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A COPEPOD PARASITE OF MUSSELS

BY

G. C. BOLSTER

Fisheries Experiment Station,
Conway, North Wales

LONDON: HER MAJESTY'S STATIONERY OFFICE
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FIVE SHILLINGS NET

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INTRODUCTION

Mytilicola intestinalis Steuer is a copepod, parasitic in the gut of two genera of molluscs. Originally classified as a dichelestid (Steuer 1902), it has since been placed in the family Clausiidae by Monod and Dollfus (1932).

It was first described by Steuer (1902) from *Mytilus galloprovincialis* Lam. found near Trieste. Since then it has also been found in *Mytilus edulis* (see below) and in *Ostrea edulis* by Baird, Bolster and Cole (1951). The parasite appears to have spread from the Mediterranean to Dutch and German ports and thence to Great Britain and Ireland.

It has been reported in *Mytilus gallprovincialis* Lam. by the following :

1.	Steuer (1902)	Gulf of Trieste
2.	Steuer (1905)	Gravosa, Italy
3.	Cerruti (1932)	Taranto, Italy
4.	Monod and Dollfus (1932)	Marseilles, Martigues, Banyuls sur Mer
5.	Heldt (1950)	South coast of France (Mussels taken to Tunisia)
6.	Korringa and Lambert (1951)	South coast of France

and in *Mytilus edulis* by :

1.	Vayssiere (1914)	Mediterranean
2.	Caspers (1939)	Cuxhaven-Wilhelmshaven area
3.	Ellenby (1947)	Blyth, Northumberland
4.	Korringa (1950)	Zandkreek, Netherlands
5.	Cole and Savage (1951)	A single specimen sent in 1937 by Miss L. Beanland to Dr. J. P. Harding from Portsmouth. In the British Museum
6.	Hockley (1951)	South coast of England
7.	Thomas (1952) (private communication)	Gareloch, Argyllshire ; Rosyth, Fifeshire, Scotland

As can be seen from the above list, Mytilicola was present in mussels on the east and south coasts of England in 1951. It had not been found on the west coast. In North Wales the only mussel bed which had been examined regularly was at Conway (Cole, 1951). Mussels from beds in Carmarthen Bay and the Menai Straits were examined from time to time, but no Mytilicola was found. Wallasey was the only other place on the west coast from which mussels had been examined. The commercially important beds in Morecambe Bay had not been surveyed for the parasite.

Cole and Savage (1951) had shown that the presence of Mytilicola is associated with a serious lowering of condition in infected mussels. Korringa (1950) found that on the Dutch beds in the Zandkreek, Mytilicola increased very rapidly in numbers during April and May. In the warm months of July and August, mortality was so heavy among the mussels there that the production of marketable fish fell to 5 per cent of normal. The possibility of a similar outbreak occurring in Britain made a quick decision regarding the first line of approach imperative. The two most urgent needs were to plot the distribution of the parasite and to investigate possible methods of cultural control. If much time were spent on investigating control before the distribution of the parasite was known, results might not be applicable to all areas. Chemical and physical means had been tried and found unsuccessful by Korringa (1950 and 1951). On the other hand, if too much time were spent on plotting the distribution of Mytilicola in detail wherever mussels were to be found, a serious outbreak might have occurred before any control measures had been started.

It was decided that the best course would be to make a rapid survey of the important commercial beds on the west coast which had not so far been examined, and if these were not found to be infected, to go on to an examination of nearby beds. In this way the nearest potential source of infection could be discovered. It would not be sufficient merely to examine the mussel beds adjacent to the main uninfected commercial beds, because infection, it was thought, could be brought in mussels attached to the bottoms of ships. For this reason it would also be necessary to examine ports and harbours.

The present paper is an account of this survey, and a record of observations made both in the field—on the west coast and at Blyth, Northumberland—and in the laboratory, which are considered to be significant to the problem of control.

METHODS

When sampling a bed, twenty mussels were taken for microscopic examination and as many individuals as time allowed examined macroscopically while walking over the beds. When a mussel was placed in the collecting tin, for later examination at the laboratory, a number of other mussels from the same clump or level were opened on the spot. On each area examined this number was usually between sixty and eighty. It was by this macroscopic examination that Mytilicola was first found at Fleetwood. It was intended that mussels taken for microscopic examination should fall within a size-range of from 5·50 to 5·99 cm. This would have tended towards a degree of standardization in results between host-size and number of contained parasites, and although the first six samples were actually collected with this aim in mind, the idea had to be abandoned. A size-range consciousness was found to interfere with random sampling. In many areas a gradation in size was noticed between mussels situated at different tide levels, both on beaches and those attached vertically on piles. Where the distribution of mussels was vertical, as on the dock walls, jetties and piers, a boat and rake were used for collection below the water level where this was necessary.

Some places from which samples were examined could not be visited personally. For these, marked with an asterisk in Table 1 (p. 21), a full explanation of the sampling requirements was given to the collectors. From such samples, comprising between 60 and 100 mussels, which were sent to Conway, 20 were taken for microscopic examination and the remainder opened and examined macroscopically.

Mussels which were to be examined microscopically were placed in an open tin and kept cool until required. Notes were taken of the date of collection, on the general factors relating to the area where they were collected, and of the date of dissection. When mussels were opened after they had been kept in the collecting tins for some time, Mytilicola, if present, was usually to be seen in or near the rectum.

On one occasion two parasites were found free in the shell cavity after ten days. In order that none should be lost from the examination, the samples were nearly always dealt with within four days of collection.

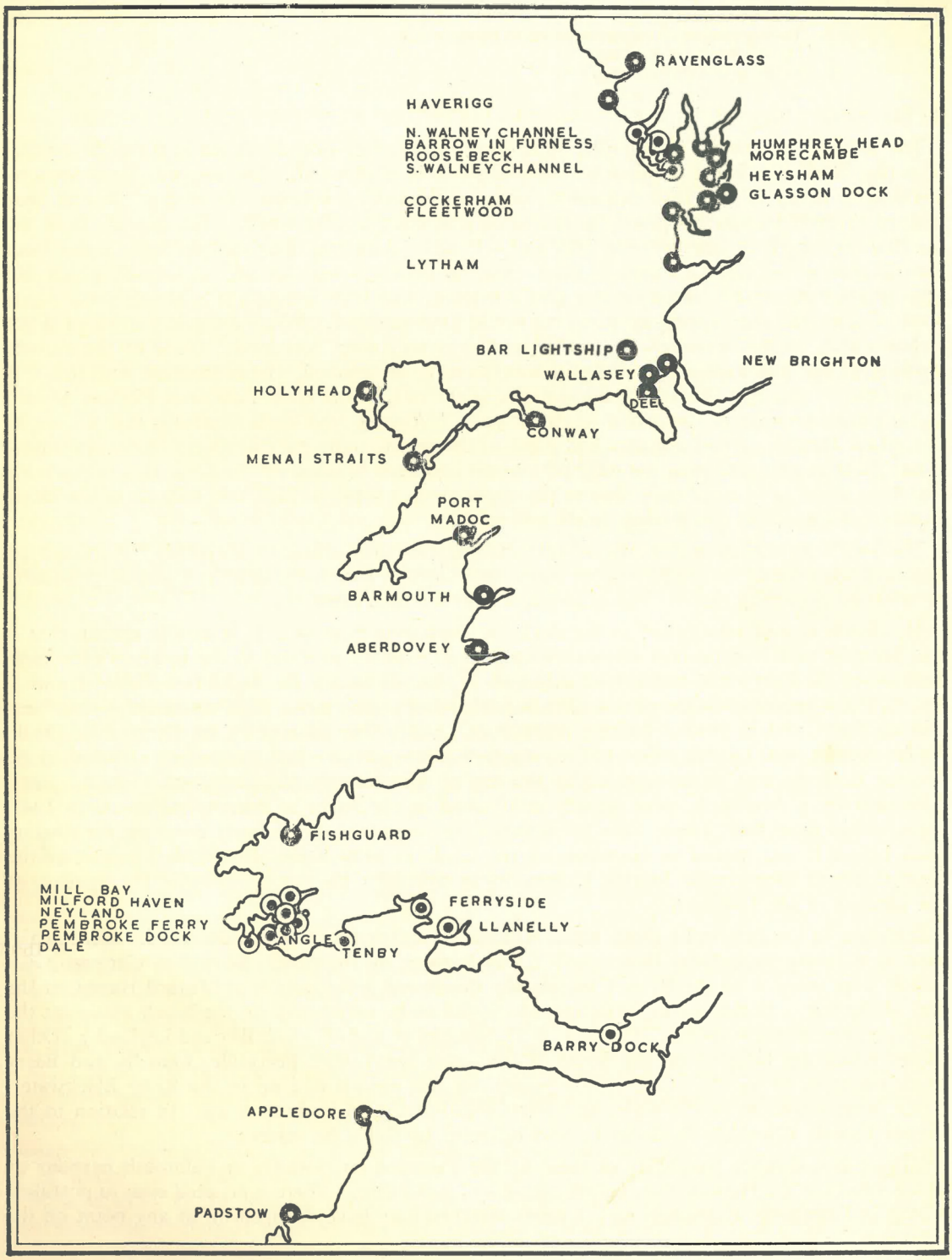
In the macroscopic examination, as much of the gut as possible was uncovered by using a thin scalpel. This revealed the presence of any adult stages of the parasite. The following procedure was adopted for detailed microscopic examination in the laboratory and during the field surveys at Fleetwood and Milford Haven. The length of the mussel was first noted, then by the method described in the Appendix (p. 30), the gut was dissected out intact from the point where it joins the stomach. It was then placed in a solid watch glass containing sea water. The digestive gland, with its contained stomach, was next removed and placed in another watch glass. Gut and digestive gland were then teased out in turn under the dissection lens. Any parasites present were counted, sexed and sorted under a binocular microscope into two groups—those less than and those greater than 3 mm.—before being stored in Bouin's fluid. They were brought to Conway in the fixative and later transferred to 70 per cent alcohol and measured under a binocular microscope. The sexes were checked again and the number of juveniles, i.e., those less than 3 mm. was noted.

Over a thousand mussels from the west coast were examined in this way. Very many more were opened and examined on the mussel beds.

INFECTION

Factors influencing spread

Infection on the west coast was found mainly in and near shipping ports (Fig. 1, and Table 1, p. 21) the main centres being at Barrow-in-Furness, Pembroke Dock, Llanelly and Barry Dock.



1. Distribution of *Mytilicola intestinalis* on the West Coast of England and Wales.

◉ Infected Stations

● Uninfected Stations

It may be postulated that there are three possible ways by which Mytilicola infection can be spread :

1. Transportation of infected host on shipping
2. Dispersion of pelagic stages
3. Relaying of infected hosts.

(1) SHIPPING

The parasite was found for the first time during the survey in mussels taken from the bottom of a tug which was being scraped on the grid dock in Fleetwood. The tug was from Barrow-in-Furness, where it was kept constantly afloat and working between the docks. It had been scraped thirteen months previously in the same grid dock at Fleetwood. The mussels from the tug bottom ranged in size between 2·26 and 4·15 cm. Although four samples were taken from various sites within the dock area at Fleetwood, no parasites were found. If mussels which had been scraped off vessels placed on this grid previously had been infected, it is almost certain that most of them and their contained parasites would have perished. When the grid was swept down at low water, all the mussels were seen to sink into very deep, soft mud. None of the mussels growing on the keel supports of the grid was found to be infected. In connection with this it is of interest to note that this same tug, FURNESS, is the only vessel from Barrow-in-Furness known to have been scraped at Fleetwood in recent years. Among Mytilicola from this tug, six out of thirty-four females carried egg-sacs and eight of the seventy-nine parasites were immature stages. If nauplii were extruded after the infected mussels had been brushed off the dock, it is improbable that they could have made their way to the upper cleaner water at high tide because of the dense muddy sediment into which their hosts had sunk.

The same tug makes twelve trips a year from Barrow-in-Furness to Heysham. Although no parasites were found in samples taken from three sites in Heysham, there is a strong possibility of infection occurring there. The same must hold for Fleetwood.

