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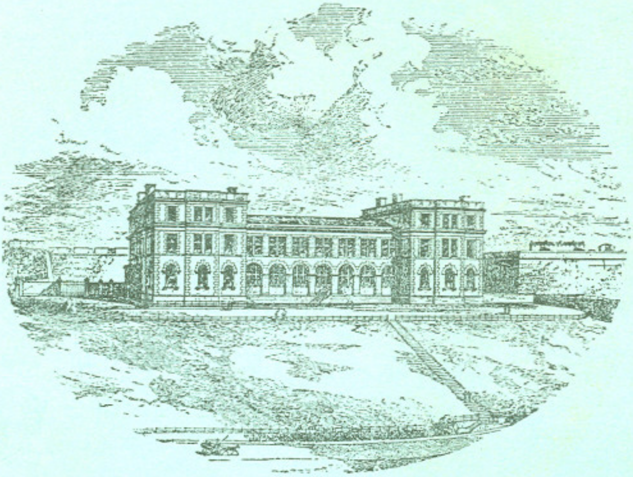

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On the Vertical Mixing of Sea-Water and its Importance for the Algal Plankton.

By

W. R. G. Atkins, O.B.E., Sc.D., F.I.C.,

Head of the Department of General Physiology at the Plymouth Laboratory.

With Figure 1 in the Text.

During the last three years determinations of hydrogen ion concentration, temperature, salinity, and phosphates have afforded evidence that sea water is at certain times far from uniform in composition from surface to bottom. Approximate determinations of the respirable organic matter, and the examination of the algal plankton of the water-bottle samples carried out by Dr. M. V. Lebour, have furnished further reasons for regarding the different levels in the sea as more or less distinct localities at certain seasons and under specified conditions. Though attention has from time to time been called to this when discussing the results of the various determinations, yet it seemed of interest to collate and compare them here.

As regards salinity, a difference between top and bottom is taken to denote the inflow either of less saline water on the surface or of more saline water beneath, according to the facts favouring either supposition. As a general rule the area covered by the cruises from Plymouth exhibits a remarkable uniformity in salinity and an almost absolute uniformity from surface to bottom. There are, however, exceptions, such as those for April 24th and 25th, 1923, for which values of S ‰ are given below:—

m.	E 1	E 2	E 3
0	35·29	34·95	34·67
15	35·28	34·94	—
25	—	35·08	34·86
50	35·27	35·11	35·01
Bottom	35·30	35·16	35·10

Here an inflow of less saline water on the French side is clearly indicated, but the May results show that complete mixing has taken place, for the salinity gradient no longer exists, save that a slight fresh-water effect had become noticeable down to 5 metres on the English side at E 1.

Similar reasoning led to the supposition that, when abrupt changes in temperature were found in the water column, a different origin was to be sought for the warmer upper layer. The evidence reviewed here is all against this view and in favour of regarding such changes as due to the incidence of radiant heat energy upon a column or sheet of water in which vertical mixing is temporarily in abeyance. Reference to the temperatures recorded in the writer's accompanying paper on hydrogen ion concentration, and in the former papers of the series, Parts I and II, shows how sharp such temperature differences may be in calm summer weather. Some of the 1923 records are plotted in Fig. 1. In this it may be seen that the gradient is less marked at E 3 than at E 1 or E 2, and is less at N 2 than at N 1 in July. Again, in August a greater amount of mixing, as indicated by the warmer bottom temperature, has taken place at L 5 than at L 6, and at L 6 than at E 1. The effect of stormy weather is well brought out by the June and July, 1922, records, a drop of 3·3° between surface and 20 metres on June 6th having been reduced to 0·8° on July 11th; a difference of 2·2° appeared again in August, but from September onwards the temperature gradient throughout the whole column was negligible; this condition was maintained till the following June, and in July the difference amounted to 4·4° between

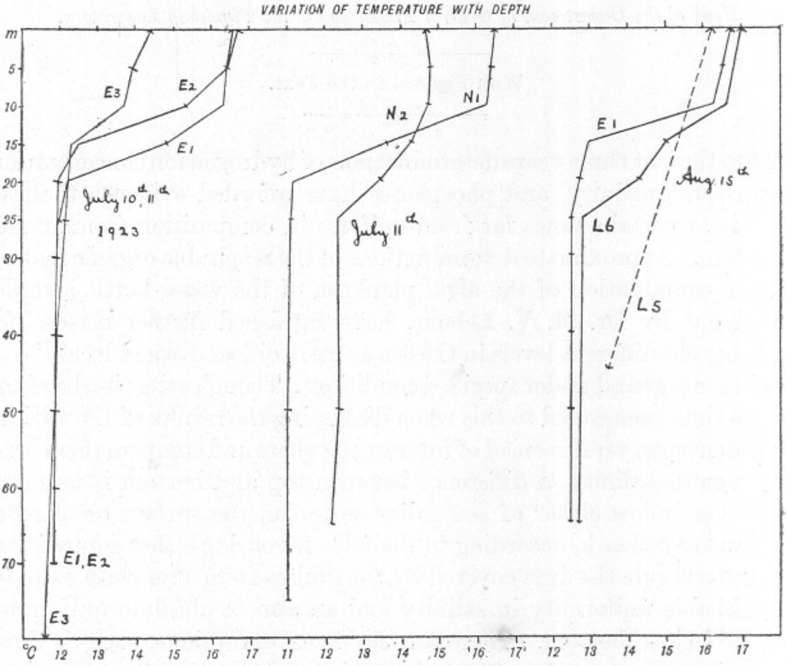

Fig. 1.

0 and 20 metres, falling to 4·0° in August and 1·7° in September, after which uniformity was attained.

Since the warmer water is also the lighter where the salinity is the same, and the density gradient is all the more marked when the bottom water is the more saline, the physical causes of the mixing must be sought. In relatively shallow water wave motion and the to-and-fro streaming of the tides over the irregularities of the bottom are jointly concerned in the mixing. Of these, wave motion is of but little importance in calm weather, but in stormy weather and in deep water it appears to be the sole agent. As the surface water cools and the density of the water column becomes more uniform, it is clear that vertical mixing may be brought about more readily. When the surface water is colder than the bottom water, mixing is automatic.

In the course of a cruise one cannot fail to be struck with the temperature differences found from station to station and with the variations in $\triangle$t, the difference between top and bottom values. Similar variations may be observed in $\triangle$pH and $\triangle P_2O_5$ in mgrms. per cubic metre. Records for the July, 1923, cruise are tabulated here, and temperature and pH values for the May, 1922, cruise are given in Part II of the hydrogen ion concentration series. In all such runs, save when stormy weather has ensured a general mixing, one is likely to encounter low temperatures at L 2, the Breakwater, at L 5, the Eddystone, at E 3, off Ushant, often at N 2 some miles south of the Scillies, and off the Lizard. The positions of the stations are shown in the map in Part I, this Journal, Vol. 12, p. 754. Low values observed during the night July 10th–11th were not due to rapid surface cooling, but to mixing with deeper water, as shown by the E 3 depth series observations; furthermore, similar low values were found at N 2, in the afternoon.

