CONTRIBUTIONS TO THE BIOLOGY OF THE CRUSTACEAN EUPHAUSID, MEGANYCTIPHANES NORVEGICA (M. SARS)

by

J. Mauchline.

Presented to the University of Glasgow
as a thesis for the degree of Ph.D.,
April, 1958.

ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
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Table of Contents.

I. Introduction.

The larvae and adults of the crustacean euphausid, Meganyctiphanes norvegica (M. Sars) were identified by the key provided by Einarsson (1945).

This is one of the largest euphausids in the northern hemisphere, attaining a length of over 40 mm. The pigmentation is exclusively characteristic of this species, the mouth region being deep red and red chromatophores on the stomach and hepatopancreas showing through the transparent integument.

The sex of living animals can be determined by eye owing to the presence of red chromatophores on the vas deferens of males. On preservation, however, the tissues become opaque and the presence in males, or absence in females, of a petasma must be determined.

M. norvegica is an Atlantic boreal species, its northern limit being correlated with the 5°C isotherm in May, its southern by the 15°C isotherm in February (Einarsson, 1945).

Briefly, for Ruud (1936) and Einarsson (1945) have described it in detail, the distribution of M. norvegica is as follows. It is found from the Murman coast to Skagerrak and Kattegat, is present round the British Isles,

in the Faroe-Shetland Channel, Iceland area, off the east and west coasts of Greenland. It occurs as far south as the Mediterranean and, on the American side of the Atlantic, is present in the Gulf of Maine.

Little need be said about the importance of euphausids in the economy of the sea. Recent work has shown the presence of high concentrations of Vitamin 'A' in the eyes but how this is synthesized by the euphausids is not yet clear.

One of the main problems faced in studying the ecology of euphausids is to find an isolated population which can be sampled and observed continuously over a prolonged period. A few species inhabit coastal waters but, being planktonic, are subject to the coastal currents. M. norvegica lives on the 'slope' throughout the winter but moves to shallower water to spawn; this again raises sampling problems. The oceanic species present even greater difficulties.

The Clyde sea area has deep troughs, up to 200 m., which are behind an extensive submarine plateau. M. norvegica are resident in these troughs all the year and are prevented from moving out of them by the shallowness of the water over the plateau. It was therefore possible

to make continuous observations on the same population.

II. Acknowledgements.

I wish to thank Professor C. M. Yonge, C.B.E., F.R.S. for his constant help and encouragement and Dr. S. M. Marshall who supervised my work at the Marine Station, Millport.

Acknowledgement is also due to the previous Director, Mr. E. Ford, O.B.E., and the present Director, Dr. C. H. Mortimer, F.R.S., and Staff of the Marine Station, Millport, not forgetting the skippers and crews of the two research ships 'Calanus' and 'Mizpah' for the facilities made available to me throughout the course of this work.

I wish, also, to acknowledge my receipt of a Fishery Research Training Grant from the Development Commission.

III. The Anatomy and Histology of Meganyctiphanes norvegica (M. Sars).

The most important contribution to the anatomy and histology of Meganyctiphanes norvegica was made by Raab (1915). This paper seems to have been overlooked by the majority of later workers. Most of his findings have been confirmed, this report being largely concerned with what he omitted, Raab's work being only referred to where this is necessary to ensure continuity.

Other authors have made valuable contributions. An account of the structure of the superposition eyes, the brain, and the incretory organs can be found by reference to Hanström (1948), where a summary of the relevant literature is given. Vallentin and Cunningham (1888) gave excellent diagrams of the photophores and an accurate account of their structure; figures of the thoracic and abdominal organs are available in Hardy (1956).

The abdominal muscular system has been studied by Daniel (1927) but the thoracic musculature, as far as can be determined, has not been investigated.

Methods: these will be described more fully under the appropriate headings. Sections of specimens fixed in 7% formalin in sea water, were cut in transverse, sagittal,

and horizontal planes. Other fixatives were tried but a number of them caused the oviducal glands in mature females to swell to such an extent that the carapace was ruptured. The sections were stained in a variety of ways, Mallory's triple staining technique being the most useful.

Specimens were dissected either fresh or after fixation in formalin or Bouin. When fresh material, killed immediately before use, was used it was found almost impossible to carry out delicate dissections owing to the opacity of the tissues. This opacity could be partly prevented by dissecting the specimens under glycerine.

To investigate the circulatory system, a dilute solution of carbon black VS paste was injected into the beating heart of a living specimen. As soon as the blood vessels were full of carbon, the specimen was plunged into 7% formalin to arrest the heart beat and then immediately transferred to glycerine. The animals were perfectly preserved for at least five months and the tissues remained transparent enough to observe the blood vessels.

Intestinal Tract.

The oesophagus and stomach of the following euphausids have been described: Stellocheiron spp. were examined by

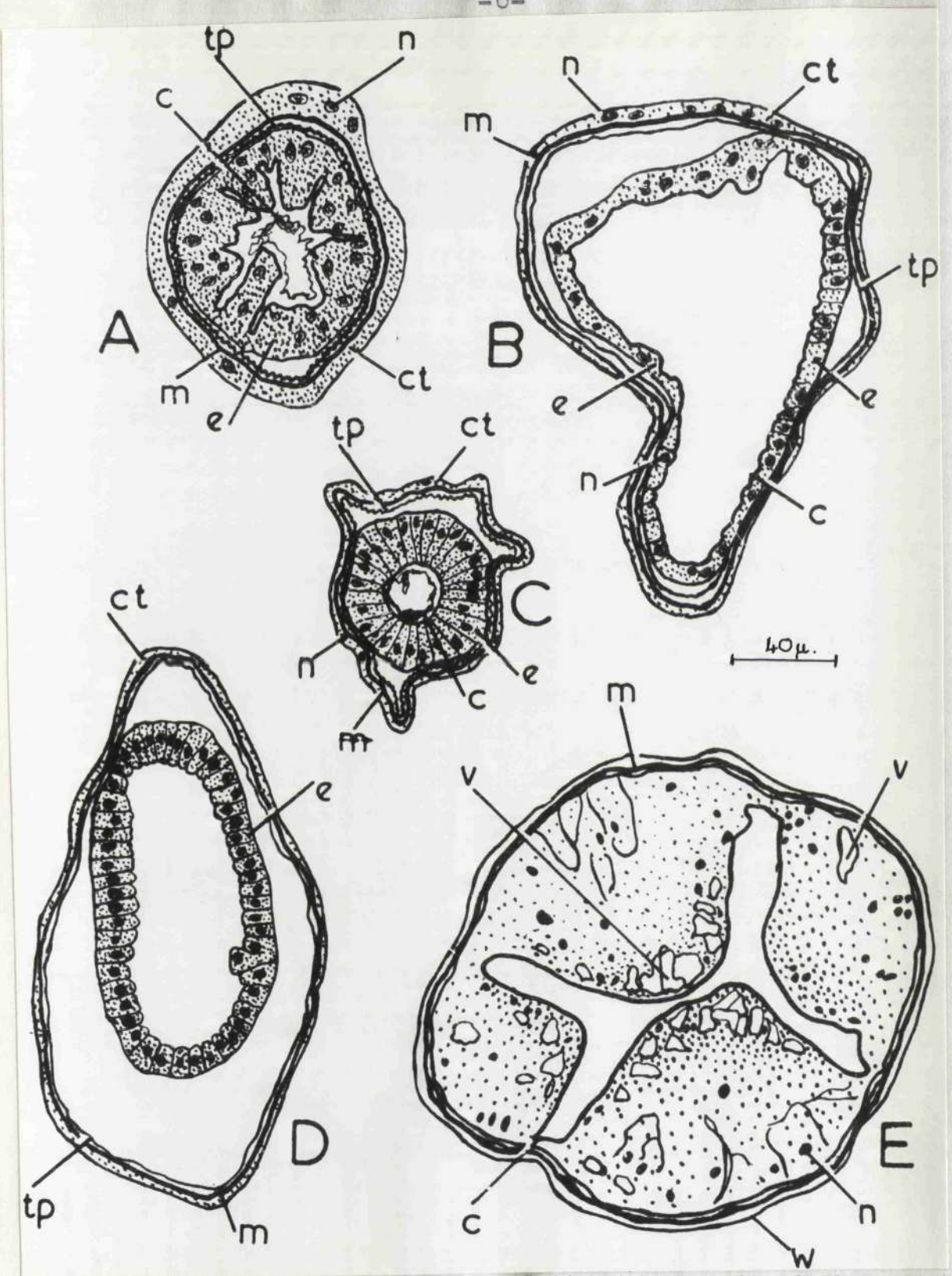


Fig. 1 . Transverse sections of the hind-gut of Meganyctiphanes norvegica. A, B, C, and D are of the 'intestine', E of the 'rectum'. c, cuticulum; ct, connective tissue layer; e, intestinal epithelium; m, circular muscle band; n, nucleus; tp, tunica propria; v, vacuole; w, 3-layered wall of 'rectum'

Chun (1896), Nyctiphanes couchii by Gelderd (1909) and Euphausia superba by Zimmer (1913). Raab, therefore, omits a description of the chitinous framework present in the stomach of M. norvegica. The present author has compared his findings with those of the above authors and, as they are all almost identical, no further description is necessary.

The mid-gut, which follows the pars cardiaca region of the stomach, is described by Raab who states that the outer layer of connective tissue is hard to see but this difficulty has not been found. What did present difficulty was the finding of the "clearly defined border of columnar cells" present in the free surface of the gut epithelium but its presence was eventually confirmed. Into the mid-gut open, ventrally, the two hepatopancreatic cavities and, dorsally, the two anteriorly projecting intestinal caecae. This region of the intestine is very short and a gradual transition to the hind-gut takes place.

It appears from Raab's figure and description of the hind-gut that its structure is uniform throughout, except for the short 'rectum'. But in the part of the hind-gut (fig. 1 B) which extends from the junction of the thorax and abdomen to the posterior end of the fourth abdominal segment, the diameter is greater than in the previous

part (fig. 1 A) and the epithelial cells become lower (fig. 1 B). The tunica propria is no longer crinkled but is often pressed against and indistinguishable from the band of circular muscle. Throughout the anterior half of the fifth abdominal segment the epithelium is of a high columnar nature (fig. 1 C) and the width of the gut diminishes. The epithelium, on fixation, tends to shrink inwards from the tunica propria thus leaving the gap seen in the figure; this same problem of shrinkage was found by Gelderd and Chun. The tunica propria is again crinkled and the band of circular muscle and connective tissue are again well defined.

The next region (fig. 1 D), which continues to the short 'rectum', is characterised by an increase in the diameter of the gut and a slight flattening of the epithelial cells. Here shrinkage is most pronounced. Some of the nuclei are more densely staining than the rest but no further differences between any of the cells could be seen. The tunica propria is still slightly crinkled and the other two layers well defined.

At the posterior end of the fifth abdominal segment the gut broadens and the walls have four multicellular longitudinal ridges (fig. 1 E). Vacuoles occur chiefly

Fig. 2. Transverse section of the intestinal caecum of M. norvegica showing a dividing nucleus, n.

around the free edges of these ridges. The nuclei are small and stain darkly unlike the cytoplasm which, though thinly granular, stains lightly. The anus opens on the ventral side of the caudal plate.

The above changes in the gut wall always take place by a gradual transition from one form to the next.

Throughout the hind-gut the chitinous covering is so thin that it can only be distinguished where it has broken free, but in the 'rectum' it is thick and can be easily seen when the sections are stained with chlorazol black or Mallory.

A conglomeration of strands having, under the high power of the microscope, the appearance of cottonwool binds the constituent particles of the faecal pellets. Preliminary tests suggest that these strands are chitinous.

Diverticula of the Gut.

Nothing can be added to Raab's description of the hepatopancreas.

He omitted a detailed description of the histology of the dorsal intestinal caeca. They are situated above the pars cardiaca region of the stomach and point anteriorly.

The epithelium consists of high columnar cells with very large nuclei, having a chromatin network. Division of these cells occurs as shown in fig. 2 while numerous small vacuoles are present in the cytoplasm. No border of columnar epithelial cells could be found in the distal regions of these organs but in the proximal part, leading into the intestine, the borders are striated. A layer of circular muscle bounds the caeca.

The Nervous System.

Raab examined the general construction of the nervous system of Meganyctiphanes and his findings have been confirmed.

A histological account of the brain and its endocrine organs can be found in Hanström 1928, 1933, 1940 and Carstam 1942.

Reproductive System.

Very little work has been done on the reproductive systems of euphausids. The only recent paper on the subject is by Bargmann (1937). She describes the anatomy, histology and development of both the male and female system

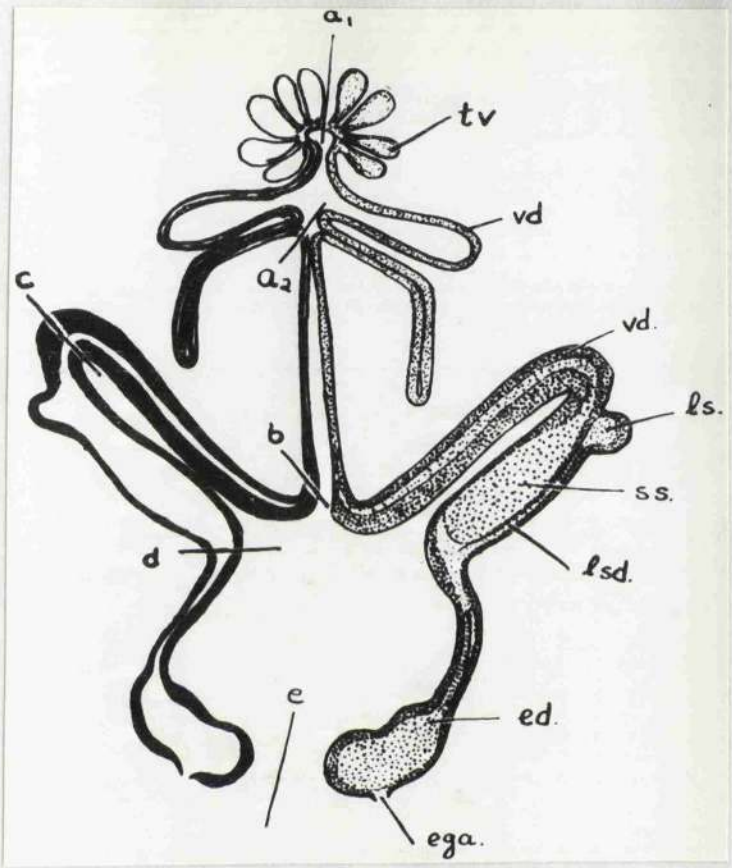


Fig. 3. Diagram of the male reproductive system of M. norvegica. The left hand side is diagrammatic and shows the regions a-a, a- b, b-c, c-d, d -e, where the various parts of the spermatophore are formed.

ed, spermatophore in ejaculatory duct; ega, external genital aperture; ls, lateral pocket; lsd, duct of lateral pocket; ss, spermatophore being formed in the spermatophore sac; tv, testicular vesicle; vd, vas deferens.

of Euphausia superba, thus advancing the work done by Zimmer (1913).

In the present investigation the male and female systems of M. norvegica were examined by vital staining with methylene blue, dissection and serial sectioning. It is possible to dissect out the male system and mount it in one piece; the female system is not so easily dealt with and only sectioning demonstrated the exact course of the oviducts.

Male System.

The testes lie dorsally against the posterior half of the hepatopancreas and are composed of 12 to 14 testicular vesicles, arranged in a horseshoe round the vasa deferentia (fig. 3). A vas deferens proceeds posteriorly from either side, turning three bends in the form of a 'W' (fig. 3), and descends round the thoracic musculature to the paired genital openings in the sternum of the 8th thoracic segment.

Raab's account of the function of the various regions of the vasa deferentia in the formation of the spermatophore does not wholly agree with the present findings. He states that the first part of the vas deferens (fig. 3, a_1-a_2) is concerned solely with the transport of the spermatozoa.

It is bounded by a pavement epithelium whereas the next region (fig. 3, a_2-b) has a thicker cuboidal epithelium and this secretes the fluid in which the spermatozoa are suspended in the spermatophore. This fluid, when the spermatophore is attached to the female, causes expulsion of the spermatozoa into the spermatheca.

The following part of the vas deferens (fig. 3, b-c), considered by Raab to have no function other than transport of the spermatozoa, is actually responsible for secreting a membrane or case around the spermatozoa. On approaching the bend (fig. 3, b) the lumen becomes elliptical until the region of the lateral pocket (fig. 3, ls). The epithelium is now columnar except at the narrow sides of the elliptical lumen where it remains cuboidal. In some decapods (Matthews, 1953), similar cuboidal cells secrete the spermatophore membrane; certainly, in the specimens examined here, there was an aggregation of secreted material against these cells but there was no evidence suggesting that they alone produce the secretion.

The vas deferens then turns posteriorly (fig. 3, c), this part being known as the spermatophore sac (fig. 3, ss). Its lumen is more pear-shaped than elliptical and a layer of circular muscle can be easily seen round the outside of the now cubical epithelium. Raab makes no mention of any

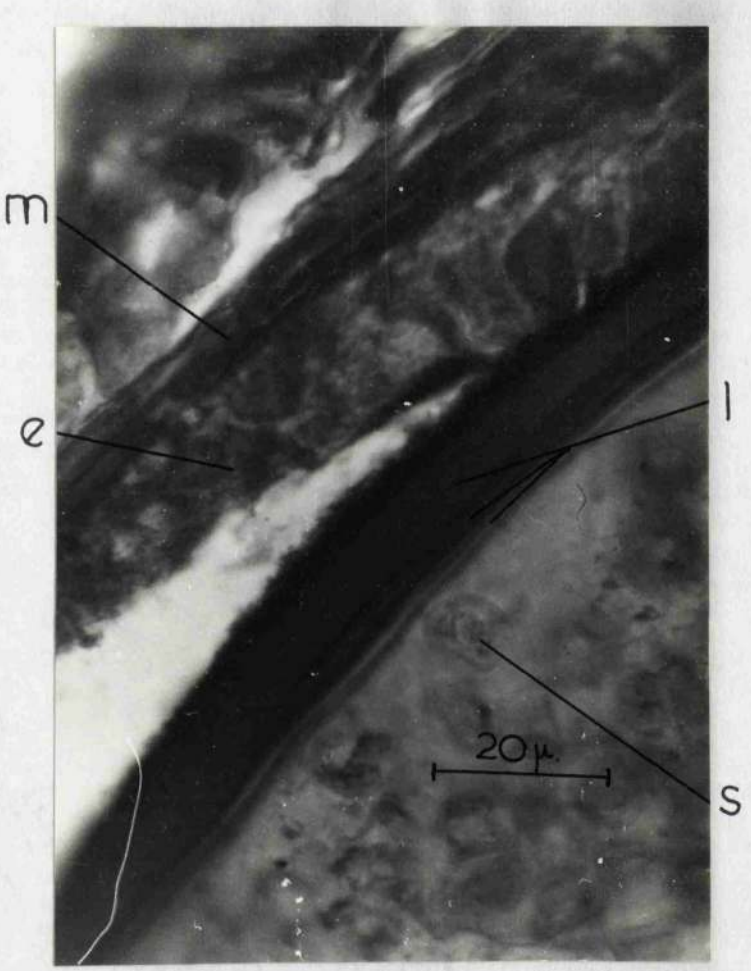


Fig. 4. Transverse section of a spermatophore and the ejaculatory duct wall.

e, epithelium and m, muscle of ejaculatory duct wall; l, l', three layers of spermatophore wall; s, spermatozoon in spermatophore.

such layer of muscle in this region. The previous parts of the vas deferens were examined in great detail to discover if there was any such layer of muscle; all that could be found was what appeared like a tunica propria but it was so thin that its staining properties could not be determined. A lateral pocket enters the anterior end of the spermatophore sac, on the side nearest the body wall, and it is in this that the cement, which attachs the spermatophore to the female, is secreted. A channel, formed by the walls of the spermatophore sac, leads from the lateral pocket to the proximal region of the ejaculatory duct where lies the part of the fully formed spermatophore which will be attached to the female.

The walls of the spermatophore sac secrete further material round the mass of spermatozoa. A third layer (fig. 4) is laid down round these two in the ejaculatory duct (fig. 3, ed) and seems to have the same staining properties as the one immediately inside it; the innermost is different and stains rather like the fluid in which the spermatozoa are suspended.

The ejaculatory duct (fig, 3, ed) extends from the spermatophore sac ventrally round the body musculature and organs to the genital opening. The epithelium is cuboidal and is bounded by a layer of longitudinal muscle

and an outer layer of circular muscle (fig. 4, m). The ejaculatory duct of a mature male is distended by the spermatophore which is stored in it for some time. As a result of this distension the genital opening lies at the side of the spermatophore so that complicated muscular movements must be required to eject it.

During the breeding season almost every male has two spermatophores present in each vas deferens, one being in the spermatophore sac, the other in the ejaculatory duct.

The spermatozoa, when they leave the testicular vesicles, are spherical in shape and have a diameter of about 9μ. By the time they reach the spermatophore sac their diameter has increased to about 14μ. Most of them are still spherical but from here onwards they are compressed into various forms, producing squares, triangles, etc. in sections.

The Female System.

A detailed and accurate description of the form and extent of the ovary, the course of the oviducts and the distribution of the uterine glands has been given by Raab. Nothing further can be added from the present investigation except a short note on the uterine glands.

Raab, in describing their extent, states that in different animals they sometimes exhibit different staining properties. In this investigation, however, there appear to be two regions of these glands which have characteristic staining reactions in all the animals sectioned. The first extends from the proximal end of the oviducts laterally and ventrally, following the course of the oviducts, into the coxae of the 6th thoracic legs; these stain predominantly pale blue with Mallory's triple stain. The second group stains reddish purple or orange-red and appears to be confined to the region round the spermatheca and external genital openings, lying between then and the nerve cord. From an examination of Bargmann's photographs it appears that there may be two differently staining groups of glands in Euphausia superba though she does not suggest this in her text. As mentioned later, the tegumental glands resemble these uterine glands closely in form and colour variations.

Investigations of the origin of the egg membranes were made (p. 58). The mass of glands round the spermatheca and genital openings contained densely stained secretions in females known to have laid eggs immediately before fixation. These secretions were not evident in females known not to have laid eggs prior to fixation. Therefore,

it was concluded that these glands secrete the cuticular membranes of the egg.

No secretions were apparent in the glands situated around the proximal regions of the oviducts. As Raab states, and the present author confirms, in sections of these glands a group of five or six cells are often found bordering a small lumen but no connection between these separate lumina could be found and no opening from them, by duct or sinus, into the oviducts. The function, therefore, of this group of glands remains unknown.

The Blood Gland and Tegumentary Glands.

The form and histology of the blood gland, located in the anterior part of the cephalothorax of M. norvegica, has been described accurately by Raab.

Closely associated with the blood gland, but neither mentioned nor figured by Raab, are groups of tegumentary glands. They have the typical rosette form, five or six cells being situated around a lumen or duct (Farkas, 1927; Yonge, 1932). Their cytoplasm is granular and the small nuclei are usually found against the wall distal to the gland lumen. When sections of the glands were stained with Heidenhein's iron haematoxylin a very conspicuous nucleolus was seen within each nucleus.

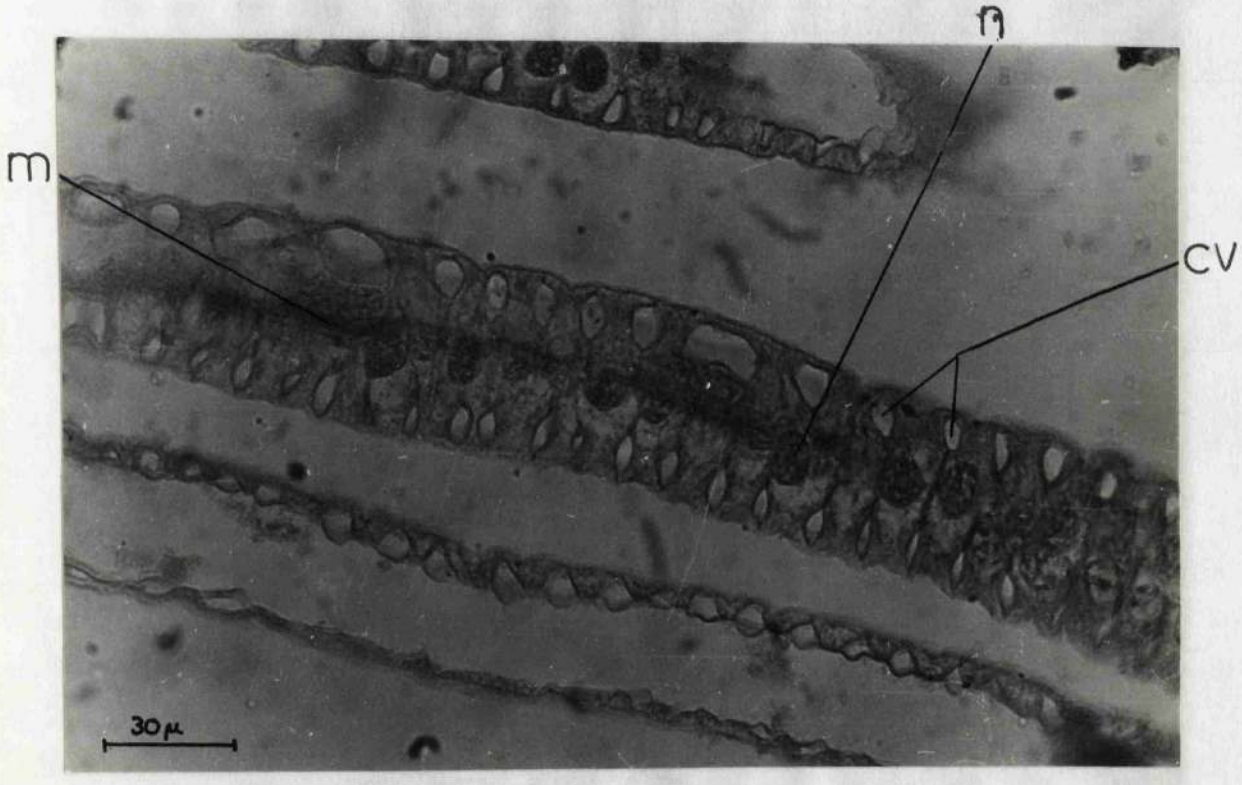


Fig. 5. Transverse section of a gill filament of M. norvegica. cv, blood vessels connecting the two branchial veins; m, muscle fibres of filament; n, nucleus of large cell of filament.

Their staining properties vary in different regions of the body. With Mallory they coloured blue, through various shades of purple, to red. Those staining blue comprised the bulk of the glands associated with the blood gland and the thoracic limbs; those staining red were found around the oesophagus. Those staining purple appear to be variants of the blue as they are often mingled with them e.g. at the posterior end of the blood gland, dorsal to the stomach; they are also present in the body epithelium immediately under the integument.

In a number of regions, close to the integument, a group of gland cells was often divided in two by its staining properties, the half lying nearest the integument staining red, the inner half blue.

As already mentioned, there is a remarkable similarity between these glands and the uterine glands, both in form and staining properties. The uterine glands secrete the outer membrane of the eggs while the tegumentary glands are responsible for the production of the outer layer of the integument. Yonge (1937) showed that the physical and chemical properties of the outer egg membranes and the superficial cuticle of the integument of Homarus vulgaris are identical. This also seems to be true in M. norvegica.

The varying staining reactions of the tegumental glands are thought to arise from varying states of secretary activity.

The Gills.

The gills represent modified epipodites of the thoracic limbs. In M. norvegica there are only seven fully developed pairs of thoracic legs, the pair on the 8th segment not being developed. Functioning gills are present in segments2 to 8, the first pair of thoracic legs having an undeveloped simple epipodite, even though there is an afferent and efferent branchial channel present. (Fig. 10, eb, 1).

The external appearance of the gills has been examined and figured by Calman (1909). The most developed branchiae are on the 8th segment, the others being smaller (fig. 10, b, 8). Histologically, the filaments are composed of large cells with large granular nuclei (fig. 5, n) which usually possess a number of nucleoli. The cell cytoplasm is also granular and striations were observed traversing the cells, most often from the walls adjoining the afferent to those nearest the efferent veins. A well developed internal muscular system was demonstrated, commencing around the branchial channels and extending into

the lamellae where it branches considerably so that each filament has a few muscle fibres running up its centre to its distal end. (fig. 5, m). Around each filament was a very thin cuticular layer.

The system of blood vessels present in the gills is described in dealing with the blood circulation.

The Excretory Organs.

An examination of the excretory organs in the bases of the 2nd antennae simply served to confirm the detailed description of Raab.

Circulatory System.

Raab (1915) dealt with the arterial system, reconstructing it from sectional material and gave an accurate though not very detailed account. He considered that his results confirmed, for the most part, those of Zimmer (1913) for Euphausia superba, and, therefore, when he does not present a detailed description of some aspects it is thought his observations were identical with Zimmer's. Other earlier papers have been reviewed by him.

Colosi (1920) described the heart of Nematoscelis megalops, including the histology of the ostia, arteries and arterial valves. No further papers on the blood

circulation of euphausids were found except Zimmer (1932) who reviewed the knowledge of the euphausid arterial system and Mayrat (1956 a) who discussed the occurrence of a 'frontal heart' in mysids and euphausids.

The present investigation was made by serial sectioning, and by injecting carbon black VS paste, diluted with tap water, into the live heart of pericardium. Very fine glass pipettes were used, their tips being inserted at the join of the carapace and the first abdominal segment and usually passing through the thin layer of chitin without breaking. If the carbon was injected direct into the heart it flowed out, by the action of the heart beat, simultaneously into all the arteries. If, however, it was injected into the pericardium the resultant effect depended on the amount injected. When less than 1 cc. was put in, this was carried into the heart and thence to the arteries but a larger amount seemed to arrest the heart beat or clog the ostia so that the carbon simply showed the extent of the pericardium in animals with a carapace length less than 7 mm.

The blood had a clotting action on the fine carbon particles in this solution thus making it easier to follow the course of the carbon-blood suspension when it

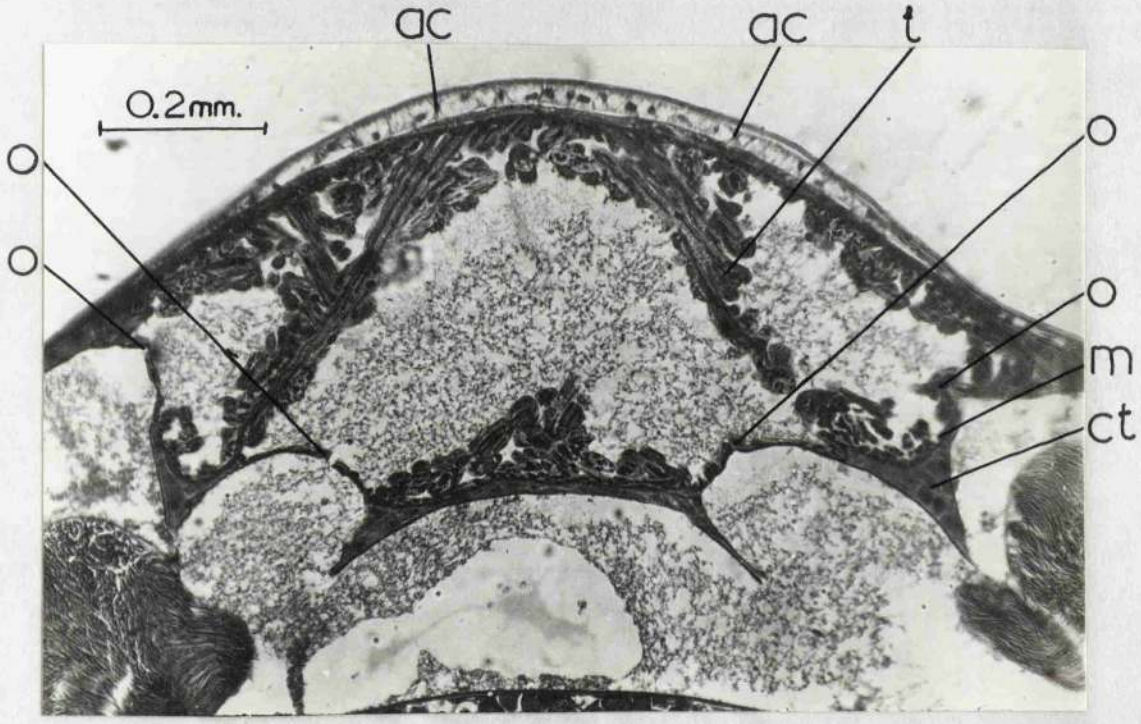


Fig. 6. Transverse section of the heart of M. norvegica showing the two pairs of ostia.

a.c, alae cordis; ct, connective tissue layer; m, internal muscular layer; o, ostium; t, trabecula.

entered the sinuses from the ends of the arteries.

The Arterial System.

The heart is dorsal, close to the carapace, in the third to the sixth thoracic segments. The lumen of the pericardium connects with the cardiac cavity by way of two pairs of ostia (fig. 6, o), the more dorsally situated pair being slightly anterior to the other as stated by Raab.

The heart possesses an extremely complex muscular system, some of the largest components (trabeculae) (fig. 6, t) of which traverse the lumen from the dorsal-lateral to the ventral median areas. The wall of the heart is composed of two layers similar to those described by Colosi (1920) in Nematoscelis. The outer layer, which completely surrounds the other layers, is connective tissue constructed of large cells with large granular nuclei (fig. 6, ct). To this layer is attached dorsally the alae cordis (fig. 6, ac) which are bands of connective tissue by which the heart is suspended in the pericardium from the dorsal body wall. Further bands of connective tissue, which are found at the anterior and posterior ends of the heart and a few which originate from its ventro-lateral borders, cross the pericardium to attach the heart

to the pericardial wall. The inner layer of the heart wall is muscular; there is an almost complete layer of longitudinal muscle running round the wall immediately inside the connective tissue layer but it is broken in places by strands of circular muscles and the origins of the trabeculae.

The ostia (fig. 6, os) which are extensions of this muscular layer of the wall, also have muscles, which cross the cavity of the heart, attached to them. They are thus opened and closed by muscular action unlike the arterial valves, to be described later, which are operated by the blood pressure alone.

Raab has described the origins of the various arteries from the heart but he does not describe in any detail the respective organs and tissues they supply.