Mytilicola is well established in the docks at Barrow-in-Furness. It is almost certain that it was brought to this important ship-breaking port in mussels attached to the bottoms of vessels. Because of the heavy and widespread infection in mussels within the docks (see Tables 1 and 2, pp. 21, 23), it appears that the parasite has been there for some years. Ex-German ships have been laid up there, and in 1947 a floating dock from Lubeck was moored in the Devonshire Dock. As far as is known, Lubeck is free of the parasite but it is possible that the mussels attached to the floating dock became paratisized on its journey to this country via the North German ports. Alternatively, if Mytilicola were already established in the docks at Barrow-in-Furness in 1947, there would have been ample time for infection to spread to the mussels covering the floating dock before it was moved to Gareloch on the Clyde in May 1950. Dr. H. J. Thomas, of the Scottish Home Department Marine Laboratory in Aberdeen, has since confirmed the presence of the parasite in the Gareloch.

Infection in the Pembroke Dock area (Milford Haven) is heavy and widespread. Here again, there is a strong probability that infection was brought by shipping. Several ex-German naval vessels were moored up the River Cleddau, the shoreward prolongation of Milford Haven, at the end of the war. In the survey, infection was found to be very heavy on the beach area near the mooring sites for these vessels. (Table 1, p. 21, samples 46 and 48—Mill Bay and Leyland.) Other places which are infected on the South Wales coast are Tenby, Ferryside, Llanelly and Barry Dock (samples 49 to 52). Cole (1952) points out that vessels laid up in the River Blackwater, Essex, were towed to South Wales and Barrow-in-Furness to be broken up. In relation to the slipper limpet, *Crepidula fornicata* L. and referring to ships, he states :

"There is a distinct possibility of their having sheltered temporarily in Falmouth harbour or at the mouth of the Helford river before rounding Land's End. There is no need even to postulate a stop at Falmouth, as mussels with limpets attached may have dropped off at any point on the voyage."

If these mussels were also carrying Mytilicola—and it is almost certain that they were (mussels in the Fal and at most places examined along the south coast are infected (Hockley, 1951))—the spread of Mytilicola was undoubtedly helped in this way.

The same inference relating to the spread of Mytilicola being helped by shipping applies in Blyth. Dr. H. O. Bull, in a private communication to Dr. Cole, states that he obtained pairs of the slipper limpet, *Crepidula fornicata* L., from Blyth in 1946. These were taken from a German

vessel which, prior to going there, had been laid up in the River Blackwater in Essex. Another vessel, the ss. CAIRO CITY, lay in the Blackwater for four years before it was taken to Blyth to be broken up in 1949. Cole (1952) states that while attempting to collect *Crepidula* from her bottom, as she lay at anchor in the Blackwater, it was noticed that most of the sides of this vessel below the water-line were encrusted with mussels. After she had been moved to Blyth, a sample of fouling material was taken from her bottom by Dr. H. O. Bull and sent to Conway. "The material sent included several chains of *Crepidula*, mostly of two individuals, but with some chains of three. The mussels to which limpets were attached included individuals 65 mm. long which were judged to be four years old. The largest limpets were 35 mm. long and therefore probably three years old" (Cole, 1952). On examination, these mussels were found to contain Mytilicola. While it is impossible to state categorically that Mytilicola was present in the Blackwater before 1946, it is certain that it occurred there shortly after that date. It is possible that Mytilicola was brought to Blyth direct from either the German or Dutch centres of infection, but there are records of ships being taken from the Blackwater to Londonderry (Northern Ireland), Inverkeithing (Fife) and Blyth (Northumberland). In addition to ships destined for breaking up, others were moved away for refitting and some were sold to firms abroad. There is no evidence to deny the possibility that the spread of Mytilicola in Britain is similar to, if not directly correlated with, that of *Crepidula*. The River Blackwater is considered as a centre from which infection was started, or added to, in ports along the west coast.

(2) PELAGIC

Mytilicola is dispersed within a more limited area by water movements. The free-swimming stages were observed to live under laboratory conditions at Conway for as long as fifteen days. Grainger (1951) kept copepodids alive in petri dishes containing filtered sea water for eleven days. Distance of spread by tidal agency is therefore governed by a time factor.

(3) RELAYING

The third method of spreading infection is by relaying infected mussels in parasite-free areas. Korringa, in a private communication, refers to mussels taken from the infected German beds and relaid in Zeeland waters, as the probable source of infection in Dutch waters. At Newbiggin, infected mussels from Blyth were relaid adjacent to parasite-free mussels from Holy Island. One of the samples of relaid mussels from Holy Island was later found to be parasitized.

Development of infection in new areas

Two localities show evidence from which it can be inferred that the spread of Mytilicola other than by human agency is slow. Once infection reaches a new area, the parasite increases in numbers and then spreads out to infect hosts within a wider radius. In Barrow it appears to have multiplied within the relatively stable and deep, still water of the docks and then spread via the lock gates to the outside channel (see Table 2, samples 3, 5 to 10).

In the Pembrokeshire area heavy infection is localized around the less enclosed Pembroke dock area, while Dale, 9 miles, and Angle Bay, 6 miles away, are lightly infected (Table 2, p. 23, samples 41, 42). In both of these lesser infected areas, the numbers and density of mussels were less than in the more heavily infected areas. These places are thought to be areas of new or very recent infection.

Apart from spatial spread, there may also be a progressive increase in concentration. This can be severe. An average of 10 to 12 parasites per mussel has been reached in two samples. (Whitstable 1950, G. D. Waugh, private communication ; Ferryside, Carmarthen 1952, with a single mussel containing 31 parasites, this survey.) This level of infestation has been accompanied, at Whitstable, by reduction in area and density of stock of mussels.

Slowness of spread is to be expected as reproduction is sexual and takes place internally in the gut of the host (Hockley, 1951). Unless at least one male and one female copepodid (the infective stage) enter the host mussel to become a breeding pair, obviously the parasite cannot become established as a reproductive unit. Samples 3 and 5, from outside the docks at Barrow-in-Furness, and samples 41 and 42, which were collected away from the main centres of infection in the Pembroke Dock area, all show only one parasite per host (Table 2, p. 23). In these places mussels

were not as numerous as they were in areas showing heavy parasite numbers and 100 per cent infection. Korringa and Lambert (1951) observe that the number of mussels per volume of water is a factor limiting the degree of infection. This may account for the difference in degree of infection between the densely-populated Dutch beds and the less dense beds on the French Mediterranean coast.

The possibility of any copepodid finding a host varies directly with the density of the mussels in a given habitat. On a thinly-populated mussel bed the chance of a parasite finding a host is small. It is obvious that on a densely populated bed the chance of any one copepodid finding a host is greater. Infection in any habitat is governed by the following conditions :

1. At least one copepodid of each sex must enter the same host.
2. Because of a time limit imposed on the parasite by the period of its reproductive potential, male and female copepodids must find the host within a period which allows of their developing to sexual maturity together in the mussel. The life span of the adult parasite is not known.

The chances of these conditions being fulfilled are relative to the following considerations of host density and copepodid numbers :

1. A given number of copepodids will have less chance of establishing breeding units where the density of hosts is great.
2. Conversely, where host density is less, provided that the mussels are not too far apart, the chance of establishment is greater.

This, of course, assumes ideal environmental conditions for all habitats. In the field, however, factors which affect the density of the hosts will also be directly related to the colonizing efficiency of the parasite. There is no doubt that water movement, as a single factor alone, plays a major part in controlling the rate of establishment of new infections in a locality. Once a number of breeding pairs have been established, the rate of infection will be faster when the hosts are concentrated, giving free-swimming copepodids a greater chance of entering mussels before the pelagic stage is terminated. There is in fact a reversal in the effect of host density on the parasite, and infection may proceed as a geometrical progression. Korringa (1950) found that in the Zeeland waters Mytilicola reached sexual maturity in seven weeks. The number of eggs produced by one female is in the order of from two to three hundred in the two egg-sacs. These considerations offer some explanation for the observations of Caspers (1939), Ellenby (1947), Korringa (1950) and Hockley (1951), all of whom remarked on the "sudden" appearance of the parasite.

Marine and estuarine environments

Caspers (1939) and Ellenby (1947) have remarked on the parasite being found in estuarine areas. Grainger (1951) found that of six infected areas in Ireland, four were estuarine. In the present survey, Mytilicola has been found in estuarine environments at Ferryside and Llanelly, and from open marine environments in the North and South Walney Channels (Barrow-in-Furness area), and at Angle, Dale and Tenby (Pembroke area). The other places on the west coast where it is found are ports, i.e., Barrow-in-Furness, Fleetwood and Barry. Mytilicola was not found at Heysham, Liverpool, the Dee estuary, the North Wales beds or at Fishguard. At Heysham and Fishguard mussels were abundant only outside the dock area in open marine environments. In the Mersey and Dee estuaries mussels were rather scarce—a condition attributed locally to oil pollution and sanding-up respectively. Padstow and Appledore, two places on the northern coastline of Cornwall and Devon where large beds of mussels are found, were also free. These estuaries cannot accommodate ships of deep draught, and this may account for the absence of the parasite.

These findings are in general agreement with Hockley (1951), who found that Mytilicola had become established equally well in both types of habitat on the south coast of England.

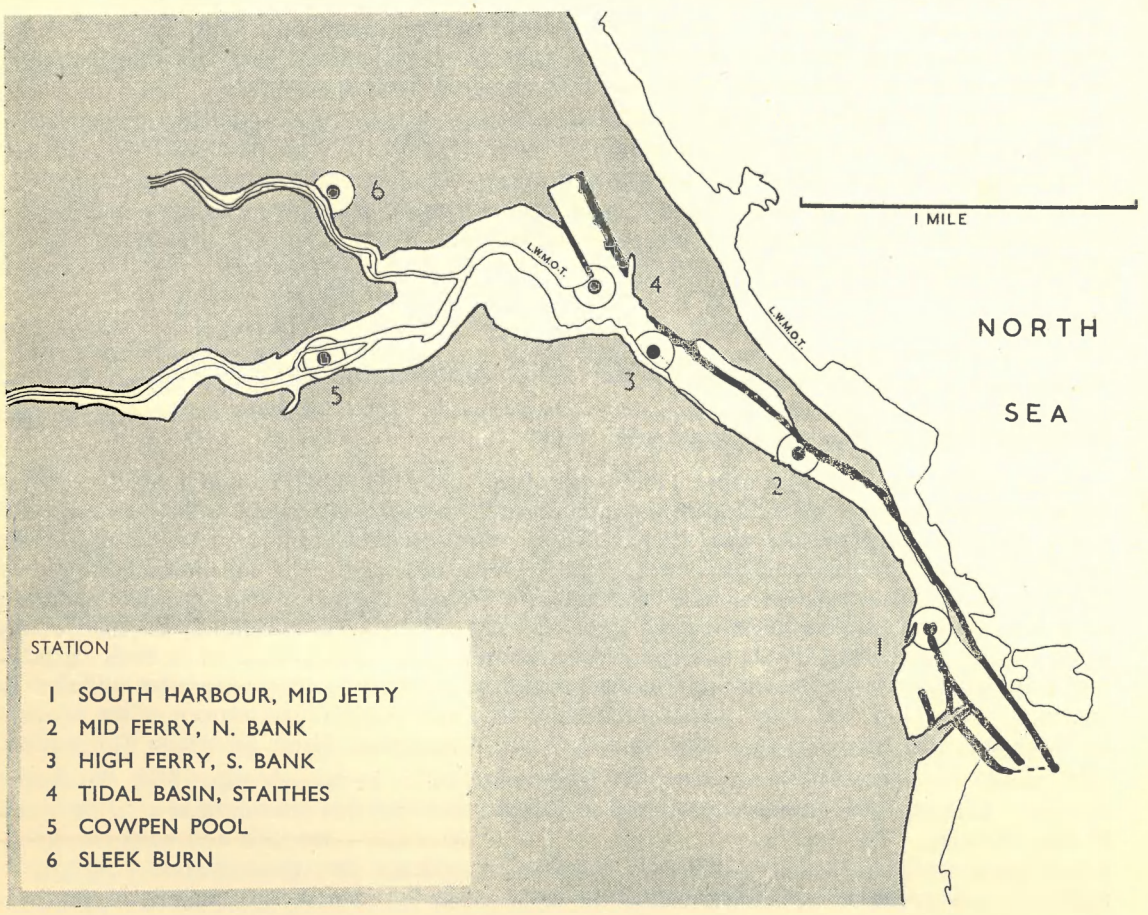
From observations made during this survey, it is considered that where Mytilicola is present in estuarine and open marine environments, it has generally spread to them from nearby ports. Where mussels are plentiful both inside and outside harbours, e.g., Barrow-in-Furness and Pembroke docks, the spread is fairly rapid. Because, as will be shown later (p. 15) the

optimum salinity level for the development of Mytilicola is rather below that of the open sea, it is to be expected that Mytilicola will become established in greater numbers and more quickly in the less saline waters of docks and estuaries. This has in fact been found during the survey and at Blyth. Hockley (1951), referring to the south coast of England, has pointed out that "in view of the power of rapid colonization, it seems likely that those few estuaries that remain free will not for long maintain their immunity." It is important to emphasize that the infective stages of Mytilicola are extremely hardy and that where once they became established in a marine environment the increased salinity will not necessarily prevent spread. The seriousness of these assertions in relation to the commercially important mussel beds, both estuarine and marine at Conway, Morecambe Bay and the Wash, cannot be over-emphasized.

