# THE LIFE HISTORY OF *MYTILICOLA INTESTINALIS* STEUER[1]

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Monthly samples of 100 mussels from Lee-on-the-Solent and Whitstable have been investigated over two years for the incidence of parasitism by *Mytilicola intestinalis*. It was found that numbers of parasites from both sites underwent seasonal variation and the change in numbers of immature stages indicated that infection occurred only once in the year; this corresponded to the time when sea temperatures were over 18 °C. It was therefore postulated that this temperature is necessary for the successful infection of mussels and thus the life cycle of the parasite is closely regulated by the environment. Any variation of life history in different localities will be due to differences in environmental temperatures. Generally in the British Isles, the critical temperature is exceeded for a short time only and therefore there is only one cycle of the parasite each year. However, mortality in the parasite population occurs twice during the year (July to September, and December to February) and corresponds to the release of eggs from mature female parasites. Eggs liberated during the winter do not infect new hosts.

## INTRODUCTION

Although the parasitic copepod, *Mytilicola intestinalis* Steuer has been the subject of many investigations because of its importance to the European mussel industries, there have been, in the past, widely differing views about its life history. Much of the controversy seems to have arisen because female copepods with egg-sacs are found throughout the major part of the year, and because results of investigations into numbers of immature parasites differ radically.

The discovery of immature stages of the copepod in mussels will indicate that breeding is occurring. Grainger (1951) believed that there was a cycle in numbers of juvenile parasites, finding they were present in highest numbers in November and December, and absent in the following June and July; few were found in May and August. Hockley (1951) seldom detected immature forms, although he stated that he had examined mussels at all times during the year. On the other hand, Korringa (1952; 1953; 1954) found them each month between March and November, the remaining months not being mentioned in his reports. Bolster (1954) with this conflicting evidence, as well as some new material in front of him, summed up the critical stage in the life history of

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*M. intestinalis* as the following: "On the east coast of England, breeding continues in most places until December and January, but ceases in February and March; it begins again in April. On the Channel coasts of England and Ireland, breeding occurs throughout the year ... Off the German and Dutch coasts sea temperatures are usually about 1 °C lower than off the east coast of England, and the non-breeding period will normally cover the first three months of the year." Unfortunately, he did not carry out a complete annual survey in any of the areas studied, and he also disregarded some of the results reported in GRAINGER's annual study. While BOLSTER believed the life span of the parasite was unknown, KORRINGA (1952; 1953) thought there was a double cycle in the year, with breeding occurring both in early and late summer. Immature parasites were produced in May and June, quickly reached maturity and having reproduced, died. The second generation of *M. intestinalis* did not reproduce that year, but hibernated during the winter months, when sea temperatures were lower than 7–8°C. As soon as the sea became warmer than this, juvenile stages became mature and all copepods that had overwintered reproduced early in the summer.

In the present studies, two populations of mussels were examined for parasites for two complete years. By studying two populations, one on the south-east coast of England, and the other on the south coast, it was hoped to be able to form definite conclusions about the length of life of the parasite, and that the time of year when breeding occurs might be established more precisely. Secondly, GRAINGER's results are the only complete record of population variation in the British Isles, although MONTEIRO and FIGUEIREDO (1961) have made an annual examination of mussels from four sites on the estuary of the river Tejo (Tagus) in Portugal. The temperatures of the water at these sites did not fall below 11·5°C, and the life cycle would be expected to follow a different pattern when sea temperatures do not reach below 6°C, because this, according to HEPPER (1955), is the generally accepted temperature under which *M. intestinalis* does not breed.

## MATERIAL AND METHODS

The two sites were Hillhead beach, Lee-on-the-Solent, Hampshire (Ordnance survey grid reference 551014) and a mussel bed at Swalecliffe, approximately two miles east of Whitstable harbour, Kent (Ordnance survey grid reference 134679). Mussels were collected from relatively small areas: approximately 20 m by 5 m (Lee-on-the-Solent) and approximately 15 m square (Whitstable). One hundred mussels were examined for parasites at monthly intervals for two years. After cutting through the posterior adductor muscle with a heavy duty scalpel, the shell of the mussel was prised open. The left valve was completely removed, leaving the body of the animal lying in the right valve, and next, the left mantle and gill were pulled away, leaving digestive gland and digestive tract exposed. These were removed and transferred to a white porcelain staining dish, where they were carefully teased out using a fine scalpel and forceps. Mature male and female copepods were easily seen against the white background. A lamp, shining at an angle of incidence of about 30° to the dish, made the movements of immature stages clearly visible. It was generally possible to examine between ten and fifteen mussels in an hour by this method.