Locality. and date.	Hour.	Surface. t °C.	Bottom. t °C.	Δt	ΔpH	ΔP_2O_5 mgrms. per m³	Notes and depth to bottom.
L 5, July 10th	Noon	15·6	12·1	3·5	0·05	0	Slight swell, slightly overcast, 46 metres.
L 6	0.45 p.m.	16·8	11·9	4·9	0·08	—	65 m.
E 1	1.30 p.m.	16·6	11·9	4·7	0·08	10	70 m.
20 miles on	5.15 p.m.	16·8	—	—	—	—	—
E 2	7.30 p.m.	16·7	11·8	4·9	0·08	10	85 m.
20 m. on	11.30 p.m.	14·8	—	—	—	—	—
E 3, 11th	3 a.m.	14·5	11·6	2·9	0·08	16	100 m.
24 m. on	7 a.m.	14·5	—	—	—	—	—
N 1	10.30 a.m.	16·5	11·0	5·5	0·09	20	Sunny, slight haze, 100 m.
20 m. on	3 p.m.	17·4	—	—	—	—	—
N 2	6 p.m.	14·7	12·2	2·5	0·04	5	Visibility bad, fog around, 85 m.
E 7	9.15 p.m.	15·8	—	—	—	—	Very calm, clear, 70 m.
6 m. on	10 p.m.	17·3	—	—	—	—	Thick fog.
L 5, 12th	6 a.m.	16·4	—	—	—	—	Fog just lifted, clear sun.
L 4	—	16·6	12·2	4·4	0·04	2	50 m.
L 3	7 a.m.	16·7	12·7	4·0	0·05	4	45 m.
L 2	—	15·8	14·6	1·2	0·00	—	14 m.
L 1	8 a.m.	16·6	15·5	1·1	0·00	—	20 m.

The abruptness of the temperature change during settled weather is often very remarkable. On account of the vertical motion of the ship it is impossible to define it precisely, but at N 2 in July, 1921, a difference of 2·05° was observed between 27 and 32 metres with △pH 0·05. On August 12th, 1921, △t was 2·12° between 20 and 25 metres at E 1, and on July 10th, 1923, △t amounted to 2·64° between 15 and 20 metres, which increased to 3·77° by the 19th; on August 15th the cold-water layer was at 15 metres, and between this and 10 metres △t was 3·32° and △pH 0·04. On July 10th △pH was as great as 0·07 between the depths 15 to 20 metres.

The values for △t and △pH are usually maxima over the same range, but on June 19th, 1923, △pH was 0·07 between 20 and 25 metres, yet △t was only 1·14°; thus high values for △pH may be met with earlier in the season than for △t.

One effect of a high pH gradient is that in the more alkaline upper layer the partial pressure of carbon dioxide is quite considerably reduced, as explained in Part II previously mentioned. With abundant sunshine it may thus result that the lower partial pressure limits the rate of algal photosynthesis.

Another factor which influences algal growth, and seems to be the limiting factor in the summer, is the quantity of phosphate available. As shown in the last issue of this Journal, pp. 119–150, the phosphate at the surface is used up completely, though a considerable amount of phosphate may still remain in the deeper water. The rate of multiplication of the algal plankton may therefore be greatly influenced by the rapidity with which this is brought to the upper layers into good illumination. Thus the stormy June of 1922, which so markedly altered the pH and temperature gradients, must have been equally effective in rendering available the phosphate of the deeper waters. For reasons connected with phosphate supply it is therefore clear that evidence upon the vertical circulation of sea water is one of the most important factors to be considered.

Reference has already been made to Dr. Lebour's examination of the algal plankton of the water-bottle samples. These extended over a period of close on two years, but no evidence was obtained that any particular organism was to be found at one depth rather than at another. During the summer when rapid vertical mixing was in abeyance a certain amount of stratification of the plankton did occur, and phytoplankton is as a rule most abundant in the upper layers. Evidence as regards this has also been obtained by observing the changes in pH value of the water samples which take place on storing. The change, as explained in this Journal, Vol. 12, pp. 772–780, is due to the production of carbon dioxide in the water through the breakdown of what has been termed the respirable organic matter. The colour changes which occur in the tubes are striking, and are most marked during summer and autumn, usually in the top 25 to 30 metres; as a rule no two tubes of a depth series give exactly the same final pH value. However, once the temperature and pH gradient vanish owing to the vertical mixing of the water all such differences from tube to tube become much less, and the total change during winter is relatively small.

We may conclude that at certain stations irregularities in the bottom suffice to cause a considerable amount of vertical mixing in the water, even during calm weather, so that the gradients in the water brought about either directly or indirectly by incident light and heat energy are much reduced. At other stations such gradients may be very noticeable during settled fair weather. These conditions may be observed from May to August, but by September stormy weather and cooling of the surface water have usually effected much vertical mixing, which is complete by October, so that the water attains and maintains a great degree of uniformity from top to bottom.

Thermal stratification and the marked differences in the dissolved gases which accompany it have been very fully treated of by Birge and Juday, in their "Inland Lakes of Wisconsin," Survey Bull. No. 64, 1922. In these lakes, the largest of which, Mendota, is 9·5×7·4 kilometres, with maximum depth 25·6 and mean 12·1 metres, the upper layer or epilimnion varies from 5 to 7 metres when first formed, but it gradually increases in thickness as the season advances, extending to a depth of 10–12 metres by the middle of September. The same authors record in Bull. No. 22, 1911, full details of the manner in which these stratifications originate, through the water immediately next the surface being heated by radiant heat.

In "Notes from the Biological Laboratory of the Wisconsin Geological and Natural History Survey," reprinted from Wisconsin. Acad., Vol. 20, and issued February, 1922, Birge continues Juday's descriptions of the limnological apparatus used, and in particular the electrical pyrlimnometer, which shows how rapidly radiant heat is absorbed by water. Thus, whereas 1·30 calories per sq. cm. per minute were recorded at a depth of 0 cm., at 25 cm. 0·41 calories was received, at 200 cm. only 0·20, at 400 cm. 0·10, and at 10 metres 0·013. The homogeneity of the upper 10 metres of the sea as regards temperature can therefore only be brought about by the mixing of the surface water, which is efficient to a depth depending upon the length of the waves from crest to crest, and beyond that but little mixing appears to occur. The writer's own experience has shown that in the still water of a large pond the surface—about 2 cm.—may be as many as 5° C. warmer than the water at 20 cm.

The data accumulated by Birge and Juday are most valuable and find application in the study of marine problems also. They appear to support the view that the stratification observed in the waters of the English Channel has arisen at each station where found, except in so far as the tidal movement may have affected it.

SUMMARY.

1. Measurements of hydrogen ion concentration, of phosphate concentration, and of temperature all show at certain seasons a well-marked gradient from surface to bottom. The upper 10–20 metres is more alkaline, notably depleted of phosphates and warmer.

2. Settled summer weather and deep water, free from irregularities of the bottom, favour the formation of such a gradient. Its breaking up is occasioned by wave action and the cooling of the surface water in autumn.

3. Thermal stratification in the English Channel arises at each station, and is not due to the inflow of warm over colder water.

The Food of Young Herring.

By

Marie V. Lebour, D.Sc.,

Naturalist at the Plymouth Laboratory.

THE Herring season of 1923–24 was a peculiarly good one, the fishery continuing from the end of October into the beginning of February.

Newly hatched Herring were first observed on December 17th, 1923, and post-larvæ were abundant up to March, 1924, in the neighbourhood of Plymouth.

Investigations were made into the food of these young Herring, and the probable depth at which they were feeding. Hauls with Young Fish Trawl were made near the surface, midwater, and near the bottom, and tow-nettings were also taken. It has, however, now been found by Mr. Russell that the samples assumed to be near the bottom were possibly in reality some distance above it.

The results of these investigations show that there are more young Herring near the surface and that they feed more there than lower down, and this is quite in accordance with Cossar Ewart's remarks (1886), who showed that newly hatched Herring ascend to the surface layers almost immediately after hatching.

Many large hauls of newly hatched Herring were taken towards the end of December and early in January at all depths, samples of 100 of each haul being examined for food, but none being found. The first seen were from the region of Bigbury Bay, by the end of December being farther west in a straight line from Plymouth Sound, and in January they were scattered in many directions, occurring inside the Sound and outwards towards the Eddystone and beyond as far as Station E1, which is the farthest station usually worked.

It was not until January 14th that any food was found inside the Herrings this year, and those measured 10 mm. with the yolk sac gone, although in previous years those still bearing a yolk sac contained small metazoa (Lebour, 1921). The contents of the alimentary canal were various, larval mollusks, small copepods, and unicellular matter being present in about equal proportions. In the larger specimens copepods are nearly always taken.