Intensity of infection in relation to current and exposure

Some observations on distribution in relation to current speed were made at Neyland in the Pembroke area. The samples comprised mussels collected from two habitats in this place. Eight mussels were taken from a small, densely populated bed situated under the ferry slips. There was a rapid flow of water over this bed at each tide. Twelve were taken from the nearby beach. Those from under the ferry slips contained 15 parasites (8 hosts), while those from the beach contained 72 parasites (12 hosts).

A second observation made at Tenby was that there was a varying degree of infection with depth. The sample was divided into four groups each of 5 mussels. These were taken from four height levels on a rock.



2. Map of Blyth Estuary, Northumberland, showing position of Stations.

Height above sand in feet	*No. of parasites in five mussels*
5	6
4	14
3	21
1	27

Although it is considered certain that flow of current must govern the possibility of a copepodid entering a mussel (Hockley, 1951, Meyer and Mann, 1951), it was decided to test the hypothesis of varying degrees of infection with depth in relatively sheltered water. Blyth was chosen as a suitable place to do this. The Blyth estuary was divided into six sections, with a station in each (Fig. 2), from which mussels were taken in samples of 20 at varying height levels. The distance between highest and lowest mussels varied considerably at the different stations. At Station 4 it was 10 feet ; at Stations 1 and 3, 6 feet ; Station 6, 4 feet ; Station 5, 3 feet ; and at Station 2 only 2 feet, which did not allow of a sample being taken for this purpose. At Station 1, two series were taken, one comprising four samples and the other two. At Stations 1, 3 and 4 (Table 5, p. 26) there was a significant difference in the degree of infection with depth. At all of these stations mussels were taken from the piles under jetties. At Stations 5 and 6 (samples 76, 77, 78 and 79) the height differences were not great ; the mussels were taken from horizontal positions on beds where the action of the tides would have tended towards a more even distribution of the infective stages.

Hockley (1951) has suggested that "because of the sinking effect in the infective copepodid stage, mussels on the bottom are much more susceptible to infection than those raised on steep surfaces". Korringa and Lambert (1951) found that in areas examined on the French Mediterranean coast, infection was lighter in mussels nearest the surface. Meyer and Mann (1951) state that, from their observations, it appears that in the Wattenmeer the parasites were more numerous where the mussels were in deep, still water. Parasites were absent or occurred only in small numbers where the current was strong. They found that while isolated mussels situated high up on rocks were free, those in deep crevices between piles were heavily infected. They add that "research on mussels which are situated in deep water has not been carried out yet".

Varied infection with depth is not considered to be the result of any single factor. Obviously mussels on the lower range of their distribution are covered by the tides for longer periods than those which are higher placed. This is the most probable reason, but the environmental conditions of speed of current, light, salinity and temperature will exert a modifying effect. It has been observed (above) that the degree of infection increases with depth more markedly where mussels are found growing on piles.

BIOLOGY—NOTES AND OBSERVATIONS

Influence of light on dispersal of planktonic stages

Steuer (1905), Pesta (1907), Caspers (1939) and Meyer and Mann (1951) found a positive phototropic response in the nauplius and metanauplius, and a negative one in the infective copepodid stage. Grainger (1951) found that the nauplius is positively phototropic and very active. The metanauplius is less active and has a weaker phototropic response. The copepodid he found to be an active swimmer but notices that "individuals differ considerably in their response to light ; some have positive, some a negative, and some scarcely any response to ordinary daylight". As noted by Hockley (1951), it was observed in the laboratory at Conway that while both nauplius and metanauplius were photopositive in their response to daylight, the copepodids differed in behaviour from these two stages and were usually seen swimming at the bottom of the beakers in which they had been reared. This appears to be an important factor governing distribution.

We have seen that infection is generally found to be heavier in mussels taken from the deeper parts of a habitat. It is submitted that a partial explanation for this phenomenon is to be found in the following. The first two free-living or planktonic stages—nauplius and metanauplius—are photo-positive to daylight. Although there is no evidence that these migrate vertically in nature, it does appear that, if the observations made in the laboratory apply equally in the field, there will be a tendency for nauplius and metanauplius to swim towards the surface. The work of Hardy and Gunther (1935) on the dynamics of water currents has shown that dispersal of

plankton is accelerated over a greater area on the surface than in lower water levels. If this holds for the smaller water masses significant in the present problem, it would make for a generally wide dispersal of the first two larval stages of Mytilicola in the time taken by them to reach the copepodid stage ; that is, about 36 to 48 hours at a laboratory temperature of 18°C. It is thought that because of the observed positive geotropism and the weak positive phototropism of the copepodid, there would be a tendency for this stage to sink to the bottom in nature. In the laboratory, the copepodid has lived for as long as 15 days. It is doubtful that a period as long as this would prevail in the field. If the copepodid sank on to a densely populated mussel bed the chances of a host being found quickly would be good. If on sinking to the bottom, the copepodid were presented with a set of adverse environmental conditions, such as turbulence or heavy sedimentation, its chances of survival could be lessened. Nothing is known concerning predators of the planktonic stages of Mytilicola.

Breeding and development in relation to season and water temperature

The intensity of breeding at different seasons may be determined by noting the proportion of large females carrying egg-sacs and relating it to the number of juveniles in a sample.

Korringa (1951) found in the Netherlands that breeding began early in March and reached its height in June and July. Meyer and Mann (1951) record a maximum percentage of females with egg-sacs in August 1950 in the German Wattenmeer, declining to nil towards the end of January 1951. No breeding females were present in February and March 1951. The statement in the same publication that "le pourcentage des femelles porteuses d'ouefs est très élevé pendant les mois de janvier à octobre . . . mais vers fin octobre leur nombre diminue, et vers janvier 1951 on en rencontre peu or plus du tout" is not in good agreement with the table of percentages to which it refers and suggests that the first reference to "janvier" may be a misprint.

Grainger (1951), on the other hand, examining mussels from near Cork, Ireland, concluded that "females carrying egg-sacs were found throughout the year, but more carried them in summer". His lowest percentage of females bearing egg-sacs occurred in January (44·4 per cent) and his highest (77·3 per cent) in July. These figures were obtained by dividing the number of females bearing egg-sacs ($\times$ 100) by the total number of females, including those too small to breed. A more reliable picture of breeding intensity is obtained by substituting "total females 5 mm. or more in length" for "total females" in this calculation, since the presence of a large proportion of immature females may result in an apparent low breeding intensity and the smallest females bearing egg-sacs measure 5·0 mm. Grainger (1951) further states that immature stages "were present in highest numbers in November and December. None was found in June and July and very few in May and August". This scarcity of juveniles during the summer when, as noted above, the percentage of the total females carrying egg-sacs was at its highest suggests that egg-sacs may have been retained throughout the summer without hatching. However, it is usually considered that the eggs of copepods are fertilized before the egg-sacs are extruded, and it has been found that hatching usually occurs within eight days at summer temperatures in egg-sacs removed from the parent female.

It is possible that Grainger's material included a proportion of unfertilized females, since the average number of female Mytilicola per host in his material never exceeded three and was, during the summer, about half that density. This suggests the occurrence of a substantial number of mussels carrying only one or two parasites. In these circumstances a proportion of the females would be unable to breed. Several instances were noted during our investigations of single females bearing egg-sacs in mussels which contained no other parasites. Unfortunately it was not determined whether these egg-sacs contained developing nauplii. There is the possibility, however, that the males may not survive for long after fertilization has taken place.

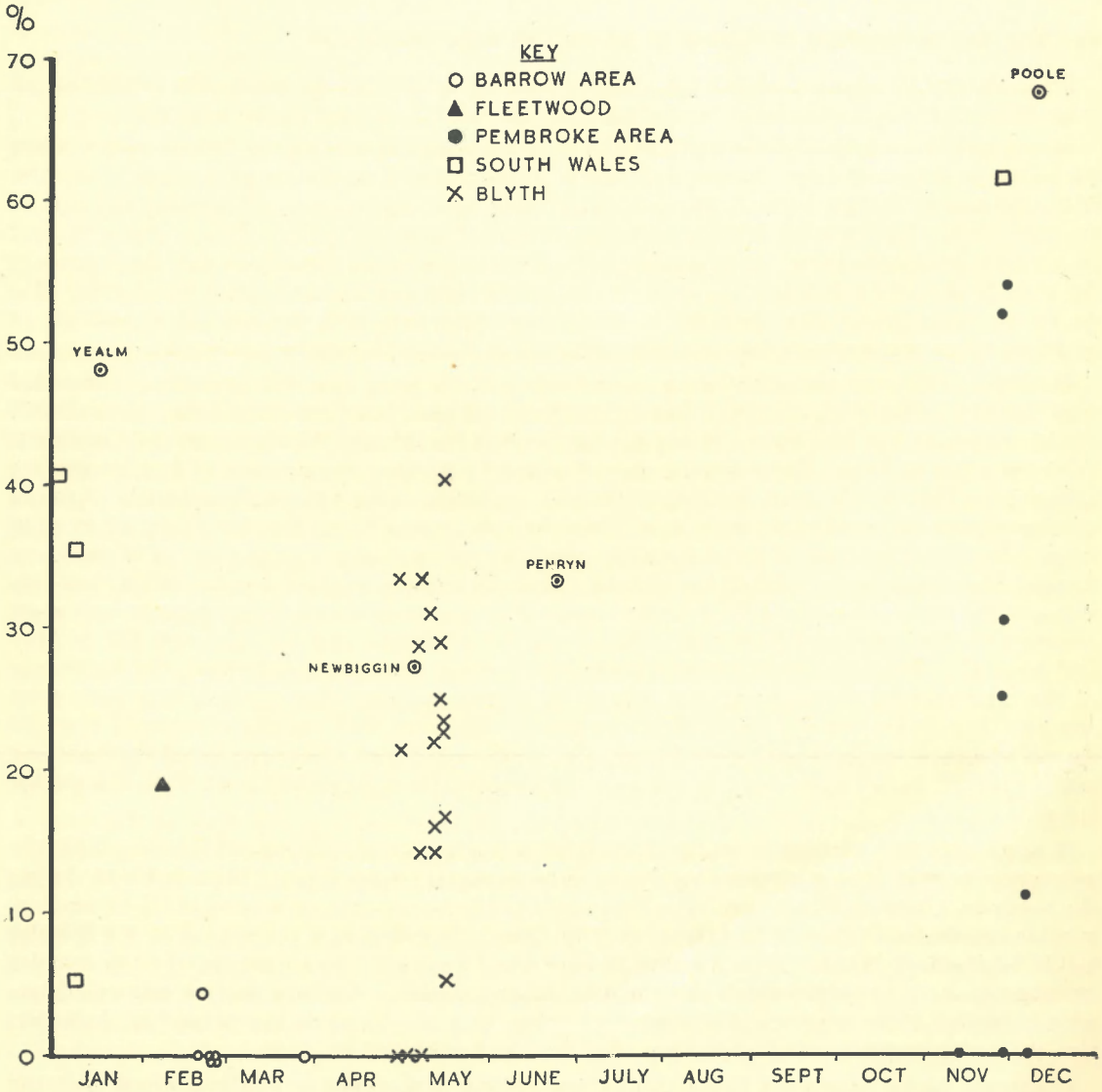
Immature stages have been found during the present investigations in the stomach and the diverticula of the digestive gland. Grainger (1951) does not record having found parasites in these parts of the host, nor did he observe any copepodid stages in the mussel, so that it is possible that juveniles may have been overlooked.