He states that the median aorta cephalica supplies the cerebral ganglion and eyes but did not show that it also serves the antennules, the dorsal half of the blood gland, and part of the stomach. This artery travels anteriorly immediately below the carapace until almost vertically above the cerebral ganglion where it divides to supply the antennules by means of two lateral antennary arteries (fig. 7, Al). Next a dorsal median branch (fig. 7, bd) serves the dorsal half of the cephalothoracic

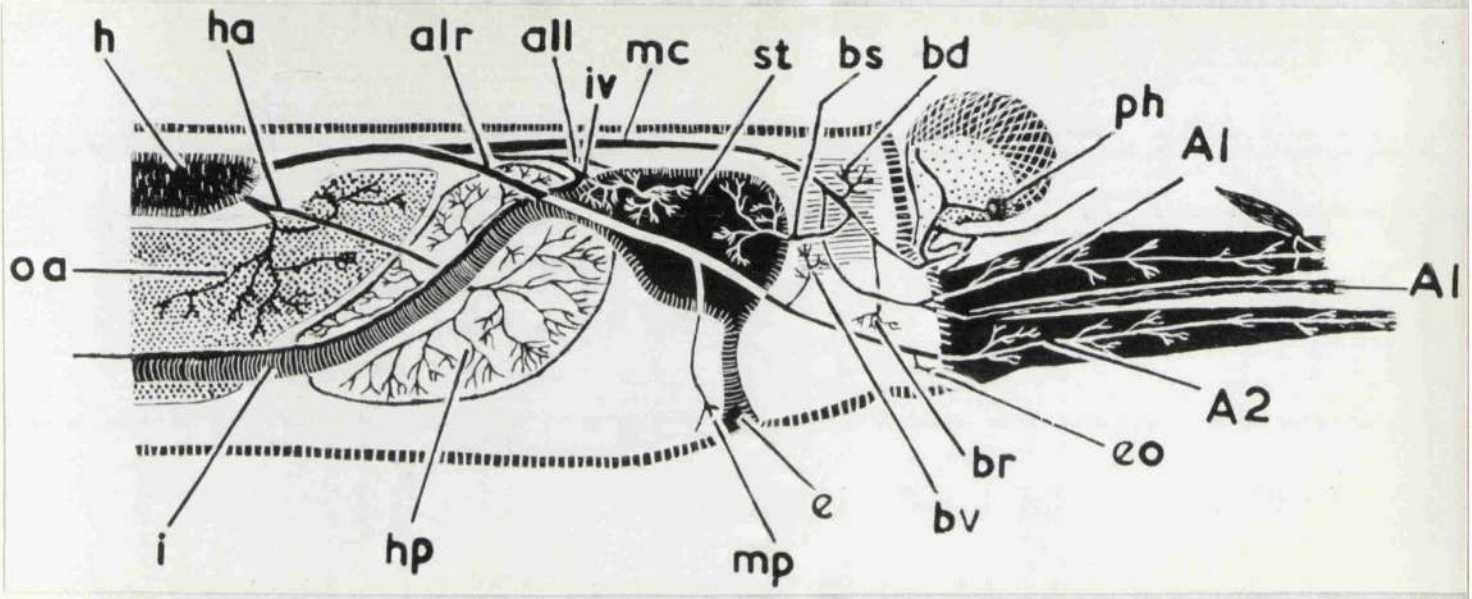


Fig. 7. Diagrammatic drawing of anterior part of thorax of female M. norvegica to show the distribution of the main arterial vessels. The right-hand half of the hepatopancreas has been wholly removed, as has part of the ovary.
A1, first antenna; A2, second antenna; all, left arteria lateralis; alr, right arteria lateralis; bd, dorsal vessels to blood gland; bv, ventral vessels to blood gland; br, vessels to brain; bs, vessel to stomach; e, mouth; eo, excretory organ; h, heart; ha, left hepatic artery; hp, hepa-topancreas; i, intestine; iv, intestinal vessel; mc, median aorta cephalica; mp, vessel to mouthparts; o, ovarian blood vessel; oa, optic arteries; ph, photophore with branch from optic artery to it; st, stomach.

blood gland. Two very thin ventral branches (fig. 7, bs), just anterior to the blood gland artery, give origin to a system of very fine vessels spread over the dorsal anterior surface of the stomach. These vessels are so fine that a successful injection is very difficult. The brain is supplied by a ventral median branch (fig. 7, br), the main artery afterwards dividing into the two optic arteries (fig. 7, oa).

The blood vessels in the eyes were of special interest and will be described later.

No frontal heart, such as described by Chun (1896) in Stylocheiron abbreviatum, was found associated with the median aorta in M. norvegica. Mayrat (1956 a) has described this organ and the species in which it occurs.

Raab only mentions that the paired anterior arteriae laterales supply the antennal excretory organs. Their detailed course is as follows. They run anteriorly and diagonally (fig. 7, 8; all, alr) from the heart, each producing a branch which supplies the body epithelium and musculature (fig, 8, sb). Next the mandibles and maxillules, along with the muscles and tissues associated with the oesophagus, receive a supply of blood by a branch (fig. 7, 8; mp) from the arteria lateralis of that side. The main limbs of the arteries continue towards the antennae, each supplying

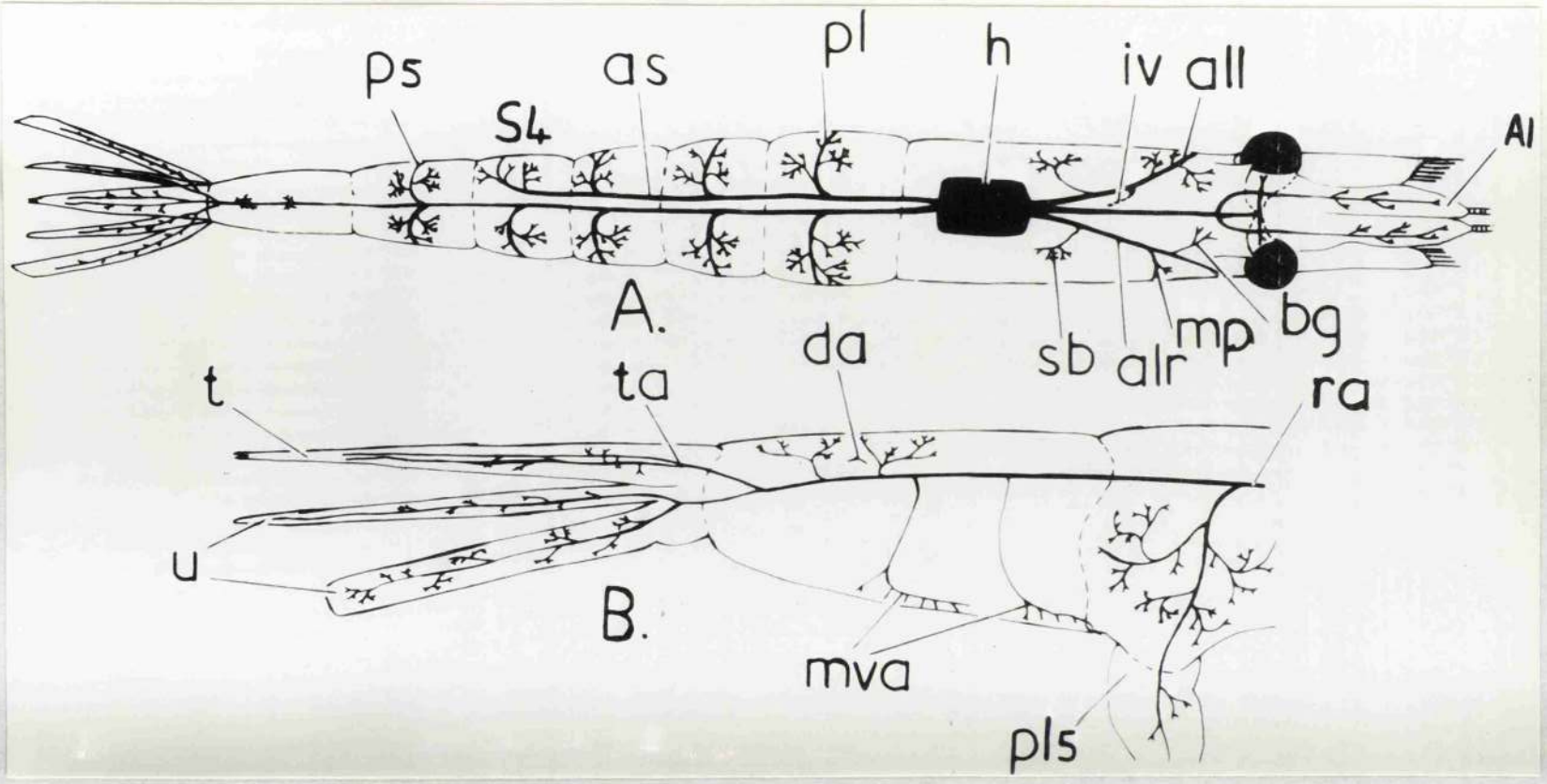


Fig. 8. A. Drawing, from injected specimens, of the dorsal arterial system. B, Lateral view of the arteries in the sixth abdominal segment, telson and uropods. Al, first antenna all, left arteria lateralis; alr, right arteria lateralis; as, left arteria abdominalis superior; bg, vessels to blood gland; da, dorsal branches; h, heart; iv, intestinal vessel from left arteria lateralis; mp, artery to mouthparts; mva, median ventral branches; pl 5, pleopod with artery; pl, p5, left-hand branches to pleopods 1 and 5 respectively; ra, right arteria abdominalis superior; S4, fourth abdominal segment; sb, small dorsal blood vessel supplying muscles and epithelium; t, telson; ta, arteries of telson; u, uropods with arteries.

the blood gland with a fine branching vessel (fig. 7, bg). After serving the excretory organ (fig. 7, co) they terminate in the antennae (fig. 7, A, 2).

The left arteria lateralis, but not the right as far as can be determined, produces two branches (fig. 7, 8; iv), just posterior to the branch to the mouth parts, which supply the gut. The first turns posteriorly and runs along the dorsal side of the mid- and hind-gut, also supplying, by an anterior system of fine vessels, the posterior dorsal half of the stomach. The second vessel travels inward to the posterior end of the stomach and supplies the ventral half of it.

Ventral to the origin of these three anterior arteries are found the paired hepatic vessels (fig. 7, ha), which descend anteriorly to their respective halves of the hepatopancreas. In that organ (fig. 7, hp) they divide into four main trunks, two anterior and two posterior, which subdivide into numerous fine vessels ramifying throughout the tissue. Small branches (fig. 7, obv) from these arteries supply the anterior half of the ovary or the testicular vesicles. Raab does not describe these branches to the gonads nor does he describe the form of the hepatic vessels.

Five arteries emerge from the posterior ventral region

of the heart. Most anterior is the large single aorta descendens which Raab has described. He states that the posterior branch, the arteria abdominalis inferior, extends through the whole abdomen, but in fact it terminates in the fourth abdominal photophore, which it supplies.

Posterior to the origin of the aorta descendens, a thin pair of arteries, the gonadal arteries, emerge ventrally from the heart and, travelling horizontally and posteriorly, supply the vas deferens, or the posterior half of the ovary. This was not noted by Raab who stated correctly that they terminate in the anterior abdominal musculature.

The remaining two vessels of the five are the two large arteriae abdominalis superiores (fig. 8, as). Raab describes them as extending posteriorly and dorsally through the total length of the abdomen, supplying the pleopods by means of lateral branches. In each of the first four abdominal segments a lateral branch (fig. 8, p1, p5) is given off to each pleopod from the artery on that side. These branches, during their course ventrally round the abdominal musculature, supply the muscles and the body epithelium by means of fine branching systems of vessels. In M. norvegica, however, the left arteria abdominalis superior ends in segment 4 (fig. 8, s4) where it supplies

the left member of the 4th pair of pleopods. In segment 5, the right artery supplies both members of the 5th pair of pleopods (fig. 8, p5) as well as the tissues on both sides of the body. In segment 6 there are no pleopods and only fine lateral branches of the artery are found, the main distribution of the blood being by way of two median ventral branches (fig. 8, mva) which supply the ventral tissues of the segment and two median dorsal branches (fig. 8, da) which serve the dorsal tissues. By dichotomous branching, the posterior part of this artery produces a branch to each member of the two pairs of uropods and two branches to the telson (fig. 8, t,u).

Zimmer (1913), in his figure of the arterial system of Euphausia superba, shows the left hand arteria abdominalis superior stopping in segment 4. As described above, this takes place in M. norvegica. Some specimens, however, of Thysanoessa raschii were injected and two forms were found in about equal numbers; in the first the left-hand artery terminated in segment 4, in the second the right-hand one. In both cases the other artery supplied both sides of the remaining two segments. About 40 specimens of each species were injected.

At the origin of each artery or group of arteries, there is a non-muscular valve which is opened and closed by

the pressure of the blood. Zimmer (1913) figures the valve in the aorta descendens of Euphausia superba; in M. norvegica the corresponding valve is a tetrahedron with concave lateral faces and appears to be similar to that of Zimmer though he figures it as a cone. A more complicated kind, hexahedral in shape with concave lateral faces, also occurs. The bases of the polyhedrons are adjacent to the heart, the vertices pointing up the lumen of the blood vessels.

The tetrahedral valve of the aorta descendens has, in two of its opposite lateral edges, a slit through which the blood passes from the heart to the artery. A similar valve is found at the proximal ends of the paired hepatic arteries, gonadal arteries and arteriae abdominalis superiores; here, however, each artery is served by one slit. In the three alternate edges of the hexahedral valve, located at the common origin of the median aorta cephalica and the two arteriae laterales, is a slit; each, again, supplies one artery.

The Sinus System.

No account has been found of the sinus system of euphausids. Investigations were made on that of M. norvegica by experimental injection of live animals, and

by serial sectioning. As mentioned previously, the carbon suspension, when injected into the heart of live animals, is pumped out by the heart into the arteries. Its course through the arteries can be followed to their finest branches where it is passed into the various sinuses. In the sinuses a certain amount of clotting of the carbon particles occurs with the result that small lumps are formed which are carried by the blood back towards the pericardium and can be observed under the binocular microscope.

Carbon particles in the abdominal cavities travel anteriorly in the spaces present between the muscles, etc., all the cavities being components of the abdominal sinus. This was confirmed by an examination of serial sections though in them there appeared to be an aggregation of blood corpuscles in a ventral median line. This, however, is almost certainly explained by the fact that the main flow of blood from the arteries to the abdominal sinus takes place ventrally from the region of the pleopods and photophores. The blood flows anteriorly to the ventral posterior region of the thorax.

In the thorax and head, owing to the body organs and muscles, the cavities are very much reduced and broken up, as compared with the abdominal ones, but in sections there

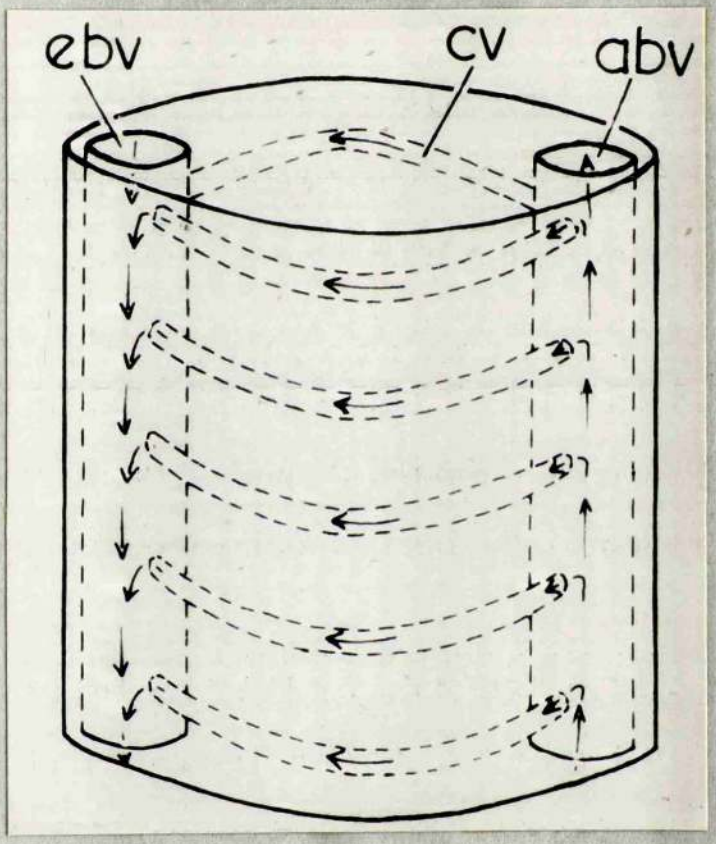


Fig. 9. The flow of blood in part of a tubular gill filament of M. norvegica is shown by the arrows.

abv, afferent branchial vein; ebv, efferent branchial vein; cv, connecting vessel.

is a suggestion of a dorsal and ventral sinus. The dorsal sinus is restricted to the anterior region round the blood gland and extending posteriorly to the anterior end of the pericardium. Blood from this region is carried to the posterior ventral part of the thorax. The ventral sinus collects the blood from the eyes, antennae, mouth parts and thoracic legs, etc., all of it being carried to the posterior end.

Thus the blood from all parts of the body reaches the gills. Here it enters the afferent branchial channels, which lie between the efferent branchial channels (fig. 10, eb) and the body wall. There are various muscles associated with these channels and they, along with the action of the pericardial wall (George, Nair, and Muthe, 1955), presumably drive the blood into the gills. Certainly when carbon is injected into the afferent branchial channels it "spurts round" the gills and this was not due to the pipette. The afferent branchial channels lead into the afferent branchial veins which are in the branchiae. These by means of sub-branches, supply each gill filament. A sub-branch of the afferent vein (fig. 9, abv) carries the blood terminally on one side of each filament, a sub-branch of the efferent vein (fig. 9, ebv) returning it on the opposite side. Connecting

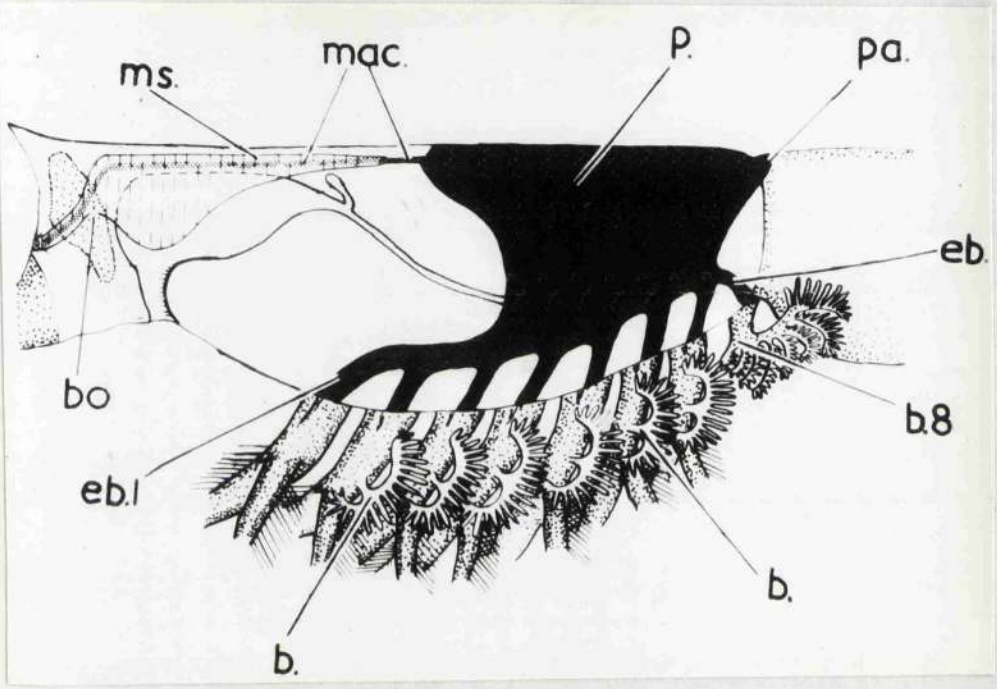


Fig. 10. Drawing of the thorax of M. norvegica to show the extent of the pericardium and membrane round the median aorta cephalica.

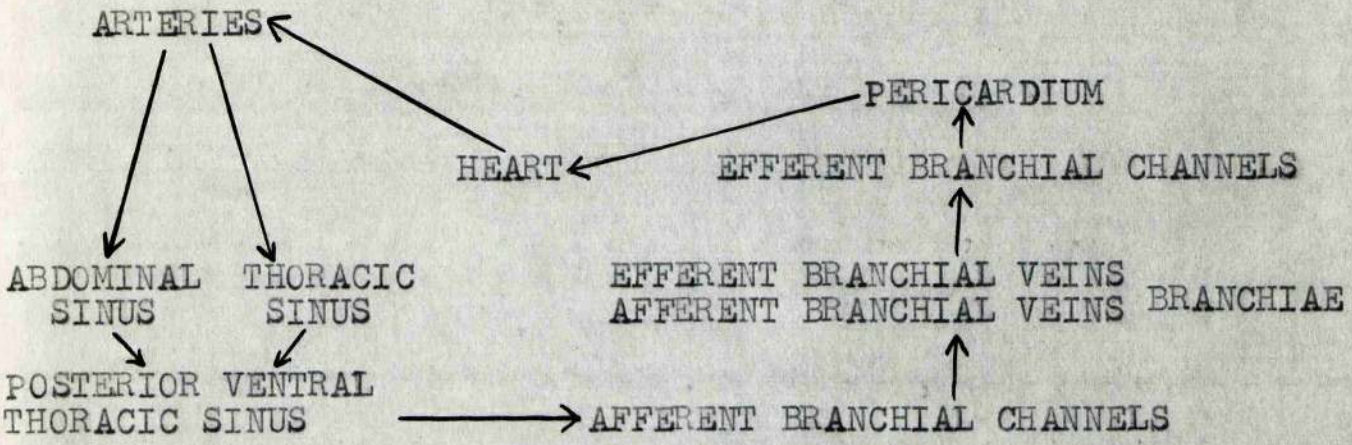
b, branchiae; b8, branchiae of eigth thoracic segment; bo, possible opening of membranous structure in blood gland; eb, efferent branchial channel; eb1, efferent branchial channel to first limb; mac, median aorta cephalica; ms, anterior membranous structure round the median aorta cephalica; p, pericardium; pa, pericardium in first abdominal segment.

the two vessels are numerous small vessels (fig. 9, cv) passing from the afferent, round the circumference of the almost tubular filament, to the efferent vessel. The efferent branchial veins lead to the pericardium (fig. 10,p) via the efferent branchial channels (fig. 10, eb).

Raab has described the pericardium but only mentions the efferent branchial channels. Briefly, the pericardium (fig. 10, p) extends from the region, just anterior to the heart, posteriorly into the first abdominal segment (fig. 10, pa) where it is attached to an endophragmal chitinous band from the dorsal body wall. On each side of the thorax, it has a lateral extension in the 3rd to 8th segments into which the eight efferent branchial channels flow (fig. 10, ebl, eb). From near the posterior end of the heart to its attachment to the chitinous band in the abdomen the pericardium has a complicated system of muscles traversing its lumen. This posterior part is known as the pericardial sinus. Connective tissue composes the greater part of the pericardial wall but in the region of the sinus and in its lateral extensions towards the gills muscular fibres are present.

A schematic representation of the circulation of blood in M. norvegica is shown in Table 1.

Table 1.



In the region of the anterior dorsal thoracic sinus, the closed membrane (fig. 10, ms) mentioned by Raab, round the median aorta cephalica, was observed but found to be more complex than he described. It is associated with the artery shortly after it leaves the heart and at its posterior end has the appearance of a few connective tissue fibres connecting the artery with the dorsal body epithelium. More anteriorly, however, it is a definite membrane enclosing the artery; a well-defined space is present between the two and it continues as a tube until the artery is dorsal to the posterior end of the stomach. The membrane then spreads out laterally and ventrally (in the form of a saddle) over the stomach, the lateral extensions reaching as low as the opening of the oesophagus into the stomach. Just anterior to the oesophagus these extensions shorten and, immediately anterior to the stomach,

disappear, the most anterior part of the membrane being in the form of a tube round the artery. A ventral opening (fig. 10, bo), undetected by Raab, may be present in the region of the blood gland. It was found in two specimens but was not clearly defined and its presence could not be confirmed from an examination of a further two animals. Similar, though less perfectly closed membranes, were found round the arteriae laterales.

In general outline the structure round the median aorta cephalica resembles the pericardium very closely except for the lack of musculature and also the fact that very little blood is found in it except around the possible ventral opening in the region of the blood gland. Raab states that its purpose is to regulate the flow of venous blood but does not support this statement with any evidence. The fact that there are similar structures associated with the arteriae laterales would suggest some function associated with the arteries themselves. Moreover, it is thought that the heart beat and gill musculature control the arterial and venous flows.

The function of these membranes is more likely to be discovered from embryological studies as it is possible that they are vestigial structures originating from anterior extensions of the pericardium.

The Blood Vessels of Compound Eyes.

While working on the general morphology of M. norvegica sections of the eyes were examined and a group of conspicuous "cells", whose function was unknown, was found proximal to the basement membrane. The question arose as to whether these structures were peculiar to euphausids, and possibly the site of Vitamin A synthesis, or were present in other crustacean eyes. Dr. T. H. Waterman (personal communication) had suggested that they might be blood vessels.

The eyes of M. norvegica were then examined in detail and these structures identified in sections as sub-branches of the optic artery. The eyes of some other crustaceans were similarly investigated, but not in detail, to see whether there is a general pattern in the vascular system of compound eyes.

Blood vessels are rarely mentioned in the numerous descriptions of compound eyes. The only relevant paper found is that of Mayrat (1956 b) which was published while the present work was in progress. He describes the vascular system in the eye of the mysid, Praunus flexuosus (O. F. Müller).

Hanström (1948) has reviewed the work done by him and

Carstam on the morphology of the eyes of M. norvegica.

The following crustaceans, other than M. norvegica, were examined:

Macrura Natantia	Leander squilla (Linn.)
Macrura Reptantia	Nephrops norvegica (Linn.)
Anomura	Eupagurus bernhardus (Linn.)
	Eupagurus prideauxi (Leach)
	Galathea squamifera (Leach)

A solution of 50% carbon black VS paste was injected, using very fine glass pipettes, into the live heart of M. norvegica, Nephrops norvegica, Eupagurus bernhardus, and E. prideauxi. When the anterior arteries were full of carbon the heart-beat was arrested in 10% formalin in sea water. The eyes were immediately severed from the specimens and dissected under glycerine which served to prevent the nerve ganglia becoming opaque.

Sections of Leander squilla, Eupagurus spp., and Galathea were examined, as also were sections of the eyes of M. norvegica injected with carbon.

In M. norvegica the median aorta cephalica travels anteriorly and ventrally from the heart, as already described, finally dividing at the base of the eye-stalks into the two optic arteries, one to each eye.

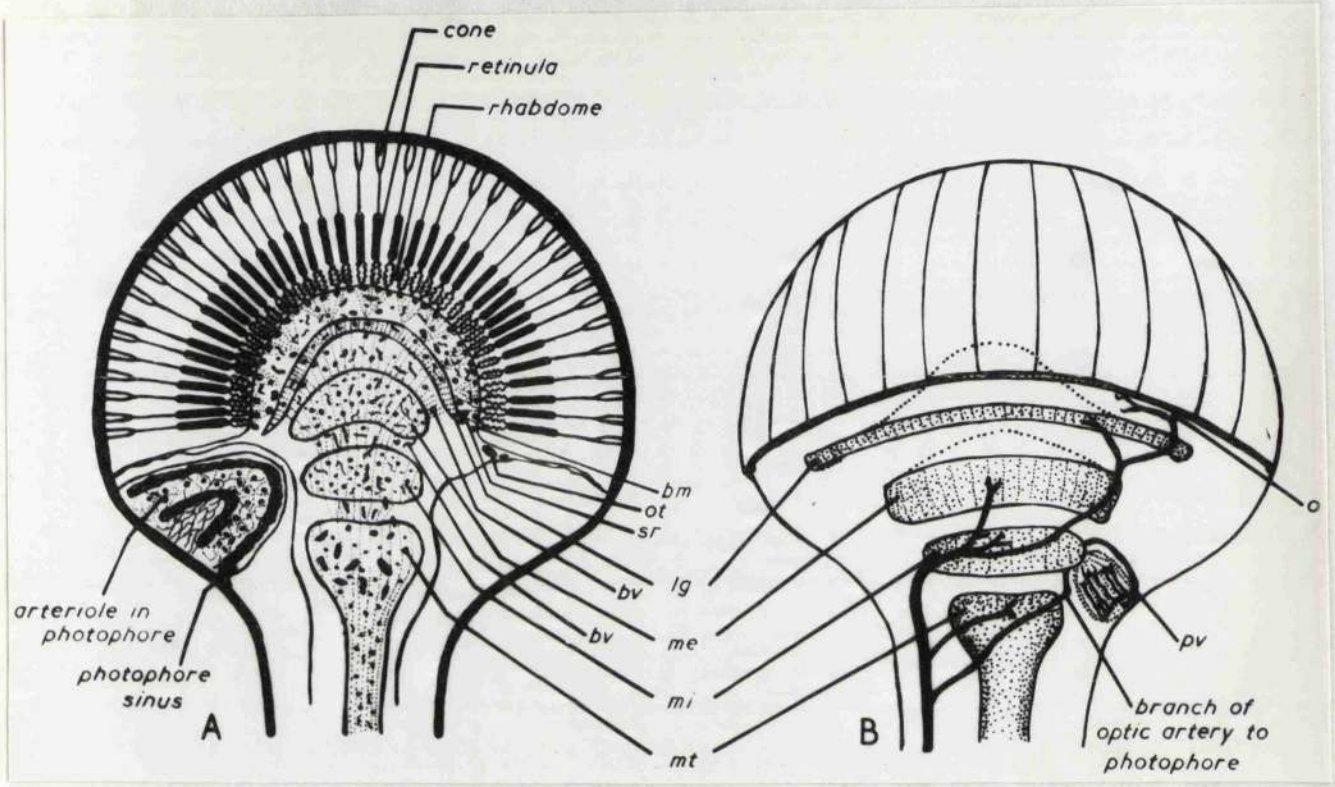


Fig. 11. A. Schematic drawing of a section of an eye of M. norvegica showing the distribution of fine blood vessels in the ganglia, the regions of the eye between the ganglia, and the photophore. B. Schematic drawing of an eye showing the course of the optic artery and its branches.

bm, basement membrane; bv, blood vessel; lg, lamina ganglioaris; me, medulla externa; mi, medulla interna; mt, medulla terminalis; ot, end of optic artery; pv, photophore branch divides in three; sr, subretinal arteriole.

The structure of the superposition eye of M. norvegica is further complicated by the presence of a photophore in the ventral region of the eye-stalk (the orientation of the eye is taken from its position in the animal). The first branch of the optic artery - which at first runs out in the inside lateral edge of the eye stalk between the cuticle and the nerve ganglia - serves this photophore and, as far as can be determined, it alone. When this branch reaches the frontal edge of the light organ it divides in three (fig. 11 B, pv), the median branch being very fine. The lateral branches produce numerous branches which ramify down through the "posterior cellular layer" (Vallentin and Cunningham, 1888) and the outer edges of the striated body. The blood from these vessels enters the ocular sinuses via a sinus (fig. 11, A) surrounding the sides and inner surface of the photophore.

The second branch from the optic artery supplies the medulla terminalis (fig. 11 B, mt) with a complex system of fine vessels which spread throughout its tissues (fig. 11, A, mt). A few fine sub-branches from it pass outwards to supply part of the medulla externa.

The main artery (fig. 11, B) then curves round the nerve ganglia towards the dorsal side of the eye, serving en route the medulla interna and medulla externa (fig. 11B, mi,me)

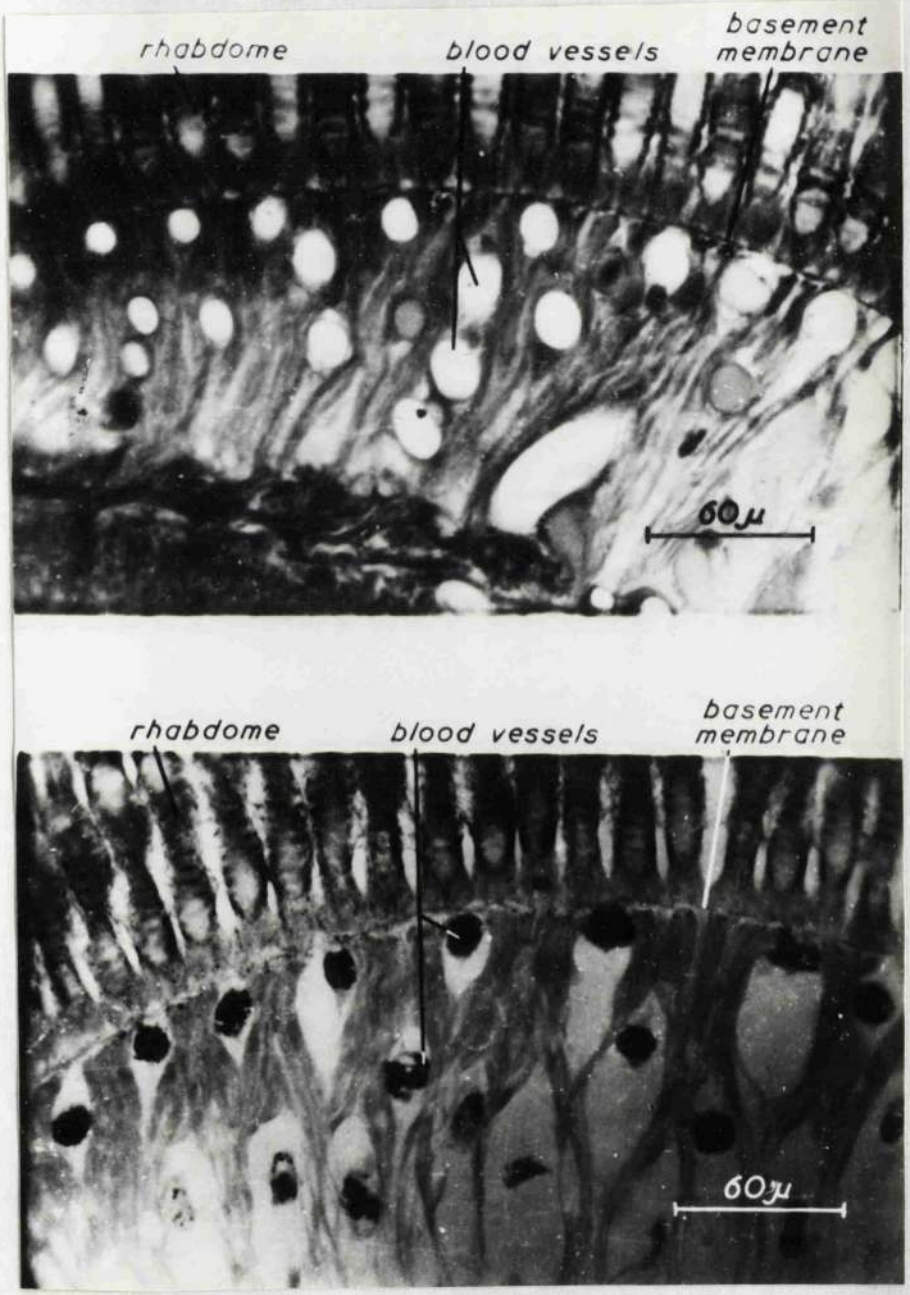


Fig. 12. Sections showing the rhabdomes, basement membrane, and subretinal region of the eye of M. norvegica. In A the blood vessels were not injected; in B they were filled with carbon black.

These two ganglia are very rich in blood supply, the two systems being connected by vessels travelling across the intervening space in both directions.

The lamina ganglionaris (fig. 11, lg) and the region (fig. 11, A, st) of the eye between it and the basement membrane are each supplied by a sub-branch of the optic artery, which is now found in the dorsal region of the eye. A high concentration of blood vessels is present among these nerve fibres below the basement membrane.