When possible 100 Herring from each sample were examined for food, and it was found that more empty specimens occurred in the lower layers than near the surface. After March very few young Herring were to be found.

The following is a list of all food taken by the Herrings up to 12 mm. long :—

Mollusks	Larval bivalve.
	,, gastropod.
Copepods	*Pseudocalanus elongatus.*
	Acartia Clausi.
	Corycæus anglicus.
	Oncæa sp.
	Harpacticid indet.
	Copepod nauplius.
	,, juv.
	,, egg.
Infusoria	Egg indet.
	Tintinnopsis beroidea.
	T. ventricosa.
Flagellate	*Halosphæra viridis.*
Diatoms	*Hyalodiscus stelliger.*
	Coscinodiscus excentricus.
	C. concinnus
	C. sp.
	Paralia sulcata.
	Green remains.

In the following list the food of all the young Herring examined is given, with the size, locality, and date. For the sake of brevity the contents of the alimentary canal have been divided into copepods, mollusks, eggs, and unicellular food, the last including green remains, diatoms, Halosphæra, and tintinnids, copepods including adults, young and nauplii, mollusks including larval gastropods and larval bivalves. The numbers after the specified food indicate the individual food organisms present. In the case of unicellular matter if food organisms could be identified the numbers are given, the sign + after the number indicating indistinguishable green remains ; a query (?), indicating green remains alone ; S.=Surface ; M.=Midwater ; B.=near bottom ; Y.F.T.= Young Fish Trawl ; T.N.=tow-nets.

1924, January 14th, L6, S., Y.F.T., 6 in sample, all examined, 10 mm. long ; 2 contained mollusks alone (4–6), 2 contained mollusks + copepods (3–6), 1 contained copepods alone (1), 1 empty. L6, B., Y.F.T., between

10 and 30 in sample, 10 examined, 7 contained mollusks alone (1–2), 1 contained mollusks + unicellular matter (5), 2 empty.

January 21st, Rame N.E., 4 miles, Y.F.T., S., between 100 and 1000 in sample, 100 examined, ca 10 mm. long, 5 contained mollusks alone (1), 2 contained mollusks + copepods (2), 1 contained mollusks + unicellular matter (3), 11 contained copepods alone (1–3), 1 contained copepods + eggs (2), 5 contained copepods + unicellular matter (2–3), 1 contained copepods + eggs + unicellular matter (3 +), 3 contained eggs (1–3), 21 contained unicellular matter (1–2 +), 53 empty ; B., Y.F.T., 100 in sample, all examined, ca 10 mm. long, 6 contained mollusks alone (1–2), 2 contained copepods alone (1), 6 contained unicellular matter (1–2 +), 1 contained a dark indistinguishable mass, 85 empty.

January 23rd, T.N., near S., 20 in sample, all examined, ca 9 mm., Downderry N.E., Looe N., 2 contained copepods alone (2), 11 contained unicellular matter (?), 7 empty.

January 24th, Breakwater Light N., Mewstone N.E. by N., Y.F.T., S., over 1000 in sample, 100 examined, ca. 10 mm., 2 contained mollusks alone (2), 5 contained mollusks + unicellular matter (1 + to 3 +), 1 contained mollusks + copepods + unicellular matter (2 +), 2 contained copepods (1–2), 8 contained copepods + unicellular (1+), 47 contained unicellular matter (?) ; Breakwater Light N.N.E., Mewstone N.E., B., Y.F.T., over 1000 in sample, 100 examined, ca 10 mm., 1 contained mollusks (1), 2 contained copepods (1), 2 contained unicellular matter (1), 95 empty ; T.N., under Penlee, near S., over 100 in sample, 100 examined, ca 10 mm., 40 contained mollusks alone (1–3), 1 contained mollusks + copepods (2), 1 contained mollusks + unicellular matter (1 +), 10 contained copepods alone (1–4), 48 empty.

January 28th, 13 in sample, all examined, T.N., Whitsand Bay, near S., ca 11 mm., 1 contained mollusks (1), 7 contained copepods (1), 5 empty.

January 28th, Y.F.T., Eddystone, S.S.E., 4 miles, S., over 100 in sample, 100 examined, ca 10–11 mm., 9 contained mollusks (1–2), 1 contained mollusks + eggs + unicellular (3 +), 1 contained mollusks + unicellular (3 +), 19 contained copepods (1–2), 2 contained copepods + unicellular (1–2 +), 5 contained unicellular matter (?), 47 empty. M., 50 in sample, all examined, ca 10–11 mm., 2 contained copepods (1), 1 contained eggs (1), 2 contained unicellular matter (?), 45 empty. B., over 1000 in sample, 100 examined, ca 10–11 mm., all empty.

February 1st, Y.F.T., Eddystone S. by W. 2 miles, S., over 1000 in sample, 50 examined, ca 10–11 mm., 1 contained mollusks + copepods (2), 1 contained copepods (1), 15 contained eggs (1–4), 3 contained eggs + unicellular matter (1–2 +), 6 contained unicellular matter (3 +), 24 empty. M., over 50 in sample, 50 examined, ca 10–11 mm., 4 contained copepods (1), 6 contained eggs (1–2), 2 contained eggs + unicellular matter (1–2 +), 4 contained unicellular matter (?), 34 empty.

February 4th, Y.F.T., Eddystone S.E., 1 mile, S., between 50 and 100 in sample, 50 examined, ca 11 mm., 6 contained copepods alone (1), 1 contained copepods + eggs (3), 2 contained copepods + unicellular matter (2–3), 1 contained eggs (2), 5 contained unicellular matter (?), 37 empty.

February 7th, Y.F.T., Bolt N.E., Prawle E.N.E., S., 100 in sample, all examined, ca 11 mm., 17 contained mollusks alone (1–6), 8 contained mollusks + copepods (2–5), 10 contained mollusks + unicellular matter (1–3 +), 20 contained copepods alone (1–3), 3 contained copepods + unicellular matter (2–3 +), 6 contained unicellular matter (2 +), 36 empty. (N.B.—Several sand grains and larval trematodes in these.) M., between 100 and 1000 in sample, 100 examined, ca 11 mm. long, 22 contained mollusks alone (1–2), 9 contained mollusks + copepods (2–4), 10 contained mollusks + unicellular matter (3–7), 1 contained mollusks + eggs + unicellular matter (2 +), 8 contained copepods alone (1–2), 1 contained copepods + unicellular matter (2), 2 contained unicellular matter (1–3 +), 29 empty. Many sand grains in these. B., between 100 and 1000 in sample, 100 examined, ca 11 mm., 8 contained mollusks alone (1–2), 5 contained mollusks + copepods (2–3), 1 contained mollusks + unicellular matter (2), 22 contained copepods alone (2–4), 1 contained copepods + unicellular matter (2), 1 contained eggs (1), 1 contained eggs + unicellular matter (2), 5 contained unicellular matter (?), 52 empty.

February 14th, Y.F.T., Rame N.W., Breakwater Light N.N.E., S., between 100 and 1000 in sample, 100 examined, 10–14 mm., 8 contained mollusks alone (2), 3 contained mollusks + copepods (3), 1 contained mollusks + unicellular matter (3), 19 contained copepods alone (1–3), 1 contained copepods + unicellular matter (1 +), 1 contained eggs (1), 3 contained unicellular matter (?), 64 empty. M., between 100 and 1000 in sample, 100 examined, ca 11 mm., 1 containing mollusks alone (1), 9 containing copepods alone (1), 2 containing eggs (1), 1 containing unicellular matter (?), 87 empty. B., between 100 and 1000 in sample, 100 examined, ca 10–11 mm., 1 containing mollusks alone (1), 13 containing copepods alone (1–2), 1 containing copepods + eggs (2), 1 containing eggs (1), 2 containing unicellular matter (2 +), 80 empty.