Hockley (1951) states that he has examined mussels from the neighbourhood of Southampton "at all times of the years 1948-50, and no significant seasonal variation (in the intensity of breeding) was detected. Males were always the more numerous, a typical sample yielding 182 males, 52 females. Larval stages were seldom found. Although some may have been overlooked

because of their small size, I believe it safe to infer that the time occupied by the three larval parasitic instars is short when compared with the average span of adult life".

Cole and Savage (1951), reporting upon material received in January from Blyth, Northumberland, found abundant juvenile Mytilicola in the hosts—up to 45 per mussel.

In the samples of mussels examined during the course of this investigation the proportion of adult females bearing egg-sacs varied from 67·6 (Poole, Dec.) to nil (Fig. 3). Other samples from infected beds on the east coast of England examined at the Ministry's Burnham-on-Crouch Fisheries Laboratory by Mr. G. D. Waugh gave similar results. Mussels from Whitstable, Kent, collected in July 1950 gave 82 per cent of adult females carrying eggs, while two samples collected from Southend-on-Sea and Leigh-on-Sea, Essex, in February 1950, gave corresponding figures of 0·0 per cent.



3. Percentage of female parasites carrying egg-sacs in relation to season of the year. No samples were collected during the summer months.

From these superficially conflicting statements there emerges a definite pattern in relation to the breeding of Mytilicola and water temperature. 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. If we examine the records of sea temperature in these areas (*Atlas de temperature et salinité* : International Council for the Exploration of the Sea, 1933), we find that off Newcastle the mean temperatures for January, February, March and April are 6·5, 5·7, 5·5, and 6·4°C. respectively. Off Southampton the corresponding temperatures are 8·0, 7·25, 7·0, and 8·0°C. Off Cork they are slightly higher still (Proudman, Lewis and Dennis, 1937). It seems, therefore, that about 6°C. is the critical temperature for the breeding of Mytilicola, and in areas where the temperature does not fall so low in normal years breeding may occur throughout the year. The continuous breeding area will include the whole of the south and west coasts of England and Wales, south of Anglesey. 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.

Turning to the size at maturity, there are indications that this is not the same at all localities. Grouping the samples from Pembroke and South Wales (Table 3, p. 24), the mean lengths for breeding females are 8·06 and 7·49 mm. respectively.

At Blyth the mean lengths of breeding females at Stations 1 to 5 were 8·17, 8·20, 8·14, 8·54 and 8·48 respectively (Table 7, p. 28). At Station 6, where fresh water influence was most evident, there was a slight but definite dwarfing effect, breeding females averaging 7·58 mm. only. Many molluscs extending into brackish water show a similar diminution in size at maturity.

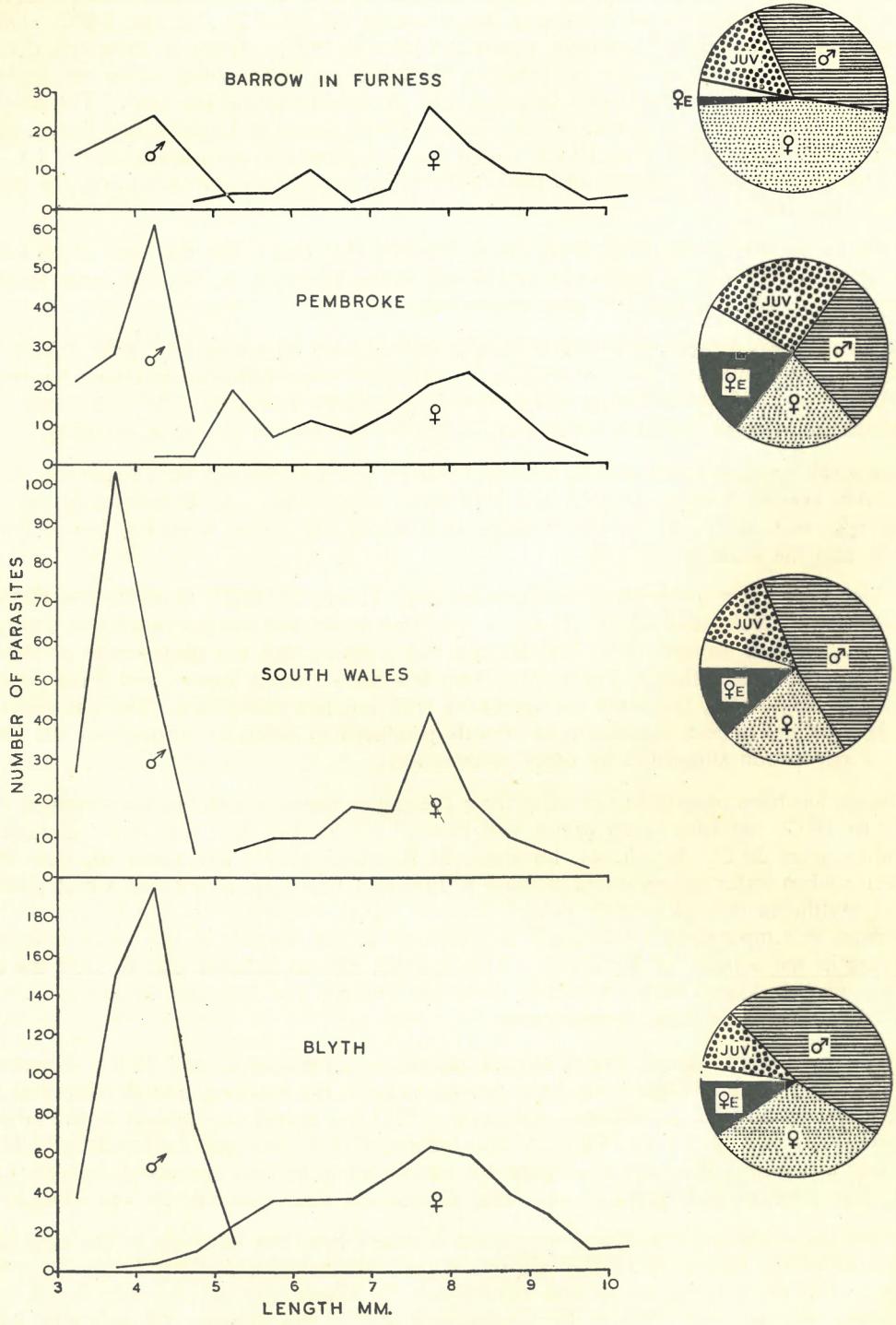
On the south coast, at Poole and R. Yealm (Table 3), breeding females were larger than in South Wales, with average lengths of 8·75 and 8·30 mm. respectively. At Barrow only one female carrying eggs was obtained. In the samples as a whole the largest breeding female measured 10·5 mm. and the smallest 5·0 mm.

Fig. 4 gives the size distribution of parasites over 3 mm. in length from Barrow-in-Furness, Pembroke, South Wales and Blyth. It will be seen that males and females overlap to a very small extent (*cf.* Cole and Savage, 1951, Fig. 3), and this suggests that the growth-rate of the female parasites greatly exceeds that of the males. Very few males exceed 5 mm., and if the population is divided at this length, the sexes are separated with but few exceptions. The size distribution of the females indicates a succession of broods produced at intervals throughout the breeding season—a conclusion supported by other observations.

Mytilicola has been observed to develop from the egg to the copepodid in temperatures ranging from 6° to 19°C. *Mytilus edulis* grows well in cool waters and does not thrive in water of a temperature over 20°C. Mytilicola, however, as Korringa (1951) has observed, does become more active when water temperatures increase in June and July. He found that a high percentage of larval Mytilicola thrived in their pelagic state at higher temperatures, and he associates with this increase in temperature a falling-off in condition of the mussels in the warm months, and an increase in the activity of Mytilicola. This enabled him to forecast that in 1950 the critical time for mussels in Dutch waters would be sometime between mid-July and the end of September, the period of maximum water temperatures.

The temperatures of coastal waters around Britain vary between 0° and 25°C. Temperatures within the upper range of this scale have proved suitable for hatching and development of the parasite under controlled conditions. Grainger (1951) has reared copepodids in the laboratory at a temperature of from 13° to 14°C. A temperature of 18°C was used for hatching by Hockley (1951), and at Conway this higher temperature was found to be very successful—nauplii hatched in from 2 to 10 days in beakers of unaerated filtered sea water (salinity 29·0 to 31·4‰).

Grainger has suggested that lower temperatures retard both the hatching of the eggs and the development of the larvae up to the infective stage. He suggests that "It is not unlikely that the eggs laid in the autumn are carried throughout the winter and develop very slowly because of the lower temperatures. When the temperature rises in the summer the eggs may hatch to produce larvae which enter the mussels in numbers in the autumn." This appears contrary to the seasonal pattern of breeding shown above. Grainger's theory might account for the low numbers of females with egg-sacs found in Barrow-in-Furness in February and March, 1951, but the percentage of immatures found in this area at this time (15·19) suggests that there had been some breeding shortly before this date. It is impossible to offer any reasonable explanation of the seasonal absence of juveniles from Grainger's samples.



4. Size-distribution and composition of the populations of *Mytilicola intestinalis* found in mussels from infected areas on the West Coasts of England and Wales. The plain segments in the circles comprise the parasites damaged during dissection of the host-mussels and therefore not sexed.

Copepodids were immobilized when kept in water at 0°C. for four days at Conway. When the temperature of the water was raised to 18·5° C., many of the copepodids recovered and were successfully used to infect mussels in water at room temperature (*ca.* 14°C.).

The higher temperatures in the summer are correlated with greater activity on the part of the copepodids. If larvae hatch in the summer it is most unlikely that they will remain in the free-swimming stages for 8 to 12 weeks to enter mussels in the autumn. If they do, in fact, then it is to be expected that Grainger would have found large numbers of juveniles in the summer. This was not the case. Copepodids have not been kept alive in the laboratory for longer than fifteen days unless they enter a host. Because of the passive method of infection, there is no known reason why the copepodids should not enter their hosts during the summer months unless it be that the feeding of mussels was considerably retarded. This, however, cannot hold. In fact the reverse is true—mussel feeding activity is greatly increased after the spawning period finishes in June.