Pressed close to the basement membrane is a layer of fine arteries which seem to present a constant pattern; they run out round the membrane from the dorsal to the ventral side of the eye. This subretinal supply is extremely rich and it was at first thought that here was the source of nutrients for the ommatidia. Later, however, carbon was found in the spaces between ommatidia and the main optic artery was seen to end against the basement membrane. No blood vessels were found distal to the basement membrane.

In Leander squilla also (see later) the optic artery ended against the basement membrane and an opening was found in the membrane at the end of the artery; the blood appeared to pass into the complex of cavities between the ommatidia, the ommatidial sinus. The same thing must take

place in M. norvegica.

In the ventral side of the eye there is a complex of sinuses between the photophore and basement membrane. It is through these that the blood from the ommatidial sinus must gain access to the eye sinuses proper.

It is well known that there is an outer and inner eye sinus present in the eye stalk, the two becoming one at the base of the eyes where the blood then enters the cephalothoracic sinus. The blood from the complexes of fine vessels is simply voided from their distal ends into the eye stalk sinuses whence it is finally returned to the heart.

In Leander squilla a similar pattern of vessels is found. The three medullas each have a ramifying system of fine vessels as has also the lamina ganglionaris. Here again there is a very rich supply lying between the lamina ganglionaris and the basement membrane. No blood vessels were found distal to the membrane. In serial sections the optic artery was seen to open through the basement membrane in the dorsal region of the eye, into the ommatidial sinus. In the ventral region of the eye a complex of sinuses, similar to that found in M. norvegica, was seen and it is through these that the blood from the ommatidial sinus reaches the outer eye stalk sinus.

The eyes of Nephrops norvegica were examined by dissection only. A branch of the optic artery was found associated with each nerve ganglion and a rich subretinal supply was observed.

In Eupagurus spp. the ganglia were riddled with blood vessels and an extremely rich subretinal supply was present. No blood vessels were found distal to the basement membrane though a large amount of blood was present in the ommatidial sinus. Again the ommatidial sinus opened into the outer eye stalk sinus.

In the sections of Galathea squamifera a branch of the optic artery to each ganglion was found. The eye has a rich subretinal circulation and also a copious supply to the lamina ganglionaris. Again no blood vessels were found distal to the basement membrane though blood was found between the retinulae.

A constant pattern of blood vessels is thus apparent in all the eyes examined, a branch of the optic artery being associated with each of the three medullas and with the lamina ganglionaris. The final branching of the main artery supplies the groups of optic nerve fibres proximal to the basement membrane as well as producing a very rich subretinal layer of fine vessels. In all cases the artery

terminates at the basal membrane, the remaining blood passing into the ommatidial sinus.

The blood from the ommatidial sinus and from all these systems of ramifying vessels flows into the eye stalk sinus, whence it is returned to the heart via the gills.

If the above results are compared with Mayrat's for the mysid, Praunus flexuosus, a similarily is immediately apparent. His drawing shows more detail than fig. 11 but if this figure was made comparable to that of Mayrat the basic pattern would be obscured. He shows five main branches of the optic artery, supplying the nerve ganglia and the subretinal region but has not found the main artery terminating in the basement membrane as found in the euphausid and decapods examined here.

In M. norvegica there is an extra branch, the one to the photophore, no comparable branch being present in any of the other crustacea investigated.

IV. The Egg.

No account has been found of the growth relationships of the egg and nucleus within the ovary.

An adequate revue of the literature on the egg membranes in Crustacea has been presented by Yonge (1937) who outlined the various hypotheses regarding their origin and number. He showed that the egg of Homarus vulgaris had an inner chitinous membrane, secreted by the oviducts, and an outer cuticular one, secreted by glands in the pleopods.

Similar secreted membranes were found round the eggs of astacuran and brachyuran Crustacea (Yonge, 1935).

Mawson and Yonge (1938) demonstrated an inner chitinous membrane secreted by the oviduct, and an outer cuticular membrane, secreted by uterine glands, in Chirocephalus diaphanus (Anostraca). An inner thin transparent membrane and two outer membranes were found round the eggs of this species by Hall (1953).

Marshall and Orr (1954) found two membranes round the eggs of the copepods Calanus finmarchicus, C. finmarchicus var. helgolandicus, Metridia longa, Acartia clausi, Pseudocalanus minutis, Euchaeta norvegica, Oithona similis and the freshwater species Cyclops agilis

and C. viridis. They also found two similar membranes round the harpacticid Tigriopus fulvus and in the semi-parasitic copepod Caligus rapax. The author (unpublished results) concluded that the eggs of Euchaeta norvegica had only the chitinous membrane round them, the cuticular secretion forming primarily the matrix of the egg mass and only secondarily an outer membrane round most eggs.

The permeability of the egg membranes of Homarus vulgaris was investigated by Yonge (1946) who showed that the outer membrane is semi-permeable whereas the inner one is freely permeable. He concluded that the outer membrane served to protect the embryo mechanically and chemically.

No description of the origin and nature of the egg membranes of any euphausid has so far been published and therefore it was decided to make the following investigation.

Development in the Ovary.

The mature ovary in M. norvegica lies partly against the hepatopancreas, passes posteriorly below the pericardium and extends into the first abdominal segment. Its form and histology have been adequately described by Raab (1915).

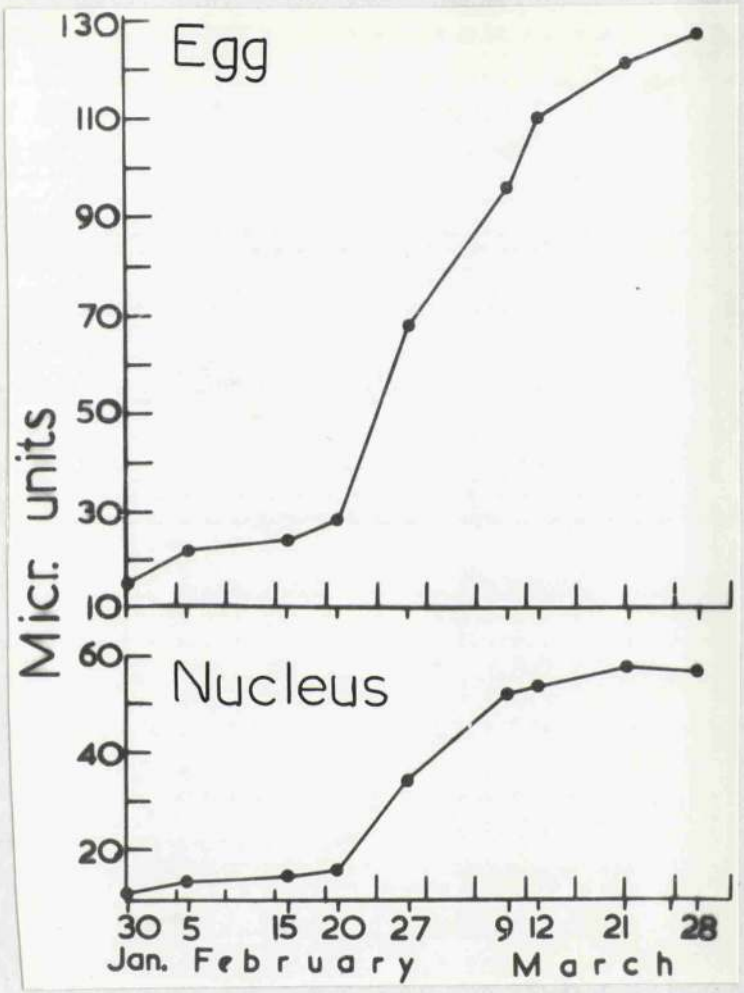


Fig. 13. The growth rates of the egg and its nucleus in the ovary during 1957. Each micrometer unit equals 0.003mm.

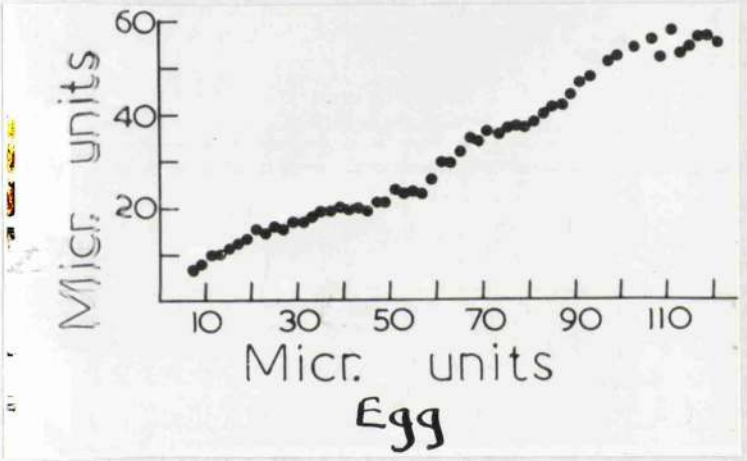


Fig. 14. The relationship of the nucleus diameter to the cell diameter of eggs developing in the ovary. Each micrometer unit equals 0.003mm.

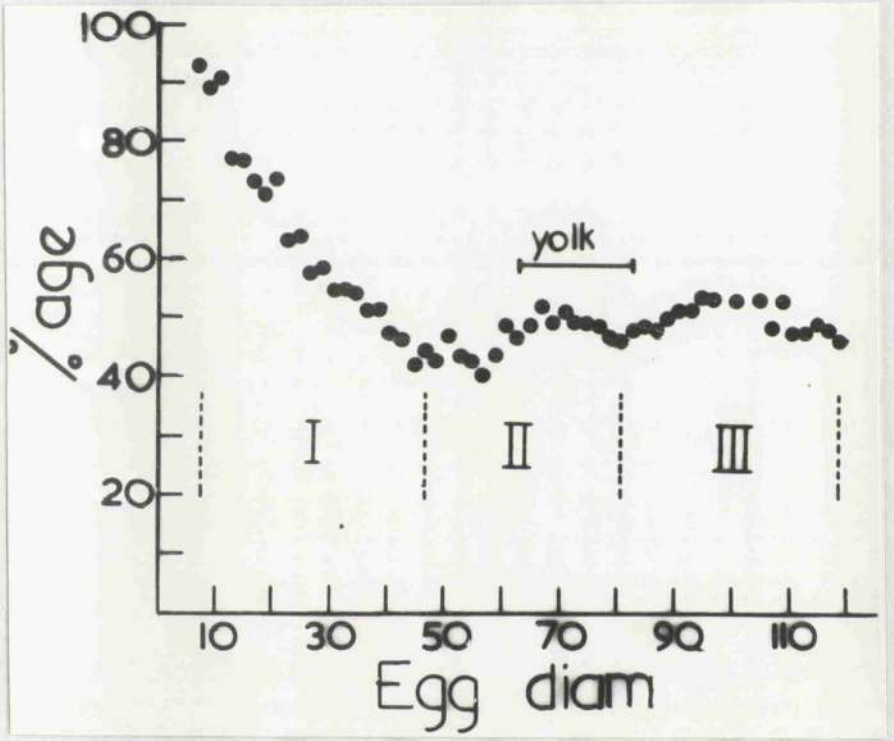


Fig. 15. The diameter of the nucleus shown as a percentage of the egg diameter. I, II, and III are the three phases in the development. The stage at which yolk globules appear in the cytoplasm is shown.

The growth of the eggs within the ovary is a continuous process starting 2 to 3 months before egg-laying takes place. The eggs are packed closely together so that they are not spherical but if they are teased out of the ovary their diameter can be approximately determined. On release from the germinal site of the ovary the diameter is about 0.03 mm. The ovary increases in size as the eggs grow larger and more are released from the germinal areas. Raab has described the cytology and development of the eggs in the ovary.

The ovaries are at about the same stage of development at the same time in all individuals of one population of M. norvegica so that the mean diameter of the eggs in the ovaries can be taken as representative of the state of maturity of the population. Samples were taken and the mean size at a given date was calculated (fig. 13). The initial growth of the eggs is slow but is followed by 5 weeks of very active growth, the eggs in the ovaries being fully developed by the end of March. The final size attained by the eggs was 0.36 to 0.38 mm diameter which is the diameter of the egg minus the perivitelline space once it has been laid.

The growth rate of the nucleus was investigated (fig. 13). Again the initial increase was slow but when

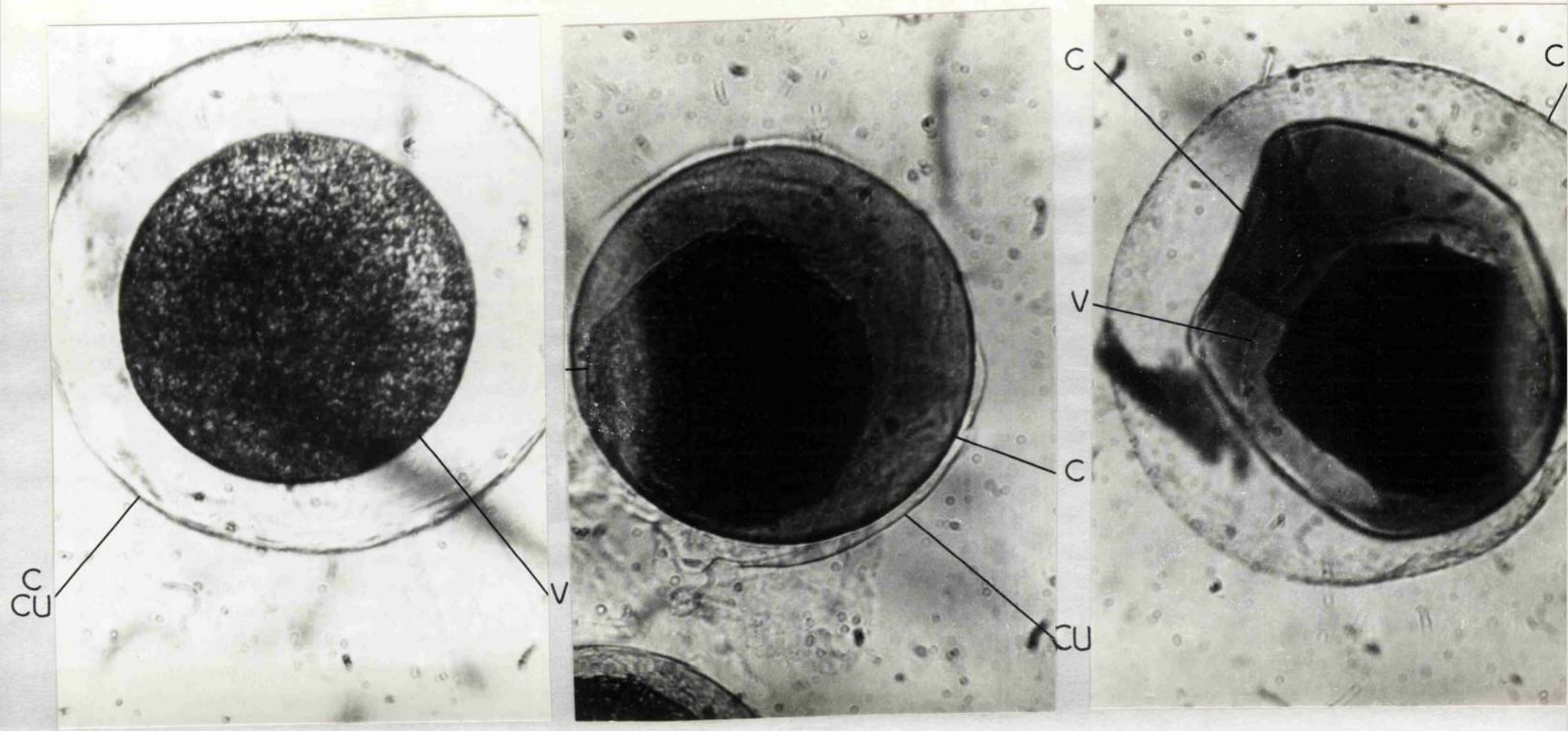


Fig. 16.A. Control egg in sea water. B. Egg after immersion in cold saturated KOH. C. Egg after immersion in cold concentrated HCl.

C, chitinous membrane; cu, cuticular membrane; v, vitelline membrane.

the egg started to grow at a faster rate the expansion of the nucleus accelerated but did not follow the same pattern as that of the cytoplasm. This can be clearly seen when the diameter of the nucleus is graphed against (fig. 14) and as a percentage of (fig. 15) the egg diameter. There then appear to be three phases in the growth of the egg. Since the growth curve for the nucleus is smoother than the growth curve for the egg, and the egg measurement is an inclusive measurement, the variations of the nucleus/egg ratio must be caused primarily by alterations in the rate of growth in volume of the cytoplasm.

In the first phase, the cytoplasm increases in volume faster than does the nucleus. Then two phases follow in each of which initially the cytoplasm increases in volume at a slower rate than the nucleus. Almost the same increase, about 0.12 mm., in the egg diameter takes place in each phase though the middle one has a smaller increase, about 0.10 mm. It is in the latter part of this middle phase, which is of shorter duration than the other two, that the yolk globules appear in the cytoplasm.

Nature and Possible Origin of the Egg Membranes.

There is a space between the vitelline membrane and

the two outer secreted membranes which are usually indistinguishable from each other. The vitelline membrane is closely applied to the egg cell and is rarely distinguishable from it (fig. 16 A).

In the following account the vitelline membrane is referred to as such while the other two are referred to as the inner and outer membranes respectively. The eggs used in the following experiments were taken in townets and fixed in 10% formalin in sea water. The mean diameter of the egg cells was 0.40 mm., the mean total diameter of the eggs being 0.66 mm.

Twenty eggs were covered with a cold saturated solution of KOH. After 30 minutes the outer membrane had separated from the inner one in a number of cases and was being dissolved in others (fig. 16 B). The vitelline membrane was separating from the cell of the egg. Twenty-seven hours later the outer and the vitelline membranes had disappeared and the egg cells were disintegrating. The inner membrane remained intact.

A further twenty eggs were placed in a test tube and covered with about 10 cc. of cold saturated KOH. This was then heated slowly in a glycerine bath until the temperature was 160°C. It was kept at this temperature for 15 minutes and then allowed to cool in this bath. At

120°C. the eggs were no longer recognisable and the solution was becoming discoloured. At 160°C. the eggs had disappeared and the solution was a definite brown colour. After cooling, the pieces of material which remained were removed, washed and a 0.2% solution of KI added to them. A blackenning of the material took place suggesting that it was chitin.

The membranes were further tested by immersing twenty eggs in cold concentrated HCl. After 3 hours the outer and inner membranes had contracted to 0.52 to 0.55 mm. in diameter. There was then a slight swelling but after 27 hours of immersion they had a diameter of 0.52 mm and the inner membrane was starting to separate from the outer. It continued to do so until they were completely separated (fig. 16, C). It then began to dissolve, further suggesting a chitinous nature, while the outer and the vitelline membranes remained intact.

Since the outer membrane was dissolved in KOH and remained intact in HCl it would seem to be cuticular (i.e. protein) in nature.

Eggs were also immersed in absolute alcohol and distilled water but no noticable swelling or shrinking took place.

An attempt was made to find the origin of the membranes. Females which had laid or were about to lay eggs were fixed in 10% formalin in sea water and sections cut of the ovary and oviduct. Eggs were never found in the distal regions of the oviduct of any of the specimens examined.

The ripest eggs are found in the wide proximal regions of the oviducts and though it is thought that they may be invested with a chitinous membrane at this stage it has been impossible to prove. Chemical tests were made on the eggs in this region but the results were negative.

The glandular regions of the oviducts are near their proximal ends which are thick walled whereas the greater mass of the uterine glands is around their distal ends where the walls are one cell thick and the lumen is much larger. In females which were fixed immediately after eggs had been laid, no secretion was found in the proximal regions of the oviducts but some was found in the openings of the oviducts to the exterior (fig. 17, s). It stained orange-red with Mallory's triple stain and was identical in colour with the granules in the glands surrounding this part of the oviduct (fig. 17), which would indicate that it originated

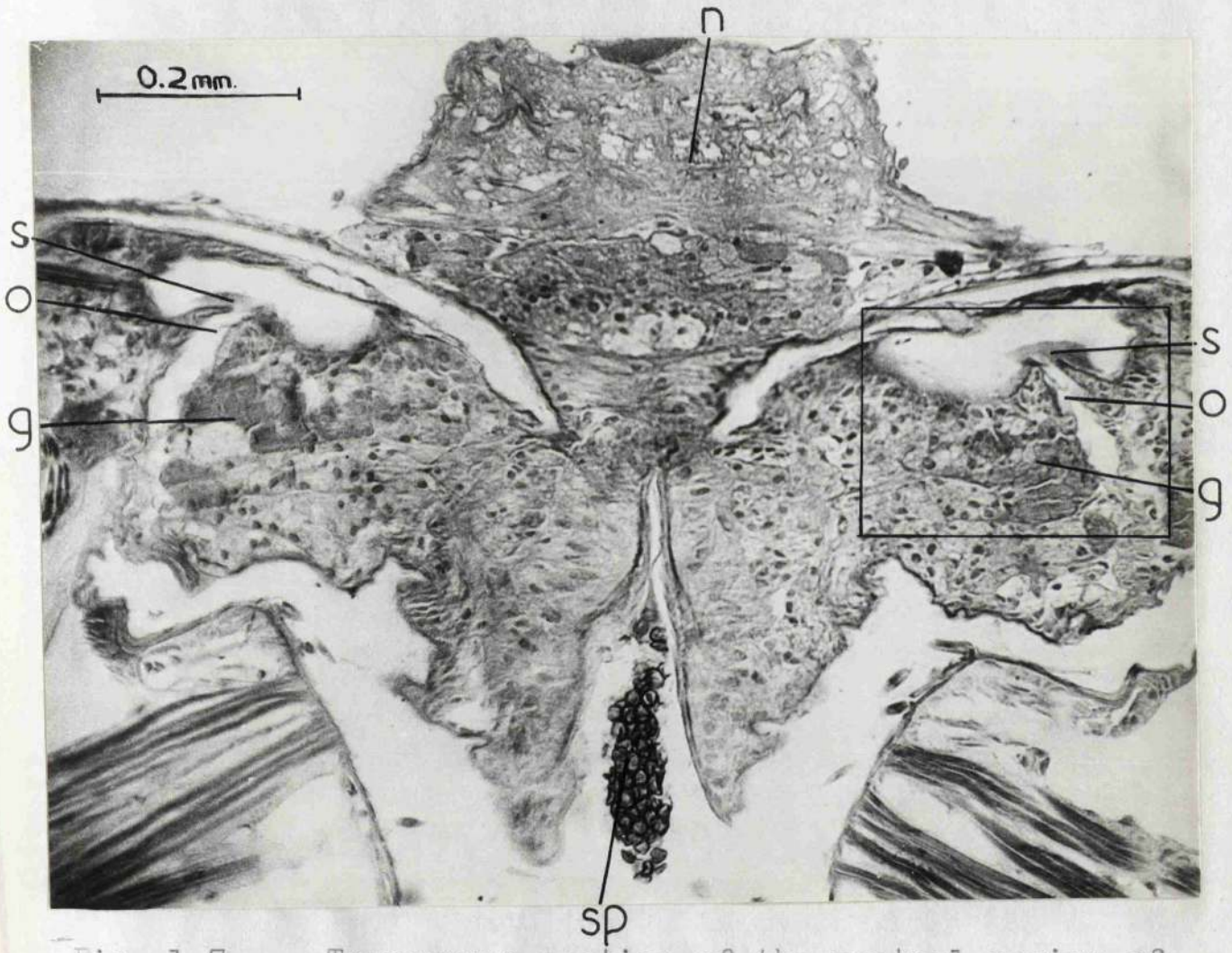


Fig. 1 7. Transverse section of the ventral region of the thorax of M. norvegica showing the external genital openings with some secretion present.
e, external genital openings; g, glands which secrete the cuticular egg membrane; n, nerve cord; o, oviduct; s, secretion of glands; sp, spermatozoa in spermatheca.

from them. Yonge (1937) showed that the cuticular membrane round the egg of Homarus vulgaris stained this orange-red colour with Mallory but the membrane in M. norvegica is too thin for valid staining tests. It is, therefore, concluded that the secretions which form the cuticular membrane in M. norvegica are secreted through the walls of the oviducts into the wide lumen present here. This supports the conclusions of Bargmann (1937) who worked on Euphausia superba.

The eggs must be invested with both membranes before fertilisation takes place for spermatozoa have never been found inside the oviducts in this or any previous investigation. A description of how fertilisation may be effected is given by Raab (1915) and supported by Bargmann (1937). Fertilisation seems to be external, the eggs being fertilised as they pass out of the oviducts past the sperm mass.

On extrusion, the egg has a total diameter of 0.64 mm. while the diameter of the cell is about 0.38 mm. In the laboratory, however, M. norvegica laid small eggs which had a very small perivitelline space, their mean total diameter being 0.36 mm., but these developed normally and nauplii hatched from them about 60 hours after they were laid.

Since the chitin membrane must be acquired prior to the cuticular and the eggs in the ovary do not seem to possess it while newly extruded eggs do, the glandular proximal regions of the oviducts presumably secrete it.

Some euphausids, Nyctiphanes couchii (Einasson, 1945), N. simplex (Boden, 1951) and N. capensis (Boden, 1955), retain their eggs in sacs. These are attached to the endopodites of the 6th and 7th thoracic legs and the exopodites of the 8th thoracic legs. No information is available on the uterine glands in these species but it would be interesting to know if each egg has only one membrane, the chitinous one, and whether the binding substance is homologous with the outer membrane in M. norvegica.

V. Larval Development.

The early work on the larvae of the Euphausiacea was concerned with identifying them in the plankton. The earliest identification was by Dana (Claus, 1863) who thought they were adult forms and named them separately. G.O. Sars employed the names given by Dana to distinguish between the different phases of larval development.

The eggs of some euphausids are shed freely into the sea, in others they are retained in egg sacs. Nauplii hatch from these eggs and these moult to a second nauplius stage followed by a metanauplius stage. The abdomen develops during the following three calyptopis stages, the 3rd calyptopis larva having an abdomen with the full compliment of segments before it moults to the first furcilia stage. Fully developed pleopods are usually acquired in the first 2 or 3 furcilia stages but they can develop in several ways thus giving rise to the various forms of larvae within one stage. This variability of form is not confined to the earlier furcilia stages but is found throughout the later development. Early workers described each form as a stage and the first 2 furcilia stages were thus subdivided into 11 stages by Macdonald (1927b).

Larval stages were also classified on the presence or absence of photophores, larvae with the full complement being known as cyrtopia stages, but this term is now obsolescent.

The work remained in this descriptive phase until Macdonald (1927b) suggested that the larvae in the Clyde passed through fewer stages than elsewhere. Rustad (1934) also found certain larval forms present in much greater numbers than others and his conclusions supported Macdonald's suggestions.

Fraser (1936) was the first to recognise clearly that each larva does not pass through each form found in the plankton but that there were certain dominant forms, the bulk of the larvae moulting from one dominant form to the next. He showed that non-setose pleopods became setose at the next moult and suggested that forms represented by small numbers of specimens in the plankton were variant forms.

A further advance was made by Einarsson (1945) who described and classified the various larval forms in the northern Atlantic.

Attention has been centred on pleopodal development in the early furcilia stages and the variation in the general morphology of the larvae has tended to be less

considered since the work of Fraser and Einarsson. Heegaard (1948) and Bary (1956), however, have emphasized that the morphological characteristics of the larvae within each stage vary very much. Heegaard suggests that ecdysis and morphological development may be independent and hence larvae moulting into the next stage may not have the same morphological characteristics.

Sheard (1953), working with very large numbers of larvae of Nyctiphanes australis, showed the various ways by which a larva of that species can attain the adult form. Consequently, he classified the larvae into 3 classes, furcilia I, II, and III, in order to provide a basic nomenclature for comparing larval development in different species. His furcilia I comprised larvae with the eyes free of the carapace and the pleopods absent or present as non-setose rudiments; his furcilia II comprised larvae with some or all pleopods setose and the pair of long lateral telsal spines unaltered at the base; his furcilia III comprised larvae with all pleopods functional and the shape of the base of the long lateral spines altered.

In this work, new data on the larval forms of M. norvegica in the Clyde sea area are presented. Lebour (1925) described the various larval forms found

in the plankton of the Plymouth area. The larvae originating from the population of M. norvegica in Upper Loch Fyne were studied by Macdonald (1927b). Einarsson (1945) investigated the larval development of this species in the northern Atlantic. Heegaard (1948) described the early furcilia forms in the Bonnefjord and discussed the variations which he demonstrated in the morphological characteristics of larvae within one stage.

The earlier larval stages were sampled by 4 fine townets so arranged on the warp as to fish the following depths simultaneously: surface, 50m., 100 m., and 150m. Four medium townets were substituted to catch the older larvae.

Samples were taken at least once a week in various regions of the Clyde sea area throughout the breeding season.

The larvae of M. norvegica have been classified into furcilia stages according to Einarsson's (1945) descriptions which were found to be accurate. Thus no detailed morphological descriptions of the larvae are presented here.

The calyptopis stages of M. norvegica were examined and the mean measurements, from the rostrum to the distal

point of the telson excluding the setae, are compared in Table 2 with those presented by Lebour (1924), Einarsson (1945) and Heegaard (1948).

Table 2.

	Lebour	Einarsson	Heegaard	Author
Calyptopis I	1.02 mm.	1.0 mm.	0.85 mm.	1.03 mm.
II	1.6 mm.	1.5 mm.	1.57 mm.	1.59 mm.
III	2.4 mm.	2.5 mm.	2.13 mm.	2.40 mm.

Personal measurements of the three stages are identical with those of Lebour and are very close to Einarsson's. Heegaard's measurement of the first calyptopis stage in Gulmarfjord is at the lowest end of the range in size found in the Clyde. He measured only 12 calyptopis specimens and does not state how many of each stage there were but his measurement for the third stage is less than that of the smallest one found in this investigation, which suggests that his third stage larvae were indeed smaller.

The percentage incidences of the various morphological forms found in the first two furcilia stages were investigated. In order to compare these results with those of Macdonald (1927b) and Einarsson (1945) the form with no pleopods has been included with those having

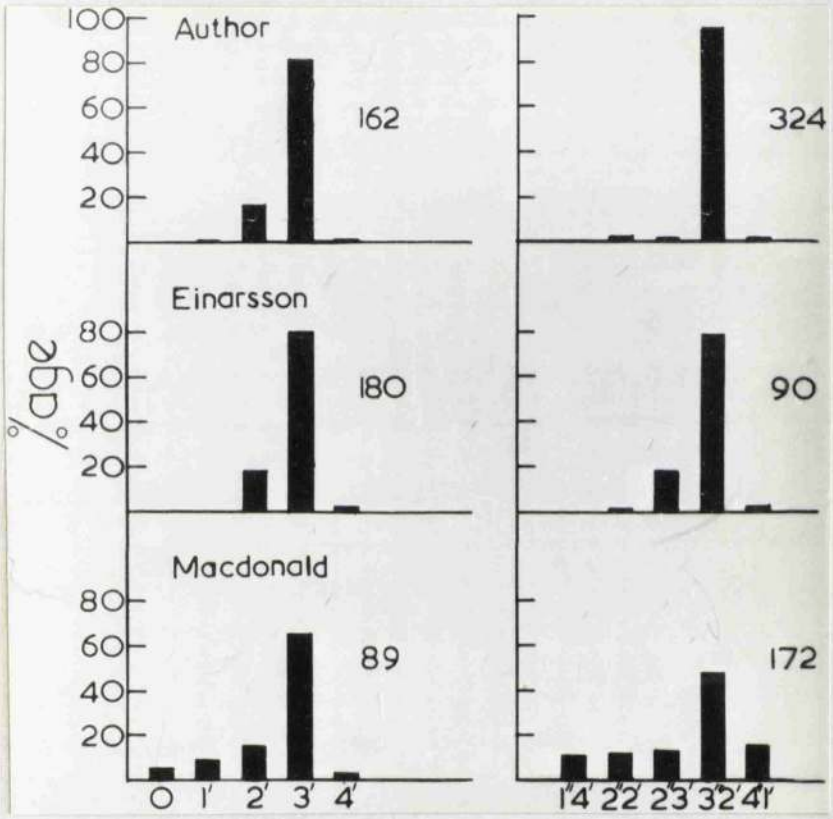


Fig. 18. The frequencies, shown as percentages within each stage, of the various forms found within the first two furcilia stages by Macdonald, Einarsson, and the author.

The sign ' designates a non-setose pleopod; the sign " designates a setose pleopod.

non-setose pleopods. The furcilia II specimens are those with both setose and non-setose pleopods present. The percentages were calculated separately in both stages (fig. 18).

The results for furcilia I are more like those of Einarsson than Macdonald. The form with two non-setose pleopods occurred later in the larval season, which extended from the first week of April until mid-July. Three specimens with 2, and 122 with 3 non-setose pleopods were caught before 13th May. On 13th May, however, 24 specimens with 2, and 40 with 3, non-setose pleopods were found in the townettings examined. After the 13th very few furcilia I and II larvae were caught in the Clyde sea area even though sampling continued every week until July.

The furcilia II results present a different picture from that of both previous authors. Macdonald found 52% and Einarsson 21% of the specimens in this stage varying from the dominant form. In the present investigation, however, only 5% of the total were variants.

The furcilia were classified according to Einarrson's descriptions, the range of measurements within a stage being shown in fig. 19. Both the third and fourth furcilia stages have terminal spines but in the third stage the

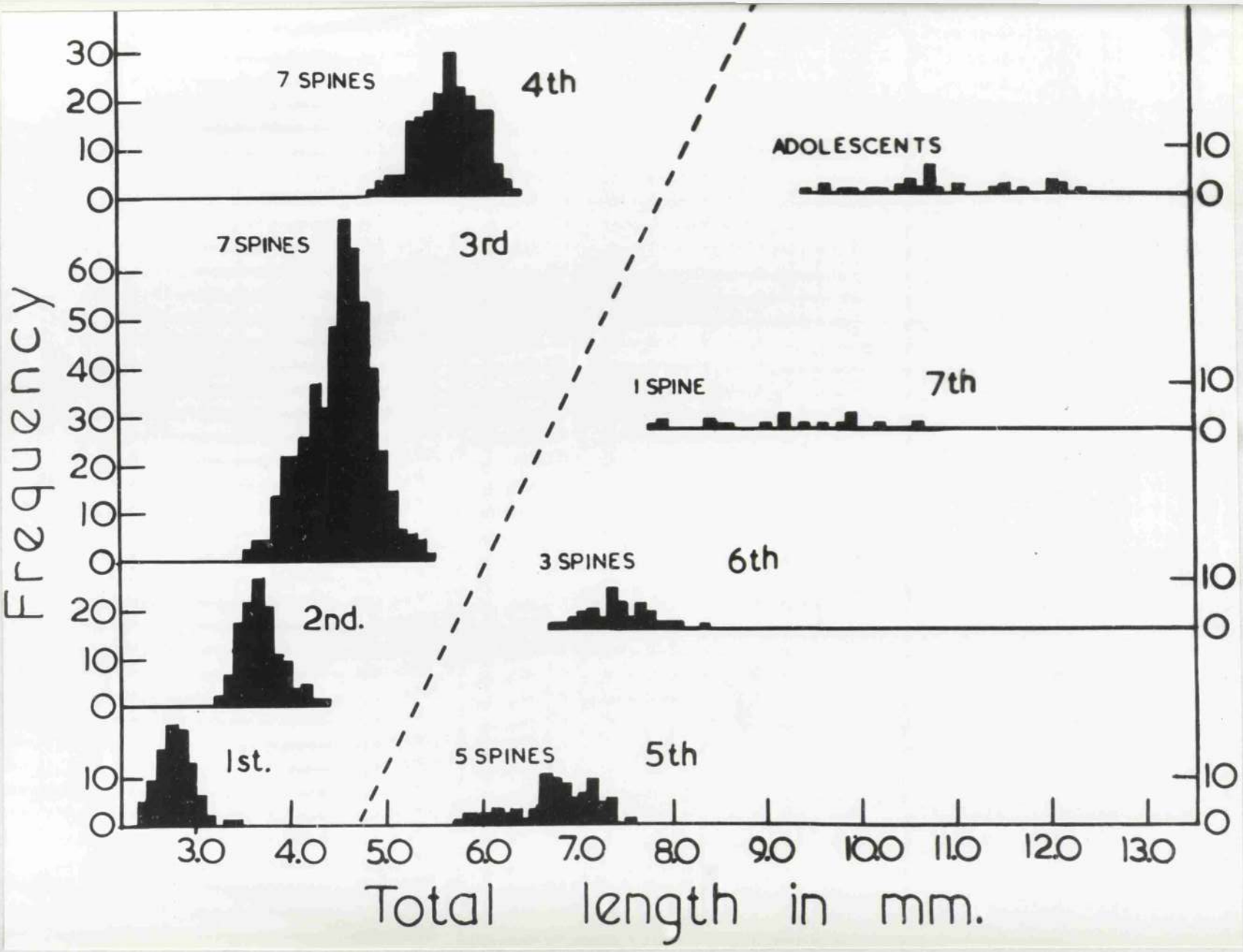


Fig. 19. Length/frequency histograms of the furcilia stages of M. norvegica.

endopod of the antenna is not segmented. The mean size of each stage is compared with Einarsson's measurements in Table 3.

