0 (10)	2.80	10.0
	Females	78.6 (14)	3.27	14.3
Oct. 25	Unknown	8.7 (138)	2.67	0.7
	Males	24.8 (113)	2.57	3.5
	Females	17.9 (145)	2.62	1.4
Nov. 28	Unknown	13.6 (44)	1.83	0
	Males	25.8 (31)	2.37	0
	Females	16.7 (42)	1.43	0
Dec. 20	Unknown	0 (85)	0	0
	Males	0 (29)	0	0
	Females	0 (28)	0	0

September and October. By December 20th moulting had ceased and all the spots had been reabsorbed.

There was insufficient material to give definite results for the 1954-hatched age group (Table IX). The percentage of 1954-hatched males bearing spots decreased from 27% to nil by April, probably due to the increase in the metabolic rate in the spring enabling the reabsorption of all the calcium left from the last moult of the previous season. However, the increase in the mean spot number for the February sample suggests that some males may moult in this month. The only other sign of a moult was in one animal in the May sample. Thus males may moult only once, perhaps twice, in their second spring; some may not moult at all.

As in the males, the percentage of 1954-hatched females bearing spots is reduced from 25% in January to almost nil by April. However, the increase in percentage and mean spot number in the March sample suggests that a few of the females may have a spring moult. In May all the 1954 females in the sample had moulted on becoming berried. By late June these females would be moulting out of the berried condition and at this time most of them would die (JEFFERIES, 1958). The small number of 1954-hatched females found berried and in the normal condition in July and August could be either representatives of the few second year females breeding twice or females (similar to No. 8 of Table IV) which did not berry until

TABLE IX.

Occurrence of moulting spots or nodules in 1954-*hatched animals caught at Moreton in* 1956 (figures in brackets refer to the numbers of animals examined).

Date of sample	Percentage of animals bearing spots	Mean number of spots on rostrum	Percentage of animals bearing spots on pereiopods
Females:			
Jan. 18	25.0 (32)	1.25	0
Feb. 15	12.5 (8)	2.00 (1 result)	0
Mar. 9	34.4 (32)	2.54	0
Apr. 19	3.8 (79)	2.33	0
May 16	Normal — (0)	—	—
	Berried 90.0 (10)	1.78	0
June 21	Normal 50.0 (2)	14.00 (1 result)	50.0
	Berried 27.8 (54)	2.93	1.8
July 13	Normal 100.0 (2)	2.50	0
	Berried 75.0 (8)	3.83	0
Aug. 13	Normal 100.0 (1)	2.00 (1 result)	0
	Berried 75.0 (4)	2.33	0
Males:			
Jan. 18	27.3 (11)	1.00	0
Feb. 15	15.0 (20)	1.67	0
Mar. 9	17.6 (17)	1.00	0
Apr. 19	0 (31)	0	0
May 16	14.3 (7)	10.00 (1 result)	14.3
June 21	1 animal — no spots		
July 13	1 animal — 1 spot.		

early July. The field data thus shows that the majority of the second year females moult at the beginning and end of the berried period and perhaps once in the spring preceding it; a total of 2—3 times before death.

On collecting the field samples the water temperature was measured and a sample analysed for chloride content. As the temperatures were only taken at monthly intervals and reflect only the temperature on the day of collection (the May sample, for example, was collected after a warm period), they are not as accurate a record as that obtained by the daily laboratory measurements. However, they provide an indication of the environment for comparison with that used in the laboratory (Table X). They show that, on the whole, temperatures were probably lower in the field than in the aquaria; possibly due to the larger volume of water. The salinity of the pool was not very different from that used in the laboratory, being just below that of 50% sea water for most of the year.

TABLE X.

Monthly water temperatures and chloride contents of the pool at Moreton and the laboratory aquaria. The laboratory results are the means of daily temperature readings whereas those for Moreton are single results.