Influence of salinity

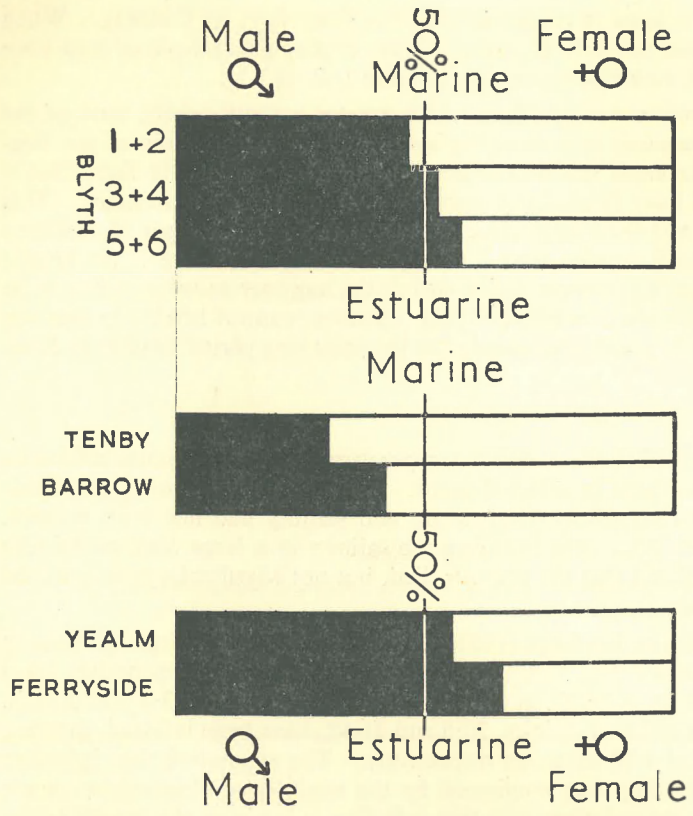
Korringa (1951) states that it is not likely that either temperature or salinity limits infection, because there is plenty of variation in these in infected areas. In 1950, the year of catastrophic mussel losses on the Dutch beds, the changes in temperature and salinity had not been noticed. Salinity is thought to have been about 28‰. On lowering the salinity in a large tank containing mussels to as little as 10‰, Korringa found that the mussels died, but not Mytilicola, which proved to be more euryhaline than their hosts.

Meyer and Mann, reported by Leloup in Korringa (1951), have shown that the minimum salinity in which Mytilicola can survive is about 5‰. In the laboratory at Conway copepodids have been reared successfully at a temperature of 18°C. in waters of salinity 17·2, 18·5, 23·0 and 30·8‰. Mussels placed in dishes containing sea water of salinity, 20·5 and 31·4‰ have been infected, showing an average density per host of 2·37 and 4·70 parasites respectively. The suggestion that infection occurs less readily at much reduced salinity was confirmed by the analysis of observations made at Blyth (Table 8, p. 29). These observations also show that infection is less near the mouth of the estuary, where salinity is rarely reduced below that of the sea outside, than in the middle section of the estuary, where moderate fresh water influence is discernible.

Table 8 shows that the percentage infection was least at Blyth at Station 1 (Fig. 2), where it was little more than half that observed at Station 4 up-river. The average number of parasites was also least in the most marine habitat near the mouth of the estuary (21·62 parasites per 20 mussels at Station 1 ; 96·50 per 20 mussels at station 4). The range in salinity observed in April at Station 1 during a tidal cycle was from 32·7 to 33·6‰, whereas at Station 4 it was 30·79 to 32·16‰. It is not suggested that salinity alone was responsible for the differences observed, as the degree of exposure and the speed of the current also varied. It has already been shown that these influence infection. It is probable, however, that a small admixture of fresh water results in optimum conditions for the survival and development of the parasite.

There was a slightly lower percentage infection and a markedly smaller number of parasites per host in the Sleek Burn (Station 6, Fig. 2), the station most affected by fresh water discharge. At this station salinity was observed to range from 5·63‰ at low water to 32·52‰ at high water. At Station 5 (Cowpen Pool) the mussels examined were taken from the bank, well clear of the low water stream, and the observed salinity range to which they were exposed during a tidal cycle was 30·0 to 32·52‰, i.e., markedly less than at Station 6. It seems, therefore, that frequent exposure to water of low salinity may limit infection. Further investigation is clearly needed in estuaries where mussels are present below low water mark (this was not the case at Blyth) over a wide range of salinity conditions. There is also need for extended work in the laboratory to determine the extent to which infection occurs in mussels maintained constantly at salinities near the limit of their toleration. It is also desirable to investigate the changes in parasite content which result when infected mussels are moved from a marine to a fully estuarine environment and vice versa.

There is evidence from Tables 2 and 6 (pp. 23, 27) to suggest that salinity may affect the sex ratio of the parasites. In the lower part of the Blyth estuary (Stations 1 and 2), where the salinity is very little reduced from that of open sea water, female Mytilicola were slightly more prevalent than males (91 ♂♂ : 106 ♀♀). At Stations 3 and 4 in mid-estuary, the two sexes were very nearly equal in numbers (255 ♂♂ : 233 ♀♀). The same tendency is evident to some extent in Table 2. Ferryside



5. The influence of salinity upon sex-ratio. Percentages of male and female Mytilicola in the different sections of the Blyth Estuary (numbering of station from mouth to headwaters) and at representative marine and estuarine stations.

and the River Yealm, both estuarine stations, show a prevalence of males, while at Tenby and Barrow, both marine habitats, the females are far more numerous (Fig. 5). Possibly some other factor such as exposure also influences the survival of male and female parasites ; perhaps also males may not long survive after effecting fertilization. The latter hypothesis receives some support from the relative scarcity of males at Barrow in late winter when the breeding season had practically ended. It is possibly significant that the two samples from Pembroke Ferry and Mill Bay, which include a high percentage of juveniles—showing that breeding was in full swing—also show an almost equal number of males and females. In this part of Milford Haven the conditions are marine but sheltered. None of the samples for Pembroke was taken from a habitat substantially influenced by fresh water discharge.

Effect on host

Cole and Savage (1951) concluded from their study of Blyth mussels that "the presence of Mytilicola is associated with a serious reduction of condition in infested mussels". Korringa (1951) points out that a preliminary survey of mussel beds in the Zandkreek area showed a loss of condition in mussels where infection was in the order of 5 to 10 Mytilicola per host. This loss of condition was not apparent where the occurrence of the parasite was light (1 to 3 per mussel). During the present survey it has been observed that the presence of the parasite is usually associated with poor condition in the host. In the Pembroke area the condition of mussels, whether infected or not, was poor, while in the sample from Llanelly (sample 51) the general condition was noted as "good", even in a host containing 19 adult parasites.

Although the study of condition in relation to parasite content of mussels was outside the scope of this survey, the impression gained is that the sample from Llanelly was an exception. It is possible that in some areas, through the agency of some unknown set of conditions, infection, though heavy, may not be apparent in its effect on the condition of the host. This is suggested only as a possible secondary explanation for infection escaping detection until it has become widespread and heavy. Infected mussels may hold their condition more easily if the degree of infection is increased at a time when the gonads of the host are developing or have developed. Korringa (1950) remarks that infected mussels are unable to breed. Fecundity is certainly diminished in infected mussels. This probably results from a diversion of products which are normally used in the development of the gonads to a form of compensatory metabolism in the host.

Meyer and Mann (1951) have shown that the filtering capacity is reduced in infected mussels in proportion to the degree of infection ; that the absorption of albumen is more rapid and that their respiration rate is twice that of healthy mussels. They found that although the host could, if it was fully developed, live with little difficulty while containing three parasites, the very young

PLATE I. View across the mussel beds at Whitstable, showing in the foreground great reduction in population of mussels as the result of very heavy attack by Mytilicola. *Photo :* D. Key.

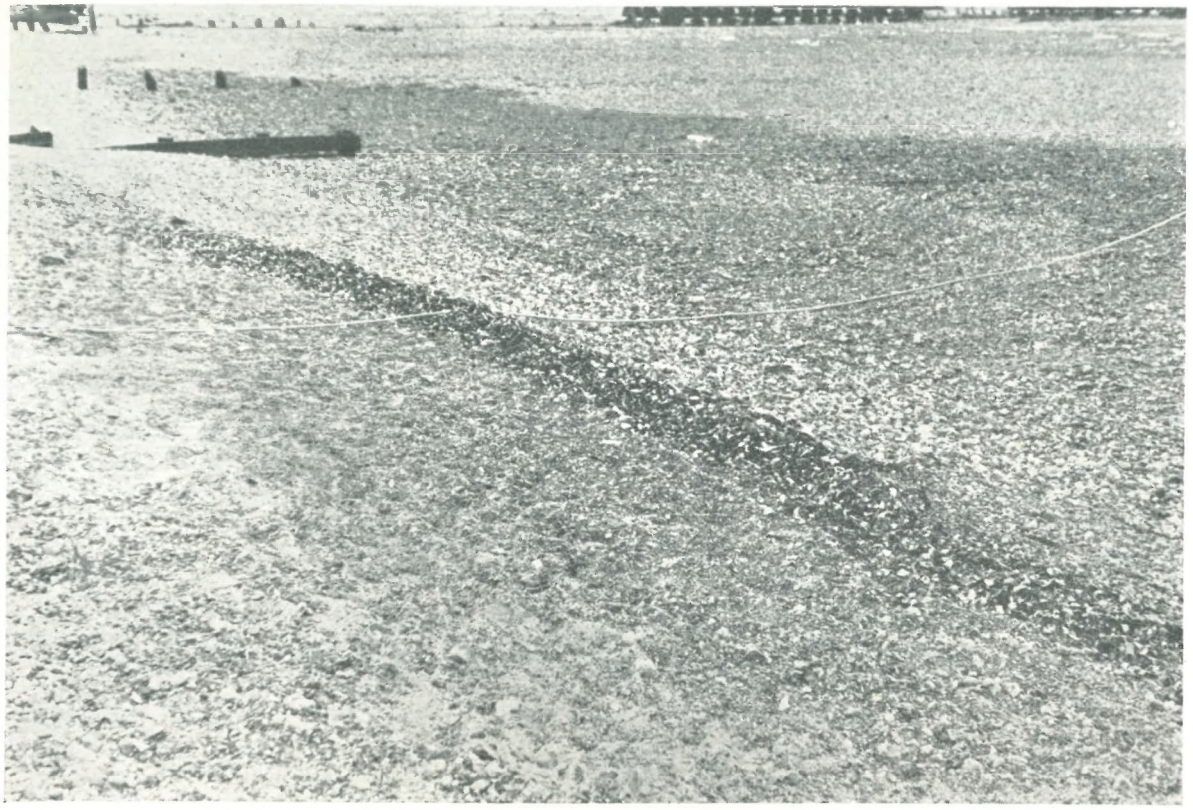


PLATE II. Shells of recently dead mussels forming windrow at high water at Whitstable following devastation of beds by Mytilicola. *Photo :* Dr. G. E. Newell.

though lightly infected mussels showed a high mortality. In the mussels from Blyth examined by Cole and Savage (1951) the minimum infection causing serious loss of condition seemed to be rather higher.

In the German Wattenmeer, Meyer and Mann (1951) found that infection occurred in "young" mussels during the breeding season as much as in mussels which had finished breeding. Korringa and Lambert (1951) found a 30 per cent infection of 1 or 2 parasites per host in mussels between 29 and 35 mm., growing on a pile in a mussel bed near Mèze on the south coast of France. Cole and Savage (1951) found an average of 14·25 parasites in mussels between 3·5 and 4·99 cm. collected at Blyth in January.

In sample 70 (Table 5), which was taken from the uppermost mussels at Station 3 in the Blyth estuary in May, the ten smallest, ranging in size between 3·48 and 4·28 cm., with an average length of 3·87 cm., contained in all 28 parasites. The other ten mussels of this sample, ranging in size between 4·46 and 5·66 cm., with an average length of 5·23 cm., contained 24 parasites. In sample 9, (Barrow-in-Furness), the ten smallest mussels, ranging in size between 3·57 and 3·83 cm., with an average length of 3·68 cm., contained 15 parasites. The ten largest mussels, ranging between 3·84 and 5·89 cm., with an average length of 4·29 cm., contained 16 parasites. At Newbiggin (Table 5, sample 80) the smallest infected mussel was 3·34 cm. long and contained 14 parasites, the largest was 6·79 cm. and contained 10 parasites. The two samples from Blyth and Barrow are the only ones in which the difference in the size of hosts allows of such comparisons. In most of the other samples the difference in size was less. Grainger (1951) found that the smaller mussels contained few copepods, but he does not record having found immature parasites in the digestive gland, and some may have been overlooked ; nor was consideration given to the fact that the growth-rate of young mussels is retarded by infection. There is no definite evidence from this survey to show that smaller mussels in any one habitat are less heavily infected than larger mussels.