Table 3.

Furcilia	I	II	III	IV	V	VI	VII	VIII	
Einarsson	3.0	4.0	5.0	6.0	7.0	7.5	8.0	8.5	mm.
Author	2.8	3.7	4.5	5.7	6.8	7.5	9.1	10.9	mm.

Einarsson does not state how many specimens of each stage were measured but it is most interesting that the increase in size at moulting seems to be relatively less in his later stages than in those here examined.

The mean sizes of the variant and dominant forms in the furcilia stages were calculated (Table 4) and the number of specimens of each form measured is shown in brackets.

Although the numbers are small, increasing size is associated with greater structural complexity. The specimen with four telsal spines is an exception as it is larger than the mean size of those with three spines.

A similar correlation has been shown for various species by Sheard (1953) and by many other authors with fewer numbers of larvae available to them.

Heegaard (1948) thinks that each nauplius stage lasts

Table 4.

Non-setose pleopods	Setose and non-setose pleopods	Furcilia Stages III	IV	6 spines	V	4 spines	VI
0' 2.76 mm (1)	2"3' 3.65 (5)	4.5mm	5.7mm	6.0mm	6.8mm	7.7mm	7.5mm
2' 2.85 mm (19)	3"2' 3.70 (154)	(446)	(206)	(1)	(76)	(1)	(40)
3' 2.85 mm (83)	4"1' 4.0 (6)						
4' 3.35 mm (2)							

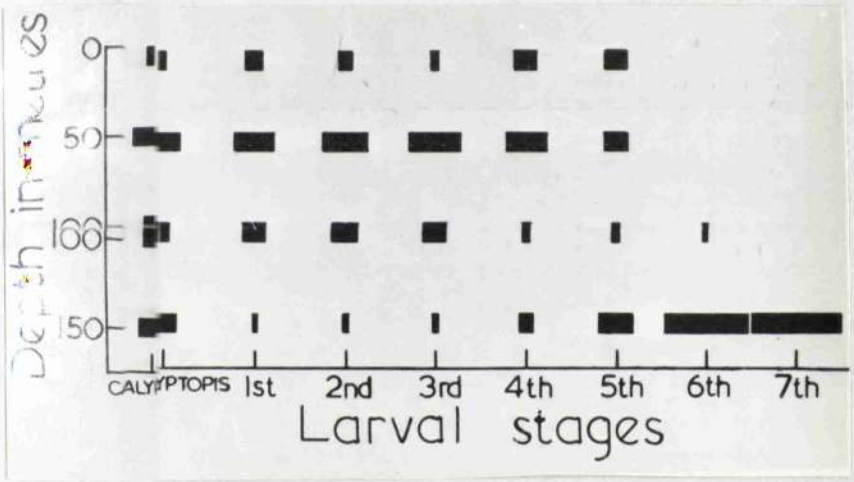


Fig. 20. The vertical distridution of the different larval stages of M. norvegica in the sea during daylight hours.

3 - 4 days, each calyptopis stage a little longer, and each furcilia stage about 7 - 8 days. In the present investigation each nauplius stage lasted 3 days and each calyptopis 3 - 4 days. No furcilia larvae moulted in the laboratory but from the continued sampling of the natural population the average duration of each stage is thought to be 5 - 6 days.

The vertical distribution of the larvae of M. norvegica in the sea during daylight hours was investigated (fig. 20). All stages except furcilia VII and VIII were found from surface to bottom but the layer of greatest abundance was about 50 m. Furcilia VII and VIII lived much closer to the bottom than the rest and behaved more like the adults.

A diurnal vertical migration of the larvae takes place but since there are always larvae present in the surface layers it is not so marked as that of the adult.

The gut of the nauplius is not functional. Sars (1898) thought that the metanauplius feeds but Taube (1915) states that there is no connection between the mouth and mid-gut. Macdonald (1927a), states that the gut is functional but he did not find food in it. A green mush, almost identical to the substance Macdonald (1927a) calls flocculent detritus, was found in the stomachs of 10% of

the metanauplii here examined.

Vegetable detritus, a few diatoms, some filamentous algae and algal spores, fragments of dinoflagellates and mud particles were present in the gut of the larvae examined. Green mush was also present, more so in the earlier furcilia stages than the later ones.

A few of the furcilia VII and VIII specimens examined also contained crustacean remains.

When a crustacean larva moults it increases in size. If a large sample of the larvae of one species is measured and the results analysed on a length/frequency distribution a regular polymodal distribution is obtained. The increments of the modes at each moult is not usually constant but is always significant. If one larval stage, that is one mode, is missing or there is one too many then the curve becomes irregular in that region. Measurements of the larvae within a stage conform to a normal distribution on a length/frequency graph.

As already shown (Table 1) Heegaard's measurement for the calyptopis III stage of M. norvegica is smaller than that of other authors but this may be because there is an extra instar, the form with no pleopods, in the Gullmarfjord.

Heegaard refers to Lebour (1925) and Madonald (1927b)

who found this form without pleopods and asks "... does (sic) the oceanic specimens of M. norvegica develop without this stage at Iceland, whence Einarsson obtained his material, contrary to the development in the three other investigated localities with neritic specimens?"

He suggests that Einarsson may have overlooked this form but if Macdonald's (1927b, p. 790) results are examined it will be seen that he found only 6 specimens with no pleopods as compared with 80 specimens with non-setose pleopods, which suggests that the form with no pleopods was a variant form. The present author found one specimen (fig. 8) and Lebour (1925) does not state how many she found; her measurements of the calyptopis III larvae and the larvae with non-setose pleopods are identical to those found here so that it is unlikely that a distinct stage with no pleopods existed between them. It would seem, therefore, that the larvae in Gullmarfjord are peculiar in having this form as a distinct larval stage.

Macdonald worked in Upper Loch Fyne and found a large number of variant forms in the first two furcilia stages (fig. 18) whereas the author sampled Lower Loch Fyne and the Firth of Clyde and found even fewer variants than Einarsson at Iceland. M. norvegica seems to have been

more plentiful in Upper Loch Fyne in 1927 than in recent years and it may be that the environmental conditions have changed.

All the variant forms of the furcilia stages occurred in the plankton some time after the dominant forms were common. Whether food conditions or hydrographical conditions caused this is not known but Broad (1957) showed that the quantity and type of food available affects the frequency of moulting and the rate of development of larvae of Palaemonetes pugio and P. vulgaris. The frequency of moulting was found to be independent of the rate of development so that variation in form and frequency of larval stages arose.

It has been suggested that the oceanic conditions would be more uniform than the coastal ones and that this is why oceanic euphausids have fewer variant forms within the larval stages. Einarsson showed that the degree of dominance of a form within a larval stage of M. norvegica varies at different stations and Sheard (1953) has presented even more conclusive results for Nyctiphanes australis.

Thus in order to elucidate the development of any one euphausid species samples have to be taken throughout the whole period and area when and where larvae are present.

Nomenclature of Euphausid larvae.

The nomenclature used to describe the larval development of the Euphausiacea is still a major problem. Sequential stages in crustacean larvae are usually associated with sequential moults but this is not so in the Euphausiacea unless the larval stages are named separately for each species.

It is now recognised that the number of larval moults in a species is not constant but that most of the larvae follow the same developmental path while the remainder pass through various numbers of moults. When several authors refer to the larvae of various species as "furcilia III" it is of advantage to know that these larvae are at comparable stages of development.

Sheard suggested that the furcilia larvae should be classified under the following headings:

Furcilia I Pleopods absent or present as non-setose rudiments.

II Some or all pleopods setose.

III All pleopods setose and functional.

If all calyptopis larvae moult to furcilia larvae without any pleopods then these form a distinct stage as they need another moult to acquire non-setose pleopods.

This form is found in most of the Stylocheiron spp. (Frost, 1935; Lewis, 1955) and Thysanoessa spp. (Rustad, 1930, 1934; Einarsson, 1945) investigated. It may or may not form a distinct larval stage in Nyctiphanes spp. (Sheard, 1953; Boden, 1955). Therefore it may be a larval stage in some species of a genus and not in others.

Heegaard (1948) records it as a distinct stage in the development of M. norvegica in the Gullmarfjord whereas Einarsson (1945) at Iceland and Macdonald (1927b) and the author in the Clyde sea area found it present only as a variant form. It seems, then, that there may be a variation within a species in the number of moults passed through by the greater percentage of the specimens when several sea areas are compared. This affects the numbering of the stages so that the furcilia I described by Heegaard (1948) does not have the same morphological characteristics as that described by Einarsson (1945).

In species which do not have a furcilia larva without pleopods the calyptopis III larvae moult directly to a larva with non-setose pleopods. The number of pleopods present may vary from species to species or within a species. Usually, however, one form is present at a higher frequency than the others and this has been

termed the "dominant form". The non-setose pleopods in all larvae, whether derived from calyptopis III larvae or furcilia larvae without pleopods, acquire setae at the succeeding moult in all the species investigated.

It would seem of value, therefore, to group these larvae together as furcilia I and describe each form found, their range in size and numerical incidence.

A pleopod develops first as a non-setose rudiment which at the next moult acquires setae. The anterior abdominal segments acquire non-setose or setose pleopods first. That is, a furcilia I larva with non-setose pleopods usually moults to a furcilia II larva in which the non-setose pleopods are setose and the blank segments have non-setose pleopods. At the following moult all the segments have setose pleopods.

There are, however, exceptions to this. In Nyctiphanes simplex (Boden, 1951) the furcilia I larva with 3 non-setose pleopods usually moults to a larva with 5 setose pleopods. Where most larvae in furcilia II of a species have one or more of the posterior abdominal segments without pleopods and the most anterior segments have setose pleopods, two moults are required to produce a larva with 5 setose pleopods. This happens in

Stylocheiron longicorne (Frost, 1935), Euphausia longirostris, E. spinifera (John, 1936) and possibly in a few others. In other species, where this is not the normal path of development, a variable percentage of the larvae develop in this way and so have an extra moult.

The number of moults from the time a larva acquires non-setose pleopods until the pleopods become functional can thus vary. Sheard has ascribed all forms with setose and non-setose pleopods to furcilia II but has also included with them forms with 5 setose pleopods.

The larval form with 5 setose pleopods and the telsal spines, usually 7 in number, unreduced is the cause of some disagreement in the literature. Euphausia species (Bary, 1956; John, 1936) have only one larval instar with 7 terminal telsal spines and 5 setose pleopods. Boden (1951), however, suspects that there are several larval stages of this type in Euphausia pacifica. Thysanoessa inermis has 3 and T. raschii 4 consecutive stages (Einarsson, 1945) which have 5 setose pleopods and 7 terminal spines on the telson, the stages being identified by the comparative development of the thoracic appendages. M. norvegica has two such stages whereas Pseudeuphausia latifrons (Tattersall, 1936) has no such stage, the telsal spines being reduced by the time the

larva has 5 setose pleopods.

Boden (1950, 1951, 1955) has used the presence or absence of antennal endopod "segmentation" and the reduction sequence of the telsal spines to classify the larvae of the species he investigated. In Euphausia pacifica about 40% of the larvae with 5 telsal spines and in Nyctiphanes simplex and N. capensis about 50% of the larvae with 3 spines had the antennal endopod segmented. These seem to be valid stages judging by the measurements he presents.

The point, however, at which endopod "segmentation" takes place is variable when related to the telsal spine reduction sequence in various species within a genus and differs very much from genus to genus.

In almost all euphausid species, however, the sequential reduction of the terminal telsal spines seems to be a constant feature although reduction occurs in various ways. The larvae with setose and non-setose pleopods usually moult to larvae with 5 setose pleopods and the telsal spines not reduced in number. The known exceptions to this rule are Pseudeuphausia latifrons (Tattersall, 1936) and Nematoscelis microps (Gurney, 1947). The terminal spines may be reduced in number at the next moult (some Euphausia spp.) or as many as 4 successive

moults may take place before the reduction begins (Thysanoessa raschii).

Therefore, considering all these facts it would be better to exclude all specimens with 5 setose pleopods and 7 telsal spines from furcilia II unless they were obviously derived directly from furcilia I larvae with 5 non-setose pleopods or their morphological characteristics made it obvious that they should be classed with furcilia II larvae. Instead, it is suggested that these larvae be classified by themselves as furcilia III and the number of instars, their form, incidence and size-range described.

There now only remain the larvae in which the telsal spines are reduced in number. Various authors (Einarsson, 1945) have examined the possibility of using the lateral telsal spines as characters for identifying the later furcilia stages but have concluded that there is far too much variation between species to make this useful.

Boden (1955) has criticized Sheard (1953) for 'lumping' the late furcilia larvae together as furcilia III. He suggests that the concept of dominance is still useful and so they should remain separate and distinctly named. Sheard's including them together under one heading, however, does not obscure this concept as one provision is that the several instars should be described. One strong criticism

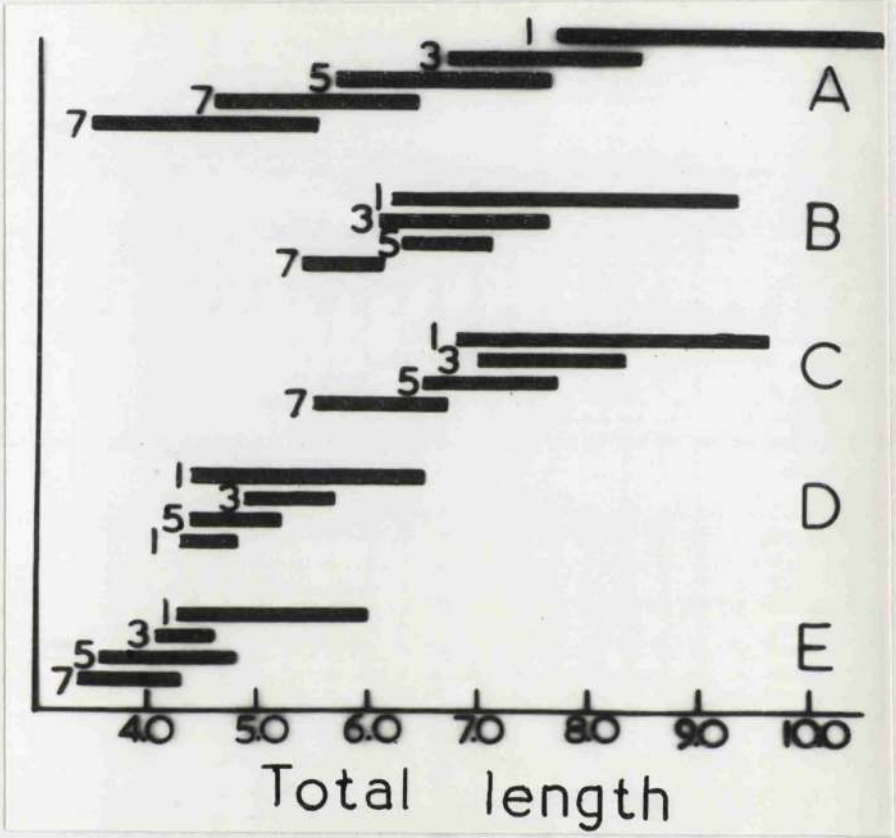


Fig. 21. Size ranges of the larval stages of some euphausids.

A, M. norvegica; B, Euphausia vallentini, (John, 1936); C, E. frigida, (John, 1936); D, Nyctiphanes australis (Bary, 1956); E, N. australis, (Sheard, 1953).

The numerals at the left-hand sides of the histograms refer to the number of terminal telsal spines.

made by Boden of Sheard is that his furcilia II larvae are distinguished from his furcilia III larvae by an alteration in the shape of the base of the lateral spines on the telson. This is certainly unsatisfactory and lends support to the suggestions made here.

The size range of larvae within a stage, which on a size/frequency histogram should conform to a normal distribution curve, should not decrease when larvae moult to the following stage. Instead, it should remain constant, according to theoretical mathematics, or according to some biological theories it should increase. In M. norvegica (fig. 21) it remains almost constant until the instar with 1 telsal spine when it increased by a half.

The range in size of the larvae of Nyctiphanes australis (fig. 21, Sheard) with 3 telsal spines is less than half that of larvae with 5 telsal spines. Since there is a relationship between the size of a larva and its morphology the author would suggest that the larger specimens with 5 spines had them reduced to one at the next moult and thus omitted a 3 spine stage and that the 3 spine larvae Sheard found were derived from the smaller larvae with 5 spines. Sheard found that larvae with 5 telsal spines did indeed have them reduced to one at the next moult. He also found that 7 telsal spines could be

reduced to 3 in one moult and a similar explanation would fit this.

Bary (1956) with fewer numbers of larvae of N. australis did not find this decrease in size-range but the lower limit of the size range of larvae with 1 telsal spine (fig. 21) is much less than the lowermost limit of the supposed preceeding stage. This seems to be a fairly common phenomenon (fig. 21, E. frigida, E. vallentini) and would be explained if a number of the larvae omitted a stage in the telsal spine reduction sequence.

The reduction sequence is 6-4-2-1 in Stylocheiron suhmii (Lebour, 1926) and there are very many species where the possible sequence is not known. Thus it is by no means obvious that the telsal spine reduction sequence is a valid way of classifying the larvae. It would, however, be of value to classify these larvae together as furcilia IV and describe the dominant instars, their size-range and frequency.

Conclusions.

No ideal larval classification can be devised for the Euphausiacea and consequently the most useful form should be adopted. An attempt has been made in this paper to show that the larval development in euphausids

can be split into 4 phases.

In the first phase, the calyptopis larva moults to a larva which either has or acquires at the next moult non-setose pleopods. There are thus either one or two moults in this phase depending on whether there is an instar without pleopods.

In the second phase the larvae with non-setose pleopods moult to larvae with setose and non-setose pleopods. In a few species there are larvae with 5 setose pleopods derived from a dominant furcilia I form with 5 non-setose pleopods and these should be included here and the situation made clear. Usually there is one moult in this stage but in a few species the first instar in this stage has one or two abdominal segments without pleopods; this instar requires 2 moults to acquire 5 setose pleopods.

The third phase is characterised by the continued development of the thoracic appendages and the non-reduction of the terminal spines on the telson. The antennal endopod very often becomes segmented in this stage. The number of moults varies considerably, being one in some Euphausia spp. and 4 in Thysanoessa raschii.

In the fourth phase, the terminal telsal spines are reduced and sometimes the "segmentation" of the antennal

endopod takes place. The thoracic limbs continue to develop. The number of moults is questionable but is thought to be three. The sequence of the spine reduction shows some variation in different species and possibly within a species.

The author suggests that these phases be termed as follows:

Phase I ..... Furcilia I
Phase II ..... Furcilia II
Phase III ..... Furcilia III
Phase IV ..... Furcilia IV

Since the most important conception in our consideration of euphausid development is that of 'dominant forms' it must not be obscured. All the instar forms must be described and where there is much variation as many larvae as possible should be examined and measured. The measurements are very important and should be presented either as range of size within an instar, the mean size and number of specimens measured being indicated, or in the form of length/frequency histograms for each larval form or instar.

VI. The Relationship between vertical Migration and Feeding.

A diurnal vertical migration in euphausids has been described for a very large number of species. Einarsson (1945) has reviewed knowledge of the north Atlantic species and, of the six dominating species in this area, three have been shown to migrate vertically; Thysanopoda acutifrons, Nyctiphanes couchii and Thysanoessa raschii. Marshall (1948) has since obtained evidence of a vertical movement in Thysanoessa inermis.

Euphausia pacifica and Nyctiphanes simplex migrate vertically in the San Diego region (Esterly, 1914). Hardy and Gunther (1935), working on the euphausids of the South Georgia area, demonstrated vertical migration in Euphausia superba, E. frigida, E. triacantha, Thysanoessa macrura, and T. vicina. Pseudeuphausia latifrons was shown to avoid the surface layers during daylight in the Great Barrier Reef area (Tattersall, 1936).

Of the 20 species examined by Lewis (1954) in the Florida Current region 5 occurred rarely in his hauls, 7 showed a definite vertical migration and 5 appeared to migrate towards the surface at night, but, in the case of

some species, the numbers present made conclusions inconclusive. The remaining three species, Stylocheiron elongatum, S. longicorne and S. suhmii did not occur in appreciable numbers in his hauls but Moore (1949) found evidence of vertical migration at night.

Where a worker has failed to demonstrate a vertical migration in a euphausid species it is generally because the numbers present were too few and later workers with greater numbers have proved its presence. From the above cited literature it is apparent that a euphausid which does not at least come nearer the surface at night than during the day is exceptional.

The possible relation of euphausids to the deep scattering layer has been discussed by Moore (1950) and Tucker (1951).

Various authors have failed to demonstrate diurnal vertical migration in the populations of M. norvegica (Smith, 1879; Paulsen, 1909; Bigelow, 1926). Vertical migration was, however, demonstrated by Tattersall (1910) although not so marked as in other euphausids and mysids he studied. Hickling (1925) found movement of M. norvegica away from the sea bottom at night but he did not determine the upper limit of migration.

The population resident in Upper Loch Fyne was shown

to perform a regular diurnal migration by Macdonald (1927a) who also found that smaller specimens tended to approach nearer to the surface at night than larger ones. Einarsson (1945), in reviewing the subject, reaches the conclusion that "negative phototropism of this species reveals itself in areas of slight current movements, while strong vertical currents and not the search for food would account for the appearance of this species in the surface layers of turbulence areas".

The discontinuity layer was shown by Hansen (1950) to be the upper limit of the vertical migration of M. norvegica in the Bonnefjord but the numbers on which he based his results were very small. Marshall (1948) has presented data which suggests that a vertical migration takes place in the North Sea.

Cannon and Manton (1929) found that M. norvegica is a filter feeder. No further work on this aspect of euphausids seems to have been done except for that of Barkley (1940) on Euphausia superba. He found it to feed by filtering Fragillariopsis antarctica and secondarily other diatoms and protista, and showed that the distance between the setules of the filtering setae was 7μ, the food particles in the stomach being less than 40μ in size.

The nature of the food has been studied by Paulsen

1909 (M. norvegica, Thysanoessa inermis), Lebour, 1924 (Nyctiphanes couchii), and Hickling, 1925 (M. norvegica, N. couchii, Thysanoessa spp.).

The conclusions drawn from this earlier work, as pointed out by Einarsson (1945), are that euphausids feed on phytoplankton, protista, Crustacea and detritus.

Land and marine detritus were shown to be important constituents of the food of M. norvegica by Macdonald (1927) who also found that diatoms and copepods were eaten in considerable quantities. He stated that crustacean remains seemed to be found more often in the stomachs of larger than smaller specimens and that the opposite was so for diatoms and "wet dust".

Einarsson (1945) found, in his own investigations, that M. norvegica fed mainly on detritus and fragments of Crustacea and hardly at all on phytoplankton. Of the four species of euphausids, from the Sea of Japan, examined by Ponomareva (1955) only one, Thysanoessa raschii, fed on diatoms to any extent, the dominant food being copepods (Ponomareva, 1954, 1955). She reports the presence of entire or parts of crustacean compound eyes in the stomachs of three species of euphausids and suggests that the "reddish-brown substance" found by Einarsson may originate from macerated eyes.

Investigations were made on the populations of M. norvegica

resident in Loch Fyne. Preliminary examinations of vertical migration, feeding methods and food showed that a detailed correlated account was desirable. The purpose of this report is not to present a qualitative account of the food eaten but to examine the interrelationships which exist between vertical migration, feeding methods and food eaten at any one time of day.

It was desirable to carry out two full-scale experiments, one with a night period of about 15 hours in the winter and a summer one with a 5 hour period of darkness.

Two investigations extending over 24 hours were made on the population in the deep water just north of Tarbert, Lower Loch Fyne. The first set of hauls was taken at 4-hourly intervals from noon, 14th to noon 15th, November, 1956, when the period of darkness was about 15 hours. In the experiment on 22-23rd July, 1957 it was necessary to take samples at hourly intervals through the 5 hour period of darkness in order to analyse the vertical movements; daylight hauls were made every 3 hours.

Each haul was made with four 1 m. open stramin nets so arranged on the warp that the following depths were fished dimultaneously; surface, 50m., 100m., 150m. The nets were towed at these depths for 20 minutes so that the

proportion of specimens caught at lesser depths when the nets were being hauled was negligible. The hauls were sorted on the ship, fixed in 10% formalin in sea water, and brought back to the laboratory for subsequent examination.

The sex of each animal was determined and its carapace length measured. Stomach contents of specimens in the winter hauls at each depth and time were examined, the presence or absence of diatoms, filamentous algae, dinoflagellates, Sagitta spp, Euchaeta norvegica, unidentifiable crustacean remains, compound eyes, organic detritus and mud being noted.

A number of supporting observations and experiments were made in various parts of the Clyde sea area and these are mentioned under the relevant headings.

The methods employed in the investigations of feeding mechanisms are described with the results of the experiments.

Vertical Migration.

In describing the results reference is made to the 0- and I-year classes. The 0-group is defined as that which has not yet laid eggs or produced spermatophores. The I-group are animals which have taken part in one

breeding season.

Winter Analysis.

The first attempt, on November 8-9th, 1956 had to be cancelled during the night owing to deterioration in the weather but the hauls which were taken were useful in supplying duplicate material for checking the results of the following experiment.

This experiment was commenced at noon, 14th November when there was a bright sun, clear sky and fresh north wind which did not affect the ship working close to the northern shore of Loch Fyne. By 1600 hours a few clouds were in the sky, the sun was low and the wind dropping.

Darkness fell about 1700 hours, though official sunset was at 1600 hours.

By 2000 hours the sky had cleared again but the moon, which was in its last quarter, was veiled by cloud for some time before and during the haul. The moon was still veiled at midnight and showers of rain were rather frequent. The haul at 0400 hours was taken in the darkest part of the night, the moon being no longer visible and the sky overcast.

Sunrise was at 0730 hours.

At 0800 hours the sea surface was agitated by a fresh

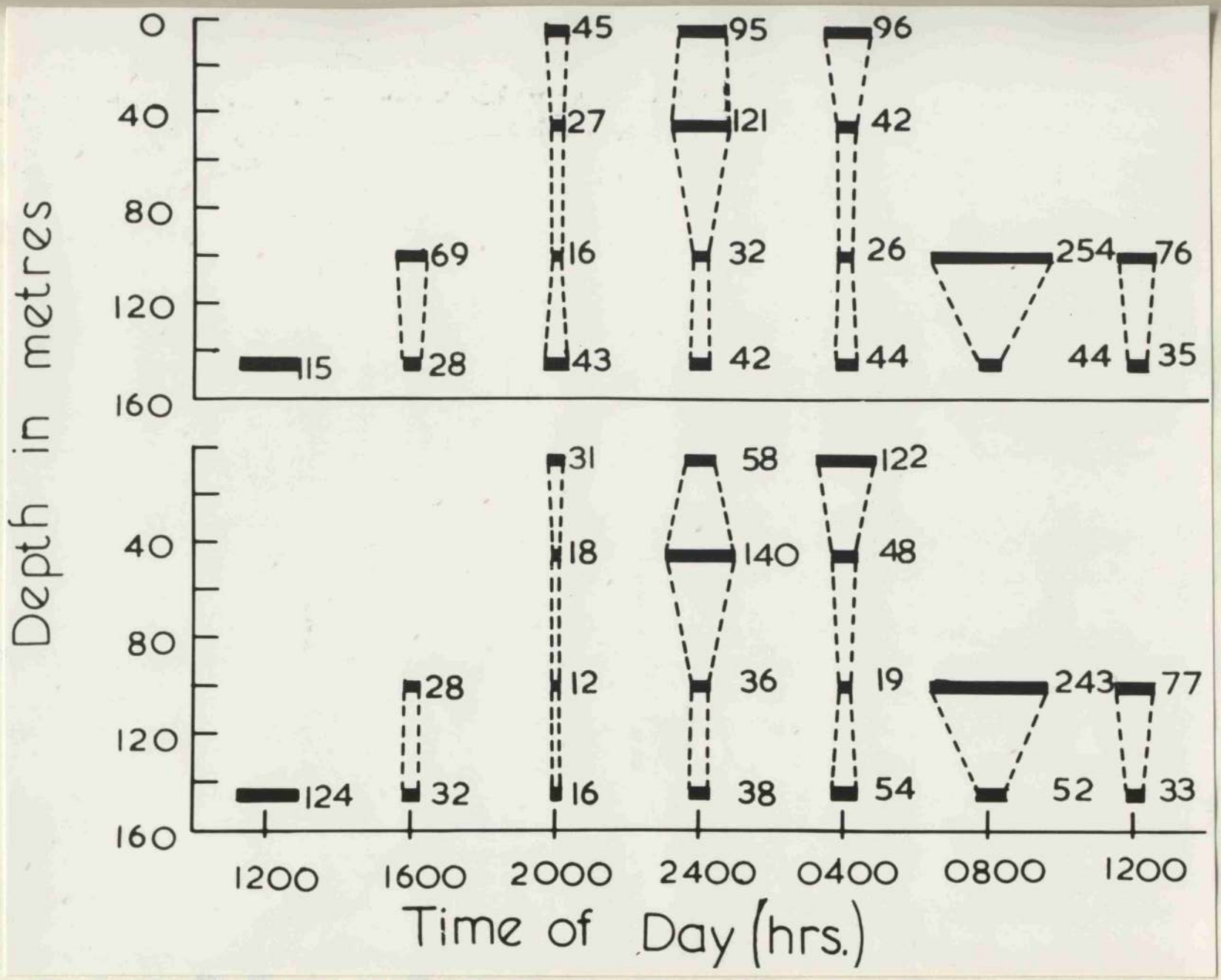


Fig. 22 . The vertical migration of M. norvegica on the 14 and 15th, November, 1956. The numbers refer to the numbers caught at different depths and times. Females, upper graph; males, lower graph.

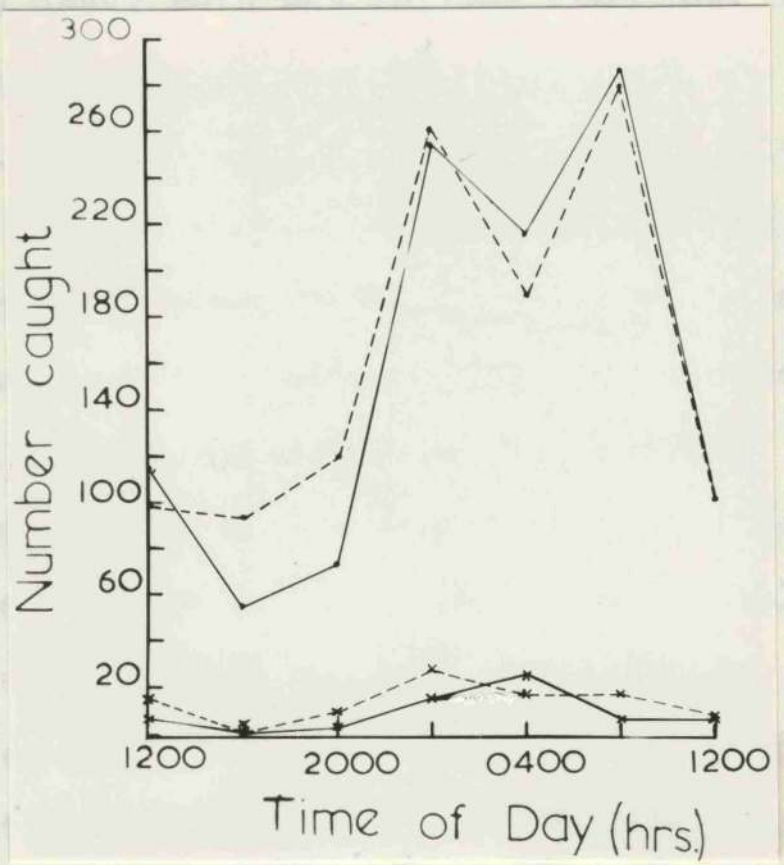


Fig. 23. The total numbers of M. norvegica caught by the 4 nets at any one time of day from noon, 14th to noon, 15th, November.
The upper pair of lines are the 0-group animals, the lower pair the I-group. Females, broken lines; males, solid lines.

north wind and heavy rain was falling from low, dark clouds. At noon on 23rd November there was low cloud, rain and wind.

Thus the experiment started on a bright day and continued through a night in which the moon was not thought to have much influence. The following day was very dull and misty with stormy sea conditions.

A vertical series of sea temperatures was taken but the difference between surface and bottom was only 0.6°C, the surface being 10.7°C, the bottom 11.3°C.

Both males and females began their upward migration as the sun set at 1600 hours (fig. 22). The number of animals in the surface layers increased to a maximum at 0400 hours but by 0800 hours, thirty minutes after sunrise, all had moved downwards.

It is interesting to note that a greater total number of males and females were fished at 0800 hours than at any other time (fig. 23). In the course of the present work it has been shown that a large part of the day population of M. norvegica lives in the bottom 20m. layer of the sea. It is impossible to sample this layer quantitatively owing to the nature of the bottom (fine mud) and the chances of loosing the gear. Even at night this layer is still populated, though much more thinly, so that the population

may be considered as mobile vertically as well as horizontally. When it sinks slightly, then proportionately more animals accumulate in the bottom 20m. than elsewhere. Since the lowermost net fished at 150m. depth, and the animals seemed to be spread uniformly throughout the vertical range, the total number of animals caught by the 4 nets at any one time (fig. 23) is an estimate of the number of animals above this bottom layer. It can be seen (fig. 23) that between noon and sunset there was a slight sinking of the population as a whole though part of it rose (fig. 22). An upward movement from the bottom then began, becoming accelerated between 2000 hours and midnight. After midnight the population as a whole sank but at 0800 hours more 0-group animals were caught above the bottom 20m. than even at midnight. The numbers caught at noon on the 15th were about the same as the previous day but were distributed in the two lowermost nets.