Month of 1956	Field environment (Monthly readings)		Laboratory environment (Daily readings)	
	Water Temperature in °C.	Chloride content mg./litre	Water temperature in °C.	Chloride content mg./litre
Jan.	4.0	12,710	5.3	9,900
Feb.	1.0	8,950	2.7	,,
Mar.	7.5	6,240	8.5	,,
Apr.	9.5	7,290	11.6	,,
May	17.5	7,450	18.6	,,
June	15.5	8,520	20.9	,,
July	16.5	8,160	21.2	,,
Aug.	16.0	5,010	15.7	,,
Sept.	16.0	2,720	16.8	,,
Oct.	8.5	8,190	9.9	,,
Nov.	5.5	6,610	9.9	,,
Dec.	3.0	4,180	9.8	,,

DISCUSSION

Examination of the laboratory and field data shows that the two sections agree fairly well. Both show that moulting in the 1955-hatched animals began in March in 1956 and finished in early December with the shortest intermoult period occurring in July. Also the information on the 1954 and '56 age groups is similar and the females became berried at the same time (Tables II, IV, VII and IX). Thus it seems possible that the more detailed results of the laboratory approximate quite closely to the moulting paths which were present in similar conditions in the field in 1956. Although it is probable that the intermoult periods were not as short at Moreton as they were in the laboratory during June and July (owing to lower temperatures), other smaller pools which were sampled had summer temperatures as high as those found in the aquaria (JEFFERIES, 1958) and their *Palaemonetes* would presumably have similar intermoults. The laboratory results can thus be used to plot the moulting history and estimate the number of moults within the lifespan of one animal. This moulting cycle is shown diagrammatically in Fig. 1; the first six months being covered by Fig. 2, the centre twelve months by Fig. 3 and the last few months by Tables IV and IX.

After hatching in the summer, the larval moults follow each other rapidly at intervals of two to four days. These short intermoult periods (c. 4—5 days) are continued after the animal has become post larval until the autumn temperatures begin to decrease. There are at least five moults per month during the first few warm months decreasing to three per month by October. The moulting season ends in early December by which time the temperature has usually lowered the metabolic rate below the level at which moulting is maintained. In mild winters, such as the one of 1956—57, those animals which moulted too late in November to moult again in early December are able to moult in mid-winter (January). In this first six months of life there may be from 15 to 25 moults. The number depends on the date of hatching.

Moulting starts in the following year when the water temperature has risen to about 9—10°C. Thus moulting usually starts in March but may be as early as February in unusually mild winters. The males start to moult before the females; probably because they require a slightly lower temperature for initiation of moulting. This second moulting season extends from March to November. The number of moults occurring in this period varies. In the males there are 10 moults whereas in the females the number varies from 8 to 10 according to the dates of berrying. There are 11 moults in the females of the previous years late brood; these being too young to breed.

In the final moulting season the first moult of the majority of both males and females occurs at the time of the second moult of animals in their second moulting season (May in 1956; March in 1957). At this moult the majority of the females become berried (Table IV). A few animals of both sexes may also have an earlier moult in February or March as is shown by Tables IV and IX. Death usually occurs after breeding has been completed. The field samples of 1956 contained very few two-year-old males after May (Table IX); death probably occurs after copulation. Thus males complete only 1—2 moults in their final moulting season. The majority of two-year-old females berry at their first moult and die after finishing the berried intermoult. In 1956 this occurred at the end of June (Tables IV and IX). Thus females complete 2—3 moults in their final moulting season. A few may not berry until July or may berry twice (Tables IV and IX). Information from Table III, column 6 and Table IV, column 8 shows that these could complete 6—7 and 4—5 moults respectively (assuming death at the moult after hatching the eggs).

Summing the information presented above enables one to estimate the number of moults completed by an animal of either sex which lives for the full term of two years. Thus a male, if one of the early-hatched animals of its year, may complete 37 (25 + 10 + 2) moults but only 27 (15 + 10 + 2) if it hatches from one of the late broods. Similarly, early-brood females may complete 38 (25 + 10 + 3) or exceptionally 42 (25 + 10 + 7) moults in their life. In late-brood females these figures would be 29 (15 + 11 + 3) and 33 (15 + 11 + 7) moults respectively. These totals are quite large considering that at the time of moulting the animal is at its most vulnerable to the only common predator in its immediate environment; that is other *Palaemonetes*. It must be remembered that the above totals are not standard but relate to moulting under the temperature conditions of 1956 and a salinity of 50% sea water. Variations in the number of moults per year may occur with variations in temperature. Thus a particularly warm spring, as in 1957, may increase the number by one or two (the time of the first moult of Group B in 1956 coincides with the time of the third moult in 1957; Figs. 2 and 3). Similar increases may be expected during a warm autumn. The salinity of the water may also affect moulting rate (JEFFERIES, 1958).