The parasite enters by the current of water made by the mussel. This is confirmed by observations made during infection experiments at Conway. Because of this passive method of infection, other conditions being equal, the intake of parasites will be proportionate to the filtering efficiency of the host. Jørgensen (1949) has shown that filtering efficiency may vary in small *Mytilus edulis*. In experiments where suspensions of flagellates and Nitzschia were used, he found feeding rates (= water transport) of 80, 32 and 40 ml. per hr. per mg. N in mussels of average lengths 1·5, 2·9 and 3·2 cm. respectively. "The feeding rates are shown to be comparatively larger in the smaller animals than in the bigger ones." Fox, Sverdrup and Cunningham (1937), on the other hand, have shown that in *Mytilus californianus* there is an appreciable increase in filtration rate with increase in size of mussel. Mussels of average size 74, 102 and 178 mm. gave filtering rates of 0·5 to 2·1, 2·2 to 2·9, and 1·8 to 18·1 litres per hour respectively. Although the filtration rate of small mussels per unit of flesh weight may be greater than that of large mussels, the absolute volume of water passing through the gills will almost certainly be less. It may well be, however, that the young mussels may filter more at a time when the larger mature mussels are in the process of spawning—a time when food intake is considerably reduced.

It has been noticed that young mussels often settle on the older, already existing, stock on a bed. It is possible that this position may be more favourable for the intake of parasites.

Though at first there is no visible difference between free and infected mussels on external examination, severely infected mussels are later seen to break away from the byssal attachments and die. Plates I and II show the result of severe infection at Whitstable in July 1950. These mussel beds have now been almost totally destroyed. A sample of mussels from this area, received at Conway in October 1949, included one containing no less than 57 adult parasites. On internal examination, there is a marked change in the appearance and volume of flesh in heavily infected mussels. The digestive gland, which is dark brown in healthy mussels, turns to an ochre colour and, in dying mussels, to yellow or cream. The appearance of the mussel bed changes gradually as the mortality increases. At first, empty and gaping valves are to be seen ; later, when the byssal attachments disintegrate and the empty valves are washed away by the tides, naked patches appear. These bare patches may be scoured clean or sanded-up, depending upon the swiftness of the currents ; successful recolonization of denuded areas has not so far been observed. The surviving mussels at Whitstable are still heavily infected with Mytilicola.

Dollfus (1951) is not convinced that infestation with Mytilicola results in the death of mussels. He considers that the epidemic mortality in the Netherlands must have been due to another cause—

a bacterium or virus ; and that mussels infected with Mytilicola may be weakened and thus become more susceptible to the disease. Such a contention is very difficult to prove or disprove. The basic fact with which the mussel farmer has to contend is that heavily infected mussels are thin and weak and are liable to die in quantity when environmental conditions become unfavourable, e.g., during very hot summers.

Cross-infection of oysters and mussels

Mytilicola was found in *Ostrea edulis* in the Penryn and Blackwater rivers, in Cornwall and Essex respectively, by Baird, Bolster and Cole (1951). Copepodids hatched from egg-sacs removed from a parasite found in one of these oysters were used successfully to infect four Conway mussels. The mussels were kept in water of salinity 31·8‰ at temperatures from 13° to 15° C. and dissected six weeks after the copepodids had been introduced ; 23 parasites were found, an average of 5·75 per host. Experiments were also made to determine whether there was any difference between the susceptibility of mussels and oysters to infection by the parasite. In this experiment five mussels and five oysters were placed together in each of two glass vessels containing water of salinity 28·3‰, at a temperature of 13° to 15° C. After four weeks all the molluscs were dissected. In none of the oysters was the parasite found, but mussels in both vessels were infected. In one, four out of five mussels contained a total of five parasites, in the other vessel, two out of five mussels contained sixteen parasites. All parasites were less than 3 mm.

These preliminary experiments suggest that Mytilicola does not easily invade oysters, and this conclusion was confirmed by other experiments made at Conway, in which oysters placed in vessels of sea water, to which copepodids had been added, failed to become infected. Mussels treated by a similar technique almost invariably became infected.

Few oyster beds have so far been examined for parasites, but mussels from all the major oyster-producing areas in Britain are already infected. There is, therefore, the maximum chance of the parasite becoming established in oysters if susceptible strains exist, or if the parasite should become adapted in such a manner as to increase its chances of entering and surviving in oysters. *Mytilicola orientalis* (Mori) is already well established in *Ostrea gigas* in Japan (Mori, 1935) and on the Pacific coast of the United States (Wilson, 1938), and in *Ostrea lurida* at Puget Sound, Washington (Odlaug, 1946). Odlaug concluded that the presence of the parasite adversely affected the condition of the host oysters. Further work is needed to show whether *Mytilicola intestinalis* is capable of infecting oysters to a sufficient degree to bring about a loss of condition. Mussels in the vicinity of oyster beds form a risk to the oysters. This danger is not, as far as we know at present, very great, but it may be wise to remove the mussels whenever this is practicable.

CONTROL

The possibility of using immune strains has been discussed by Dollfus (1951). It was successful for oysters in eastern Canada following an outbreak of contagious disease (Needler, 1941). There is also the possibility that the incidence of Mytilicola may in time become adjusted in a degree that is not deleterious, (*cf.* Korringa and Lambert, 1951). The indications at present, however, point to mussel culture as most hopeful, as adopted in France (Lambert, 1935) or the Netherlands, because Hockley (1951) found heavy infestation of mussels on flat beds at Plymouth, but few parasites in mussels from the dock walls, and because of the observations reported in the present paper. It must be admitted, though, that it may not always be advantageous to seek the lower rate of infection between tidemarks, because growth and fattening are best when the mussels are fully submerged (Newcombe, 1935).

Apart from such a constructive reform as the wider use of cultural methods, there appears to be a need for consideration of the best methods of reducing the spread of infection.

SUMMARY

1. *Mytilicola intestinalis* is recorded for the first time in mussels on the west coast of England and Wales at Barrow-in-Furness, in Milford Haven and along the coast of South Wales. It was also found in mussels taken from the bottom of a tug scraped at Fleetwood, and plying between

Barrow and Heysham. Evidence is adduced to show that transport of infested mussels on the bottom of ships, particularly those destined for breaking up, has been the chief means by which the parasite has been distributed. Natural spread by means of the planktonic stages is slow, as they are of brief duration.

2. Mytilicola continues to breed while water temperatures exceed 6°C. Breeding is interrupted on the average for about two months (February and March) on the east coast but usually continues throughout the year on the Channel coast, in the south-west and in South Wales.

3. In the Blyth estuary, Northumberland, the percentage infection and the average number of parasites per infected mussel were lowest near the mouth and at a maximum in mid-estuary, being slightly reduced again at the top of the estuary where the salinity at low water was much reduced. At the mouth of the estuary female Mytilicola were more abundant than males, in mid-estuary the proportions of the sexes were about equal, at the top of the estuary males predominated. These tendencies were also evident in samples examined from other parts of the coast, but the observations were insufficient to give firm conclusions.

4. Mussels exposed high on the shore were less heavily infected than those at low water mark. Other factors believed to limit infection are turbulence and current speed.

5. Although oysters have been found to be lightly infected by Mytilicola in a few localities, experiments with mixed mussels and oysters did not result in infection of the oysters, although the mussels became parasitized. Copepodids hatched from egg-sacs removed from females found in oysters were successfully used to parasitize mussels.

6. Hatching of copepodids has been achieved at temperatures of from 6° to 19°C., with salinities of from 17·2° to 30·8‰. Successful infection experiments have been made at salinities down to 20·5‰.

ACKNOWLEDGMENTS

I would naturally wish to thank the Development Commission for their support and my senior and other colleagues in the Ministry for advice and guidance ; but I am informed that this is unnecessary. I may, however, express my thanks to others, without whose help the work would not have been accomplished in the time available : the Superintendent, and Staff, of the Lancashire and Western and the South Wales Sea Fisheries Committees.

REFERENCES

BAIRD, R. H., G. C. BOLSTER and H. A. COLE, 1951. *Mytilicola intestinalis*, Steuer, in the European flat oyster (*Ostrea edulis*). *Nature*, Lond., **168**, 560.

CASPERS, H., 1939. Uber Vorkommen und Metamorphose von *Mytilicola intestinalis* Steuer (Copepoda Paras.). In der südlichen Nordsee. *Zool. Anz.* **126**, 161.

CERRUTI, A., 1932. Molluschicoltura : In Pesca nei mari e nelle acque interne d'Italia. Vol. 2.

COLE, H. A., 1951. Le Mytilicola en Angleterre. *Rev. des Trav. (de l'Office Sci. et Tech. des Pêches Marit.).* **17**, 9-13.

COLE, H. A. and R. E. SAVAGE, 1951. The effect of the parasitic copepod, *Mytilicola intestinalis* Steuer, upon the condition of mussels. *Parasitology*, **41**, 156-161.

COLE, H. A., 1952. The American slipper limpet (*Crepidula fornicata* L.) on Cornish oyster beds. *Fish. Inv. 2*, **17**, No. 7, 1-13.

CONSEIL PERMANENT INTERNATIONAL POUR L'EXPLORATION DE LA MER, 1933. *Atlas de temperature et salinité de l'eau de surface de la Mer du nord et de la Manche*. 1-32. Copenhague.

DOLLFUS, R. Ph., 1951. Le copepode *Mytilicola intestinalis*. A Steuer peut-il être la Cause d'une maladie épidémique des moules. *Rev. des Trav. (de l'Office Sci. et Tech. des Pêches Marit.).* **17**, 81-85.

ELLENBY, C., 1947. A copepod parasite of the mussel new to the British fauna. *Nature*, Lond., **159**, 645.

FOX, D. L., H. U. SVERDRUP and T. P. CUNNINGHAM, 1937. The rate of water propulsion by the California mussel. *Biol. Bull. Woods Hole*, **72**, 417-438.

GRAINGER, J. N. R., 1951. Notes on the biology of the copepod *Mytilicola intestinalis* Steuer. *Parasitology*, **41**, 135-142.

HARDY, A. C. and E. R. GUNTHER, 1935. The plankton of the South Georgia whaling grounds and adjacent waters, 1926-27. *Discovery Reports*, **11**, 1-456.

HELDT, J. H., 1950. Observations sur *Mytilicola intestinalis* Steuer parasite des moules. *Bull. Soc. Sci. Nat. Tunisie*, **3**, 57-64.

HOCKLEY, A. R., 1951. On the biology of *Mytilicola intestinalis* Steuer. *J. Mar. Biol. Assoc. U.K.*, **30**, 223-232.

JØRGENSEN, C. B., 1949. The rate of feeding by Mytilus in different kinds of suspension. *J. Mar. Biol. Assoc. U.K.*, **28**, 333-344.

KORRINGA, P., 1950. De aarval van de parasiet *Mytilicola intestinalis* op de Zeeuwse mossel cultuur. *Visserij Nieuws*, No. 7, supplement 1-7.

KORRINGA, P. et L. LAMBERT, 1951. Quelques observations sur la fréquence de Mytilicola intestinalis Steuer (copepoda parasitica) dans les moules du littoral Mediterranéen francais, avec une note sur la presence de *Pseudomyicola spinosus* (Raff. et Mont.) (Copepoda parasitica). *Rev. des Trav. (de l'Office Sci. et Tech. des Pêches Marit.)*, **17**, 15-29.

KORRINGA, P., 1951a. Le *Mytilicola intestinalis* Steuer (Copepoda parasitica) menace l'industrie moulière en Ze'lande. *Rev. des Trav. (de l'Office Sci. et Tech. des Pêches Marit.)*, **17**, 9-13.

KORRINGA, P., 1951b. Over *Mytilicola intestinalis* (Copepoda parasitica) en enkeleandere ongewerste vreemdelingen in onze wateren. *Overdruk uit Vakblad voor Biologen*, **31**, 63-74.

LAMBERT, L., 1935. L'Ostreiculture, la Mytiliculture et la Conchyliculture. Leur control sanitaire. *Mem. de l'Off. des Pêches Marit. Spec. Ser.*, **12**, 119-137.