February 16th, Y.F.T., off the Lizards, S., 12 in sample, all examined, 3 contained mollusks alone (1–2), 1 contained mollusks + copepods (3), 4 contained copepods alone (1), 1 contained eggs (1), 3 empty. M., 12 in sample, all examined, 10–12 mm., 4 contained mollusks alone (1–3), 1 contained mollusks + copepods (2), 1 contained mollusks + eggs (3), 2 contained copepods alone (1), 1 contained eggs (2), 3 empty. B., 3 in sample, all examined, 11 mm., 1 contained a copepod, 2 empty.

February 22nd, Y.F.T., Knap, S., 17 in sample, all examined, ca 12 mm., 7 contained copepods alone (1–4), 1 contained eggs (1), 9 empty. B., 2 in sample, 12 mm., both contained copepods (2).

March 3rd, Y.F.T., L4, B., 9 in sample, all empty.

March 8th, Y.F.T., L4, midnight, B., 20 in sample, 12–23 mm., all empty.

March 20th, Y.F.T., Mewstone N.N.E., Yealm Point E.S.E., B., 12 in sample, all examined, 12–26 mm., 4 contained copepods alone (1–5), 1 contained copepods + eggs (4), 7 empty. Y.F.T., Shagstone N.E., Mewstone S.E., M., 6 in sample, 8–24 mm., 2 contained copepods alone (1–3), 4 empty.

March 31st, 1 in sample, 24 mm., L4, Y.F.T., empty.

We find from these records that out of 1593 Herring examined, 768 came from surface hauls, 269 from midwater and 556 from near the bottom; 978 were empty, 265 from the surface, 169 from midwater and 341 from near the bottom. Thus more than half those from near the bottom and from midwater were empty, and only a little more than a third were empty from the surface. Further, those which had food inside usually contained more when from the surface than from the lower layers. The food of the small Herring is varied, unicellular matter, larval mollusks and small copepods (including nauplii) occurring in about equal proportions. In a former paper on the food of young clupeoids (Lebour, 1921) the writer has shown that larval gastropods are of special importance. It now seems that unicellular matter may be taken just as freely, possibly the mollusks (both gastropods and bivalves) being taken in preference if present. Many of the little Herring contain green material, which is probably the remains of diatoms or flagellates. *Halosphæra viridis* is present as food frequently in one or two hauls. Indeed, it seems that in certain hauls certain food has been taken. At a length of 10 mm. such copepods as *Pseudocalanus elongatus*, *Acartia Clausi* and *Corycæus anglicus* are often taken, usually, however, not more than one to four at a time. These are the common copepods of the plankton at this time, and the larval mollusks are also plentiful. Few diatoms were recognised, amongst these being *Hyalodiscus stelliger*, *Paralia sulcata* and *Coscinodiscus excentricus*, again the common forms in the winter plankton. It was noticed in one surface haul (Rame N.E., 4 m., 21.1.24) that Acartia was very abundant in the plankton, and the little Herring were eating it. Inside the Acartia taken from the Herring were many diatoms—*Paralia sulcata*, *Coscinodiscus* sp., *Thalassiosira* sp., *Thalassiothrix nitzschioides* and small naviculoid diatoms. These are also the essential food of

Pseudocalanus, which is breeding in the early winter months. At this time of year the surface is swarming with small plankton, diatoms, larval mollusks, larval and small adult crustacea. Herrings hatch at the bottom and make their way to the surface where food is most abundant, begin to feed before the yolk has entirely disappeared, at first on unicellular matter, larval mollusks and small copepods, and as they grow live chiefly on copepods. *Paralia sulcata* is a diatom having profound significance from the point of view of food. It may be eaten directly by the baby Herring or indirectly by the small organism serving for its food, larval mollusks, copepod nauplii, adult copepods, which are all common food of the baby Herring, or the adult Herring may eat it indirectly, as it is also a common food of many other copepods (Calanus, etc.) and schizopods, much eaten by the Herring.

Besides the food for the Herring there are many enemies eating the tiny fishes. Even the adult Herring itself, Mackerel and Pilchard were sometimes found full of the newly hatched Herring. Medusæ of many kinds, Pleurobrachia and Sagitta all abound and eat the Herring (Lebour, 1922–23). Taking Paralia as a base we can thus see many food chains reaching to the fishes. Paralia is eaten by Acartia, other copepods, larval mollusks and other crustacea which are eaten by the young Herring, which, in their turn, may be eaten by various cœlenterates, worms and older fishes.

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Temperature and the Viscosity of Protoplasm.

By

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With 1 Figure.

DURING the investigation of amœboid activity (**17**) it became necessary to know the effect of temperature on the viscosity of protoplasm. In the marine amœbæ studied the viscosity appeared to rise as the temperature fell, especially near 0° C. Greely (**9**) has noted similar changes in the protoplasm of fresh-water amœbæ and other protozoa. An increase in viscosity with a fall of temperature also accounts for the parallel effects of cold and loss of water on the protoplasm of various animals (Greely, **7** and **8**).

The amœbæ were not suitable for the quantitative determination of relative changes in viscosity. Weber (**20** and **21**) investigated these changes quantitatively in certain plant cells. He found that the viscosity rose as the temperature fell in the same way that it does in protein solutions, but more rapidly. Perhaps this might be expected since Chick (**3**) has shown that for protein solutions the rise in viscosity as the temperature falls becomes greater as the concentration of protein increases, and the protein concentration in protoplasm is probably high.

However, Heilbrunn (**11**) has shown that the viscosity of sea-urchin eggs falls as 0° C. is approached. In his most recent paper (**13**) he has determined quantitatively the effect of temperature on the viscosity of Cumingia eggs. He finds the viscosity to be maximum near 15° C., and to fall rapidly as the temperature is raised or lowered from this point. Near 0° C. the viscosity rises again very sharply.

Heilbronn (**10**) has obtained somewhat similar results with certain Myxomycetes, though the variations of the viscosity are less marked. He suggests that the viscosity of protoplasm, as opposed to a purely physical system, can undergo " auto-regulation " by the protoplasm itself.

Temperature thus has widely different effects in different cases, and until more have been studied it is difficult to draw conclusions as to the general effect of temperature on the viscosity of protoplasm. But since the viscosity of the constituents of protoplasm must rise as the temperature falls, we would expect the rise in viscosity first mentioned, noted by Weber (**21** and **22**) and others, to be the normal effect of a fall in temperature on protoplasm, unless secondary changes occur. Weber points out that in other cases the peculiar variations of viscosity are probably brought about by such secondary changes (e.g. changes in permeability).

Again, variations in the viscosity must arise from changes in the state of the protoplasm itself, and such changes must have an influence on processes taking place in the protoplasm. But although Heilbrunn (**13**) points out that the viscosity temperature curve for Cumingia eggs is roughly similar to the curve showing the relation of crossing-over in Drosophila to temperature, yet the curves showing the relation of the majority of biological processes to temperature show no relation to such a viscosity temperature curve. For instance, the curve relating temperature to the rate of beat of the Terrapin heart (**19**) is a smooth curve gradually reaching zero near 0° C. : if the state of the protoplasm changed with the temperature, as in Cumingia eggs, one would expect the change to be reflected by a deviation from the observed smooth curve, this deviation being maximal where the viscosity was maximal. On the other hand, the gradual manner in which this and similar curves reach zero near 0° C. is in keeping with the assumption that in most of these cases the viscosity rises regularly as the temperature falls, becoming very great near 0° C.

Material, Methods, and Results.

The viscosity of the protoplasm of the immature eggs of *Nereis diversicolor* (the normal, not the heteronereis form) appears to rise as the temperature falls. The following experiments were performed to determine this rise quantitatively, and thus to find the order of magnitude of the viscosity changes in cases such as this.