It was noticed that there was a vertical size gradient of animals at midnight as Macdonald (1927) realised with much smaller numbers in his samples. Surface nets caught only 0-group animals while nets near the bottom caught mostly large ones.

The animals were sexed and grouped in 1 mm. size

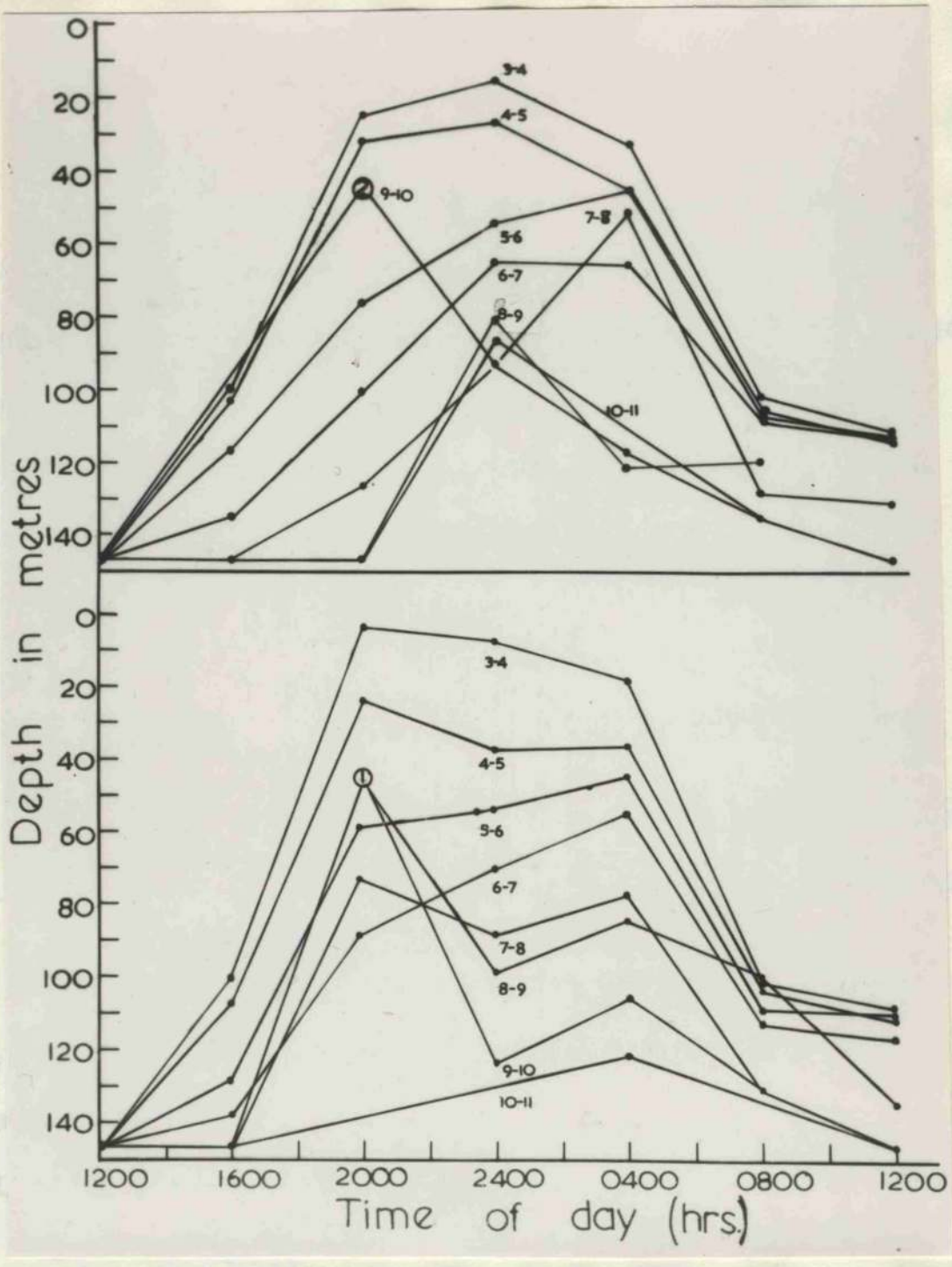


Fig. 24. The vertical layering of the size classes on the 14th and 15th, November. The numbers associated with the lines refer to the size classes, i.e. 3-4mm. The numerals in circles refer to the number of specimens of each size class represented by that point. Females, upper graph; males, lower graph.

classes. The mean depth of occurrence of each size class of males and females was calculated for each time of day (fig. 24). The 3.0 mm. size class was represented by a total of 20 females and 12 males, the mean depth and time at which they were caught being presented in Table 5.

Table 5.

	noon 14th	1600	2000	midnight	0400	0800	noon 15th
♂				3.7 m.		100.6m.	100.6m.
♀		100.6m.		3.7 m.	3.7m.	100.7m.	112.1m.

It is noticeable that, even with the small numbers present, the size class tends to be nearer the surface than the 3-4mm. class.

All size classes between 3 and 7 mm. show a clearly defined relationship to each other in their depth of occurrence. The larger size classes are represented by fewer specimens and, consequently, some results, in the 8 to 10 mm. classes, do not follow the general trends of the graphs. These points have been appropriately marked in fig. 24 to show the number of specimens in each size class which they represent.

The relationship of increasing size of M. norvegica

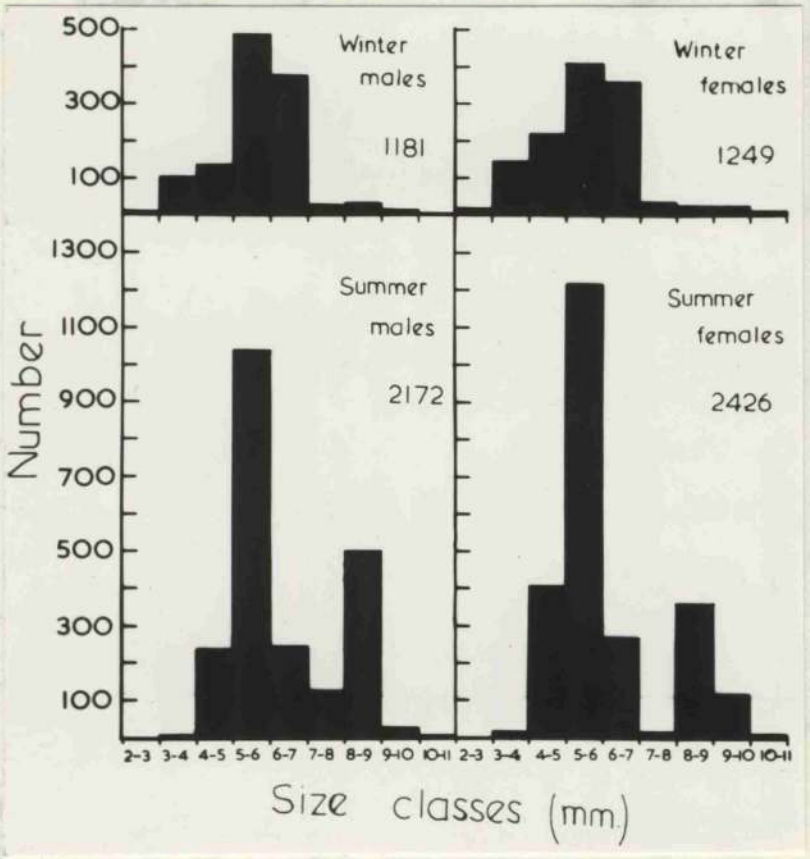


Fig. 25. Histograms of the populations of M. norvegica investigated in November, 1956, and July, 1957.

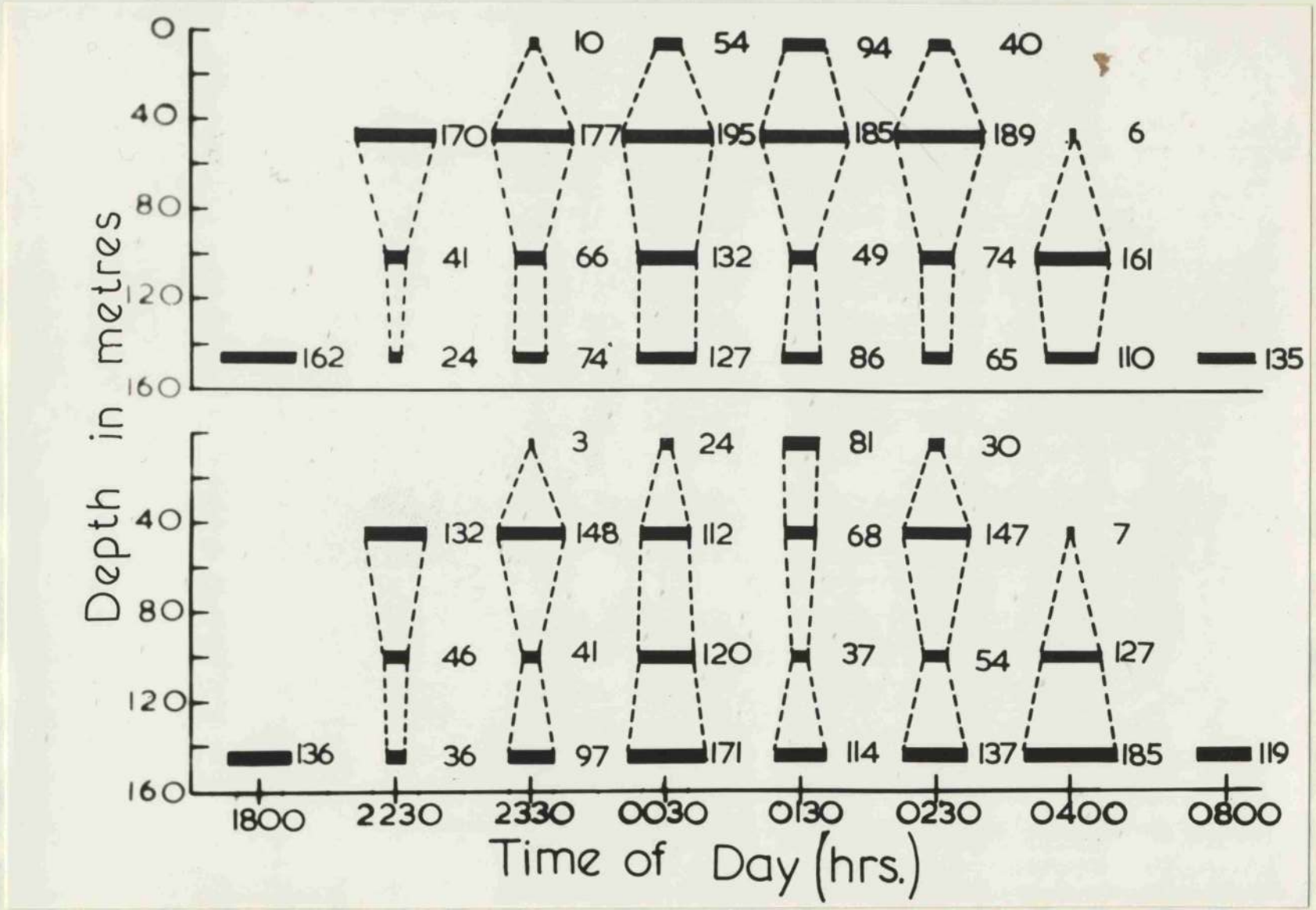


Fig.-266 The vertical migration of M. norvegica on the 22nd and 23rd July, 1957. The numbers refer to the numbers caught at different depths and times. Females, upper graph; males, lower graph.

to increasing depth of occurrence is present even at noon on the 15th when the two lowermost nets caught specimens and the mean depth of occurrence could be calculated. Confirmatory evidence had been gained on various occasions when a net has hit the bottom and caught a larger percentage of larger specimens than any net kept clear of the mud.

There appears to be a tendency in males for smaller size classes to reach their summit of vertical movement earlier in the night than larger size classes but this is not so clear in the case of females.

Summer Analysis.

The vertical migration in the summer is complicated by the fact that the period of darkness available is about one third of that of the winter. The size composition of the population has also altered (fig. 25), the previous winter's 0-group having grown in the spring and early summer to become the I-group without a very great mortality, even through the breeding season. The eggs laid in April-May have given rise to the new 0-group by July.

There was very little difference between the various hauls taken during daylight hours on 22-23rd July, 1957, the population remaining mostly in the bottom 20m. layer.

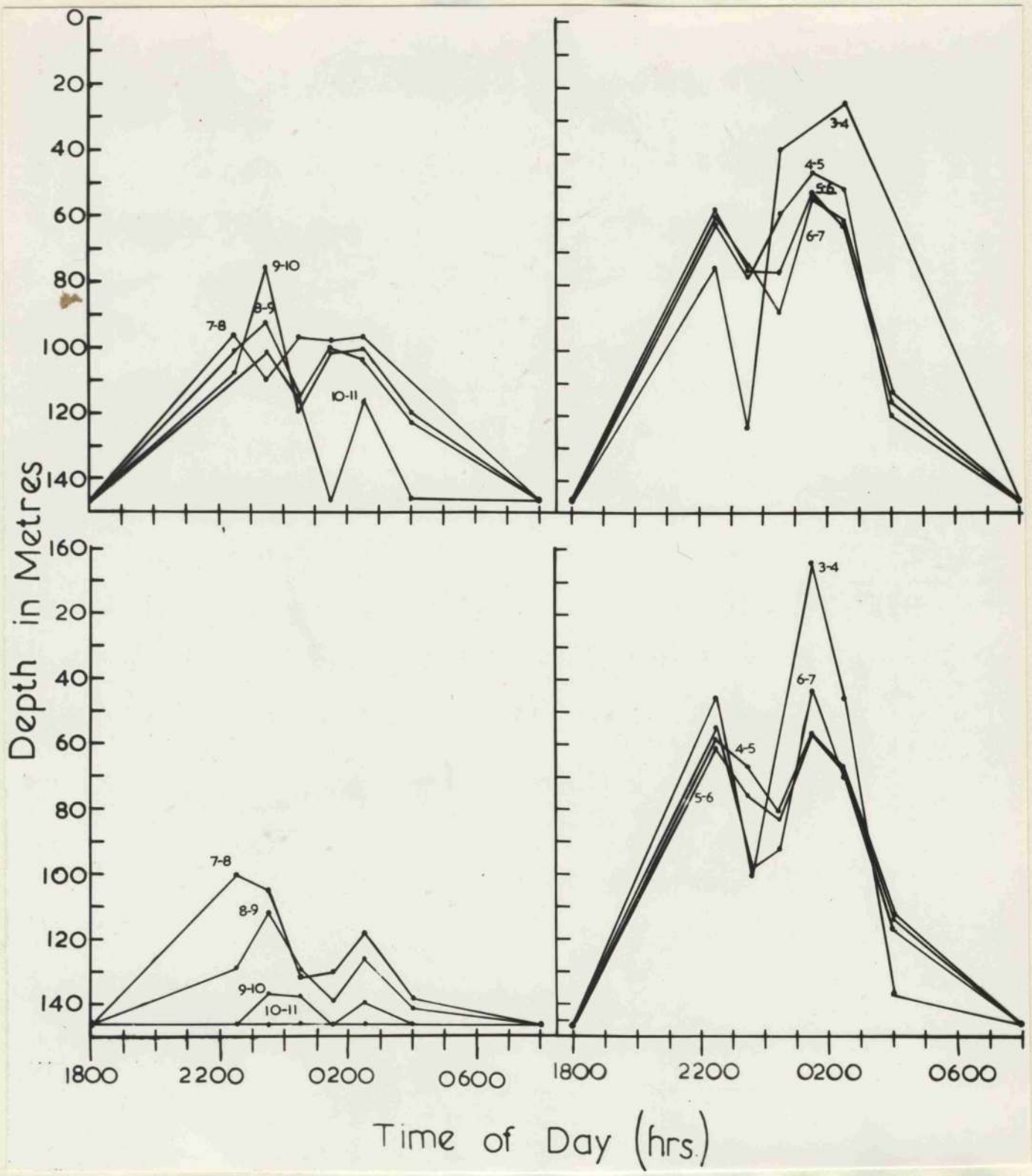


Fig. 27. The vertical layering of the size classes in July, 1957. The numbers associated with the lines refer to the size classes, i.e. 3-4mm. Females, upper graph; males, lower graph.

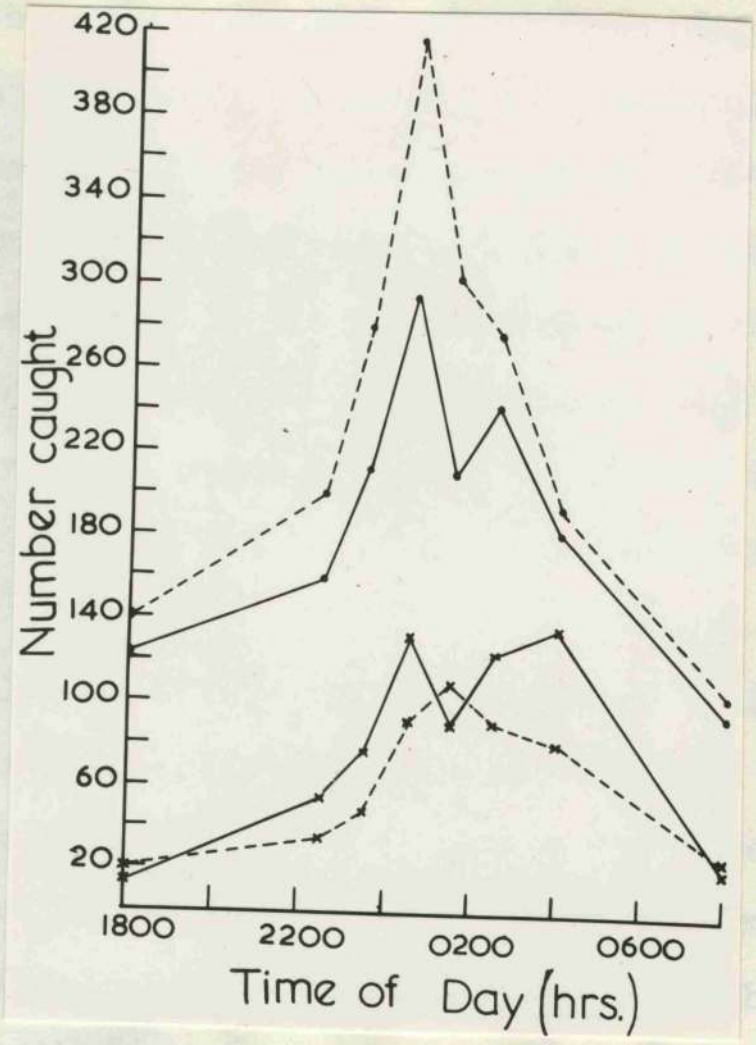


Fig. 28. The total number of M. norvegica caught by the 4 nets at any one time of day on 22nd and 23rd July.

The upper pair of lines are the O-group, the lower the I-group. Females, broken lines; males, solid lines.

Consequently the data presented extend from 1800 hours on the 22nd to 0800 hours on the 23rd. Since the period of darkness was only five hours, hauls were taken every hour from dusk at 2300 hours to dawn at 0400 hours.

The weather was calm throughout the period but at 0300 hours there were clouds in the eastern part of the sky which delayed the onset of daylight so that the 0330 hours haul was delayed and taken at first light at 0400 hours.

The animals had started to move upwards by 2230 hours (fig. 26) while the western sky was still bright with the afterglow of the sun. One hour later a few specimens were at the surface, the number increasing to a maximum at 0130 hours. They started to sink before daylight was apparent and by 0400 hours were absent from the surface layers.

The mean depth of a given size class at a particular time was calculated (fig. 27) and it was found that the 0-group tends to be separated vertically from the I-group.

After the initial ascent at dusk the 0-group classes sink after dark and rise again between 0130 and 0230 hours, to migrate down again at first light. Even if there is a midnight sinking the total numbers caught in the four nets (fig. 28) increases to a maximum at 0030 hours suggesting

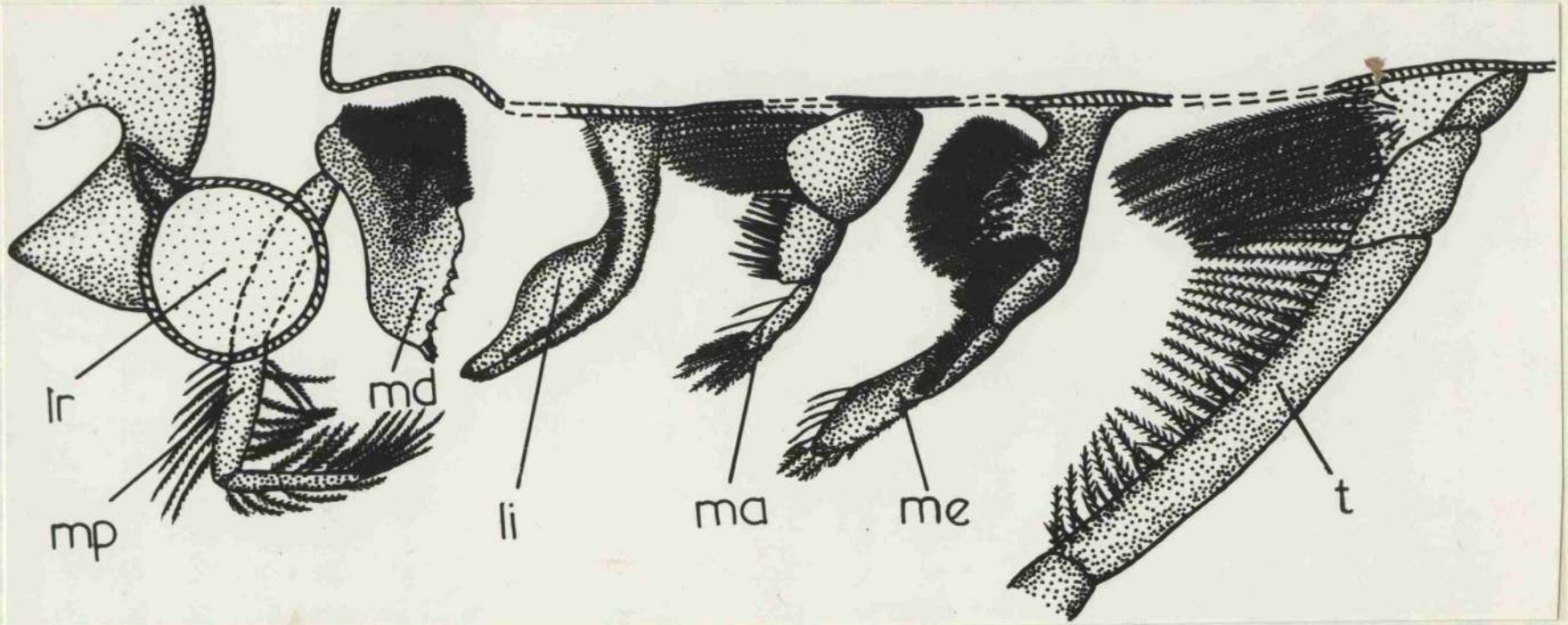


Fig. 29. Diagrammatic drawing of the right-hand mouthparts of M. norvegica to show the distribution of the filtering setae.

li, labium; lr, labrum; ma, maxilla; me. maxillule; md, mandible; mp, mandibular palp; t, fourth endite of 1st thoracic limb.

that those in the bottom 20m. are still migrating upwards. The numbers at the surface drop after 0030 hours but the males rise again at 0230 hours whereas only a slowing down in the sinking of the females takes place. The numbers then revert to the same order of magnitude as found at 1800 hours on the previous day.

In the I-group (fig. 27) the size classes of the males are more clearly distributed vertically than those of the females. The general trend in the I-group would appear to be a rise starting at dusk and continuing until about 2330 hours. A sinking then takes place followed by a further rise by the males, a slowing of the downward movement in the females, before dawn. At first light both sexes migrate downwards.

Feeding Methods.

An investigation of the feeding methods of M. norvegica was made to interpret the results of the stomach content analysis. Cannon and Manton (1929) described M. norvegica as a filter feeder.

Some experiments were done using starch granules coloured with iodine since these tended to stick to the setae through which the feeding streams passed thus enabling their routes to the mouthparts to be traced. Carbon black

VS paste, diluted with sea water, was ejected from very fine pipettes into the water around the animal in order to trace the origin of the water in the feeding currents.

The filtering apparatus is found on the mouthparts and first thoracic limbs (fig. 29). The mouthparts in situ fit closely together so that the setae of the various parts overlap to form a lateral filtering wall and the food-groove between them becomes closed ventrally by the 4th endites (fig. 29, t) of the first thoracic limbs. Food suspended in the water passes through this tunnel and is filtered off by the setae of the mouthparts and first thoracic limbs. The setae of the filtering areas are of three main types:

I, the setules are on two sides of the seta and in one plane, the distance between each setule being about 4 to 5μ.

II, the setules are on different planes on the seta with a distance of about 8μ between any two setules in the same plane.

III, the setae are spine-like with serrated distal edges or a few setules.

The exopodites of the first thoracic limbs of the left side are rotated laterally and vertically in an anticlockwise direction, those on the right in a clockwise

direction. This causes currents of water to flow down the vortex of their movement and pass through the setae on the proximal endites of the thoracic limbs into the medial food-groove. The setae on the proximal segments of the thoracic limbs prevent large particulate matter entering this food-groove. The fine particulate food is carried anteriorly to the mouthparts by the action of the mouthparts themselves. The most posterior elements of the mouthparts move before the anterior ones. Thus the maxillae are moved laterally and posteriorly and are then returned to their original position. Immediately after the maxillae have started to move the maxillules and then the labia follow their movement. The inward part of the movement of the maxillae forces the water laterally between them and the maxillules thus causing the food to be strained off by the filtering setae. The movement of individual parts of these appendages must of course contribute considerably to the production of this current but the main point is that such a current can be produced by the mouthparts.

Excellent figures of these mechanisms have been presented by Cannon and Manton in several papers.

The exopodites of the thoracic limbs were removed from a number of M. norvegica which were then placed in

a starch suspension. Starch was ingested to almost the same extent as by normal animals showing that the mouthparts must be the primary feeding current producers. The exopodites would appear to aid the mouthparts in passing the food anteriorly along the food-groove but probably their main function is to draw water from a greater area than the mouthparts.

The food on the filtering setae of the first pair of thoracic limbs and maxillae is transferred to the spines on the maxillules or directly to either of the rows of hairs on the labia (fig. 29, li). The food which accumulates on the hair-row on the posterior face of a labium is transferred on to the lateral hairs of the other labium by movements of the labia. The mandibular cusps then collect the food and, with the aid of the mandibular palps, labrum and pulsations of the oesophagus, it is macerated and passed into the stomach. The peculiar dentition on the inner dorsal edges of the mandibles (Manton, 1928) appears to comb the fine particulate food from the filtering setae of the proximal regions of the maxillules and maxillae. The posterior face of the labrum has a number of ridges which oppose the dentition on the anterior faces of the mandibles, fine maceration of the food being performed by rubbing it

between them.

M. norvegica was observed to stir up mud by the action of its pleopods from the bottom of laboratory tanks and to feed on the resulting suspension by the filtering method described above. There is evidence that this is also done in the sea. Cannon and Manton (1927) have described an identical feeding mechanism in the mysid, Hemimysis lamornae.

Raptatory methods of feeding, as defined by Cannon Manton (1929), are also employed. When large particles of organic detritus are available M. norvegica will often swim about pushing a mass of material collected between the thoracic limbs and antennae. This material is brought to the mouthparts by sudden lateral-ventral movements of the thoracic limbs which cause it to be drawn into the "food-basket" formed between them and the mouthparts.

These methods of feeding have been noticed in animals of all size classes. One further method, however, has only been seen performed in animals of the larger size classes. They can produce a strong enough "inhalent current" by the lateral-ventral movements of the thoracic limbs to draw living prey into the food-basket. Live Euchaeta norvegica and Sagitta spp. have been secured in this way but no hunting or stalking of prey takes place.

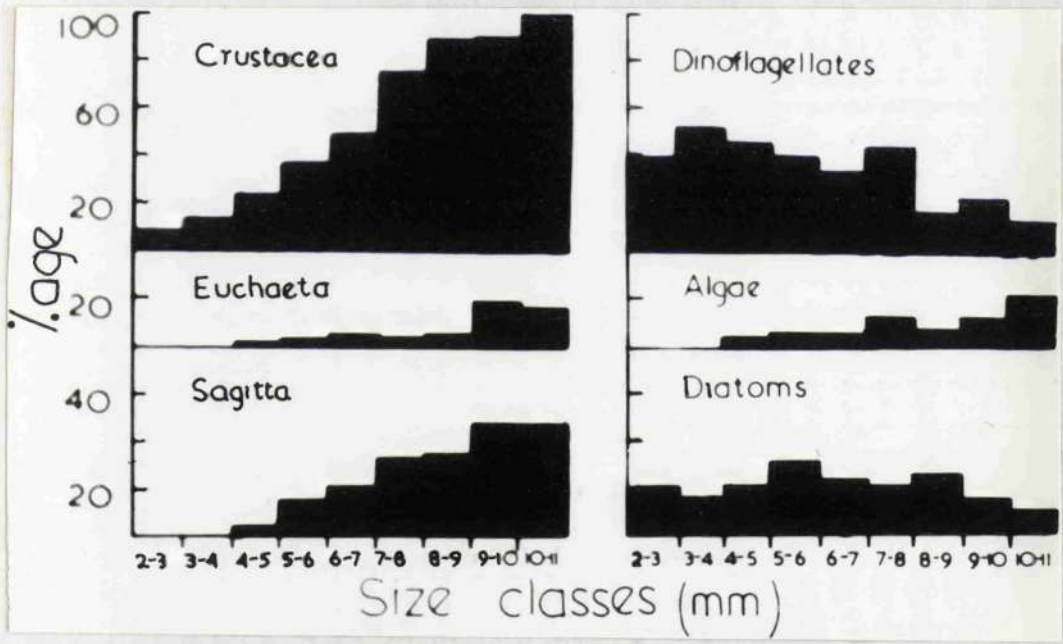


Fig. 30. The percentage of each size class of M. norvegica with a particular food present among the stomach contents.

If a large M. norvegica comes in contact with a Euchaeta or Sagitta which is not moving then it can draw it into the food-basket but no M. norvegica have been seen to catch actively swimming prey of these dimensions.

Ponomareva (1954) describes the method used by euphausids to eat out, with the mandibles, the soft parts of copepod bodies. No account, however, of the method by which these copepods are caught is given.

Stomach Contents.

The percentage of animals of a given size class with crustacean remains, other than Euchaeta norvegica, present in their stomachs was calculated (fig. 30). A continual increase in their occurrence with increasing size of M. norvegica is apparent, the greatest single increase being at the transitional class, 7-8 mm. which is predominantly I-group animals.

The mandibles ground the crustacea into such small pieces that identification was difficult. The percentage occurrence, however, of recognisable Euchaeta norvegica remains (fig. 30) is correlated with increasing size of M. norvegica and it is found to form an appreciable part of the diet of the larger animals.

Similarly, increasing occurrence of remains of

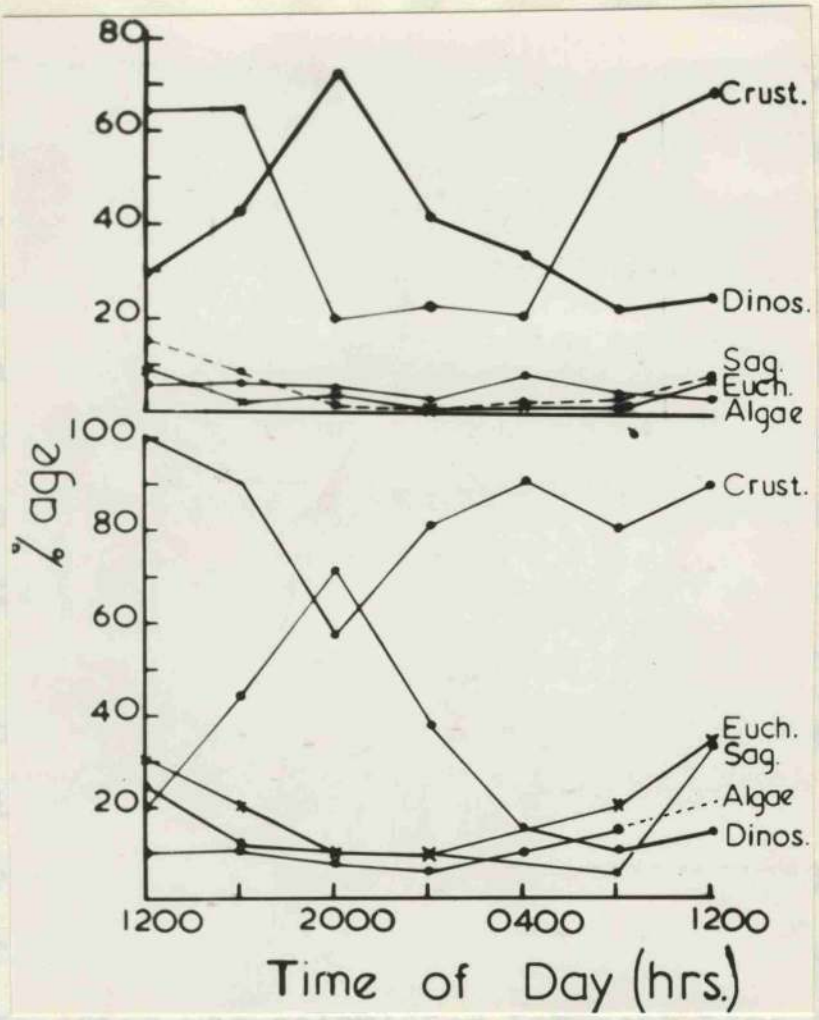


Fig. 31. The percentage of 0-group (upper graph) and I-group (lower graph) M. norvegica with a certain food present in their stomachs at a given time of day.

Sagitta spp. (fig. 30) and filamentous algae (fig. 30) is related to increasing size of the feeding animals.

A reverse correlation to those above exists for dinoflagellates (fig. 30) where the average number of specimens was 10 to 15 in each stomach whereas diatoms only occurred in ones and twos. It is noticeable that the presence of diatoms is not correlated with the size of M. norvegica (fig. 30). Though they do not form a significant part of the diet, they are presented here, along with the dinoflagellates, as an index of the amount of filter feeding done by the various size classes.