MEYER, P. F. and H. MANN, 1950. Betrage zur Epidemiologie und Physiologie des parasitischen Copepoden *Mytilicola intestinalis*. *Archiv. fur Fischereiwissenschaft*, **2**, 120-134.

MEYER, P. F. and H. MANN, 1951. Recherches allemandes relatives au "Mytilicola", copépode parasite de la moule, existant dans les watten allemandes 1950-51. *Rev. des Trav. (de l'Office Sci. et Tech. des Pêches Marit.)*, **17**, 63-75.

MONOD, Th. and DOLLFUS, R. Ph., 1932. Les copépodes parasites de mollusques. *Ann. Parasit. Hum. Comp.* **10**, 129.

MORI, T., 1935. *Mytilicola orientialis*, a new species of parasitic copepoda. *Dobutsugaku Zasslu (Zool. Soc. Japan)*, **47**, 687-693.

NEEDLER, A. W. H., 1941. Oyster farming in Eastern Canada. *Bull. Fish. Res. Bd. Canada*, No. **60**, 1-83.

NEWCOMBE, C. L., 1935. A study of the community relationships of the sea mussel, *Mytilus edulis* L. *Ecology*, **16**, 234-243.

ODLAUG, T. O., 1946. The effect of the copepod *Mytilicola orientalis* upon the Olympia oyster *Ostrea lurida*. *Trans. Amer. Micr. Soc.* **65**, 311.

PESTA A., 1907. Die Metamorphose von *Mytilicola intestinalis* Steuer. *Zeit. f. Wiss. Zool*, **88**, 78-98.

PROUDMAN, J., H. M. LEWIS and A. L. DENNIS, 1937. On the temperature of the surface waters of the Irish Sea. *Phil. Trans. Roy. Soc.*, **236**, 261-302.

STEUER, A., 1902. *Mytilicola intestinalis* n. gen. n. sp. aus dem Darme von *Mytilus galloprovincialis* Lam. *Zool. Anz.* **25**, 635.

STEUER, A., 1905. *Mytilicola intestinalis* n. sp. n.g. *Arb. Zool. Inst. Univ. Wien.* 15, 1.

VAYSSIÈRE, A., 1914. In CAILLOL, H. and A. VAYSSIÈRE. Zoogeographie in les Bouches du Rhône. *Encyclopédie departementale*, 3 partie, **12**, 278 (not seen in original, quoted from Monod and Dollfus, 1932).

WILSON, C. B., 1938. A new copepod from Japanese oysters transplanted to the Pacific Coast of the United States. *J. Wash. Acad. Sci.*, **28**, 284-288.

TABLE 1

DISTRIBUTION OF SAMPLES AND PARTICULARS OF INFECTION—WEST AND SOUTH COASTS

Sample No.	*Locality*	*Date*	*Average length of host cm.*	*Percentage infection*	*Heaviest infection*	*Total of parasites per 20 mussels*	*Average per infected host*
	CUMBERLAND						
1	Ravenglass	20.2.51	5·63	0	—	—	—
2	Haverigg	20.2.51	4·95	0	—	—	—
	LANCASHIRE						
3	N. Walney Channel ..	22.2.51	5·17	10	1	2	1
4*	S. Walney Channel (1)	30.3.51	5·85	0	—	—	—
5*	S. Walney Channel Outside Docks .. (2)	28.3.51	5·68	15	1	3	1
6	Barrow-in-Furness .. (1)	21.2.51	5·78	85	6	45	2·65
7	,, (Docks) .. (2)	21.2.51	5·61	45	1	9	1·00
8	,, ,, .. (3)	22.2.51	5·67	90	11	77	4·28
9	,, ,, .. (4)	22.2.51	3·99	75	7	31	2·07
10	,, ,, .. (5)	22.2.51	5·51	65	9	37	2·85
11	Roosebeck	6.2.51	5·60	0	—	—	—
12	Humphrey Head	16.2.51	5·26	0	—	—	—
13	Morecambe North	7.2.51	5·47	0	—	—	—
14	Heysham North	12.2.51	5·52	0	—	—	—
15	Heysham	13.2.51	5·24	0	—	—	—
16	Heysham Dock	13.2.51	5·10	0	—	—	—
17	Glasson Dock	6.2.51	4·77	0	—	—	—
18	Cockerham	13.2.51	5·55	0	—	—	—
19	Fleetwood .. .. (1)	5.2.51	5·80	0	—	—	—
20	,, ... (2)	27.2.51	5·58	0	—	—	—
21	,, ... (3)	15.2.51	5·26	0	—	—	—
22	,, ... (4)	6.2.51	3·42	65	14	79	6·08
23	,, ... (5)	2.3.51	5·58	0	—	—	—
24	,, ... (6)	8.3.51	6·53	0	—	—	—
25	,, ... (7)	8.3.51	5·78	0	—	—	—
26	,, ... (8)	15.2.51	5·29	0	—	—	—
27	Bar Lightship	21.7.51	2·83	0	—	—	—
28	Lytham	5.2.52	6·24	0	—	—	—
	CHESHIRE						
29	New Brighton	5.3.51	4·47	0	—	—	—
30	Wallasey	5.3.51	5·80	0	—	—	—
31	Dee Estuary	23.1.51	5·73	0	—	—	—
	CAERNARVON						
32	Conway	1.1.51	5·73	0	—	—	—
33	Menai Straits	7.1.51	5·73	0	—	—	—
34	Portmadoc	9.1.51	5·73	0	—	—	—
	ANGLESEY						
35	Holyhead	6.1.51	5·34	0	—	—	—
	MERIONETH						
36	Barmouth	11.1.51	5·73	0	—	—	—
37	Aberdovey	12.1.51	6·17	0	—	—	—
	PEMBROKE						
38*	Fishguard .. .. (1)	4.6.51	5·80	0	—	—	—
39	,, ... (2)	30.11.51	5·29	0	—	—	—
40	,, ... (3)	30.11.51	5·72	0	—	—	—
41	Dale	5.12.51	5·17	10	1	2	1
42	Angle	12.11.51	5·00	6·25	1	1	1
43	Milford Haven .. (1)	4.12.51	5·33	30	5	12	2
44	,, ,, .. (2)	27.11.51	6·00	15	1	3	1
45	Pembroke Dock	27.11.51	6·28	85	12	67	3·94
46	Mill Bay	29.11.51	5·74	100	15	159	7·95
47	Pembroke Ferry	29.11.51	5·76	100	23	107	5·35
48	Neyland	29.11.51	5·88	100	31	87	4·35
49	Tenby	29.11.51	4·55	80	10	68	4·25

*Not personally collected.

TABLE 1 (*continued*)

Sample No.	*Locality*	*Date*	*Average length of host cm.*	*Percentage infection*	*Heaviest infection*	*Total of parasites per 20 mussels*	*Average per infected host*
	CARMARTHEN						
50	Ferryside	2.1.52	4·80	100	26	217	10·85
51	Llanelly	8.1.52	4·70	90	26	141	7·83
	GLAMORGAN						
52*	Barry Dock	9.2.52	6·53	60	4	27	2·25
53*	Sker Point	29.3.52	2·51	0	—	—	—
	DEVON						
54*	Appledore	8.2.52	6·47	0	—	—	—
	CORNWALL						
55*	Padstow	1.2.52	7·00	0	—	—	—
	SOUTH COAST						
57*	Poole	11.12.50	5·73	90	19	109	6·05
58*	River Yealm	15.1.51	5·73	100	15	173	8·65
59*	River Penryn	29.6.51	5·67	15	2	4	1·33
60*	Lympstone	19.10.51	6·20	—	—	—	—

*Not personally collected.

TABLE 2

ANALYSIS OF MUSSEL SAMPLES

(EACH COMPRISED 20 MUSSELS)

Sample No.	*Locality*	*Date*	*Males*	*Females with egg-sacs*	*Females without egg-sacs*	*Juveniles less than 3 mm.*	*Damaged*	*Total*	*Ratio* ♂♂ : ♀♀	*Hosts having only*			*Per cent infected hosts with 1 parasite*
										1♂	1♀	1 *Juvenile*	
	BARROW												
3	N. Walney Channel	22.2.51	—	—	2	—	—	2	—	—	2	—	100·0
5	S. Walney Channel	28.3.51	—	—	2	1	—	3	—	—	2	1	100·0
6	Barrow-in-Furness .. .. (1)	21.2.51	14	1	24	2	4	45	1 : 1·79	1	4	—	29·4
7	,, ,, ... (2)	21.2.51	3	—	4	2	—	9	1 : 1·33	3	4	2	100·0
8	,, ,, ... (3)	22.2.51	27	—	36	13	1	77	1 : 1·33	2	2	—	22·2
9	,, ,, ... (4)	22.2.51	12	—	13	5	1	31	1 : 1·08	2	3	—	33·3
10	,, ,, ... (5)	22.2.51	14	—	15	8	—	37	1 : 1·07	1	4	—	38·5
	Totals		70	1	96	31	6	204	1 : 1·39				
22	Fleetwood .. .. .. (4)	6.2.51	25	6	28	8	12	79	1 : 1·36	1	1	—	15·4
	PEMBROKE												
41	Dale	5.12.51	—	—	2	—	—	2	—	—	2	—	100·0
42	Angle	12.11.51	—	—	—	1	—	1	—	—	—	1	100·0
43	Milford Haven .. .. (1)	4.12.51	3	1	8	—	—	12	1 : 3·00	—	3	—	50·0
44	Milford Haven .. .. (2)	27.11.51	1	—	2	—	—	3	1 : 2·00	—	—	—	0·0
45	Pembroke Dock	27.11.51	27	14	13	8	5	67	1 : 1·00	1	2	—	17·6
46	Mill Bay	29.11.51	47	14	34	48	16	159	1 : 1·02	—	—	—	0·0
47	Pembroke Ferry	29.11.51	31	15	15	37	9	107	1 : 0·97	—	1	2	15·0
48	Neyland	29.11.51	19	7	21	34	6	87	1 : 1·47	4	3	—	35·0
	Totals		128	51	95	128	36	438	1 : 1·14				
	S. WALES												
49	Tenby	28.11.51	17	24	15	6	6	68	1 : 2·29	1	1	—	12·5
50	Ferryside	2.1.52	108	22	35	46	6	217	1 : 0·53	—	1	—	5·0
51	Llanelly	8.1.52	68	22	40	9	2	141	1 : 0·91	—	1	1	11·1
52	Barry Dock	8.2.52	—	2	11	11	3	27	—	1	3	—	33·3
	Totals		193	70	101	72	17	453	1 : 0·89				
	S. COAST												
57	Poole	11.12.50	36	23	15	27	8	109	1 : 1·06	—	2	—	11·1
58	R. Yealm	15.1.51	68	25	30	39	11	173	1 : 0·81	—	—	—	0·0
59	R. Penryn	29.6.51	0	1	2	0	1	4	—	—	2	—	66·6

TABLE 3

AVERAGE LENGTH OF PARASITES (in mm.)