TABLE 1. Analysis of *Mytilicola intestinalis* population at Lee-on-the-Solent

| Date | % Infection | *Mytilicola*/ *Mytilus* | Number parasites in 100 mussels Immature | Male | Female Total | Female % with eggs | Male/ Female | Sea temp. °C |
|---|---|---|---|---|---|---|---|---|
| 19 Jan. 1966 ..... | 88 | 2·07 | 5 | 126 | 76 | 28·6 | 1·66 | – |
| 17 Feb. 1966..... | 67 | 1·35 | 4 | 79 | 52 | 3·7 | 1·52 | – |
| 21 March 1966... | 79 | 1·97 | 16 | 111 | 70 | 12·9 | 1·59 | – |
| 19 April 1966 .... | 73 | 1·67 | 23 | 86 | 58 | 9·4 | 1·48 | – |
| 17 May 1966..... | 59 | 1·07 | 15 | 57 | 35 | 34·3 | 1·63 | – |
| 21 June 1966..... | 62 | 1·03 | 13 | 57 | 33 | 63·6 | 1·73 | – |
| 18 July 1966 ..... | 56 | 0·94 | 6 | 62 | 26 | 57·7 | 2·38 | – |
| 15 August 1966... | 61 | 0·99 | 21 | 48 | 30 | 56·7 | 1·60 | – |
| 19 Sept. 1966..... | 64 | 1·29 | 28 | 66 | 35 | 31·4 | 1·89 | – |
| 18 Oct. 1966..... | 70 | 2·04 | 40 | 100 | 64 | 29·7 | 1·56 | – |
| 13 Nov. 1966..... | 76 | 1·83 | 32 | 92 | 59 | 28·8 | 1·56 | – |
| 11 Dec. 1966..... | 82 | 1·99 | 23 | 105 | 71 | 31·0 | 1·48 | – |
| 9 Jan. 1967 ..... | 84 | 2·49 | 35 | 125 | 89 | 20·2 | 1·40 | – |
| 6 Feb. 1967..... | 85 | 2·39 | 18 | 120 | 101 | 11·9 | 1·19 | – |
| 12 March 1967... | 83 | 2·20 | 15 | 120 | 85 | 24·7 | 1·41 | 4 |
| 9 April 1967 .... | 79 | 2·50 | 19 | 130 | 101 | 18·8 | 1·29 | 8 |
| 7 May 1967..... | 77 | 1·78 | 20 | 105 | 53 | 35·8 | 1·98 | 6 |
| 11 June 1967..... | 76 | 1·75 | 4 | 114 | 57 | 57·9 | 2·00 | 16 |
| 9 July 1967 ..... | 62 | 1·30 | 3 | 91 | 36 | 58·3 | 2·53 | 18 |
| 6 August 1967... | 72 | 1·46 | 40 | 79 | 27 | 44·4 | 2·93 | 22 |
| 9 Sept. 1967..... | 79 | 2·37 | 63 | 118 | 56 | 39·3 | 2·11 | 15 |
| 15 Oct. 1967..... | 87 | 3·26 | 31 | 179 | 116 | 37·9 | 1·54 | 13 |
| 19 Nov. 1967 .... | 93 | 4·42 | 29 | 248 | 165 | 46·1 | 1·50 | 8 |
| 17 Dec. 1967..... | 92 | 4·09 | 26 | 226 | 157 | 34·4 | 1·44 | 5 |
| 14 Jan. 1968 ..... | 94 | 4·38 | 34 | 221 | 183 | 18·0 | 1·21 | 6 |

## RESULTS

The complete analysis of results from Lee-on-the-Solent and Whitstable can be found in Tables 1 and 2, respectively.

### PERCENTAGE INFECTION OF MUSSELS

The percentage of infected mussels was not constant, but showed definite seasonal fluctuations which were more clearly demonstrated by the figures for Lee-on-the-Solent. The highest incidence of infection here was found during the early winter months, being between 82% and 85% in 1966–67, and between 93% and 94% in 1967–68. From March onwards, there was a gradual decrease in the level of infection until July, when the lowest incidence was found both in 1966 and 1967. The incidence of infection was higher at Whitstable, varying between 91% and 100%. The same fluctuations were apparent, with the lowest levels of infection occurring in July 1966 and June 1967. Higher levels were present in autumn months, the 100% level being found mainly between August and November.