Another interesting facet of the above results is the reduction in the number of moults per season as the animals grow older. During the first half-season there are 15 to 25 moults; in the second, 8 to 11 and in the third and last, only 1 to 3. Thus the moulting rate is also affected by the age of the animal. A further indication of this slowing down of the moulting "mechanism" with age is given by the data on rostral spots. In the first winter all the nodules are reabsorbed when moulting is completed for the year (Table VIII) whereas in the second, many remain (Table IX and Figs. 5 and 6).

On examination of Table VI it will be noted that when environmental conditions are such that the embryonic development period is shortened (high water temperatures), the parent females also follow the favourable conditions for a shortened intermoult and moult not long after the hatching of the larvae. The berried intermoult is thus always the right length for the embryonic development period and would make one think that the latter controls the former. Although the parent female can have no "knowledge" of the condition of the embryos, the act of hatching or maybe the release of the weight of the egg mass could provide sufficient stimulation to set the moulting "mechanism" into motion again. I have not witnessed hatching in *Palaemonetes* but HÖGLAND (1943) working on *Leander squilla* noted that the female now and then facilitates the bursting of the egg membranes and the liberating of the larvae by violently whisking her pleopods. This at least is evidence of "knowledge" of hatching. It may be stated against this theory of the length of the embryonic development period governing the length of the berried intermoult, that in females which lose their eggs after a few days (unsuccessful copulation) the berried intermoult period is still as long as when the eggs are retained until hatching. It is even shortened in females having the intermoult period during July. On the other hand, support is given by the fact that females which lose their eggs within an hour of release from the ovary, due to lack of cement production (no copulationary stimulus), have the normal short intermoult period of non-breeding females. A possible explanation is that a long intermoult period is automatic after the stimulation of either copulation or cement production irrespective of whether these are successful. The length of this long intermoult appears to be governed by both the environment and the embryonic development period. I think that the latter is probably the prime factor. The female never moults while she is still carrying the egg load but moults soon after the stimulus of its removal. In three females having the berried moult within a few days of each other in early June, the first hatched in 33 days and moulted at 36, the second hatched in 35 days and moulted in 39 but the third did not hatch until 40 days after fertilization, the moult following in 2 days time. Thus if the third female had moulted to the same environmental stimulus as the first two, the eggs would have been lost before hatching. The act of hatching appears to provide the stimulus for bringing the long intermoult to a close. When the eggs are lost early in the period, the intermoult continues automatically for approximately 40 days (varying slightly with the environmental temperature as does the normal intermoult), the females in question being unable to alter the "mechanism" set in motion by the attempted copulation and cement production. Without the stimulus of copulation the breeding intermoult appears to be controlled solely by the environmental temperature.

HÖGLAND (1943) has put forward the theory that "for the cementing of the eggs to be successful (in *Leander squilla*) the co-operation of one or more substances from the male is evidently necessary, which are undoubtedly to be sought in the packets of sperm attached by the male to the female at mating." The work reported here would support HÖGLAND's theory; female *Palaemonetes* releasing eggs without the stimulus of copulation do not produce cement. The present work also provides the information that the copulation itself (or even an attempt at copulation) stimulates the female into producing the cement. However, without the presence of the spermatophore from the male this cement would seem to be deficient in some factor and the eggs are lost. Perhaps, as HÖGLAND suggests, the spermatophore possesses the key to correct cement formation.

With regard to the growth at each moult it is unfortunate that the results of the laboratory experiment cannot be used to see if this is uniform throughout the year. This is because the animals composing the laboratory population did not grow much during the course of the experiment. However, this is a common phenomenon in animals maintained in small aquaria and does not detract from the results obtained. Histograms resulting from analysis of samples from the field (JEFFERIES, 1958) clearly show that in the period 6—18 months, growth starts in late June and continues until November. This late start is probably due to the maturation of the germ cells in both sexes. Both the laboratory and rostral spot data, on the other hand, show that moulting starts in March; this being supported by the discovery, for the first time in the year, of cast exoskeletons in the water during the collection of the March samples. This means that the first few moults of the year are not accompanied by growth. Unless the spring and summer at any locality are cooler than usual, most females berry in either early or late May. Fig. 3 shows that the former will moult 7 times from late June to the end of November, and the latter 6 times. Females too young to breed will moult 7 times before the end of November as will the males. Thus the males and females moult the same number of times within the duration of the short season of growth. The histograms also show that growth is greater in the females in this period than it is in the males. Thus the reason for the females being larger than the males must be due to greater growth at each moult.