The percentages of 0-group and I-group animals with crustacean remains, Euchaeta, Sagitta, filamentous algae and dinoflagellates was calculated for each time of day (fig. 31). The stomach functions primarily as a gizzard so that the food rarely remains in it for as long as four hours, the period between successive hauls in this analysis. In the 0-group there is a drop in the percentage with crustacean remains, Euchaeta and Sagitta present in their stomachs throughout the period of darkness when the 0-group has migrated towards the surface. A similar drop in percentage is present in the I-group (fig. 31) but during the mid-darkness period a rise in the percentage consuming Crustacea is apparent followed by a drop which may coincide

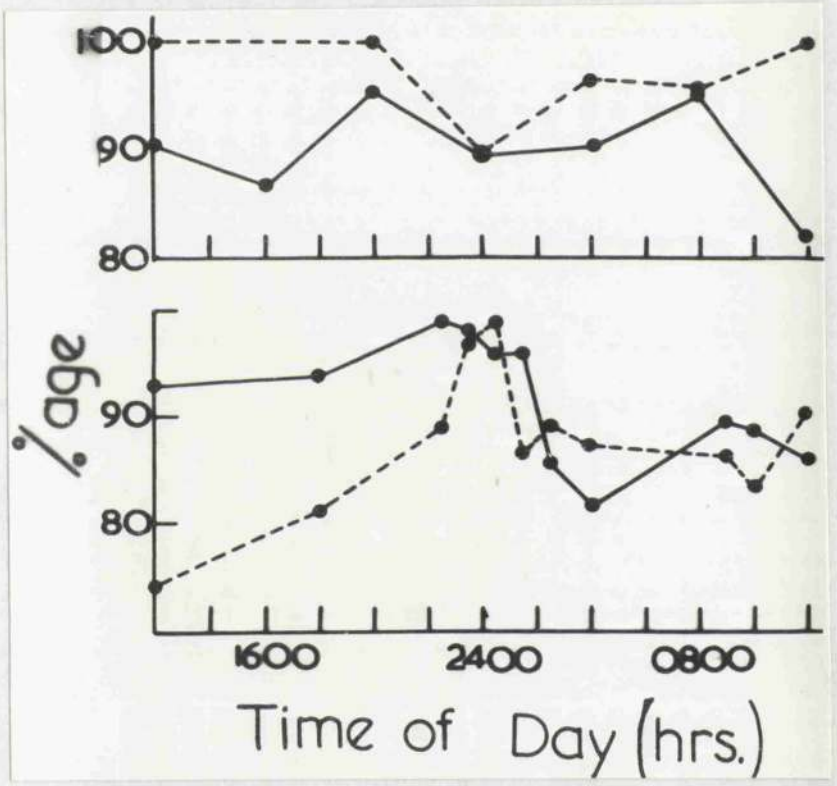


Fig. 32. The percentage of 0-group (solid lines) and I-group (broken lines) M. norvegica with food present in their stomachs at a given time of day during winter (upper graph) and summer (lower graph).

with the dawn-rise of M. norvegica.

The incidence of filamentous algae consumed by 0- and I-group animals (fig. 31) remains fairly constant throughout the 24 hours, none of the fluctuations in percentages being significant.

An investigation of the percentages of 0- and I-group animals with food in their stomachs at a given time of day (fig. 32) showed an increase at night for the 0-group specimens. The initial increase coincides with the upward dusk migration between 1600 and 2000 hours. The percentage then drops slightly but remains at a high level throughout the hours of darkness, a secondary increase coinciding with the dawn-rise and downward migration. The stomach contents comprised mostly of a "green mush" of small particle size which seems to be synonomous with Macdonald's "flocculent detritus".

In the I-group M. norvegica decrease in feeding is evident at night. This lasts until the animals are back in the bottom layers at 0800 hours.

The greater part by volume of the stomach contents of about 60% of the M. norvegica examined comprised organic detritus with mud particles. Since filamentous algae, parts of small polychaetes and crustacean remains were often

associated with the mud it was decided to examine the surface layers of mud in the deeps where M. norvegica lived. A Jenkin's mud sampler, which samples a core of about 9 sq. ins. was used because with it an undisturbed core, with the water above it, could be obtained.

Filamentous algae, including a Cladophora sp. of littoral origin, were found living though not attached and growing at that depth (175 m.). All the species of algae found in the mud had already been identified in the stomachs of M. norvegica.

As regards diatoms only 4 cells of a Biddulphia sp. were found in the eight samples taken. Ciliates were plentiful and what is thought to be their remains have been occasionally identified in the stomachs. Small polychaetes averaged two and isopods three per sample. Various cumacids were present at a density of 1-2 per sq. in. of mud surface, but their remains, though probably present, have never been recognised in the stomachs. The molluscs and brittle-stars found in the mud have not been noted in the stomachs, and they may be too hard to be eaten.

Ponomareva (1955) identified parts of compound eyes in the stomach contents of three of the species of

euphausids she examined and remarks that no previous mention of them has been made except possibly by Einarsson (1945) who described a "reddish-brown substance" which Ponomareva thinks may be derived from ingested compound eyes. The present author thinks this identification may be correct as entire or parts of compound eyes have been identified in the stomachs of M. norvegica in the present investigation (Table 6).

Table 6.

	Size Classes							
No. of specimens with	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10
Eyes present	1(?)			7	4	2	3	2
Eyes absent	17	65	147	444	457	93	58	20
% age with eyes	3.5	0	0	1.6	1.0	2.0	5.0	9.0

There was a very little reddish-brown material, which might have originated from a compound eye, present in the stomach of one specimen on the 2-3 mm. class; no crystalline cones were present to confirm the identification. If this specimen were omitted there would be a correlation of presence of compound eyes with increasing size of M. norvegica which would be expected if they were obtained by predatory methods. As Ponomareva

has remarked, specimens with one eye missing or damaged eyes are not uncommon but this may partly be caused by the net. The fact that they are thought to be euphausid eyes may not be very significant as the cuticle of euphausid eyes tends to be softer than that of other crustaceans of similar size and thus may be more easily ingested. It has been suggested that the eyes are attacked when the photophore in the eye stalk luminesces but no evidence to support this has been found.

Discussion.

Vertical Migration.

In the winter the regularity of the spatial inter-relationships (fig. 24) of the size classes, especially those between 3 and 7 mm., throughout the upward and downward migrations would suggest control by some discrete factor or factors. If the speed of swimming, combined with specific gravity, were acting to produce this distribution then the layering in the midnight period would not be so regular. The factors controlling it would seem to be physical properties of the environment rather than the distribution of food organisms or other biological properties. The work of Harris and Mason (1956) suggests that light intensity is the most important

factor involved.

The temperature in Loch Fyne from surface to bottom was almost uniform in the winter, the difference being 0.6°C on 14th November, 1956. Therefore temperature gradient would have no effect. The vertical variations in salinity would also be ineffective at this time of year.

Various observations have been made in the winter on the effect of differing weather conditions on the uppermost day-level of M. norvegica. The effect of the bright sun on this level at noon on the 14th can be compared with the higher level at noon on 15th November (fig. 22) when the sky was heavily overcast. In all the observations made, when the light intensity decreased the animals rose upwards but if the sun brightened then almost immediately they sank lower.

At sunrise, animals in the surface layers of the sea will be affected by the increasing light intensity slightly before animals in the mid-water regions with the result that the surface specimens start their downward migration first. The light intensity continues to increase and progressively deeper animals commence to move down so that there will tend to be a vertical layer of greater density of M. norvegica associated with the

deepening isolume layers. It is suggested that the nets sampled this layer at 0800 hours on 15th November.

It is difficult to confirm this hypothesis without data on the isolumes but repetition of this post-dawn haul suggests that there does seem to be a much denser layer of M. norvegica present in the sea and that this layer is sinking and finally disperses when it reaches the deep water layers.

Another phenomenon which is difficult to demonstrate is an upward movement of the population just prior to dawn. This dawn rise is not apparent in fig. 22 as the samples were too far apart in time but if a haul is taken at first light then more animals are found in the surface layers than in the mid-darkness period. This is a fairly common phenomenon (Cushing, 1951) and has been shown for Euphausia pacifica and Nyctiphanes simplex by Esterly (see Cushing, 1951) and possibly for Stylocheiron carinatum (Lewis, 1954).

The vertical interrelationships of the size classes are not so regular in the summer but they exist. The separation vertically, however, of the two age groups is more clearly defined. In the summer (fig. 25) there is a clearer separation on a size/frequency graph of the 0- and I-group than in the winter and thus if more overlap

in size of the two groups were present this vertical separation might not exist. But conversely the 0-group classes are much more intermixed and close together vertically in the summer (fig. 27) and so the age as well as size would seem to be involved.

In all the summer observations on the effect of weather conditions on M. norvegica light again seems to be the main factor controlling vertical movements.

A surface net caught three specimens at the surface on 12th September, 1957, when an almost full moon was and had been continually clear of cloud. On dark nights at this time of year 60 to 80 specimens were caught in a comparable haul at the surface. This has been observed several times and in every case the moon-light caused them to sink lower. Fisher et al (1953) caught M. norvegica in the port of Monaco during the night by using light lures and hand-nets. Why they should be attracted to a light lure is not known.

The direct influence of light intensity on vertical movements of M. norvegica is very apparent in both summer and winter but the mechanism whereby the size classes are distributed vertically in unknown. Various authors have shown a vertical layering of size classes in copepods (Cushing, 1951) and Ponomareva (1955) remarks that the

largest size classes of the euphausid Thysanoessa longipes have a reduced vertical migration never rising above 100 m. depth. It would seem that the optimum light intensity for some planktonic Crustacea decreases as they grow older and increase in size.

One consequence of a vertical layering of size classes is apparent at the breeding season when spermatophores are transferred from males to females. The population of M. norvegica has a wide range in size, the smallest mature animals being about one third the total length of the largest. It is not known whether large males and small females are compatible, or vice versa. The spermatophore of a specimen with a carapace length of 10 mm. contains about 12 times as many spermatozoa as that of an animal with a carapace length of 5 mm. and, since spermatophores are transferred in pairs, a large male produces about 24 times as many spermatozoa as a small one. A large female of comparable size produces about 12 times as many eggs as a smaller one. Hence the most efficient system of spermatophore transference would be between males and females of like sizes. This can take place because of the vertical layering of size classes present at night in the winter when mating takes place. A few females have been found with the spermatophores still full of spermatozoa

and it is probable from the measurements of the spermatophores that they originated from males of similar size.

Females M. norvegica about to lay eggs do not conform with the described pattern of vertical migration. The eggs are laid in the surface layers and, though egg extrusion is mainly at night, a few gravid females have been caught at the surface during daylight. No other M. norvegica have been caught at the surface in daylight and no surface swarming has been observed by the author. An account of the known instances of surface swarming by M. norvegica is given by Fisher et al (1953).

Feeding Methods.

M. norvegica can feed by three methods. They can a) strain off the food particles suspended in the sea water, b) stir up the mud and detritus on the sea bottom and filter the resulting suspension or c) use a raptorial technique (Cannon and Manton, 1929). The first method can be used at any depth, the second on or near the bottom and the third mostly on the bottom. Larger animals, however, can feed on live prey at any depth.

Vertical Migration, Food and Feeding Methods.

It is impossible to estimate with accuracy the amounts of organic detritus and nannoplankton eaten by M. norvegica as almost every animal has some present in its stomach at all times of the day. In the stomachs of small specimens some mud particles, vegetable detritus and a green mush, thought to be synonomous to Macdonald's 'flocculent detritus', often occur together. The relative proportions of these materials differ in different size classes and it is noticeable that larger animals have a higher proportion of mud particles and vegetable material present with the green mush than the smaller ones.

A considerable amount of vegetable detritus of land and littoral origin is found in suspension in the waters of Loch Fyne. It is, therefore, concluded that the larger animals obtain the vegetable material mostly from the sea floor while the smaller animals acquire it pelagically.

Since filamentous algae, reds and greens, occurred, in a fresh state, in the stomachs of larger specimens with mud it was thought that they must be obtained from the bottom and the mud samples proved this to be possible.

The 0-group, however, ingest them at night (fig. 31) in the upper water layers while filter feeding.

Crustacea, Euchaeta and Sagitta are found more often in the stomachs of larger than of smaller M. norvegica and the former occur deeper in the sea than the latter. Fewer specimens have these remains in their stomachs at night than during the day.

From the above evidence it is concluded that remains of Crustacea, Euchaeta and Sagitta in the stomachs originate from the bottom water layers.

These zooplankton organisms can only be fed on by raptatory methods owing to their relatively large size.

A reverse correlation (fig. 30) with size of M. norvegica exists for dinoflagellates which are fed on more frequently at night (fig. 31). Thus it is evident that they are acquired in the upper water layers by filter feeding methods, green mush being associated with them in the stomachs.

Diatoms did not occur in the stomachs in sufficient numbers to justify conclusions about their origin. Possibly they are obtained in the deeper water layers, frustules of the larger diatoms (Coscinodiscus spp., Biddulphia spp.) being present more often in the stomachs of larger M. norvegica.

Thus during the day the smallest M. norvegica which feed predominantly on green mush and detritus, must employ primarily filter feeding and secondarily raptatory mechanisms. The middle size classes feeding on detritus, green mush and some zooplankton must rely to about the same extent on the two mechanisms. The larger animals ingesting mostly organic detritus and zooplankton must be predominantly raptatorial. During the night, however, the dominant method of feeding is filtratory, the raptatory method possibly being used to some extent in the deeper water layers.

In several species of copepods, including Calanus finmarchicus, large specimens are found deeper than smaller ones. C. finmarchicus has been shown to feed mainly on diatoms and protista (Marshall and Orr, 1955). An increase in the percentage of C. finmarchicus feeding takes place at night in the winter (Marshall, 1923) but in the spring and summer the percentage feeding remains at a constant high level throughout the day and night.

The present author has examined the gut contents of a few C. finmarchicus caught at 150 m. depth in the Clyde and found that up to 20% by volume of the stomach contents was composed of grit and what looks like vegetable detritus. Their gut contents were very similar to those

of 0-group M. norvegica caught during the day at this depth except that diatoms were present in the stomach of C. finmarchicus in appreciable numbers.

The above comments suggest that the same relationships between vertical migration, size and food may exist in the case of C. finmarchicus and possibly to some extent in all predominantly filter feeding planktonic animals which perform a vertical migration taking them below the main layers of photosynthesis in the sea.

VII. The Significance of Carapace Measurements.

Measurements of carapace length are now considered preferable to measurements of total length in prawns and shrimps. The total length, that is the distance between the tip of the rostrum and the end of the telson, is difficult to measure accurately owing to the rostrum often being damaged and the abdomen flexed. Recent authors (e.g. Horsted and Smidt, 1956; Mistakidis, 1957) have measured carapace length (in Pandalus spp.) in different ways but the relationship of the carapace measurements to total length is usually stated.

Macdonald (1927a) and Einarsson (1945) measured the distance between the tip of the rostrum and the end of the telson in M. norvegica while Ruud (1936), using Mediterranean specimens, measured the distance from the centre of the eye to the posterior margin of the 6th abdominal joint. Ruud gives the relationship of total length to this measurement as 1.2 which agrees closely with the value found in this investigation, namely 1.23.

It was decided to adopt carapace length, from the base of the eye notch to the posterior dorsal median edge of the carapace, as a measurement of the size of the animals throughout the course of investigations of the

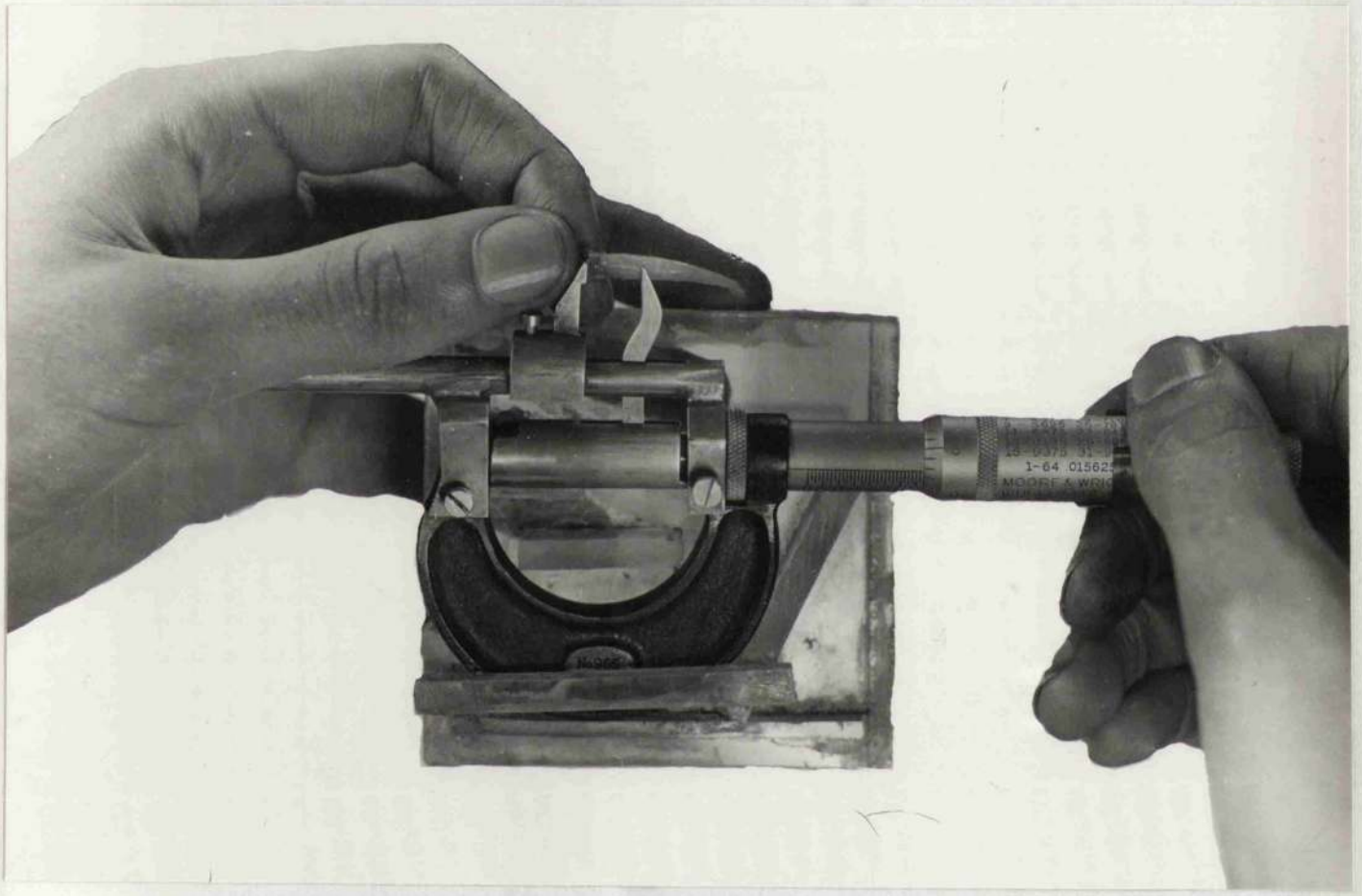


Fig. 33. A M. norvegica being measured with the modified screw micrometer.

biology of M. norvegica and consequently it was necessary to discover the relationship of total length to carapace length. The carapace length did not bear a constant relation to the lengths of other parts of the body, such as the abdomen and telson, and it was desirable, therefore, to discover by how much and when it varied.

Fresh M. norvegica were used and the measurements compared, in a number of cases, with those made on specimens preserved in 10% formalin in sea water. It was found that if the animals were measured within two weeks of preservation no significant difference occurred.

Measurements of carapace length were made with an ordinary screw micrometer (Mauchline, 1958a) which was modified (fig. 33) so that measurements could be made between two jaws, one fixed and one floating. The fixed jaw is independent of the fixed micrometer anvil and its position, relative to the floating jaw, can be altered to allow a wide range of measurements to be made. The measurements were made with an accuracy of 0.1 mm.

Total, telson and abdomen lengths were measured with an accuracy varying from 1.0 to 0.5 mm. using a Beck Vernier measuring microscope.

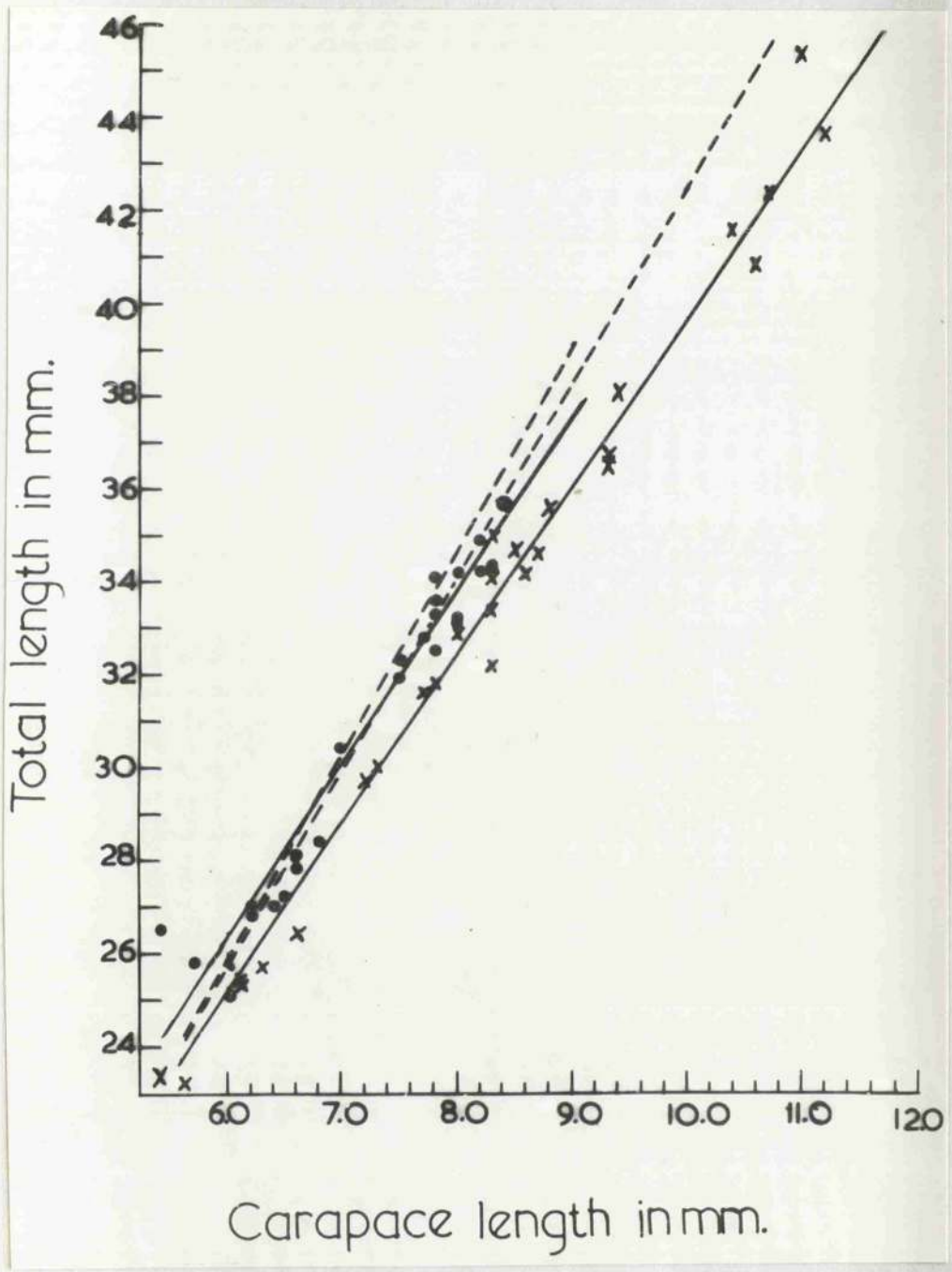


Fig. 34. The relationship of total length to carapace length in M. norvegica.

Males, short lines; females, long lines; immature, broken lines; mature, solid lines.

• mature males; × mature females.

Results.

The carapace length, from the base of the eye notch to the posterior dorsal median edge of the carapace, and the total length, from the base of the eye notch to the end of the telson, of 190 males and 221 females caught in October, when the gonads were immature, were measured. The ratio of total length to carapace length varied from 4.03 to 4.87 in males and from 3.87 to 4.58 in females. The mean ratio in males and females was 4.33 and 4.27 respectively; these were usually found to provide a sufficiently accurate means of deriving total length from carapace length measurements. When the regression lines were calculated (fig. 34) it was found that males tended to have a slightly greater total length than females of the same carapace length but the difference is not very significant owing to the amount of scatter. It is also made less significant from a practical point of view because very few males with a carapace length greater than 9.0 mm. occur.

The abdomen and telson of 27 specimens of each sex, caught in March when the gonads were mature, were measured and the results graphed against carapace length (fig. 35, 36). Males were found to have larger abdomens

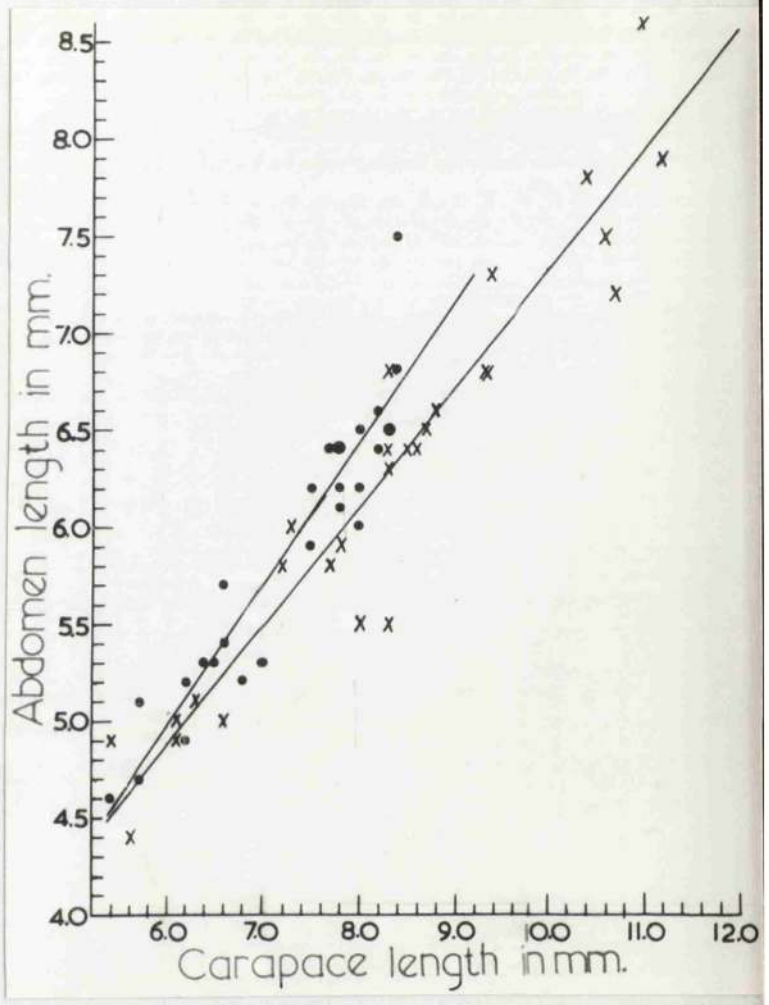


Fig. 35. The relationship of abdomen length to carapace length in mature M. norvegica.

Males, short, females, long line.

• males; × females.

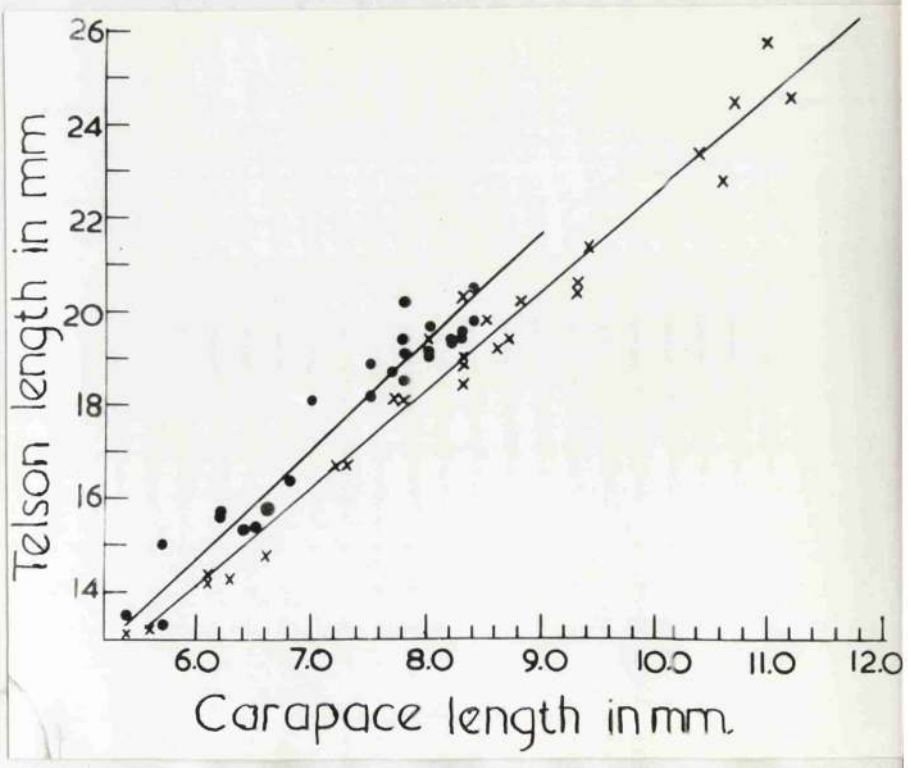


Fig. 36. The relationship of telson length to carapace length in mature M. norvegica

Males, short line; females, long line.

• males.

× females.

and telsons than females of corresponding carapace length. There is much more scatter in the measurements of telson length than in those of abdomen length even though only animals in good condition were selected for these investigations. The relationship of total length to carapace length varied from 4.12 to 4.91 in males and from 3.86 to 4.33 in females. The mean ratios in males and females were 4.27 and 4.05 respectively. The regression lines for these relationships are shown beside those for October in fig. 34. The length of the carapace in both sexes has increased relatively to the total length as the gonads matured but the increase is much greater in the females than in the males. Why the male carapace should tend to swell at all is not known as there is no corresponding swelling of the male gonads.

This change in the total length/carapace length relationship has been confirmed while investigating the growth rates of males and females. During the period January to June, when the gonads are maturing or mature, the difference between the mean carapace length of males and females within a sample tends to be slightly greater than at other times. In the 0-group, the male carapace does not change its proportions significantly, though there is a tendency for it to swell slightly; this is not

shown in fig. 34 owing to the line being skewed round to accommodate an errant measurement (at total length, 26.5). The carapace length of 0-group females increases in length by about 5%.

The carapace length of the I-group males and females increase by about 2.5 and 6% respectively but since the mean length of the I-group females is often higher than that of the males the mean increase is often as high as 8%.

This increase takes place before the diatom and general productivity increases of the sea area, as the eggs are laid during the diatom increase. Hence the estimate of the time of onset of the spring growth of M. norvegica may be too early, in the case of females, owing tb the swelling of the carapace being mistaken for growth in length.

Conclusions.

Carapace length, from the base of the eye notch to the posterior dorsal median edge of the carapace, is a good estimate of body length in both sexes when the animals are not mature. The relationship is almost the same in males and females though there is a tendency, not statistically significant, for the males to have a slightly

greater body length per unit carapace length. During the breeding season, however, carapace length, on average, over-estimates total length by about 1.5% in males and by about 4.2% in females, the error becoming greater in larger animals. The carapaces are swollen in males from January to July and in females from February or March to July.

The following regression equations were calculated:

Total length (L) on Carapace length (C):

Immature animals.

Males ..... L 4.44C - 0.74

Females ..... L 4.18C + 0.74

Mature animals.

Males ..... L 3.72C + 4.09

Females ..... L 3.61C + 3.60

Distance between base of eye notch to base of telson (L) on carapace length (C):

Immature animals.

Males ..... L 3.94C - 2.30

Females ..... L 3.53C - 0.05

Mature animals.

Males ..... L 3.21C + 1.60

Females ..... L 3.11C + 1.44

VIII. Growth, Maturity and Mortality.

The life cycles of euphausids are difficult to determine owing to the usual necessity of sampling oceanic areas where there is no guarantee that the same population is in the same area all the time. Bargmann (1945) has presented extensive data on the life history of Euphausia superba, whose breeding season she found to extend over 5½ months, the resulting males and females maturing 22 and 25 months later respectively. She was unable to determine whether they survived their first breeding season.

The life histories of the northern Atlantic species have been described by Einarsson (1945). He found that Thysanopoda acutifrons matured at the end of its second year but did not think it survived much later than the breeding season. Thysanoessa longicaudata, in the Gulf Stream areas of the north Atlantic, matures at the end of one year and dies after breeding; off Greenland, however, it survives its second summer and breeds again the following spring. T. inermis and T. raschii have similar life histories, neither maturing in northern waters until the end of their second year. They may breed twice after this, reaching an age of 3 years and,

according to Einarsson, possibly more. In southern waters these species mature at the age of one year and spawn again the next summer at the age of 2 years.

Poulsen (1926), examining samples of M. norvegica from Skagerrak, found two size groups in May: they ranged in size (total length) from 22 to 31 mm. and from 27 to 35 mm. respectively. The former group was always present in larger numbers than the latter which he considered to be one year older.

The growth rate and duration of life of M. norvegica in the Mediterranean, Cadiz Bay and the Bay of Biscay were investigated by Ruud (1936). He concluded that the animals matured at one year old, increased in size between the breeding season and the following winter, and possibly bred for a second time the following spring.

Einarsson (1945) confirmed Poulsen's results and suggested that the second time spawners (I-group) are normally more prominent in the population than Poulsen found. The 0-group animals had attained a length of about 25 mm. by their first breeding season, grew to about 30 mm. in their second summer season and bred again the following spring.

The present investigation was made in the Clyde Sea

area which is ideal for such studies. M. norvegica is distributed in the deep troughs (next chapter) which are narrow and consequently relatively easy to sample efficiently. Furthermore the mouth of the Firth of Clyde is closed by an extensive submarine "plateau", of average depth about 50m., and since there are no known dense populations of M. norvegica immediately beyond this plateau, the number of animals joining the Clyde population from other areas is likely to be negligible. The plateau region has been sampled, with negative results, for adults and larvae during in- and out-going tides in the breeding season.

Though there are several distinct sub-populations of M. norvegica within the Clyde at certain times of the year (next chapter), the growth rates in these are almost identical so that samples taken at the same time in several different areas have been lumped together after preliminary analyses.

The populations were sampled as often as possible using 2 m. and 1 m. stramin nets. It was suggested that M. norvegica, owing to its large size and agility, could escape from these nets during the day and so several tests were made. The ship steamed at three speeds over a course fixed by landmarks. Tows were thus of equal

distance and, to combat discrepancies caused by currents, the nets were towed an equal number of times at the same speed up and then down L. Fyne. The slowest and medium speeds (ca. 2½ and ca. 4 knots respectively) produced very similar results but the sample taken at the fastest speed (ca. 5½ knots) contained twice as many specimens over 35 mm. total length; little difference was found in the numbers of specimens smaller than this. It was concluded, therefore, that except for these larger size classes, which are a minority group of the population, the speed of towing did not matter and so the net was constantly towed at about 4 knots.

The samples were preserved on board ship in 10% formalin in sea water and brought back to the laboratory where the sex of each individual was determined and its carapace length measured. A sample of 150 M. norvegica was measured before and at intervals after preservation in formalin. After 10 days of preservation the mean carapace length only varied by 0.036 mm. from the result obtained from the specimens when fresh, and this is ascribed to errors of measurement. After this the carapaces of individuals within the sample tended to change their proportions and errors of up to 0.2 mm. appeared. All samples, therefore, were measured within

a week of preservation whenever possible.