### NUMBER OF *M. INTESTINALIS* PER MUSSEL

The average number of parasites infecting the mussel population at Lee-on-the-Solent followed the percentage infection closely, with highest numbers discovered between October and March, the peaks being in January 1967 and November 1967. Lowest numbers of parasites were found in July in both years.

TABLE 2. Analysis of *Mytilicola intestinalis* population at Whitstable

| Date | % Infection | *Mytilicola*/ *Mytilus* | Immature | Number parasites in 100 mussels Male | Female With eggs | Female No eggs | Female Total | % with eggs | Male/ Female | Sea temp. °C |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 June 1966.. | 97 | 4.68 | 35 | 294 | 92 | 47 | 139 | 66·2 | 2·12 | – |
| 5 July 1966.. | 94 | 5·05 | 103 | 298 | 68 | 36 | 104 | 65·4 | 2·87 | – |
| 8 Aug. 1966 . | 100 | 8·01 | 491 | 211 | 51 | 48 | 99 | 51·5 | 2·13 | – |
| 5 Sept. 1966 . | 99 | 8·30 | 405 | 274 | 65 | 86 | 151 | 43·0 | 1·81 | – |
| 3 Oct. 1966.. | 100 | 9·33 | 312 | 376 | 110 | 135 | 245 | 44·9 | 1·53 | – |
| 31 Oct. 1966.. | 100 | 8·83 | 252 | 384 | 137 | 110 | 247 | 55·5 | 1·55 | – |
| 5 Dec. 1966.. | 97 | 8·38 | 237 | 364 | 74 | 163 | 237 | 31·2 | 1·54 | – |
| 2 Jan. 1967.. | 98 | 8·53 | 168 | 424 | 34 | 227 | 261 | 13·0 | 1·62 | – |
| 30 Jan. 1967.. | 98 | 8·35 | 133 | 472 | 1 | 229 | 230 | 0·4 | 2·05 | – |
| 28 Feb. 1967.. | 99 | 7·12 | 96 | 394 | 13 | 209 | 222 | 5·9 | 1·77 | 2 |
| 29 March 1967 | 99 | 7·03 | 115 | 403 | 38 | 147 | 185 | 25·9 | 2·18 | 2 |
| 24 April 1967 . | 100 | 7·27 | 128 | 441 | 33 | 125 | 158 | 20·9 | 2·79 | 3·5 |
| 21 May 1967.. | 97 | 7·30 | 128 | 438 | 56 | 108 | 164 | 34·1 | 2·67 | 17 |
| 19 June 1967.. | 91 | 5·59 | 21 | 370 | 121 | 47 | 168 | 72·0 | 2·20 | 13 |
| 23 July 1967.. | 99 | 7·17 | 301 | 313 | 78 | 25 | 103 | 75·7 | 3·04 | 22 |
| 20 Aug. 1967 . | 100 | 8·45 | 394 | 341 | 58 | 52 | 110 | 52·7 | 3·10 | 16 |
| 25 Sept. 1967 . | 99 | 10·00 | 453 | 381 | 60 | 106 | 166 | 36·1 | 2·30 | 15 |
| 22 Oct. 1967.. | 100 | 9·65 | 345 | 430 | 72 | 118 | 190 | 37·9 | 2·26 | 11 |
| 20 Nov. 1967 . | 100 | 9·18 | 323 | 412 | 64 | 119 | 183 | 35·0 | 2·25 | 6 |
| 27 Dec. 1967.. | 99 | 8·63 | 243 | 403 | 20 | 197 | 217 | 9·2 | 1·86 | 6 |
| 21 Jan. 1968.. | 95 | 8·01 | 168 | 425 | 3 | 205 | 208 | 1·4 | 2·04 | 5 |
| 18 Feb. 1968.. | 99 | 7·14 | 147 | 401 | 3 | 163 | 166 | 1·8 | 2·42 | 2·5 |
| 17 March 1968 | 97 | 6·88 | 131 | 394 | 0 | 163 | 163 | 0 | 2·42 | 5 |
| 17 April 1968 . | 96 | 5·85 | 78 | 346 | 41 | 120 | 161 | 25·5 | 2·15 | 10 |
| 12 May 1968.. | 95 | 6·89 | 85 | 459 | 60 | 85 | 145 | 41·4 | 3·17 | 10 |
| 11 June 1968.. | 93 | 5·49 | 19 | 388 | 92 | 50 | 142 | 64·8 | 2·73 | 16 |

At Whitstable, the peak of infection occurred earlier, in October 1966 and late September 1967, and afterwards there was a gradual decline to the lowest numbers which were met with in June, both in 1966 and 1967.