The method employed was that of Heilbrunn (**12**). Individual worms, full of eggs, were opened and the eggs washed out with natural sea-water (pH 7·8 to 8·2 in all experiments). During the experiment the eggs were kept in a dish surrounded by water containing ice ; if kept at room temperature the viscosity was found to alter slightly before the end of the experiment. Eggs were taken from the dish and centrifuged in a hæmatocrit attachment to the centrifuge at a given temperature for different periods. The temperature was controlled by enclosing the hæmatocrit attachment in a small inner chamber, surrounded by a large outer chamber containing water (or ice) at the desired temperature. The hæmatocrit attachment was first heated or cooled to the desired temperature, and then rapidly fixed on to the centrifuge spindle in the inner chamber and the apparatus closed. A thermometer entered the inner chamber, and as soon as the desired temperature was registered the eggs were centrifuged. The hæmatocrit attachment was 14·5 cm. in diameter, and in these experiments it was turned at 108 revolutions per second.

After centrifuging for a certain time a black granular cap formed at the lower side of the egg. The time required for this cap to form was used as a measure of the viscosity of the protoplasm. Some eggs form the cap a little more readily than others, so that as the duration of centrifuging increases the proportion of eggs with fully developed caps increases. The change from the condition in which caps are absent to that in which all the eggs have caps occurs over a definite range of the duration of centrifuging.

All intermediate stages of cap development occur. An arbitrary standard was therefore applied above which the cap was considered to be developed. The standard taken was that degree to which the cap must be developed so that it be just visible when viewed normally, though readily visible when viewed in profile. In this way the number of eggs that had developed the cap could be counted for a particular duration of centrifuging. Table 1 shows the results of a typical experiment giving the ratio of capped to uncapped eggs for various periods of centrifuging at different temperatures. The experiments had to be done as rapidly as possible, so the counts were limited to 40 eggs.

TABLE 1.

Eggs of Nereis diversicolor.

Temperature.	Centrifuging time, in seconds.	Eggs not capped.	Eggs capped.	$\frac{\text{Capped.}}{\text{Not capped.}}$	Time for 50% to form cap.
−1° C.	60	0	40	∞	46 secs.
	50	11	29	2·6	
	40	28	12	0·43	
	30	40	0	0	
+10°	30	0	40	∞	23·5 secs.
	25	12	28	2·3	
	20	32	8	0·25	
	15	38	2	0·05	
+19°	25	0	40	∞	18·0 secs.
	20	4	36	9·0	
	15	33	7	0·21	
	10	40	0	0	
+30°	16	1	39	39·0	13·2 secs.
	12	28	12	0·43	
	10	37	3	0·08	
	8	40	0	0	

By interpolation an approximate value for the time required for 50% of the eggs to become capped was determined for each temperature (see last column). These times give a relative measure of the viscosity at that temperature.

The difference between the logarithm of the time required for the cap to form at any temperature and the logarithm of the time taken at 10° C. gives the logarithm of the relative viscosity compared with that at 10° C. By taking the mean of these logarithmic differences from several experiments for a particular temperature, the mean viscosity at that temperature relative to the viscosity at 10° C. is found.

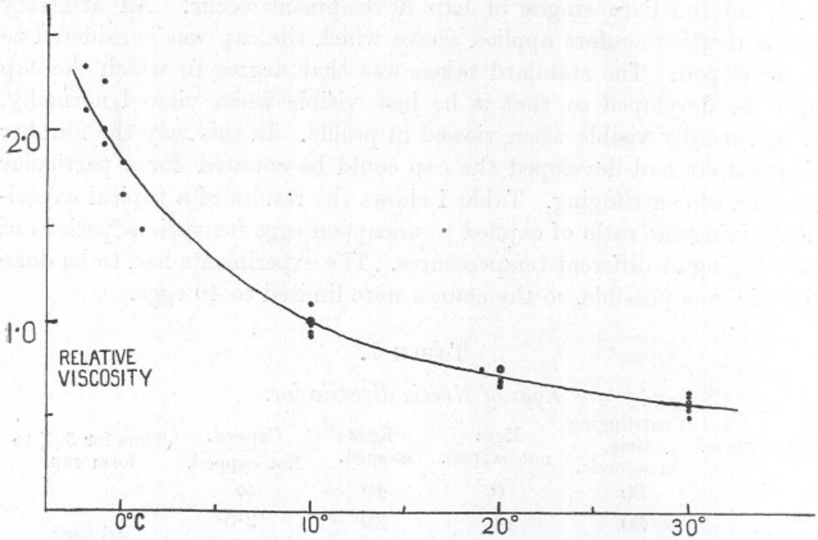

Fig. 1.—Curve showing relative viscosity of Nereis eggs at different temperatures. The curve is the mean of eight experiments, the particular values of which are plotted about the curve. Several of the values fall upon the same point.

Table 2 gives the mean relative viscosity at different temperatures from eight experiments, taking the relative viscosity at 10° C. as unity. Fig. 1 shows the curve obtained by plotting these mean values against

Table 2.

Nereis eggs.		Nereis eggs.		Protoplasm of phaseolus (**21**).
Mean temperature.	Mean relative viscosity.	Temperature.	Q 10.	Q 10.
−0·7° C.	1·95			
+10·0	1·00	0°–10°	1·84	1·51
20·0	0·71	10°–20°	1·40	1·41
30·0	0·57	20°–30°	1·26	1·37

the temperature. The individual values obtained in each experiment have been reduced proportionally and plotted about the curve to indicate the order of accuracy.

Table 2 also gives the calculated temperature coefficients, and, for comparison, the temperature coefficients found by Weber (**21**) for the viscosity of the starch sheath cells of *Phaseolus multiflorus.*

It will be seen that in both plant protoplasm and in the protoplasm of Nereis eggs the viscosity rises in a similar manner as the temperature falls, though the rise is more rapid in the latter. We are probably justified in assuming that in cases where the viscosity of protoplasm rises with a fall in temperature, the rise is of the order of magnitude shown in the above cases.

Discussion.

The velocity of a chemical reaction taking place in protoplasm must be affected by changes in the conditions of the protoplasm itself. Since no account has been taken of these changes, the validity of applying Van't Hoff's law to the rate of biological processes has been questioned (**1**) (**16**). Even if it be assumed that a chemical reaction does underlie these processes, the conditions of the protoplasm must modify its velocity considerably, because the temperature coefficient of these processes is not almost constant as it is in most chemical processes (Krogh, p. 98 (**14**).)

Various causes have been suggested to account for this variation of the temperature coefficient of biological processes. Snyder (**20**) and Rogers (**18**) have suggested that in even the simplest processes several chemical reactions with different reaction velocities are involved. It seems unnecessary to assume this until full allowance can be made for temperature changes in the conditions of the protoplasm.

It has also been suggested that limiting factors such as the availability of oxygen (**14**) may affect the velocity of underlying processes. If the temperature coefficient of the oxygen consumption of Mytilus gills is corrected for the diminished solubility of oxygen in sea-water at high temperatures, the temperature coefficient becomes constant between 10° and 30°. Gray (**6**) has suggested, tentatively, that this may be of significance. But the rate of oxygen consumption of unstriped muscle (**5**) does not vary with the oxygen tension, although the effect of temperature on the rate of oxygen consumption appears to be similar to its effect in the case of Mytilus gills.

It is therefore of great importance to determine how variations in the conditions of the protoplasm will affect the velocity of processes occurring in it. Weber (**21**) points out that changes in viscosity are directly determined by these changes of conditions in the protoplasm. Moreover, Snyder (**20**) has drawn attention to the suggestion of Van't Hoff that the temperature coefficients of even simple chemical reactions should be corrected for changes in the viscosity of the medium.

The temperature coefficient of a simple chemical reaction is not quite constant : it falls as the temperature rises, but to a smaller extent than in the case of most biological processes. Snyder shows that if the temperature coefficient of a simple chemical reaction (e.g. $H_2O_2+2H1=2H_2O+1_2$) is corrected for changes in the viscosity of the medium (water), the corrected temperature coefficient becomes almost constant. It seems probable therefore that the temperature coefficients of biological processes should be corrected for changes in the viscosity of the protoplasm, or of that part of the protoplasm in which the processes occur : and that by correcting for changes in viscosity we are approximately correcting for changes in the conditions of the protoplasm.