Wet weight was estimated by trying to partially dry the cuticle and limbs in as constant a manner as possible and then weighing the animals in previously weighed weighing bottles. The bottles with the animals were transferred to an oven at 90°C and kept at this temperature for 4 hours. They were then taken from the oven and cooled in a dessicator before reweighing.

All measurements are given as carapace length, from the base of the eye notch to the posterior median dorsal edge of the carapace, and the corresponding total lengths shown in brackets.

Results.

Egg laying begins in the Clyde sea area at the end of March or beginning of April, the time varying from year to year. Macdonald (1927a) records eggs present in the plankton in the first week of March, 1926 while in 1927 they were not evident until May. Townet and stramin net samples taken in April comprise eggs, nauplii, calyptopis and early furcilia stages, in that order of abundance, as well as the previous winter's 0- and I-groups of adults. By the middle of May, the I-group (now

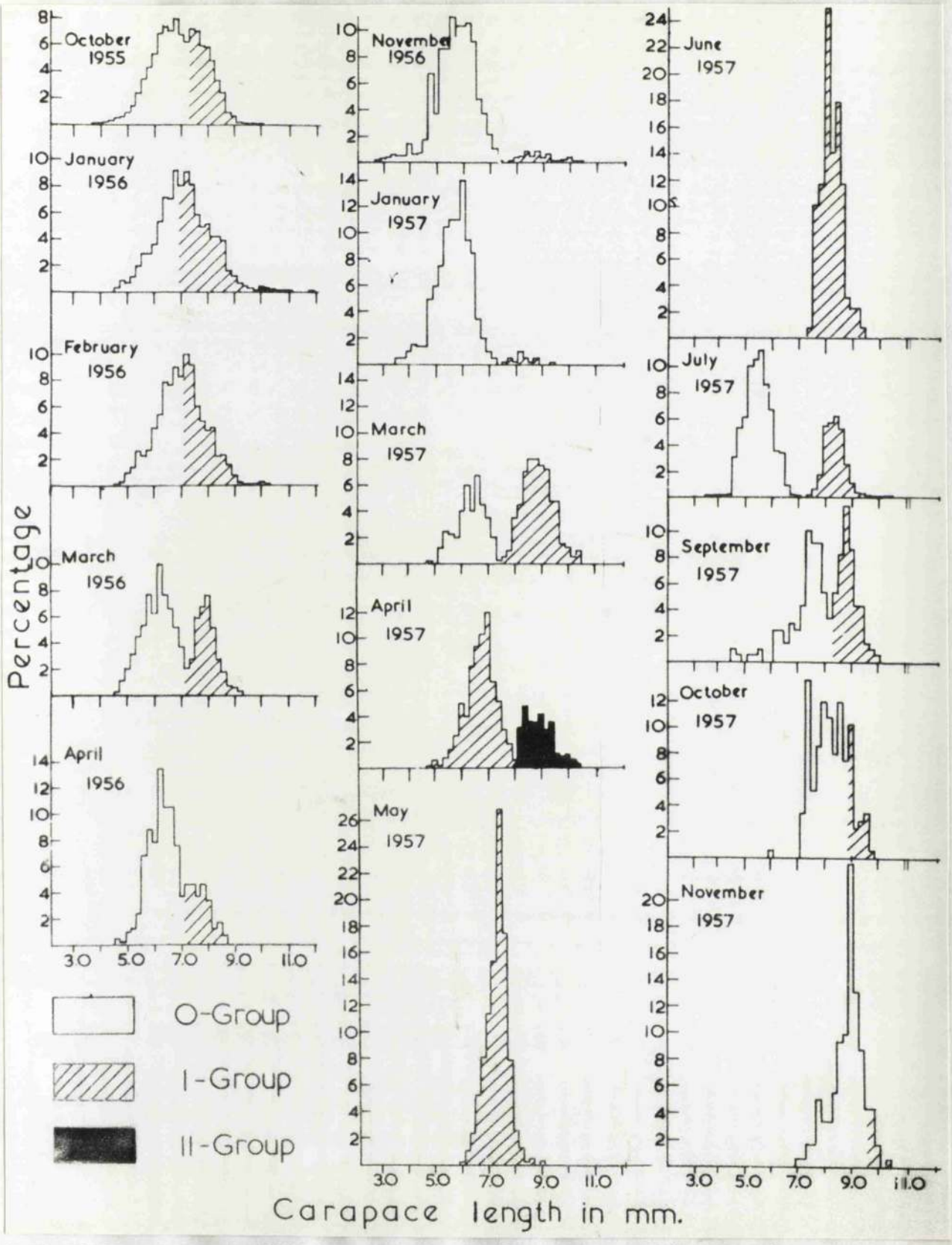


Fig. 37, A. Histograms of the populations of male M. norvegica present in the Clyde sea area from October, 1955 to November, 1957.

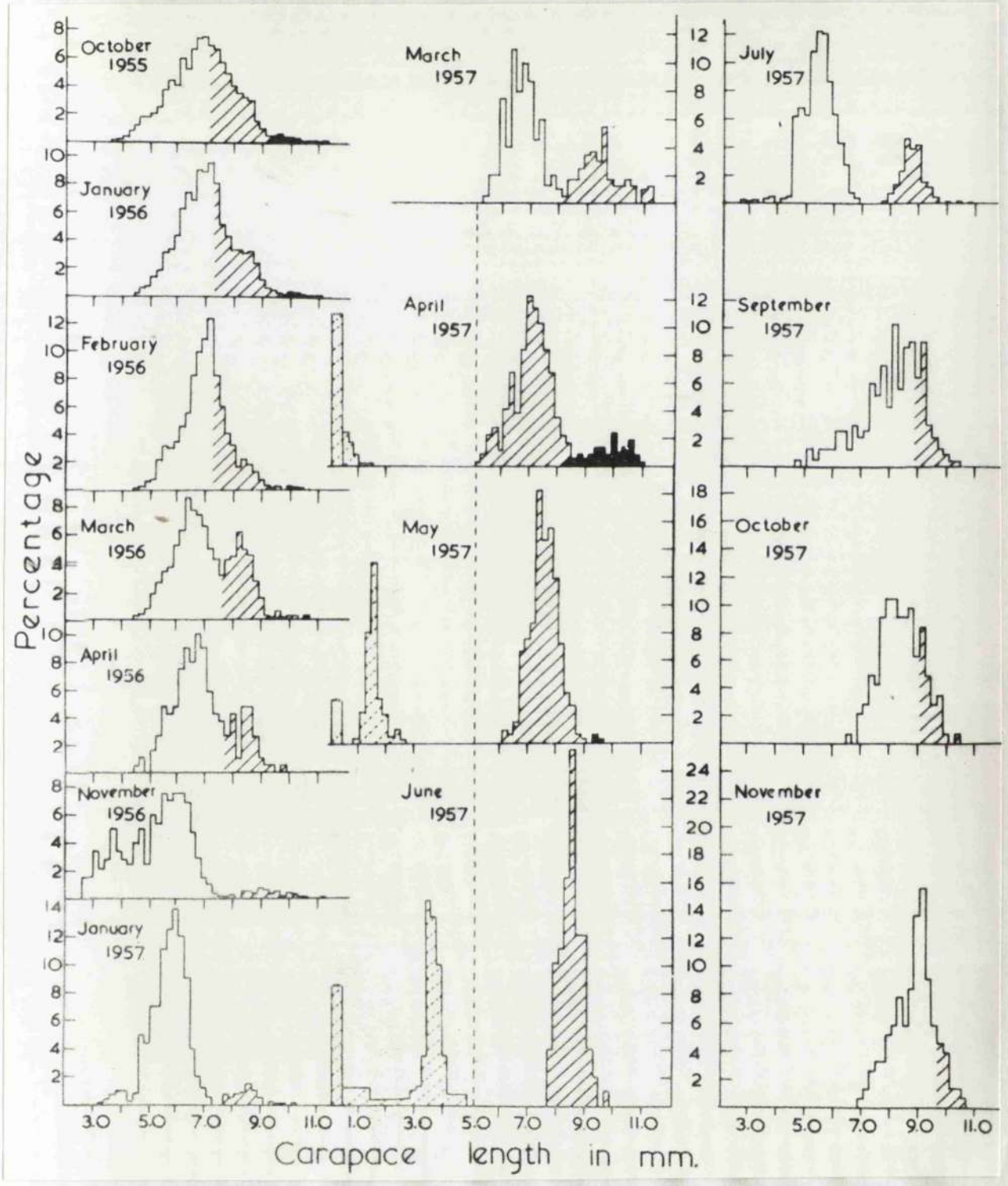


Fig. 37, B. Populations of female M. norvegica present in the Clyde sea area from October, 1955 to November, 1957. The dotted histograms to the right of the vertical broken line are of larvae and adolescents in April to June, 1957.

II-group) has declined considerably in numbers while increased numbers of furcilia larvae, now mostly 3rd and 4th stage, are present; eggs and nauplii are now scarce.

The eggs develop quickly, taking about 3 days from the time of laying for nauplii to hatch out. The duration of each of the two nauplius and one metanauplius stage is thought to be 2-3 days while that of the calyptopis and furcilia stages, about 10 stages altogether, must be about 5-6 days each as a large number of adolescent M. norvegica were found in the plankton 2 months after egg laying commenced (fig. 37, May, June, 1957).

Eggs were present in the plankton throughout the period beginning of April to beginning of July. There were, however, two peak periods of egg laying, the first at the beginning of April, the second at the end of June. All sizes of females laid eggs in the first period but the females which laid during the second period were much larger and were thought to be either large 0-group (now I-group) specimens laying for a second time or females derived from eggs laid during the second peak period of spawning of the previous year, and now spawning for the first time. The latter specimens

might be expected to grow at a faster rate than the main brood of that year and consequently become indistinguishable from them as the winter progresses and the spring acceleration in growth takes place. A proportion of the previous winter's I-group also spawns at this time.

The adults originating from this second spawning peak can be clearly seen at the lower end of the population histograms as a small peak protruding from the main 0-group one (fig. 37; 1955, to Feb., 1956).

By the winter the carapace length has increased (fig. 38) to 5.5. to 6 mm. (24 to 26 mm.). Little growth took place in the winter and only occasionally was a specimen caught which had newly moulted or was about to moult. The gonads, however, develop throughout this time, about 60% of the males having fully formed spermatophores in the vasa deferentia by mid-January (fig. 38). These were transferred to the females during January and the beginning of February (fig. 38) when, as Bargmann (1937) noted in Euphausia superba, the eggs in the ovary (fig. 37) are only about a quarter of the diameter they will attain when ripe.

This 0-group now became the new I-group and growth in length accelerated. The time of commencement of the increase in the growth rate is thought to be estimated too

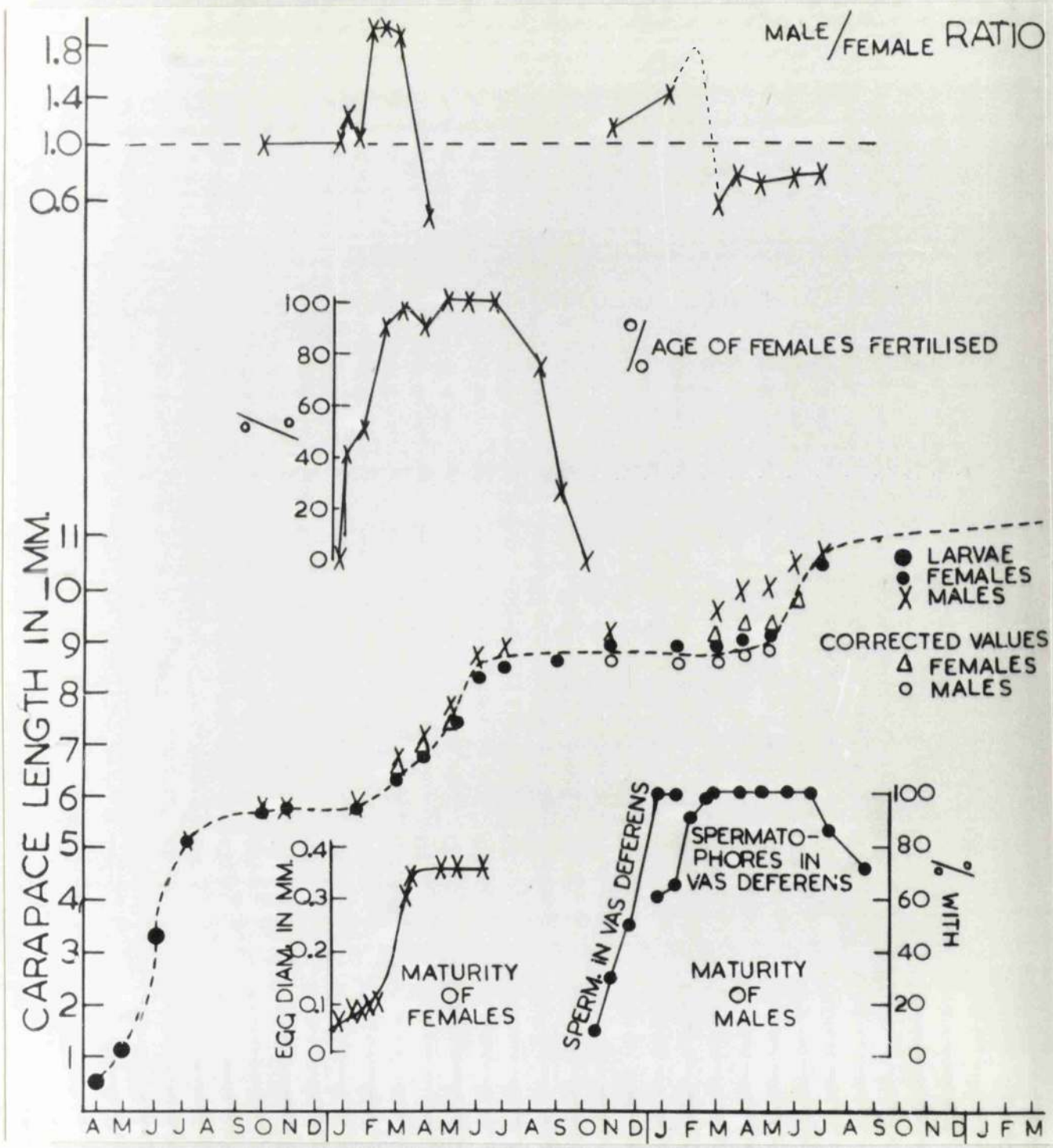


Fig. 38. The growth curve of M. norvegica showing, below it, the state of maturity of the females and males and, above it, the percentage of females with sperm-plugs on a given date. The top graph is of the ratio males/females.

early owing to the carapace swelling as the animals mature (last chapter). The curves for the state of maturity of the ovaries are shown under the appropriate parts of the growth curves (fig. 38). Most of this year group lay their eggs by the end of May while a large number of the older age group continue to lay until July. The corrected estimates of the mean carapace length of females (fig. 38), obtained from fig. 35, approximate very closely to the actual estimates of the mean carapace length in the males throughout this period. The corrections for the male carapace are negligible, not amounting to more than -0.1 mm.

Even with these corrections, the acceleration in the growth rate seems to have started some time between the beginning of February and the middle of March while the diatom and general productivity increases of the area did not appear to take place until the beginning of April, the time when the eggs were laid.

By June, the growth rate had slowed down, the mean carapace length being about 8 to 9 mm. (34 to 38 mm.). Very little growth took place throughout the winter except for the gonads again becoming mature. The females have a larger mean size owing to the presence of specimens

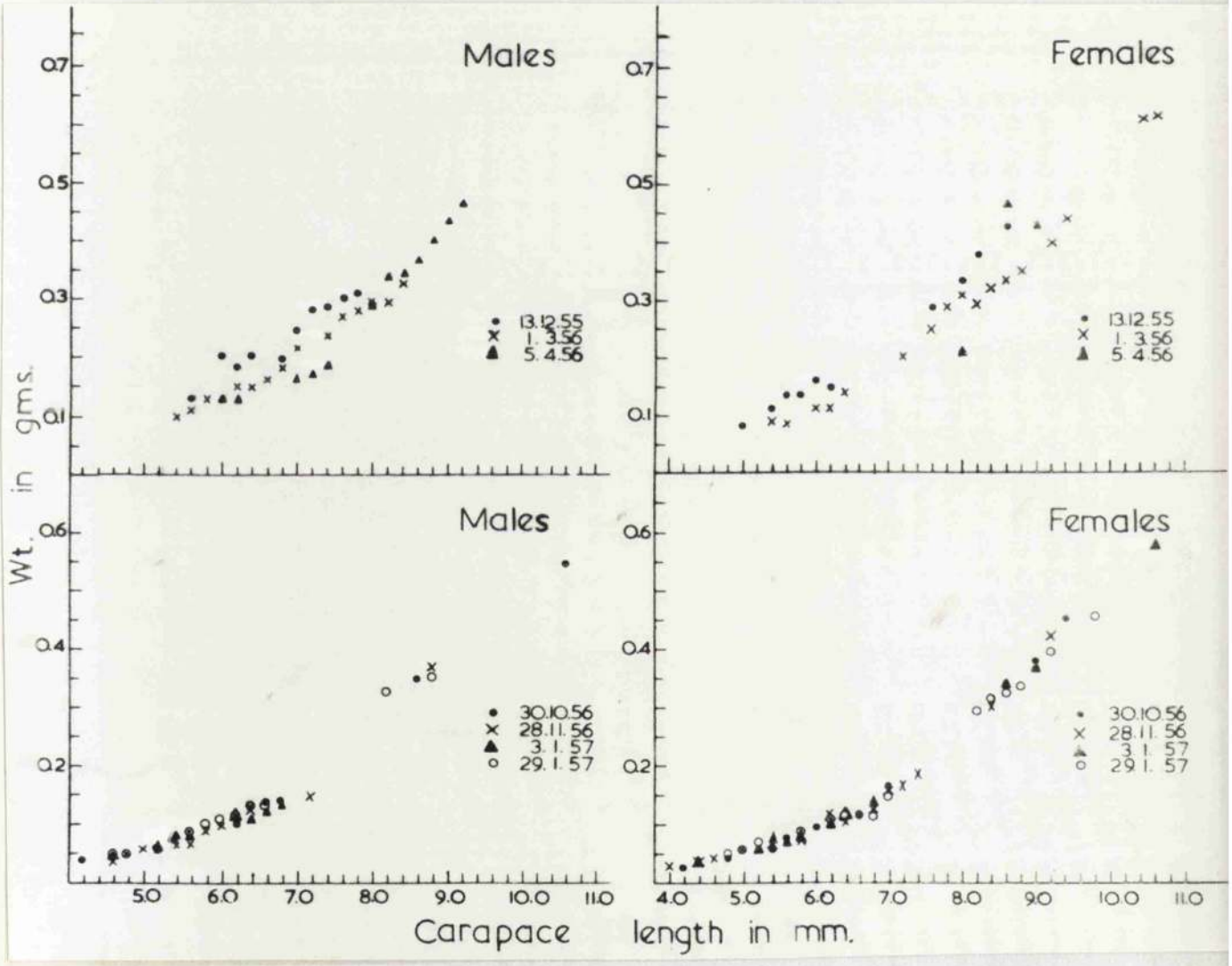


Fig. 39, A. The relationship of carapace length to wet weight in male and female M. norvegica on several dates.

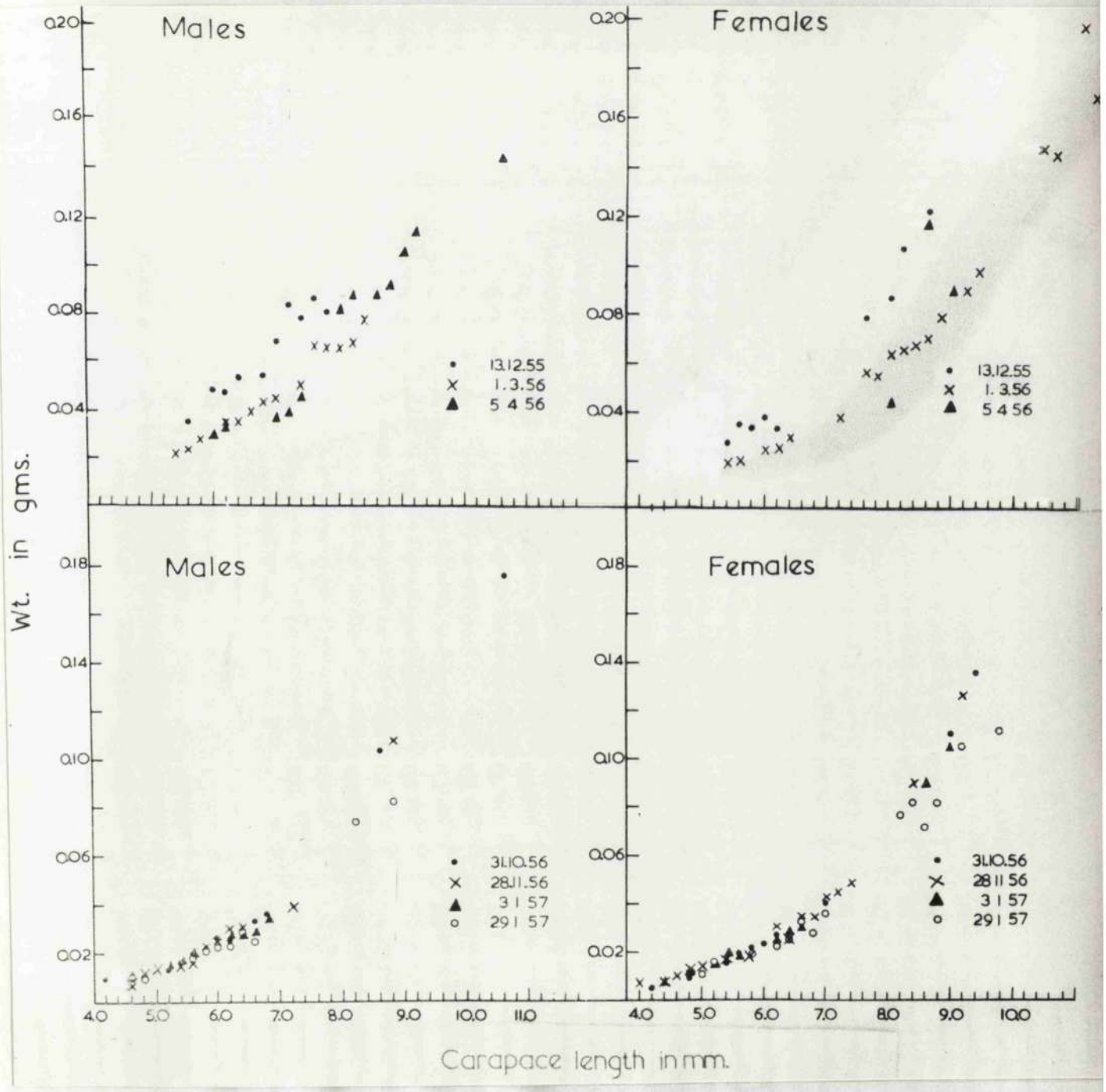


Fig. 39, B. The relationship of carapace length to dry weight in male and female M. norvegica on several dates.

measuring up to 11.0 mm. carapace length (up to 46 mm.), while males over 10.5 mm. (44 mm.) are rarely found. The spring acceleration in the growth rate of the I-group seems to be better correlated with the productivity increases of the sea area. The mean carapace length values have been corrected in both sexes and the female curve follows the male, growth starting in March to April. By July they have a mean carapace length of about 10.0 to 11.0 mm. (42 to 48 mm.). A few specimens of this group are found throughout the winter, and seem to survive until January (fig. 37, 1956) in the case of males (time of spermatophore transference) and to March (egg laying) in females.

The wet and dry weights of M. norvegica were investigated several times during the period October to April in two years (fig. 39). In December, 1955 and March and October, 1956 males were slightly heavier than females of corresponding carapace length but there were no significant differences between them in any other month investigated. During the period December, 1955 to April, 1956 an apparent decrease in the weight per unit carapace length (fig. 39) took place in both sexes. As March and April are in the breeding season, when the carapace is swollen, the measurements were corrected and

the resulting weights per unit carapace length compared. The wet weight of the males had decreased by 5% and the dry weight by 18% between December and March; an increase of 20.7% and 4.2% in the wet and dry weights respectively, took place in the females. An increase in the weight of the females is expected at this time of year owing to the growth and maturation of the gonads but why there should be a decrease in the male weight is not known. There is a high rate of mortality among the males during March (see later) and these two events may be connected. This change in weight did not appear to be taking place in 1956-57 but the experiment was not carried on long enough as the ovaries only start to mature in January. The weight per unit carapace length of the males was not changing significantly, even in the last January haul.

The mean percentage water content, that is the difference between the wet and dry weights expressed as a percentage of the wet weight, was found to increase during the winter as the animals matured (Table 7, see over).

In the 1955-56 results, the increase in percentage was greater in the females, which were mature in the March and April experiments, than in the males which were past their peak period of maturity. In 1956-57, no result is available for the peak period of maturity in the

Statistical significance between pairs of data is indicated:

Table 7.

Date	Males		Females	
13.12.55	73.56%		73.81%	
		significant		significant
1.3.56	77.40%		77.92%	
		not sign.		significant
5.4.56	76.40%		77.53%	
31.10.56	73.77%		75.07%	
		not sign.		significant
28.11.56	73.84%		73.69%	
		significant		significant
3.1.57	75.88%		74.99%	
		significant		significant
	77.39%		76.44%	

females but the last haul in January comprised mature males and the greater increase in percentage was found in the males. Thus it would seem that increasing water content is related to increasing maturity but further work is required before the specific reasons for this are known.

The ratio of males/females in all the samples available was calculated. When the value of this is greater than 1.0 females are dominant and vice versa for values less than 1.0. From October, 1955 to the first week of January, 1956 the sexes were present in equal

numbers (fig. 38). The proportion of females then rose and, following a slight relapse, the ratio reached a maximum value of 1.92. Concurrently, the proportion of 0-group to I-group males decreased (fig. 37, March), having previously dominated the population. This decrease immediately followed the time at which spermatophore transference was most frequent (fig. 38). In 1957, the females dominated the winter population and in January became slightly more dominant. No sample was available in February and so the suspected curve has been continued to the March result, when the males were dominant. This is thought to be justified owing to the spermatophore transference curve, which was almost identical in the two years including February, 1957 when enough specimens were obtained to produce valid results for it.

It would seem therefore, that there is a high mortality in the males following, and possibly owing to, the peak period of spermatophore transference in January-February.

In April, however, the proportion of the 0-group to the I-group increased but this is not evident in the male/female ratio curve (fig. 38), possibly because of the simultaneous high female mortality. The proportion of the I-group (now II-group) males which survive to the autumn is

variable and very few II-group specimens have been caught later than September.

In March, 1956 the proportion of the 0-group females increased in relation to the I-group before any eggs were evident in the plankton. At the beginning of February, only about 50%, while in the first week of March about 90%, of the females were found to have spermatozoa in their spermathecae (fig. 38) and consequently this change in the population composition may be owing to mortality caused directly or indirectly by spermatophore transference. Egg laying started slightly earlier in 1957 than in 1956, eggs being found in the plankton in the second fortnight of March instead of the first week of April. This agrees closely with the respective decreases in the numbers of females caught, thus suggesting a heavy mortality at egg laying.

No information has been gained on any increased mortality at the second peak of egg laying. The numbers of both sexes decrease considerably throughout the summer but whether this is owing to the continued breeding of the animal or to predation is not known. A part of this decrease may be false owing to the dispersal of the animals in the summer. Errors in estimating the amount of mortality taking place are known to arise after May

owing to the animals gradually spreading over a much wider area than previously.

The spermatheca of the females is lined with chitin and consequently spermatophore transference is continued throughout the summer but no second peak in the frequency of transference could be discerned. Nearly all the males carry spermatophores in the ejaculatory duct and all females, throughout May, June and July have sperm-plugs. The frequency of moulting was not examined but from the numbers of casts found in townets and from the number of specimens which moulted in the laboratory, the rate is thought to be high enough to necessitate refertilisation 2 or 3 times during the season.

Further mortality is possibly caused by the herring which are most plentiful in the Clyde from August to October, the period when the I-group declined in numbers. Examination of herring guts showed that they were feeding on M. norvegica and very little else. Other fish such as the dogfish (S. acanthias) and young hake were found to be feeding, to a large extent on M. norvegica but the amount of mortality caused by these predators could not be determined.

Conclusions.

The growth rate of *M. norvegica* in the Clyde sea area does not wholly agree with previously published results from other areas. Ruud (1936), working on *M. norvegica* in the Bay of Biscay, Cadiz Bay and the Mediterranean, the southern limit of distribution of this species, found the wintering 0-group to measure about 23 mm. Einarsson (1945), describing results obtained from populations at the northern limit of distribution, found a mean size of about 20 mm. These are both lower than the Clyde measurement of about 25 mm.

Ruud did not describe the I-group, though he considered that it existed, but Einarsson found the mean length during the winter to be about 31 mm. Even in the summer (June - July) the mean length did not exceed 32 to 33 mm. in the area south of Iceland where the fastest growth rate occurred. Poulsen (1926) has too few results to make a valid comparison with the present data.

The growth rate of *M. norvegica* is slower in colder than warmer water (Einarsson, 1945). In the Clyde, however, the growth rate is even faster than that found by Ruud in the southern areas and the older Clyde larvae,

as described previously, were larger than any described by other authors. It would seem, therefore, that the conditions in the Clyde must be extremely favourable for this species. Skagerrak would also seem to be a favourable area as Poulsen records the range of size of the I-group (then II-group) in May as 32 to 37 mm. but this group did not seemingly survive to October when he recorded the range of the new 0-group as 13 to 25 mm. and the previous winter's 0-group as 27 to 35 mm. A similar size range was found in a sample, also taken in October in Skagerrak, by Einarsson.

The author has found the size range of the winter I-group to be about 31 to 42 mm. with a mean of about 37 mm. The percentage of the population represented by this group at breeding varies, being about 40% in 1956 as compared to about 5 to 10% in 1957. No comparisons with Einarsson's data can be made owing to his samples only extending from May to October.

The actual rate of growth can vary very much from year to year. In the late summer and autumn of 1957, after an extremely successful larval season, the 0-group increased to the size usually attained by the average I-group, while the mean measurement of the I-group was comparable to measurements usually obtained from II-group

specimens. Conversely, mature males and females measuring only 12 to 15 mm. respectively have been found in the spring.

Ruud concluded and Einarsson confirmed it, that the breeding season extended for 2 to 3 months and this has proved to be so in the Clyde. The breeding season in the southern areas of distribution is from January or February to April while Einarsson states that they spawn from March to July in the northern limits, as they do in the Clyde. Lucas, Marshall and Rees (1942) concluded that there might be two breeding seasons of M. norvegica in the Faroe- Shetland Channel. It is thought, rather, that they may have detected two peak spawning periods in a continuous breeding season.

The I-group matures, on average, 2 to 3 weeks before the average 0-group specimens but seems to transfer spermatophores and lay eggs at the same time as the smaller animals and not earlier, as Ruud found in the Mediterranean.

The life history of M. norvegica therefore, is as follows: the eggs are laid from March to July, the new 0-group attaining an average length of about 25 mm. by the late autumn. Little growth takes place throughout the winter but by January the males, and by February to

March, the females are mature. Spermatophores are transferred in January and February, in the first instance, the eggs being laid at the end of March or beginning of April. The 0-group is now about one year old and grows throughout the spring and summer, reaching a mean length of about 36 to 37 mm. by the autumn. A high percentage, in some years as much as 80%, do not survive this second summer. Those living to the autumn are slowly reduced in numbers throughout the winter, a variable percentage, 10 to 40%, taking part in a second breeding season. A very small percentage of the original 0-group survive until the following winter when they are about $2\frac{1}{2}$ to $2\frac{3}{4}$ years old. A still smaller percentage seem to be able to survive to a third breeding season but no longer, having reached an age of $2\frac{3}{4}$ to 3 years.

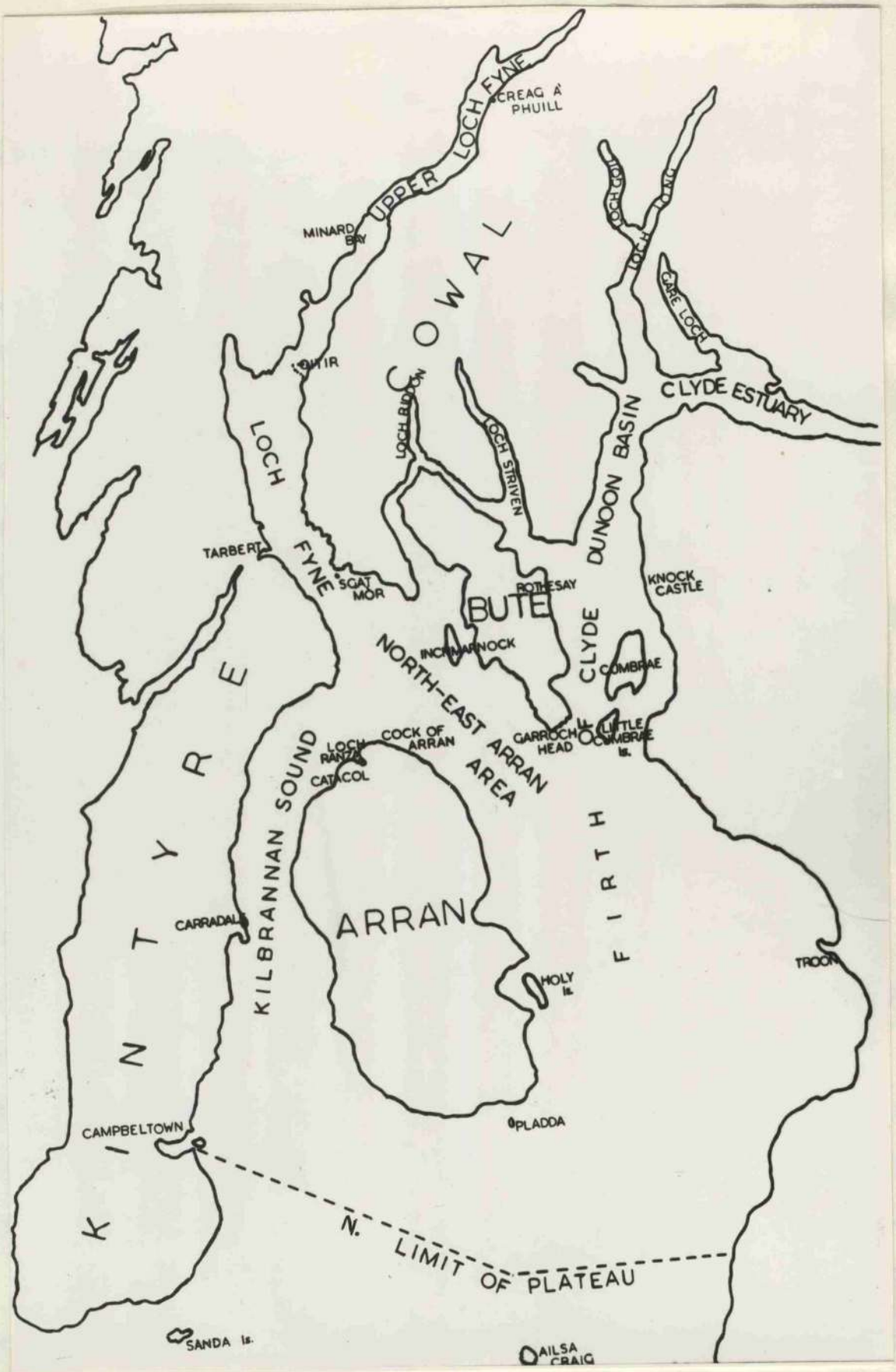


Fig. 40. The Clyde sea area.