### NUMBER OF FEMALE PARASITES

At Lee-on-the-Solent, lowest numbers were observed in July and August in both years of the survey. During the succeeding months, numbers increased rapidly until the maximum which was found around January. Numbers do not appear to begin decreasing until about April or May, although during this time of the year, there were irregular fluctuations between the monthly samples. The lowest numbers of female parasites at Whitstable were also discovered during July and August. Numbers rapidly increased in September and October, then remained more or less stable until January, when they started to decrease. There was, therefore, a slight difference in the seasonal variations occurring in the two regions.

### PERCENTAGE OF FEMALE PARASITES WITH EGG-SACS

Lowest numbers of female parasites with egg-sacs at Lee-on-the-Solent were found in February in both years, and this was followed by a gradual increase up to June and July. The percentage fell somewhat in August or September, but then remained relatively stable until the end of December. The seasonal variation was far more marked at Whitstable, with the smallest incidence observed in January to March. In late January 1967, only 0·4% of the female copepods carried egg-sacs while in the corresponding collection at Lee-on-the-Solent (6. February, 1967) 11·9% of the females bore eggs. Similarly, the greatest percentage of female parasites with eggs (75·7% on 23. July, 1967) at Whitstable was considerably higher than that (58·3% on 9. July, 1967) found at Lee-on-the-Solent. The variation in numbers followed a similar course, however, with numbers remaining moderately high from September to December, then falling sharply in January.

### NUMBER OF MALE PARASITES

In both years of the survey at Lee-on-the-Solent, the smallest numbers were found in August. By October–November, numbers were much higher and continued to increase slowly up to around January in 1966–67. This was the only complete winter studied, but in 1967–68, it appeared as though maximum numbers had been reached by November 1967. Numbers remained fairly stable until around March, and then commenced to decrease, this pattern being similar to that seen in numbers of female parasites at Lee-on-the-Solent. At Whitstable, fewest male parasites were discovered in August 1966 and July 1967, increasing rapidly up to October. In 1966–67, numbers continued to increase up to the end of January, but in the following year, the maximum had been reached by October. The numbers slowly decreased until around May–June and then fell sharply in a similar way to the numbers of female copepods from Whitstable.

It should be noted that the relative variations in numbers of male and female parasites at Lee-on-the-Solent was far greater than occurred at Whitstable. Thus between June 1966 and June 1967, the highest number of females found in 100 mussels was 101 and the lowest number 26, a ratio of 3·88:1; for males, the figures were 130 and 48, a ratio of 2·71:1. At Whitstable, corresponding results were: females, 261 and 99, or 2·64:1; males, 472 and 211, or 2·24:1.

### NUMBER OF IMMATURE PARASITES

The lowest numbers of juvenile parasites were present in mussels from Lee-on-the-Solent collected in June and July. There were rapid increases in August and September with largest numbers seen in October 1966 and September 1967. Following the peak, numbers declined until January or February and then remained fairly steady until May. Considerably higher numbers of immature parasites were found throughout the year at Whitstable. The smallest incidence, in June, was succeeded by an enormous influx, until by late August to September, juvenile parasites made up nearly half of the total parasite population. Numbers fell moderately quickly until February or March, and then remained stable until May.

### RATIO OF MALES/FEMALES

The ratio shows a definite seasonal variation, being lowest during the winter months and highest generally during June to September. The variation between summer and winter was around twofold.

## DISCUSSION

The life cycle of *M. intestinalis* is intimately related to the temperature of the environment (KORRINGA, 1952; BOLSTER, 1954; HEPPER, 1955) though there is a slight discrepancy between the figure given by the different authors for the critical temperature for breeding of the copepod. The annual variation of sea temperature at Lee-on-the-Solent and Whitstable during 1967–68 has been included in Tables 1 and 2. The temperature was measured at the time of mussel collection only, but because of the low thermal conductivity of water, mean monthly values will not vary greatly from these. It should be pointed out, however, that the spring tides when collections were made tended to occur in the mid to late afternoon at Lee-on-the-Solent, and in the early morning to midday at Whitstable. Thus the water at Lee-on-the-Solent, particularly during the summer, may have been warmed by the sun for some hours, while at Whitstable the warming time would be up to six hours shorter. Again, but this time of more importance during the winter, the sea will have been cooled by the cold night air at Whitstable, while at Lee-on-the-Solent day temperatures would have warmed the sea a little. The result will be that summer temperatures of the sea at Lee-on-the-Solent will be slightly higher than the ambient temperature, and at Whitstable, winter temperatures of the sea will be somewhat lower than the ambient temperature.