It is possible that certain structural changes might occur in the protoplasm for which no allowance was made by correcting for viscosity, although they might affect processes taking place in the protoplasm. But a particular case may be noted here. In certain cases biological activities are probably unaffected by changes in the viscosity of the protoplasm. Such a case is the development of tension by striped muscle during isometric contraction. In this case the tension developed seems to depend on the amount of the antecedent chemical reaction (production of lactic acid) rather than on its velocity, which alone would be affected by the viscosity. Nevertheless if structural changes capable of affecting biological processes occurred in the protoplasm we might expect them to affect the degree of tension developed in this case.

Now, the tension developed by muscle appears to be a surface effect (**2**). The tension developed at different temperatures during isometric contraction seems to show that the effect of temperature on the underlying physical process is unaltered : the temperature coefficient is small and negative (**4**). But if a change of temperature produced structural changes great enough to affect biological processes, they would probably be great enough to affect the temperature coefficient in the case considered : they do not appear to do so. There is some probability, therefore, that viscosity is the chief modifying factor in biological processes.

To correct the temperature coefficients of various processes for changes in viscosity with temperature demands knowledge of these changes for the particular protoplasm in each case. These are not known ; but if the relative changes are of the order of those occurring in Nereis eggs we should find that the temperature coefficients of various processes would tend to become constant if corrected by viscosity values obtained from these eggs. There will, however, be greatest divergence near 0° C. The viscosity rises rapidly in this region, and if in other kinds of protoplasm, this rise occurred a little earlier or later than it does in Nereis eggs, the correction would be imperfect. Table 3 gives the temperature coefficients of ciliary, heart and amœboid activities corrected by factors derived from the viscosity changes in Nereis eggs. It will be seen that the greatest divergence occurs near 0° C. The enormous rise in the temperature coefficient near 0° C. of, for instance, the rate of beat of the Terrapin heart, may indicate that the viscosity of the protoplasm rises far more rapidly in this case than it does in Nereis eggs.

TABLE 3.

Temperature Coefficients corrected for Changes in Viscosity.

$$\text{Corrected Q10} = \frac{\text{Q10 observed}}{\text{Q10 viscosity}}$$

Temperature range	0°–10°	5°–15°	10°–20°	15°–25°	20°–30°	22·5°–32·5°
Q10 Nereis eggs	1·84	1·59	1·40	1·30	1·26	1·24
Q10 observed	*3·1*	*2·7*	*2·3*	*2·15*	*1·95*	*1·92*
Ciliary activity—						
(6) Q10 corrected	1·68	1·70	1·64	1·65	1·55	1·55
Q10 observed	*10·2*	*3·5*	*2·2*	*2·1*	*1·9*	*1·9*
Rate of Terrapin heart beat—						
(19) Q10 corrected	5·5	2·2	1·57	1·61	1·51	1·53
Temperature range	0°–5°	5°–10°	10°–15°	15°–20°	—	—
Q10 observed	*16·9*	*3·19*	*2·31*	*2·04*	—	—
Velocity of Amœba—						
(17) Q10 corrected	8·55	1·87	1·53	1·53	—	—

In view of the previous considerations, the corrected temperature coefficients are as constant as could be expected. The values of the corrected temperature coefficients are of the order of the corrected values for chemical reactions. For the reaction $H_2O_2+2H1=1_2+2H_2O$ with an observed temperature coefficient about 2, the corrected temperature coefficient is 1·56 (**20**).

It has been mentioned that Heilbrunn (**11**) found that the viscosity of sea-urchin eggs does not rise, but falls, as 0° C. is approached. Perhaps it is significant that Loeb (**15**) found the temperature coefficient of the rate of oxidation in sea-urchin (Arbacia) eggs to be approximately constant, instead of rising as the temperature falls, as in most biological processes.

It may be pointed out finally that the rate of most biological processes gradually reaches zero near 0° C. This is in keeping with the assumption that the viscosity of a watery solution such as protoplasm is important in modifying the rate of these processes.

We may conclude that variations of viscosity of protoplasm with temperature are probably of the order of magnitude required to make the corrected temperature coefficients of biological processes constant; and that the value of the corrected temperature coefficients would probably be of the order of the corrected temperature coefficients of chemical reactions.

SUMMARY.

(1) The effect of temperature on the viscosity of the protoplasm has been determined in the unripe eggs of *Nereis diversicolor* by the centrifuge method.

The viscosity rises as the temperature falls, the rise becoming rapid near 0° C.

(2) These changes of viscosity with temperature are similar to those described by Weber (**21**) in the protoplasm of certain plant cells.

(3) Attention is drawn to the fact that the temperature coefficients of biological processes should be corrected for the viscosity of the protoplasm in which they occur.

(4) It is shown that the relative changes of protoplasmic viscosity with temperature are probably of the order required to make the temperature coefficients of biological processes constant when corrected for the viscosity factor.

(5) The magnitude of the temperature coefficients of biological processes when corrected for viscosity changes is probably of the same order as that of the temperature coefficients of a chemical process when corrected for changes in the viscosity of its medium.

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The Moulting and Growth-stages of Gammarus, with Descriptions of the Normals and Intersexes of *G. chevreuxi.*

By

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Ray Lankester Investigator for 1920.

With Plates I to XXI* and 4 Figures in the Text.

CONTENTS.

INTRODUCTION.

MANY of the difficulties found in naming and classifying Crustacea are due to the extraordinary modifications caused by growth and sex, and the confusion arising from our lack of knowledge of these developmental stages has led to many errors. In the group Amphipoda, for example, the different growth-stages of a species may be, and often are, described

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* The whole cost of producing the blocks from which the plates illustrating this paper have been printed has been met in part by the author and in part by special donations given for the purpose.—ED.

as so many different species, or sometimes even as different genera. A striking instance of this is found in the widely distributed species *Jassa falcata*, which has more than thirty synonyms.

In the hope of throwing some light on the question of development which might be applicable to the group generally, the work described in this paper was commenced in 1909. If, as seemed practicable, the life-history of one species could be worked out, and some of the problems of development solved, the results could then be applied to the other members of the group and might even perhaps add a little to our knowledge of Crustacea as a whole. Much of the work described in this paper was done whilst holding the Ray Lankester Investigatorship, and my thanks are due to the Trustees for enabling me to carry it on.

When the work was begun nothing was known as to the length of life of an amphipod, its moulting periods, the length of time taken to reach maturity, the length of the breeding period, or the incubatory period of the eggs, nor at what stage of development the sexes could first be recognised. The last point is of special importance to systematists, because in species-work as a rule the distinctions are based on the secondary sexual characters, and though there is usually a marked difference between male and female at sexual maturity, yet in the young stages the sexes are often indistinguishable. I hoped to find characters by which the sexes could be distinguished on hatching, and also to be able to trace other characters common to the young as well as to the adult which could be used in establishing the specific identity at each stage of growth.

Quite recently this question has assumed a greater importance by reason of the appearance of the phenomenon of intersexuality in one of the species under observation. Both male and female intersexes were found, but were not recognised as such until nearly mature. Experiments were therefore started to find the early stages of the intersexes, to compare them with the growth of the normal animals and to see whether or not these differed in any degree from the normal.

It is impossible to study the different growth-stages directly from the living individual, for although an amphipod is a hardy creature and can be kept under the microscope without water for a short examination, the risk of injuring it by exposure to the air is too great, especially in its feeble condition after moulting. Apart from this danger, there is also the impossibility of getting clear definition of the detail, owing to the incessant jerking and wriggling movements of the struggles to escape from the transmitted light.

It soon appeared that the only way in which the problem could be studied was by examination of the moults or cast skins of the different growth-stages. The animals would have to be kept under observation and the moults collected when cast. In order to do this, it became necessary to find a species which would live in laboratory conditions.