IX. Local Population Ecology and Distribution.

Macdonald (1927a) described the distribution of M. norvegica within the Clyde sea area. He found the species to be most abundant in Upper Loch Fyne off Creag a' Phuill (Poll) and at a station midway between the Little Cumbrae Is. light and Garroch Head. It also occurred in Lower L. Fyne (S. of the Oitir), Kilbrannan Sound, and off Cock of Arran. A few specimens were caught in Lochs Striven, Long and Goil during the summer but these disappeared towards the end of November. The exact location of each of the above stations, excepting Creag a' Phuill, is not stated nor the exact dates on which they were visited. He does, however, remark that "Adults of all sizes tend to disappear from the Clyde Sea Area from May to September. Several hauls were made in May and June in Upper Loch Fyne, where the species is usually most abundant, but no specimens were found during the day, and only a few (not more than 6 in the 1-metre stramin net) during the night."

In the present investigation, the stations (fig. 40) most often visited were immediately north of Tarbert and off Sgat Mór (island in lower Loch Fyne). A number of trips were made at varying seasons to Creag a' Phuill,

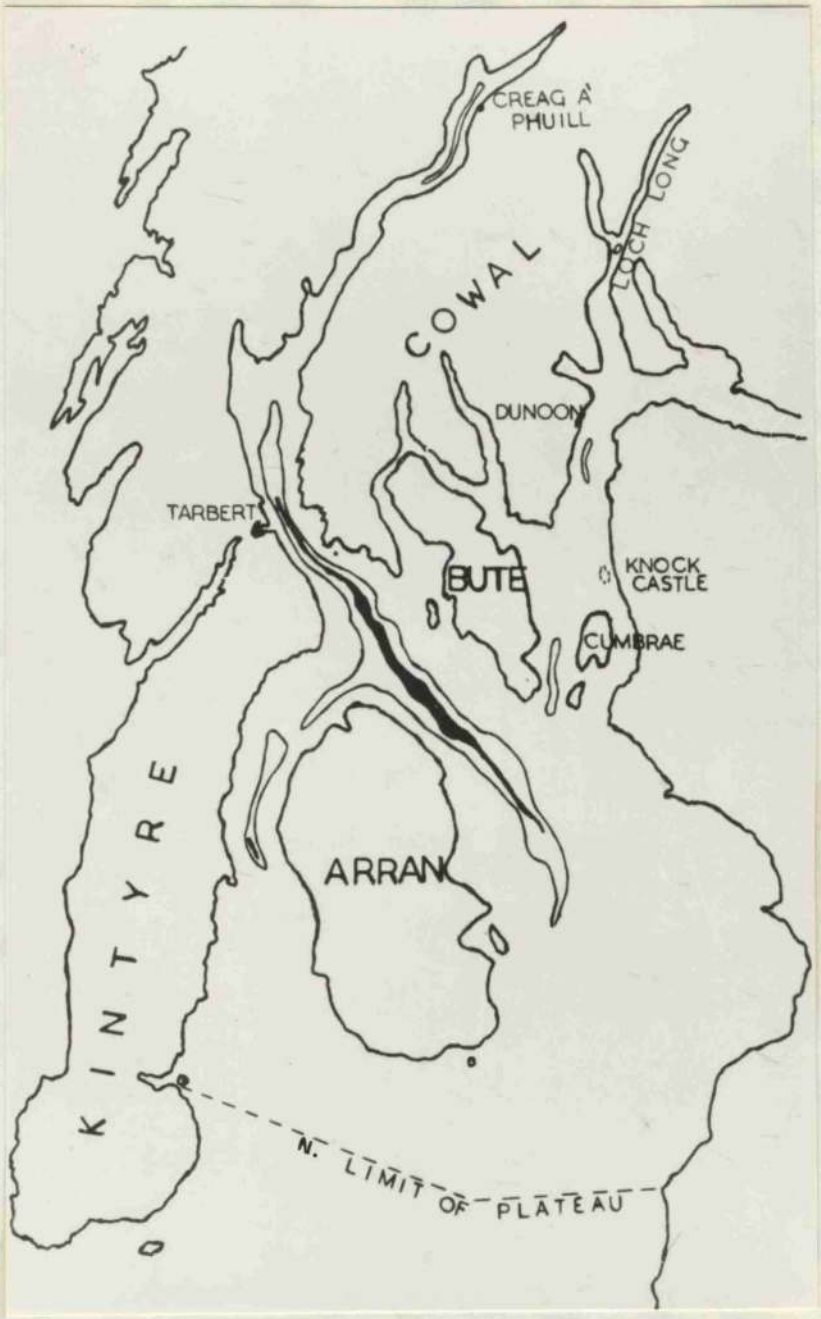


Fig. 41. Map showing the distribution of deep water in the Clyde sea area.

Black, 80 fathoms contour; line contour, 50 fathoms contour; dotted contour off Knock Castle, 40 fathoms.

L. Striven, L. Long, L. Goil, off Knock Castle, Little Cumbrae-Garroch Head, North-east Arran area, Holy Isle, Great Plateau, Carradale, Cattacol, and Loch Ranza (fig. 40).

The hauls were taken with 1 m. and 2 m. stramin nets at various hours of the day and night. Samples were sorted on board and preserved in 10% formalin in sea water for further examination.

The Clyde Sea Area.

The Clyde Sea Area is broken up by lochs entering the main basin and the presence of the islands Arran, Great and Little Cumbraes and Bute (fig. 41). The Great Plateau guards the mouth of the Firth; it has a mean depth of about 60 m. and extends right across from the southern end of Arran seawards to a line from Sanda Isl. to Loch Ryan.

A deep trough is present on the east and west side of Arran (fig. 41) these meeting round the north end and extending north-westwards into L. Fyne. The depth in these troughs is 100 - 200 m. The deep water shallows quickly at the northern end of lower L. Fyne, the part of the loch above the Oitir being entered by a narrows of 60 m. depth. The part between the Oitir and Minard Bay

does not exceed 70 m. in depth but in Upper L. Fyne depths of 150 m. are present. Macdonald worked in this deep water almost all the time.

A trough of about 130 m. depth lies between the Cumbraes and Bute but shallows at its southern limit where it enters the main trough running towards L. Fyne. A patch of 80 - 100 m. depth lies off Knock Castle (north of Largs) and off Dunoon; the remainder of the upper Firth is about 60 - 70 m. in depth, the water shoaling in various places to much less.

Loch Riddon, opening into the Kyles of Bute, is very shallow, 20 - 30 m., and no M. norvegica are found in it.

L. Striven, which in places is 80 m. in depth, opens into Rothesay Bay which is only 40 m. Macdonald found M. norvegica in this loch but none have been found by the author, Holy Loch and Gare Loch are too shallow for this species. L. Long, opening into the upper Firth, has depths of 80 - 90 m. as has L. Goil which in turn opens into it.

All these lochs must obtain a heavy drainage from the surrounding high lands and though the bulk of this fresh water travels on a surface out-flow, a large amount of the material brought in by it sinks to the bottom of the lochs, producing a rich organic substrate. Considerable

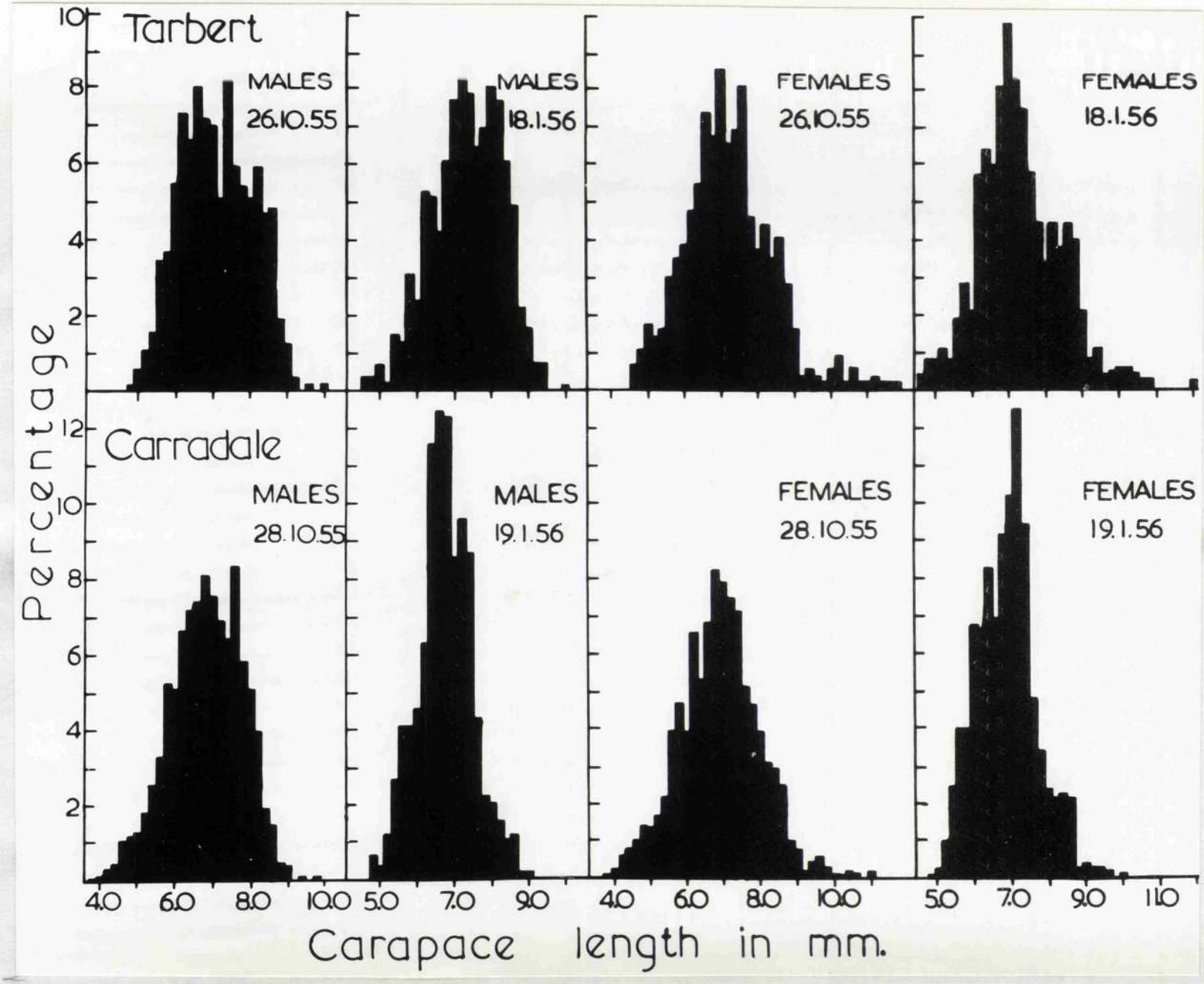


Fig. 42. A comparison of the populations found at Tarbert and Carradale.

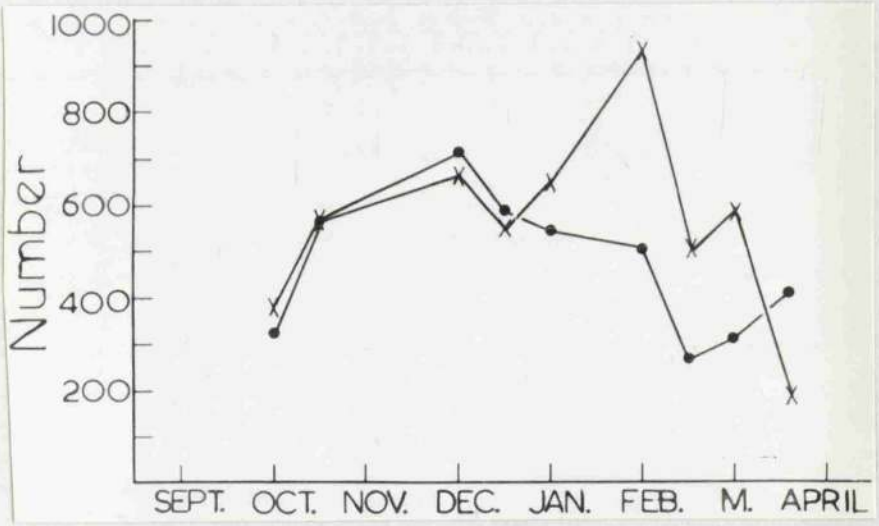


Fig. 43. The numbers caught in a standard tow at different times of the year.

quantities of land detritus are found in suspension in the waters of L. Fyne.

Winter Populations of M. norvegica.

The resident population of M. norvegica in the Clyde sea area is split up into several sub-populations which, for a part of the year, are independent of each other and static in certain areas. Two populations are more isolated than the rest; these are the one in Upper Loch Fyne, which Macdonald studied, and the one in Lochs Long and Goil. Both these groups are separated by a distance of at least 10 miles from any other populations and no adults have been found in transit either way.

The main mass of the population is found in the trough running up the east coast of Arran to Tarbert, L. Fyne. It, however, is broken up into sub-populations which tend to gather in the deeper regions of the trough north of Brodick, at Cock of Arran, off Sgat Mór and Tarbert.

A further large population is found on the west side of Arran, in the deep water west and north of Erins Bank near Carradale. Small groups have been found in the deep water running parallel with the Arran west coast,

between Cattacol and Cock of Arran.

During the winter, October to January, length/ frequency histograms of populations in these deeps (fig. 42) tend to remain distinctive and constant showing that little intercommunication takes place between the areas. There is an increase in the numbers caught (fig. 43) in certain areas as the autumn progresses and yet mortality (see last chapter) is taking place all the time. The numbers caught at stations in between those with increased population numbers decreased showing that swarming in certain areas was taking place (Table 8).

Table 8.

Depth	Station	23-25th October	8-13th November	18th December
160 m.	N. Tarbert	950	1272	1831
140m.	Tarbert-Sgat Mór	665	53	100
190m.	S. Sgat Mór	905	338	200
190m.	Ardlamont Point	312	126	486
120m.	L. Ranza	980	116	126
170m.	Inchmarnock Water	280	871	615
180m.	Cock of Arran	360	830	1123
160m.	Measured Mile	500	80	148

During January and February sampling of the populations tends to be inefficient owing to the animals occurring in

patches of high density. It is often possible to catch virtually no specimens when towing the net in one direction but on reversing the direction (i.e. altering it in relation to water currents thus causing the net to fish at a slightly different depth) up to 1000 have been caught. This indicates that M. norvegica is restricted vertically as well as horizontally. At other times of the year this discrepancy between tows in different directions rarely arises.

The stations west of Arran are of particular interest as there are usually large populations of M. norvegica found in that area during the autumn. On 28th October, 1955 a 2 m. stramin net caught 2937 specimens in 20 minutes. This was the largest single catch made anywhere in the Clyde that autumn. A further haul was taken on 17th November, and on 19th January a total of 1385 specimens were caught in a similar tow. From October, therefore, to January there were plenty of M. norvegica in this area. The spermatophores were transferred to the females in January but before the eggs were laid at the end of March to beginning of April the number of animals caught at this station had diminished to almost zero. On 23rd March tows were taken from L. Ranza to Carradale but not one specimen was caught. The net was fishing very

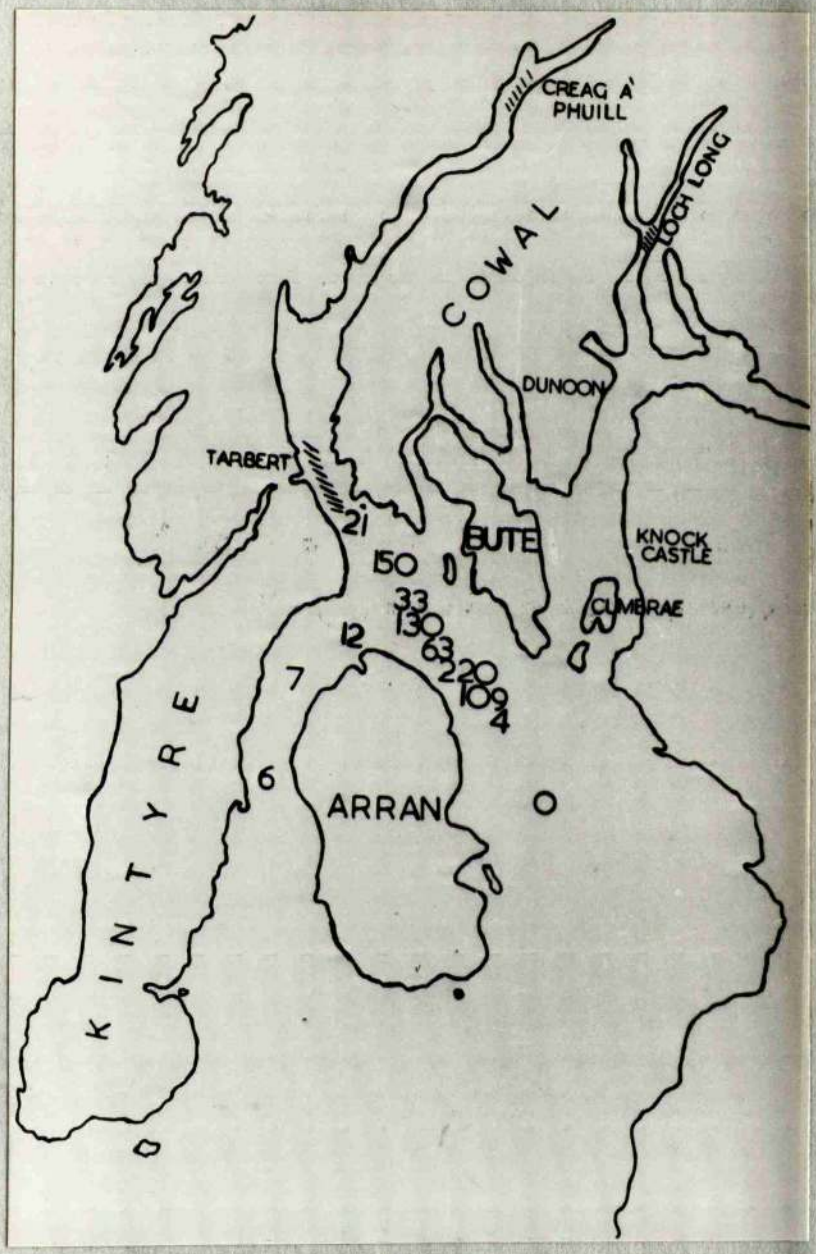


Fig. 44. The distribution of M. novegica on 11. 4. 57. The numbers refer to the numbers caught at these stations in a standard tow.

close to the bottom, as was shown by the presence of benthic animals in the catch, so that only M. norvegica extremely close to the bottom would escape it.

A similar thing happened in 1957 when only 12 specimens were caught between L. Ranza and Carradale on 12th April.

In L. Fyne, transference of spermatophores took place in the dense aggregations of animals which, in January 1956, were found at N. Tarbert and Sgat Mór. The numbers of both sexes in these two deeps, however, had fallen considerably by March (Table 9) though there were still plenty of animals present.

Table 9.

Stations	5.1.56	18.1.56	2.2.56	15.3.56
N. Tarbert	1229	1175	432	201
Sgat Mór	1431	759	886	599

Simultaneously with the fall in numbers in L. Fyne and Kilbrannan Sound, the numbers in the extensive deep area between Arran and Bute rose so that at the beginning of April the population distribution shown in Fig. 44 was found. The density is difficult to measure in this area owing to its extent but in 1957-1958 a sampling programme is being carried out the results of which again suggest a

substantial increase in the numbers present in this area. In the early autumn the centre of the local population in the north-east Arran area is usually between Cock of Arran and Inchmarnock. During the period end of January to end of March the population seems to spread but, instead of a decrease in numbers caught per haul, they remain constant and often increase considerably.

It would seem that the larger part of the population is in this area for spawning as more eggs are found in the surface layers of here than elsewhere. Furthermore, the increase in population takes place in this area between the time of spermatophore transference and egg laying.

Glover (1952) showed that M. norvegica in the North Sea moved to coastal water from January to May and then oceanwards from June to December. As far as is known, the breeding season is at the same time in the North Sea as in the Clyde, so that the Clyde movement may be related to this shoreward migration.

Why they should move to the Inchmarnock area is not clear. In the Clyde, Inchmarnock is one of the most complex areas physically, and this may be the reason why it is singled out from the others. A temperature and salinity gradient usually exists between Inchmarnock on the one hand and Kilbrannan Sound and L. Fyne on the

other, but it is not thought to be large enough for the animals to detect.

The main inflow into the Clyde is thought to come up the west coast of Arran in the deeper water and *M. norvegica* might reach Inchmarnock from there by these currents. Presumably, these currents are present throughout the year and some stimulus, therefore, must be required for the *M. norvegica* to be carried northwards. This may be provided by the cessation of luminescence (discussed later), following spermatophore transference, which might allow the population to disperse.

In L. Fyne, a smaller proportion of the population would be able to drift southwards in the surface outflow as the bulk of the population never reach the surface during vertical migration (chapter VI). Nothing is known of the deeper currents in this area but some may be carried gradually down by tidal movements.

It is thought that the currents are a more likely means of reaching Inchmarnock than following any temperature or salinity gradients.

A winter population of *M. norvegica* was found in Lochs Long and Goil. Three stations were worked several times, the first in 80 m. depth in the upper part of L. Long off Stuckbeg, the second in 90 m. depth

immediately south of the entrance to L. Goil, and the third inside L. Goil in 80 m. depth.

In the spring of 1956 a few specimens were found at all three stations but very few were found throughout the summer, though eggs were present. In April, 1957 about 150 one year old specimens were caught at station 2 and a number of these laid eggs on the journey back or that night in the laboratory. The other two stations gave negative results. A sample of about 50 one year olds were taken in June, 1957 and in October a large number of the new 0-group was present, but the I-group was poorly represented. A large M. norvegica has never been caught in either of these lochs and the numbers of the smaller I- and 0-group present seems to vary very much from year to year.

Macdonald found very few specimens at any one time in Lochs Long and Goil and they disappeared from these areas towards the end of November..

Kramp (1913) accorded the absence of M. norvegica in the North Sea during the winter to the shallowness of the area. Einarsson (1945) supports this hypothesis because M. norvegica moves to deeper water for the winter. This may be the cause of the absence of this species in these lochs in the winter and almost certainly explains

the absence of the larger size classes which as Macdonald (1927a) and the author (chapter VI) found, are always present in deeper water than the smaller.

No M. norvegica were taken in L. Striven, although Macdonald found a few there in the summer, but the loch was not visited very often.

Creag a' Phuill, Macdonald's collecting station, was visited on several occasions but rarely were M. norvegica caught in any numbers. On one occasion when they were present in large numbers south of the Oitir, only 6 specimens were caught in Upper Loch Fyne. Macdonald seems to have caught similar numbers in this area but never found comparable numbers south of the Oitir. This suggests that the character of the southern part of the loch may have changed.

He found specimens in the deep water between the Cumbraes and Bute ("Cumbrae Deep"). During the present investigation they have been caught there in small numbers throughout the autumn of each year. In November and December of 1957 they occurred in greater numbers than previously and are present in fairly large numbers (60-70 specimens per 20 minute tow with a 1 m. net) at the time of writing (13th February, 1958). A few individuals were caught at Garroch Head during the Summer.

Egg and Larval Dispersion.

As stated above the bulk of the eggs are spawned in the north-east Arran area. Fine silk nets were towed horizontally at 4 depths and counts of eggs at the different depths made (Table 10). Both hauls were made on the 18th June, 1957.

Table 10.

	Carradale	Cattacol
sufface	4682	269
20 m.	1701	175
40 m.	965	89
60 m.	437	64

Similar hauls were made throughout the season in the north-east Arran area but the numbers of eggs were much larger. Thus it is clear that, since the eggs sink in sea water, they must be laid at the surface. This is also shown by the fact that embryoss and nauplii tend to be found deeper than eggs.

Eggs are also laid in L. Fyne south of the Oitir and north of Minard Bay, off Carradale, and in L. Long but generally in much smaller numbers than in the north-east Arran area. The main breeding area extends from just

south of Sgat Mór to off the measured mile on the north-east side of Arran. Samples were taken right round Arran, in L. Fyne, North-east Arran area, round the Cumbraes, and in Dunoon Basin northwards to the mouth of L. Long. Decreasing densities of eggs were found going in every direction from north-east Arran area.

The following pattern of surface distribution emerged from this sampling. Eggs from the north-east Arran area were carried in surface currents south-eastwards down the east coast of Arran towards Holy Isle. Since, however, these eggs sink, the largest numbers were caught in this southern area below 15 m. depth instead of at the surface. They continue sinking as they approach the Great Plateau. Samples were taken on a line Girvan-Ailsa Craig-Sanda Is. on in- and out-going tides but no eggs were obtained. Only 1 furcilia larva was found and this at the northern limit of the Plateau, at a point due south of Pladda.

It is thought that the eggs reaching the area south-east of Pladda have sunk deep enough to enter the main oceanic inflow up Kilbrannan Sound. Larvae from these eggs would then tend to end up in the deep water to the east of Erins Bank near Carradale. Very few

eggs are thought to be carried round the northwest corner of Arran and down Kilbrannan Sound. Similarly few are thought to be carried into L. Fyne.

A further spread of eggs takes place from the north-east Arran area north-eastwards round Garroch Head. Again the eggs are sinking during transit and nets fishing on the east side of Garroch Head catch the largest numbers at 30 m. Decreasing numbers of eggs are caught the further up the Firth the samples are taken. No eggs, which can definitely be said to have originated from north-east Arran area, have been found north of Dunoon.

The local spawning in L. Long may give rise to the few eggs that have been found in this upper region, as they were caught at about 10-20 m. depth.

Nothing is known about the spawning in Upper L. Fyne owing to lack of time to visit this area during the breeding season, but it is hoped to examine it in the spring of 1958.

The larval dispersion described above has an effect on the relative age-group composition of the populations of the different areas. A larger number of 0-group animals are always found down Kilbrannan Sound than elsewhere.

Time of Egg Laying.

Einarsson (1945) states that "on the whole there is a certain agreement between the spawning of Euphausids and the onset of phytoplankton production, although the lack of material from April prevents any definite statement to this effect".

In the Clyde sea area there would also seem to be some correlation between these two events. In 1957, the diatom increase was well advanced on 1st April and the hepatopancreas of each M. norvegica in a haul, taken at Cock of Arran on that date, was dark green to black in colour. This phenomenon was never seen at any other time of the year. No eggs were evident in the area but on the 11th very large numbers of eggs were present. Unfortunately, no sampling was done between the 1st and the 11th but from the large numbers of eggs present in the north-east Arran area and the fact that some had reached Dunoon Basin, where no adults were present, it is concluded that laying had been in progress for some time. The diatom increase was over in the north-east Arran area by the 11th April.

On April 16th, Lochs Long and Goil were sampled. Gravid females, as well as eggs in the plankton, were found. Furthermore, a diatom increase was also in

in progress in both lochs at that time. No M. norvegica were found in L. Goil.

There would seem, therefore, to be some connection between egg laying and diatom increases. It is interesting to note that when the stomachs of the M. norvegica with the black hepatopancreases were examined, very few diatoms were found. At not time of the year (chapter VI) do diatoms form a significant proportion of the diet of these euphausids but a substance, termed "green-mush", was suspected to originate from μ-flagellates. Little evidence, however, could be found to substantiate this and it was further thought that these flagellates were too small to be caught by the filter-feeding setules of M. norvegica.

Summer Populations.

As shown in the previous chapter, a high mortality takes place in the males and females at the breeding season. This is shown in the substantial drop in the numbers of specimens caught in all areas.

It was thought that M. norvegica disappeared from the Clyde during the summer season and reappeared about September but this has proved wrong. Populations are present in the north-east Arran area throughout the

summer but, during some years, stations at Sgat Mór give virtually negative results. They disappear almost entirely from Kilbrannan Sound and the east coast of Arran and are rarely found in the deep water between Bute and the Cumbraes during April and May. During the period June to September, especially the latter part of it, specimens of M. norvegica are found all over the Clyde. Very few places of more than 140 m. depth were found to be without them and they were often fished from depths as shallow as 80 m.

The population, therefore, seems to disperse in the late summer but owing to the negative phototropism of the individuals, the dispersal is directional along the deeper channels. Consequently, the numbers at Sgat Mór, N. Tarbert, and E. and W. Arran increase while little increase is found in areas which are not accessible via channels of deep water but have to be reached by crossing a shallow bar. This prevents dispersal of adults out of the Clyde and, from the north-east Arran area, even into areas such as Dunoon Basin and Upper Loch Fyne. Adults in the deeper parts of these latter areas are thought to have originated from eggs which were spawned or larvae which were carried there.

Luminescence.

The general problem of the appearance and disappearance of euphausids from certain areas has been mentioned in the literature. Definite conclusions have been impossible owing to the areas being oceanic and the sampling techniques thus questionable. In the Clyde, however, it has been possible to gain confirmation of the fact that the total numbers caught in an area vary in a constant pattern. This pattern is owing to the amount of swarming taking place in that area at a given time.

The following experiments were planned because it was noticed that during the mid-winter period the animals were luminescing very freely when brought up in nets at sea during the night, whereas at other times of the year they were comparatively quiescent and only luminesced if stimulated mechanically or chemically. An attempt, therefore, was made to show conclusively that an annual rhythm of luminescence exists and that for the greater part of the year it serves solely as a defence mechanism.

These experiments were started in July, 1957 and are still continuing but some relevant results have been obtained and it seems, from the evidence gained in

preceeding years, justifiable to describe them.

The only previous marine studies of this kind, other than annelid studies, were made by Moore (1909) who showed a diurnal periodicity in the luminescence of copepods, and by Crozier (1920) who showed rhythms of luminescence in balanoglossids.

The apparatus used incorporated a 913A photomultiplier with power pack and D.C. amplifiers. This apparatus will be described in detail elsewhere. The whole was connected to a pen recorder so that continuous records, over 48 hours, were obtained.

The photomultiplier was housed in a small light-proof cupboard where the specimens were kept in a breffit. During the period July to October, means of keeping the breffit cool had to be devised but after October the room temperature could be kept sufficiently low. An observation window was constructed in the door of the cupboard so that the animals could be observed while luminescing and, yet, no light reach them from outside.

The specimens were placed singly in 250 ml. beakers with filtered sea water at sea temperature and allowed to stand in artificial light or daylight for about 20 minutes. They were then transferred singly to the cupboard and the recorder switched on. During the period July to August,

75 to 80% of the specimens luminesced immediately they were placed in darkness. After August, this percentage gradually decreased until November when only 10 to 20% reacted in this way.

All night records were made throughout the early autumn but no luminescence was detected after the initial burst. In the second fortnight of November, however, flashing continued steadily all night and similar records were obtained about three times a week until 20th January, 1958. Since then no specimens have luminesced throughout the night in the laboratory.

A diurnal rhythm of luminescence takes place, flashing starting at sunset, continuing through the night, and terminating at dawn. No spontaneous flashing has been observed after daylight. The records have not yet been fully analysed but there appear to be no dawn and dusk bursts of luminescence. Water temperature does not seem to alter the rhythm in any way, some records having been obtained at temperatures as high as 20°C.

During the period when positive records of spontaneous flashing at night were obtained, only 10 to 20% of the specimens flashed when they were transferred from the light into darkness. On 15th January, however, this percentage had risen to 39%, in the females, and

48%, in the males. By 20th January, spontaneous flashing during the night had ceased.

Why the percentage flashing when placed in the dark should fall as spontaneous flashing starts and should rise when spontaneous flashing falls is not yet known.

In November, when the continuous records of luminescence started, the numbers caught in several deeps were increasing. This shoaling continued until January when the spermatophores were transferred and luminescence ceased. It would seem, therefore, that luminescence serves as a shoaling mechanism to ensure efficient transfer of the spermatophores.

There appears to be a connection between the onset of luminescence and the beginning of the development of the gonads, but further work is required on this aspect before any definite conclusions can be stated.

The period April to June has still to be investigated before any full description of the function of the photophores can be presented and consequently the work is being continued.

X. Summary.

The observations of Raab (1915), on the anatomy and histology of Meganyctiphanes norvegica have been confirmed and extended. The male reproductive system was examined and an account of the formation of the spermatophores given.

In the females, the uterine glands appear to be divided into two groups; the first is associated with the proximal regions of the oviducts, the second with the genital opening and spermatheca.

The circulatory system was investigated. The blood is pumped from the heart to the various regions of the body by way of a well-developed arterial system. It passes out of the open ends of the final sub-branches of the arteries into the various sinuses, finally collecting in the posterior ventral region of the thorax. From there, by the action of the pericardium and the muscles associated with the afferent branchial channels, it enters the afferent branchial channels whence it circulates through the branchial veins, present in the branchiae, to the efferent branchial channels. The beating of the heart draws the blood into the pericardium whence it reaches the heart cavity by way of two pairs of ostia.

When the compound eyes of M. norvegica and a number of decapods were examined a constant general pattern of blood vessels was found.

The growth rates of the egg and its nucleus within the ovary are described.

The eggs, on extrusion, were found to have two membranes over and above the vitelline membrane. It is concluded that the inner membrane is chitinous and the outer one cuticular (protein).

Larval development in the Clyde sea area was investigated and found to be different from that described by Macdonald. A few notes on the larval ecology are presented.

The development of the larvae of the Euphausiacea was considered and it was concluded that it could be divided into 4 phases.

Analysis of winter and summer vertical migrations are given and the differences in behaviour pointed out. A vertical layering of size classes, larger specimens occurring deeper than smaller ones, is shown to exist during the day and night, but is more evident in the winter than in the summer.

Light is shown to be the dominant physical factor controlling vertical movements.

Four methods of feeding are described. The stomach contents were examined and the presence or absence of various types of foods is shown to be correlated with the size of the feeding animals and the time of day. The presence of crustacean compound eyes is noted.

The relationship of carapace length to total length was found to depend on the state of maturity of M. norvegica.

M. norvegica matures at the age of 1 year having attained a length of about 25 mm. Transference of the spermatophores takes place in January-February and the eggs are laid in March-April. The larvae take about 2-3 months to develop into adolescent animals. Little growth in size takes place in the winter when the gonads are maturing.

It may reach an age of $2\frac{3}{4}$ to 3 years but most of the population only survive to an age of $1\frac{1}{2}$ to 2 years.

The distribution within the Clyde sea area throughout the summer and winter is described and it is concluded that the area must be an extremely favourable habitat for the species.

Most of the population was found to move to the north-east Arran area for egg laying and this movement is

thought to be related to the shoreward migration of 'slope' populations of this species.

A swarming was shown to take place prior to spermatophore transfer and evidence is presented to the effect that luminescence is the mechanism that brings this about.

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Appendix to Reference List.

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