If it is assumed that 8°C is the critical temperature for *M. intestinalis* to reproduce (as suggested by KORRINGA), then for up to six months of the year, the copepod will be unable to breed, because between November and April–May in both areas, the water was at or below this temperature. Peaks of above 20°C occurred in July at Whitstable and in August at Lee-on-the-Solent.

### RELATIONSHIP BETWEEN SEA TEMPERATURE AND NUMBERS OF IMMATURE PARASITES

Despite the occurrence of female parasites bearing egg-sacs throughout the year, the number of juvenile copepods shows only one influx, this occurring in late July or August; it corresponds to the finding of the water temperature above 20°C. The free-living stages of *M. intestinalis* can be passed through in less than a fortnight (GRAINGER, 1951) and in fact, GRAINGER showed that the infective copepodid stage can be reached in less than 40 hours in temperatures of 13–14°C under laboratory conditions. If it can find a suitable host in a shorter time than a fortnight, the infective copepodid will enter (BOLSTER, 1954) and thus generally, the life span of the free-living copepod will be far shorter. In the present investigation, eggs have hatched and developed up to the infective larval stage in less than 24 hours at temperatures of around 20°C, and so the discovery of immature copepods in mussels during the hottest months of the year points to the conclusion that hatching had occurred, at the most, two days before collection, because of the rates of development at these temperatures. Very few young stages were found in the two months prior to the time of infection, even though temperatures recorded were around 16°C (late May at Whitstable and June at Lee-on-the-Solent) but not above 18°C. This strongly suggests that a temperature of above 18–20°C is a necessary stimulus for the release of eggs and the subsequent development of free-living larval stages. Certainly the large increase of juvenile parasites at Whitstable during July and August does indicate the existence of a sudden release of eggs throughout the female population. This release shows no correlation with the breeding cycle of the mussel, which occurs in April or May (CHIPPERFIELD, 1953).

The term "breeding period" during the life cycle of *M. intestinalis* is not a suitable description; the term can be misleading because other authors have used it as related to the infection of mussels. While females are developing egg-sacs during the early months of the year and are therefore "breeding" as described, for example, by BOLSTER (1954), the time of the year when larvae are infecting mussels is limited to a short length of time in the height of the summer. Perhaps "infection period" would be a more apt definition of the latter event, and this would not relate to the release of gametes, which BOLSTER believed to occur before egg-sacs are released.

Eggs of *M. intestinalis* have been shown to develop quite normally at temperatures lower than 18°C. GRAINGER (1951), in his experiments on hatching, had success with temperatures between 13° and 14°C. One should note that here egg-sacs were *detached* from females and allowed to stand in seawater. Also, it has been observed that eggs in egg-sacs are often 'eyed', that is, the eye of the future nauplius is visible, but this in no way contradicts the hypothesis of the necessity of 18–20°C for the release of eggs and successful infection of mussels. When egg-sacs have been seen already detached from the female in the mussel intestine, this may have been due to the mechanical stimulus of removal of the mussel from its substrate and the following dissection. Nevertheless, egg-sacs may be released for other reasons, as will be seen from later discussion.

## NUMBER OF GENERATIONS OF *M. INTESTINALIS* IN A YEAR

COSTANZO (1959) has reviewed the larval stages passed through during the development of *M. intestinalis*. He lists ten stages, the first three of which are free-living: nauplius, metanauplius and the infective first copepodid. Afterwards, there are seven larval stages in the gut of the mussel, with adult characteristics gradually being assumed. KORRINGA (1951) has stated that under warm environmental conditions, the infective larva on entering its host can become mature in seven to eight weeks, and consequently, the length of existence of each of the larval stages in the summer can be very short.