The *Jassa falcata* just referred to was first chosen. It is very common all round Plymouth Sound on the buoys, and living near the surface of the water as it does, and making its "nests" at water-level it seemed as if it might be easy to accustom it to life in shallow water in the Laboratory. Various methods were tried, but it was found impossible to keep the Jassa alive for any length of time, and in the end the plan was adopted of picking out a number of animals at one stage of growth (judged by size and development), keeping each in a separate pot till it moulted, and then preserving each animal with its moult. The stage of growth attained would then be noted and a fresh supply of Jassa at this stage would be set out for the next moult. Several hundred moults were obtained by this method, but on examining them it was seen that the results would prove of small value, as it was not possible to judge whether the moults were from immature males or from immature females, nor could the limits of individual variation be traced and defined. It was evident that the only way to get accurate information was to obtain the complete series of moults from *one* animal, the male series from one male and the female from one female.

After many efforts to establish Jassa in the Laboratory it had to be given up, and more suitable species sought for. These were fortunately found in 1912 in dredgings from the ditches which drain Chelson Meadow, a salt marsh near Plymouth reclaimed from the tidal part of the Plym a little more than a century ago, and protected from the tide by an embankment, the accumulation of drainage water being emptied through sluice-gates into the river only at rare intervals. Three species of Gammarus were taken, *G. pulex* in the freshwater stream which runs in at the far end of the meadow, and two species in the brackish water of the ditches, *G. duebenii* and a new species, *G. chevreuxi*. With these the moulting experiments were commenced, and later, two other Gammarus were added, *G. locusta* and a littoral species not yet named. *G. duebenii* had to be given up because of its cannibal propensities, but good series of moults were obtained from the other four. *G. chevreuxi* soon developed a remarkable power of producing mutations especially in connection with the eye, its shape, colour, etc. Descriptions of some of these have been published, and because of the work already done, and the new mutations which are still arising, and also because of the appearance of intersexes amongst the normal males and females, this species is the one chosen to illustrate the moulting and growth of a Gammarus. The most striking mutation, the loss of one or of both eyes, will be described in a later paper.

The differences between the species studied are very marked, in the number of moults and the time taken to reach maturity, in the size and number of the eggs, in the time of incubation of the broods, and in the time between the hatching of the young and their extrusion.

In *G. locusta*, for example, the female lays a great number of very small eggs, as many as 143 being counted in one brood. In summer the eggs take from 9 to 10 days to hatch; the young, which are exceedingly small, are extruded from the pouch almost immediately, and the female moults and lays a fresh batch the same day. The young ones moult at short intervals till sexual maturity is reached, and then at longer periods. Eggs are laid after the twelfth moult. Fifty-two of the large brood above mentioned were placed together in a jar, through which a strong current of air was kept bubbling; of the 36 which survived to maturity the first male became mature at 35 days, and the first broods of eggs were laid on the 38th day. In order to obtain exact data of the moulting periods, 32 of the others were set out singly in finger-bowls, each with air-circulation gentle in this case so as not to injure the moults. Very few of these survived, 1, a male, moulted at intervals of 5, 3, 4, 3, 4, 3, 3, 4, 4, 5, 4, and 6 days, dying after the twelfth moult. Another, a female, moulted at intervals of 2, 4, 4, 3, 5, 5, 5, 5, 4, 4, and 5 days, and then after a period of 10 days moulted and laid eggs, no male being present.

The male *G. locusta* carries the female for one or two days before the young hatch. The female, as has just been shown, can, however, lay eggs without a male being present; in one such batch, 70 eggs were counted, but they were evidently infertile, and were thrown off later.

In *G. chevreuxi*, on the other hand, the female never lays eggs unless mated. The eggs are much larger and fewer in number than in *G. locusta*. Well-grown *G. chevreuxi* females have from 30 to 40 in a batch, the highest number recorded in these experiments being 63. They take longer between moults, lay eggs after the seventh moult, and keep the young at least 24 hours in the pouch before extrusion. The male carries the female for several days before the young hatch. Sometimes moulting takes place and a new batch is laid within a few hours of the extrusion, sometimes 2 or 3 days may elapse.

This species lives well in stagnant water; *G. locusta*, on the contrary, requires a continuous supply of air. *G. pulex* also will live in stagnant water, but does better when put under the "air-circulation."

G. pulex females, like the *G. chevreuxi* females, never deposit their eggs unless mated. The eggs are very large and few in number, usually from 12 to 18 in a batch, the highest number recorded in the experiments being 28. They take from 16 to 17 days to hatch in summer conditions. The young, which are large, are kept for about a day in the pouch after hatching, and then extruded all together. The summer experiments were not successful in that none of the young survived to maturity. The early moults were at intervals of 5 to 7 days. The winter experiments, as was to be expected, gave much longer intervals between moults. One animal, a male, moulted at intervals of 12, 16, 14, 16, 18, 21, 14, and 16 days, another of the same brood, a female, at 13, 16, 12, 16, 18, 18, 16, 17, 17, and 23 days. Eggs are laid after the tenth moult.

In the littoral species (*Gammarus* sp.) the eggs are very large and few in number, only about 8 to 12 in a batch. The young hatch in about 12 to 14 days in the summer, but are kept in the pouch for several days, often having their first moult before being extruded. Sometimes the female will extrude them all together in about 4 or 5 days, sometimes she keeps them till they have all moulted and extrudes them and the moults together, or, and this is more usual, she will let them out one or two at a time, taking more than a week to do it. In one case the female kept some of the young for 13 days, and in another, one of the brood was retained for 17 days and had at least two moults before emerging. The incubation lasts for 12 to 14 or 15 days in summer, but the moulting period of the female is from 24 to 28 days. It will thus be seen that in this species the "incubatory periods," i.e. the periods from the time the eggs are laid to the time the young leave the egg (hatch), do not coincide with the "moulting periods," i.e. the periods between the laying of successive batches of eggs, which are always preceded by moulting. Indeed, it almost looks from the figures as if one moulting period in this species corresponds with two moulting periods in others, e.g. *G. chevreuxi*, the second of the two periods being occupied in protecting the already hatched young inside the brood pouch. The difference in habitat may account for this. These animals dwell on the shore fairly high up, under stones which are exposed for some hours between tides ; the other three species described live in the water, *G. pulex* in freshwater streams, *G. chevreuxi* in brackish water ditches, and *G. locusta*, a pelagic species, ranges from the water near the shore to the open ocean.

It is difficult to give the number of days to the first moult of the young in this littoral species of Gammarus. One kept for 5 days in the pouch, after emerging moulted at intervals of 8, 8, 9, 8, 10, and 12 days, and another at 8, 9, 10, 9, 9, and 9 days. None survived to maturity, owing to the difficulty of feeding them. They refused the rotted-leaf diet of the other species, and the minced shrimp with which they were fed often caused fouling of the water, pieces being carried off under the stones and so overlooked. The experiments could not be regulated easily as small stones had to be provided for shelter, and the pans had to be kept tilted to allow the animals to leave the water when they wished.

The number of moults to maturity varies with the species ; in

G. locusta eggs are laid after the twelfth moult, in *G. pulex* after the tenth, and in G. *chevreuxi* after the seventh. It is difficult to say precisely at which growth-stage the broodplates are first developed. The position of the broodplate (attached to the first joint of the leg, between the gill and the insertion of the second joint where the leg is pulled out in moulting) renders it very liable to injury during the act of moulting. This is especially so in the early stages, the cuticle being then too thin and delicate to retain its shape.