Sample No.	*Locality*	*Date*	*Males*	*Females with egg-sacs*	*Females without egg-sacs*
	BARROW				
3	N. Walney Channel	22.2.51	—	—	7·75
5	S. Walney Channel	28.3.51	—	—	8·25
6	Barrow-in-Furness .. .. (1)	21.2.51	3·63	8·30	7·84
7	,, ,, ... (2)	21.2.51	4·33	—	7·10
8	,, ,, ... (3)	22.2.51	4·05	—	7·51
9	,, ,, ... (4)	22.2.51	3·70	—	7.10
10	,, ,, ... (5)	22.2.51	4·06	—	7·51
	MEAN LENGTH		3·95	8·30	7·58
22	Fleetwood .. .. (4)	6.2.51	3·82	7·57	6·65
	PEMBROKE				
41	Dale	5.12.51	—	—	7·80
42	Angle	12.11.51	—	—	—
43	Milford Haven .. .. .. (1)	4.12.51	3·93	8·70	7·96
44	Milford Haven .. .. .. (2)	27.11.51	4·01	—	7·16
45	Pembroke Dock	27.11.51	4·00	7·75	6·30
46	Mill Bay	29.11.51	3·85	7·41	6·36
47	Pembroke Ferry	29.11.51	3·92	8·14	6·11
48	Neyland	29.11.51	3·65	8·30	6·76
	MEAN LENGTH		3·89	8·06	6·92
	SOUTH WALES				
49	Tenby	28.11.51	4·26	7·68	7·74
50	Ferryside	2.1.52	3·72	7·62	6·65
51	Llanelly	8.1.52	3·64	7·56	7·02
52	Barry Dock	8.2.52	—	7·10	6·54
	MEAN LENGTH		3·87	7·49	6·99
	SOUTH COAST				
57	Poole	11.12.50	3·76	8·75	6·65
58	River Yealm	15.1.51	4·20	8·30	7·80
59	River Penryn	29.6.51	—	7·10	7·40

TABLE 4

SUMMARY OF PARTICULARS OF MUSSEL SAMPLES

Locality	*No. of samples*	*Percentage infection*	*Average No. of parasites per 20 mussels*	PERCENTAGE COMPOSITION OF PARASITE POPULATION				
				Males	*Females with egg-sacs*	*Females without egg-sacs*	*Juveniles (less than 3 mm.)*	*Damaged*
				per cent	*per cent*	*per cent*	*per cent*	*per cent*
Barrow	7	55·0	29·1	34·3	0·5	47·1	15·2	2·9
Fleetwood	1	65·0	79·0	31·6	7·6	35·5	10·1	15·2
Pembroke	8	63·5	54·8	29·2	11·6	21·7	29·2	8·2
South Wales	4	73·7	113·3	42·6	15·5	22·3	15·9	3·8

TABLE 5

BLYTH ESTUARY AND NEWBIGGIN

DISTRIBUTION OF SAMPLES AND PARTICULARS OF INFECTION

Sample No.	*Station No.*	*Station Description*	*Date*	*Average length of host*	*Percentage infection*	*Heaviest infection*	*Total of parasites per 20 mussels*	*Average per host*	*Position on shore or piles*
61	1	S. Harbour	30.4.52	4·55	50	2	11	0·55	Vertical
62		West Side of Jetty	,,	4·81	40	3	17	0·85	Horizontal
63			1.5.52	4·87	35	2	10	0·50	Uppermost
64		N. West Side of Jetty	,,	5·01	60	3	21	1·05	2 feet lower
65			7.5.52	5·38	80	6	39	1·95	5 feet lower
66			8.5.52	5·27	90	4	35	1·75	7 feet lower
67		N. East Side of Jetty	,,	4·95	15	4	6	0·30	Uppermost
68			,,	5·73	65	5	34	1·70	6 feet lower
69	2	Mid-Ferry N. Bank	10.5.52	5·37	80	6	51	2·55	V. Distribution 2′ only
70	3	High Ferry	16.5.52	4·55	80	8	52	2·60	Uppermost
71		,, ...	,,	5·28	85	24	123	6·15	6 feet lower
72	4	Tidal Basin Staiths	12.5.52	4·75	75	4	35	1·75	Uppermost
73		(Vertical Distribution)	,,	5·16	95	15	93	4·65	5 feet lower
74			,,	5·37	100	23	143	7·15	10 feet lower
75		Tidal Basin Flats	15.5.52	5·50	95	16	115	5·75	Horizontal
76	5	Cowpen Pool	14.5.52	5·20	100	12	93	4·65	Uppermost
77		(Horizontal distribution)	,,	5·86	90	12	95	4·75	3 feet lower
78	6	Sleekburn	15.5.52	4·96	80	8	65	3·25	Horizontal
79		,, ...	,,	5·17	85	11	66	3·30	4 feet lower
80		Newbiggin	5.5.52	5·61	100	15	143	7·15	Horizontal

TABLE 6

BLYTH ESTUARY

DETAILED ANALYSIS OF MUSSEL SAMPLES (EACH COMPRISED 20 MUSSELS)

Locality	Date	Males	Females with egg-sacs	Females without egg-sacs	Juveniles less than 3 mm.	Dam-aged	Total	Ratio ♂♂ : ♀♀	Hosts having only			Percentage infected hosts with 1 parasite
									1 male	1 female	1 juvenile	
STATION 1												
S. Harbour	30.4.52	4	1	2	2	2	11	1 : 0·75	3	3	1	70·0
West Side of Jetty	,,	5	—	4	5	3	17	1 : 0·80	—	—	1	12·5
N. West Side of Jetty	1.5.52	4	—	4	1	1	10	1 : 1·00	—	2	1	42·9
,, ,, ,,	,,	5	3	11	1	1	21	1 : 2·80	2	3	—	41·7
,, ,, ,,	7.5.52	16	6	15	2	—	39	1 : 1·31	—	6	—	37·5
,, ,, ,,	8.5.52	19	2	12	2	—	35	1 : 0·74	4	2	—	33·3
N. East Side of Jetty	,,	4	—	2	—	—	6	1 : 0·50	1	1	—	66·6
,, ,, ,,	,,	14	6	12	1	1	34	1 : 1·29	1	1	—	15·4
Totals		71	18	62	14	8	173	1 : 1·13	11	18	3	36·8
STATION 2												
Mid Ferry N. Bank	10.5.52	20	8	18	5	—	51	1 : 1·30	1	2	—	18·7
STATION 3												
High Ferry	16.5.52	22	1	21	8	—	52	1 : 1·00	4	2	—	37·5
	,,	58	8	46	8	3	123	1 : 0·93	1	—	—	5·9
Totals		80	9	67	16	3	175	1 : 0·95	5	2	—	21·2
STATION 4												
Tidal Basin	12.5.52	9	3	19	2	2	35	1 : 2·44	2	2	—	26·7
	,,	49	7	28	8	1	93	1 : 0·71	1	2	—	15·8
	,,	66	8	45	18	6	143	1 : 0·80	—	—	2	10·0
	15.5.52	51	19	28	16	1	115	1 : 0·92	—	—	2	10·5
Totals		175	37	120	44	10	386	1 : 0·90	3	4	4	15·1
STATION 5												
Cowpen Pool	14.5.52	46	11	28	8	—	93	1 : 0·85	—	2	—	10·0
	,,	48	8	25	10	4	95	1 : 0·69	—	2	—	11·1
Totals		94	19	53	18	4	188	1 : 0·77	—	4	—	10·5
STATION 6												
Sleekburn	15.5.52	37	4	15	7	2	65	1 : 0·51	1	2	1	25·0
	,,	31	7	24	4	—	66	1 : 1·00	—	3	1	23·5
Totals		68	11	39	11	2	131	1 : 0·74	1	5	2	24·2

TABLE 7

AVERAGE LENGTH OF PARASITES AT BLYTH (in mm.)

Locality	*Date*	*Males*	*Females with egg-sacs*	*Females without egg-sacs*
STATION 1				
S. Harbour	30.4.52	4·25	8·30	6·40
West Side of Jetty	,,	4·17	—	8·77
N. West Side of Jetty	1.5.52	3·77	—	7·20
,, ,,	,,	3·85	7·50	8·01
,, ,,	7.5.52	3·92	8·34	6·94
,, ,,	8.5.52	4·06	7·85	7·48
N. East Side of Jetty	,,	4·50	—	8·10
,, ,,	,,	4·17	8·88	7·13
MEAN LENGTH		4·09	8·17	7·50
STATION 2				
Mid Ferry N. Bank	10.5.52	3·94	8·20	7·41
STATION 3				
High Ferry	16.5.52	3·86	7·70	6·29
	,,	3·85	8·58	6·34
MEAN LENGTH		3·85	8·14	6·32
STATION 4				
Tidal Basin	12.5.52	3·85	8·60	6·35
	,,	3·88	8·01	6·72
	,,	3·87	8·38	7·22
	15.5.52	4·48	9·19	7·62
MEAN LENGTH		4·02	8·54	6·98
STATION 5				
Cowpen Pool	14.5.52	4·10	7·97	7·28
	,,	4·33	9·00	7·54
MEAN LENGTH		4·22	8·48	7·41
STATION 6				
Sleekburn	15.5.52	3·84	7·07	6·84
	,,	3·92	8·09	6·90
MEAN LENGTH		3·88	7·58	6·87

TABLE 8

BLYTH ESTUARY

SUMMARY OF PARTICULARS OF MUSSEL SAMPLES

Station	*No. of samples*	*Percentage infection*	*Average No. of parasites per 20 mussels*	*Males*	*Females with egg-sacs*	*Females without egg-sacs*	*Juveniles (less than 3 mm.)*	*Damaged*
				per cent	*per cent*	*per cent*	*per cent*	*per cent*
1	8	54·37	21·62	41·1	10·4	35·8	8·1	4·6
2	1	80·00	51·00	39·2	15·7	35·3	9·8	—
3	2	82·50	87·50	45·7	5·1	38·3	9·2	1·7
4	4	91·25	96·50	45·3	9·6	31·1	11·4	2·6
5	2	95·00	94·00	50·0	10·1	28·2	9·6	2·1
6	2	82·50	65·50	51·9	8·4	29·8	8·4	1·5

APPENDIX

NOTES ON METHOD OF DISSECTING OUT THE GUT OF MYTILUS

1. The left valve is first removed. This is done by holding the mussel in the left hand, with the left valve uppermost and the dorsal side of the animal away from you. Next, the valves are pushed in opposite directions along the axis of the body ; the left valve away from, the right valve (the underneath one) towards you. A strong scalpel is introduced on the dorsal side of the left valve at a point just anterior to the main adductor muscle. The scalpel, with the edge close against the left valve, is drawn towards the posterior margin of the shell and then backwards around the perimeter of the valve to free the edge of the mantle on the ventral side. The scalpel is then withdrawn and passed forward, from the point of insertion to the umbo. The left valve is now twisted off. It may, however, be found necessary to probe with the scalpel blade against the inside of the left valve to detach a "sticky" piece of mantle or to sever the anterior adductor and byssal retractor muscles. The secret of opening a mussel cleanly is to ensure that the scalpel is always held closely against the upper (left) valve.

2. *Removing mantle and gills.* The right valve is placed on a folded duster under a dissecting lens. The edge of the right mantle is detached from the right valve. This is best done by introducing the joined tips of a pair of fine tweezers just in front of the exhalant aperture and, while keeping them close to the right valve, running them anti-clockwise as far as the mouth. Next, holding the left mantle just below the exhalant opening, lift it upwards and forwards. It will be found that after a little practice the mantle and gills of the left side come away together. When, however, the gills are left, they can be removed cleanly by taking them in the tips of the tweezers at a point which is level with the bottom of the posterior adductor muscle and just in front of it. Held like this, they are easily torn off.

3. *Remove the palps.* This is a most important step towards the later removal, without breaking, of the loop of the gut. The removal of the palps allows the loop to slip over the oesophagus.

4. With the back of a small scalpel, scrape away the digestive gland very carefully, beginning immediately in front of the heart. This can be made easier by pushing up the digestive gland from underneath with the first finger of the left hand placed in the valve. Follow out each arm of the recurrent intestine until the whole loop is uncovered.

5. Make an incision, commencing at a point below the junction of the direct and recurrent intestines with the digestive gland, passing beneath and parallel to the crystalline style sac and the first part of the recurrent intestine, which here lie side by side. Continue this incision back so as to free the rectum from the posterior adductor muscle.

6. With tweezers, take hold of the three thicknesses of rectum and direct and recurrent intestines just in front of the posterior adductor muscle and pull very gently upwards and forwards. Very little difficulty is normally encountered in removing the gut intact from the point where it joins the stomach to the anus. Place the gut in a watch glass of sea water.

7. Detach the digestive gland and contained stomach by lifting it out upwards and forwards with the tweezers and place in another watch glass of sea water.

8. The gut is then opened out, along its entire length and the contents removed.

9. The stomach and the main ducts of the digestive gland are opened.

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