As already mentioned, KORRINGA (1952) believes that there is a double

TABLE 3. Numbers of immature *Mytilicola intestinalis* found in 50 mussels from Lee-on-the-Solent, 1967

| Month | Length of parasite, in mm 0.5 – 0.9 | 1.0 – 1.5 | 1.6 – 2.0 | 2.1 and over |
|---|---|---|---|---|
| Jan. | 0 | 2 | 4 | 10 |
| Feb. | 1 | 1 | 1 | 5 |
| March | 0 | 1 | 2 | 4 |
| Apr. | 0 | 0 | 1 | 6 |
| May | 0 | 0 | 2 | 6 |
| June | 0 | 1 | 1 | 1 |
| July | 0 | 0 | 1 | 0 |
| Aug. | 9 | 7 | 0 | 5 |
| Sept. | 1 | 0 | 9 | 22 |
| Oct. | 1 | 3 | 1 | 7 |
| Nov. | 0 | 1 | 3 | 10 |
| Dec. | 3 | 1 | 2 | 7 |

TABLE 4. Numbers of immature *Mytilicola intestinalis* found in 10 mussels from Whitstable, 1967

| Month | Length of parasite, in mm 0.5 – 0.9 | 1.0 – 1.5 | 1.6 – 2.0 | 2.1 and over |
|---|---|---|---|---|
| Jan. | 7 | 9 | 7 | 6 |
| Feb. | 2 | 4 | 5 | 4 |
| March | 0 | 1 | 6 | 4 |
| Apr. | 2 | 3 | 2 | 9 |
| May | 0 | 0 | 1 | 6 |
| June | 0 | 0 | 0 | 2 |
| July | 23 | 2 | 2 | 0 |
| Aug. | 22 | 22 | 7 | 6 |
| Sept. | 11 | 7 | 6 | 14 |
| Oct. | 12 | 7 | 8 | 7 |
| Nov. | 11 | 13 | 6 | 10 |
| Dec. | 7 | 8 | 6 | 5 |

cycle of the parasite each year, but the results of the present survey do not agree with this. Although immature parasites have been discovered at all times during the year, their size follows a course indicating the presence of one cycle rather than two; the periodicity in numbers of immature stages is in agreement with this indication. In Tables 3 and 4, the lengths of juvenile parasites have been classified into four groups. The smallest size group of up to 0·9 mm (corresponding to COSTANZO's stages 1 and 2) will include all parasites that have recently infected the host.

The figures from Whitstable in Table 4, with rather higher numbers, show the course of events clearly. In May and June, only larger immature stages were found, but in July, the great preponderance of larvae were less than 1·0 mm long. One month later, longer, older stages were well represented, although there was still a considerable number of the earliest larval forms. By September, the majority of the juveniles which had entered mussels in July would have reached maturity, thus causing the increase in numbers of male and female parasites shown in Table 2. The water temperatures at this time were falling rapidly, with the result that the speed of development of parasites slowed down. In addition, it is unlikely that females were releasing egg-sacs between September and November, for there was little sign of a decrease in the percentage of those with eggs.

During the winter, the decline in numbers of juvenile parasites was very slow, but numbers of smallest copepods still decreased, showing that development occurred throughout the winter. Accordingly, there does not appear to be a lower critical temperature below which growth does not take place. Obviously the rate of development is slow when temperatures are low, but there is no period of 'hibernation', as proposed by KORRINGA (1952).

## LENGTH OF LIFE OF PARASITES

The course of the life history is more easily deduced by considering the results from Whitstable, because of the greater number of parasites present, and because the percentage of infection of mussels is more stable at that site. It is helpful to discuss the sexes separately, and so the length of life of female parasites will be dealt with first.

In June 1966, 139 mature females were discovered, 92 (66·2%) of which carried egg-sacs (see Table 2). By August, a fall of 40 in the total number of females can be assumed to have been caused by the death of those which had successfully released egg-sacs. Already by this time, immature stages of the parasite were found. After August, the total number of female parasites quickly increased and by November, 247 were found, 137 of which were with egg-sacs. This increase must have been caused by quick growth to maturity of the larval stages in the moderately high late-summer sea-temperatures, and nearly half of the new females had produced egg-sacs at this time. By November, all those which had successfully reproduced between July and September had died. Between November and late January, the percentage of female copepods with eggs fell quickly but there was no corresponding increase in immature stages: even though egg-sacs must have been released at this time, they did not develop. This may have been because the sea temperature (8°C or less) was too low for development, or because the developmental time was too long, allowing eggs or free-living larvae to be washed ashore or swept out to sea. The decline in numbers of females during January to May-June was caused by death of the females that had matured late in the summer and had borne eggs which were released during the winter; in other words, they died without having reproduced successfully. The remaining 50% of female copepods produced in 1966, which did not reproduce that year, started producing eggs in late February and by June or July, the majority of them were carrying egg-sacs. They died soon after having released their eggs, around August and September. What factor stimulates female parasites to release eggs during December to January is difficult to work out. It may be that reduction of food supply is acting here; even though mussels continue filtering down to 0°C (DODGSON, 1928), their metabolic state is reduced and they require less food. Thus less food will be available to the parasites and this may cause liberation of egg-sacs in the unfavourable conditions. On the other hand, cold may be the only stimulus.