HÖGLAND (1943) has said that "it will probably be impossible to determine how often the individual prawns moult under natural conditions." This may be possible, however, with a more extensive investigation based on the technique described in the field section. The laboratory experiment showed that the animals tend to moult together, there being peak weeks in which most of the population moult, separated by weeks in which few animals moult. As the numbers of animals which have just moulted is shown by the number bearing spots on the pereiopods then a percentage moult for each sample can be calculated. This could be used as a method for accurately finding the number of moults and the lengths of the intermoult periods in the field. In *Palaemonetes varians*, however, to get sufficient information to draw a moulting chart as shown in Fig. 3 would require weekly samples; the summer intermoult periods being much shorter than a month. My field samples were only taken at monthly intervals and the results are not frequent enough to yield the necessary detailed information. The monthly percentage bearing spots on the pereiopods is shown in Fig. 7 but shows very little except that moulting extends from March to December and that the October sample must have been taken in a peak week. If the trouble was taken to collect weekly samples and analyse them in the way mentioned above, then valuable information as to the moulting cycle in the field would be obtained. This method might also be applicable to other Crustacea showing similar external signs of a recent moult.

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SUMMARY

1. The moulting behaviour of the brackish water prawn, *Palaemonetes varians* (LEACH), was studied both in the laboratory and in the field during 1956.

2. Laboratory investigations showed that after hatching from June to August, the young animals completed from 15 to 25 moults before late November when moulting ceased for the winter. The second moulting season began in March when the temperature had risen to 9—10°C and continued until November. In this period males completed 10 moults and females 8 to 11 moults depending on the date of breeding. In the third and final moulting season the first moult of both sexes occurred at the time of the second moult of the second season. Only 1—2 moults were completed by the males and 2—3 moults by the females before death occurred after breeding during May—July. The intervals between the moults decreased from March to July, the warmest month investigated, and then increased from July to November.

3. Investigations based on the appearance of calcareous concretions at the time of moulting showed that moulting in the field started at the same time and continued over the same months as in the laboratory.

4. Comparison with growth measurements obtained in a previous study showed that moulting occurred without growth from March to June. During July to November growth at each moult was greater in females than in males.

5. More extensive use of the technique applied in the field investi-

gations could give complete data on the moulting behaviour of *Palaemonetes* under natural conditions. The technique may also be applicable to other Crustacea.

RÉSUMÉ

1) Le comportement de mue de la crevette d'eau saumâtre, *Palaemonetes varians* (LEACH), a été étudié tant en laboratoire que sur place au cours de 1956.

2) Les recherches en laboratoire ont montré qu'après avoir éclos de juin à août, les jeunes animaux ont fait de 15 à 25 mues avant la fin novembre, moment où la mue cesse alors pour l'hiver. La deuxième saison de mue a commencé en mars, quand la température s'est élevée à 9 à 10°C, et s'est poursuivie jusqu'en novembre. Au cours de cette période, les mâles ont fait 10 mues et les femelles de 8 à 11 mues, suivant la date de reproduction. Pendant la troisième et dernière saison de mue, la première mue des deux sexes s'est produite lors de la deuxième mue de la deuxième saison. Les mâles n'ont fait qu'une ou deux mues, les femelles que 2 à 3 mues avant que la mort survienne après la reproduction dans la période mai à juillet. Les intervalles entre les mues ont diminué de mars à juillet, mois le plus chaud en lequel on ait fait des recherches, puis ils ont augmenté de juillet à novembre.

3) Des recherches basées sur l'aspect des concrétions calcaires au moment de la mue ont montré que la mue, sur place, a commencé en même temps et s'est poursuivie pendant les mêmes mois qu'en laboratoire.

4) Une comparaison avec les mesures de croissance obtenues dans une étude précédente a montré que la mue se produisait sans croissance de mars à juin. Au cours des mois de juillet à novembre, la croissance à chaque mue était plus grande chez les femelles que chez les mâles.

5) Une application plus étendue de la technique employée pour les recherches sur place pourrait fournir des données complètes sur le comportement de mue des *Palaemonetes* dans des conditions naturelles. Cette technique peut être aussi applicable à d'autres crustacés.

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