In June 1966 (see Table 2), 294 male copepods were present, and this total had fallen to 211 by August. That year's immature parasites started adding to the total male population by August and September, but at this time, those which had lived for a year were dying. By late January, a peak in the number of male parasites was observed; then the number fell off in the same way as seen in the female parasites, this being due to the death of those which had reached maturity late in the summer. Although it is easier to follow the course of life of the female parasites because of the presence of egg-sacs, the same conclusion is reached: there are two periods of death in the *M. intestinalis* population during each year.

A number of dissimilarities were observed in the studies at Lee-on-the-Solent. There was an increase of 5–10% in the infection of mussels between 1966 and 1967, the loss of egg-sacs from female copepods during the winter was not so marked, and the number of male and female parasites did not fall markedly until after March. The temperature variations of the two areas may have caused some of these differences. At Lee-on-the-Solent in 1967, the water had reached higher temperatures later in the year and then fell more rapidly, with the result that fewer females produced eggs late in the year. In addition, winter temperatures were a little higher than at Whitstable and if this is the normal occurrence, it may have the effect of not causing the death of the late-maturing females in mid-winter, but enables them to survive until April or May. A number of them do die, because 22 (31·0%) of the females seen in December 1966 carried eggs, but by February, the number had fallen to 10 (11·9%) while no new immature stages had appeared. As there was only a small loss in the winter of 1966–67, larger numbers of the parasite remained to reproduce and to infect mussels in the following year. The male population figures followed a similar path to that taken by the female population, and differed slightly from the Whitstable results.

### EXCEPTIONS TO THE PROPOSED FORM OF LIFE HISTORY

1. If the temperature of the environment reaches 18° C early in the summer and remains high for over two months, then a second cycle can occur. This can explain the disaster observed in the North European shellfish industries in 1950. From results quoted by KORRINGA (1952), it can be seen that the mean sea temperature was much higher than usual in that year, and so a mean temperature of over 18° C was reached in June instead of July. The consequence was that infection of mussels would have occurred in June, and a second cycle could have followed in August, when temperatures were still above 18° C. Thus mussels, apart from having to withstand a longer period than usual of unfavourable temperatures, would have had a second influx of *M. intestinalis*, doubling the number of parasites in their digestive tracts.

2. When the temperature of the environment is habitually above 18° C for long periods, *M. intestinalis* will be able to breed several times during the year, and the breeding population will become 'out of phase', with no apparent cycles of infection. At Xabregas in Portugal, MONTEIRO and FIGUEIREDO (1961) recorded temperatures of 18·5° C and above between May and October. Here, smallest juvenile stages were reported at all times of the year, and the percentage of female copepods with egg-sacs varied very little between May and December (55–75%).

## SUMMARY

Two populations of the parasitic copepod, *Mytilicola intestinalis*, have been studied for two years and with the results obtained, a new form of life history for the parasite in British Waters has been proposed.

Infection of mussels occurs in late July to early September, when environmental temperatures are above 18° C. Some juvenile stages quickly reach maturity and a number of the new females develop egg-sacs, but by this time, temperatures are too low for them to release eggs normally. With the low winter temperatures, the majority of females still bearing eggs release them but even if the eggs develop, they do not infect new mussels. Larval stages which enter hosts late in the infection period mature slowly during the winter and by the spring and early summer, few of them are seen. Death of parasites occurs at two times of the year: those which have matured during the late summer die in the late winter and spring months; and the remainder, which die in the infection period, probably very soon after the release of eggs by the female parasites.

The life cycle is closely regulated by the temperatures of the environment and thus two or more cycles may be completed in a year if conditions are favourable. The latter will be the normal occurrence when the sea is above 18° C for long periods of time.

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