In *G. pulex,* where the cuticle is firmer and more substantial than in either *G. locusta* or *G. chevreuxi,* broodplates have been traced in four growth-stages preceding maturity. The development is as follows: in Moult 7 they appear as minute, rounded leaf-like plates, with margins entire; in Moult 8 they have lengthened, and increased to three times the size; in Moult 9 rudimentary hairs have developed on the margins (cf. broodplate in the upper figure of Text Fig. 4); in Moult 10 the broodplates are very large, the chitin is hard, the rudimentary hairs more numerous and more noticeable, showing under a high power as tiny conical excrescences. In the next stage sexual maturity is reached, and the broodplates are fully developed, with long fringing hairs. Three stages have been found in *G. locusta,* but in this species the cuticle is so thin in the young animals that it would be difficult to trace the earlier stages even if they were present. In Moult 10 the broodplates are very small and rounded, with margins entire; in Moult 11 rudimentary hairs appear on the margins; in Moult 12 the development is the same as in the tenth moult of *G. pulex*; and in the next stage sexual maturity is reached, and the broodplates are fully developed. Three stages have been traced in *G. chevreuxi* also. In this, the smallest of the three species, the broodplates are microscopic in Moult 5, round, with margins entire; much larger in Moult 6, with rudimentary hairs clearly indicated; in Moult 7 the hairs are seen as conical points on the margin, sometimes pushing out free of the cuticle, on the posterior margins. At the eighth growth-stage the animal is sexually mature, and the broodplates are fully developed. (See Plates III and IV, *Jour. Mar. Biol. Assoc.*, XII, 3, 1921.)

From the results set forth in this paper, it will be seen: (1) That the species sufficiently alike in structure to be included in one genus may yet differ widely *inter se* in many essential points connected with their reproduction; (2) that the bars to the interbreeding of even the most closely allied species would appear to be insuperable; and (3) that although different species may and do live together, and breed in the same place, their distinctive specific characters are preserved unchanged.

It seems important to emphasize these points, because of the help they may give in solving the difficulties systematists encounter in dealing with collections of amphipods taken in the same locality. The genus Gammarus, with which we are concerned, is an instructive example of the confusion of species. Species which have been considered distinct by some observers are regarded as one "variable species" by others, and have been grouped together under one name as a "type" and its "varieties"; or again, two or more distinct species have been described as one species with various "intermediate forms" between the two extremes.

This confusion as to the proper determination of species has risen from lack of knowledge of the life-histories of the animals. On p. 377 I have dealt with a hitherto unsuspected but fruitful cause of much of the difficulty, viz. *the different breeding forms of the male*. So different, indeed, are they that an observer who did not know their life-history would be justified in separating them into distinct species (see figures of M.8 and M.10 of the male, Plates X and XII).

The intermediate forms referred to are probably only the several growth-stages of the various species, and not, as the authors appear to consider them, new forms produced by the intermating of these species.

DESCRIPTION OF A GAMMARUS.

It may be of service here to give a brief recapitulation of the structure of an amphipod of the genus Gammarus, using the terminology established by Stebbing (*Amphipoda.* Das Tierreich, Vol. XXI, 1906).

The body of a Gammarus (Text Fig. 1) is elongate and laterally compressed, and consists of head, peræon, and pleon. The *head* carries 2 pairs of antennæ, the eyes, and the mouth-organs; the *peræon* is divided into 7 segments, and the *pleon* into 6 segments and the telson. Each of the segments bears a pair of legs, those of the peræon 7-jointed with large expansions of the first joints called *sideplates.*

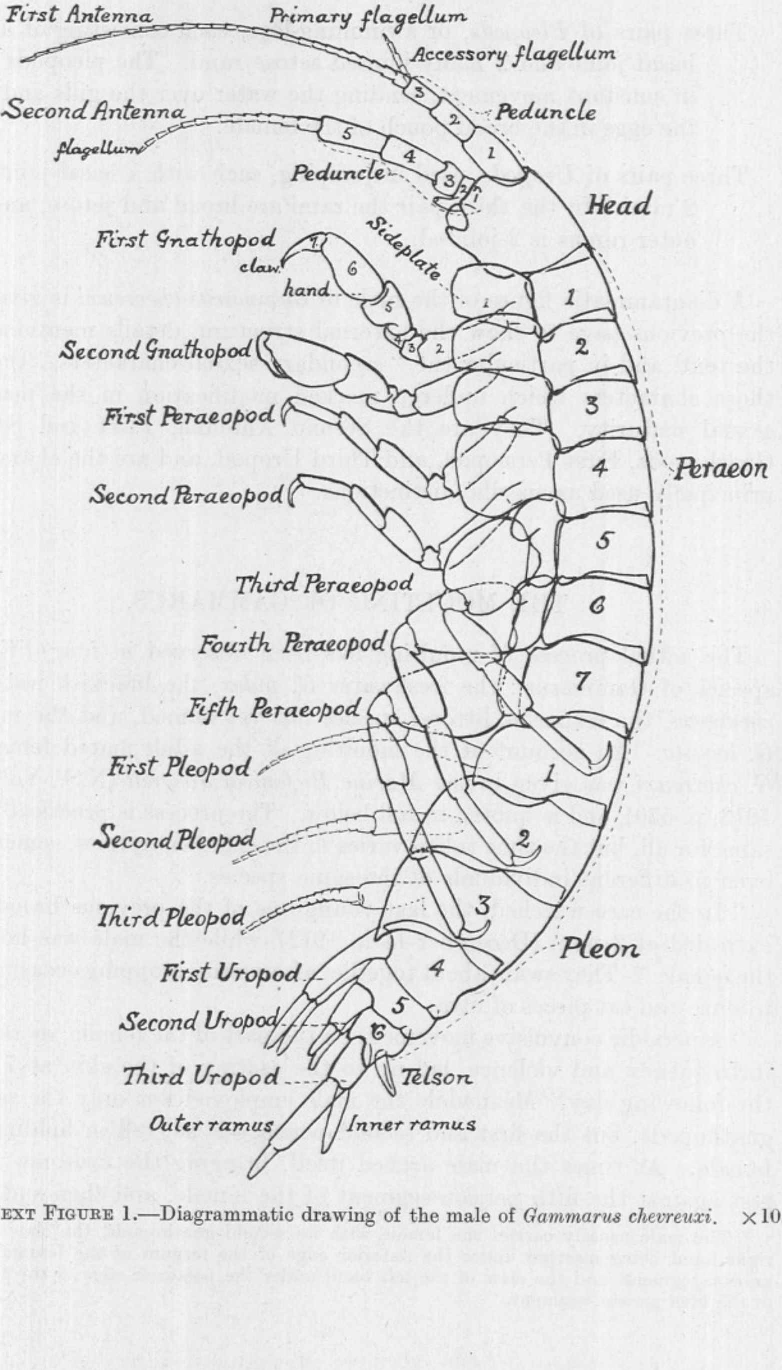
Taking the appendages in order, they are as follows :—

First Antenna, with a 3-jointed peduncle, and 2 flagella, a long many-jointed *primary,* and a much shorter *accessory.*

Second Antenna, shorter than Antenna 1, with a 5-jointed peduncle and 1 many-jointed flagellum.

Mouth-organs, *mandibles, maxillæ,* and *maxillipeds,* not dealt with in this paper.

First and Second Gnathopods, used as grasping organs, with expanded hands, much more developed in the male than in the female (see p. 360).



TEXT FIGURE 1.—Diagrammatic drawing of the male of *Gammarus chevreuxi*. ×10.

Five pairs of *Peræopods*, or walking-legs, the first two pairs bent forward at the third joint, the three hind pairs bent backward.

Three pairs of *Pleopods*, or swimming-legs, each consisting of a long basal joint and 2 many-jointed setose rami. The pleopods keep in constant movement, sending the water over the gills and over the eggs in the brood pouch of the female.

Three pairs of *Uropods*, used in jumping, each with a basal joint and 2 rami. In the third pair the rami are broad and setose, and the outer ramus is 2-jointed.

A diagrammatic figure of the male of *Gammarus chevreuxi* is given on the previous page to show the external structural details mentioned in the text, and in particular the " secondary sexual characters," that is, those characters which undergo marked modification in the male at sexual maturity. They are the Second Antenna, First and Second Gnathopods, First Peræopod, and Third Uropod, and are the characters principally used as specific distinctions.

THE MOULTING OF GAMMARUS.

The actual process of moulting has been observed in four different species of Gammarus : the freshwater *G. pulex*, the brackish water *G. chevreuxi*, the estuarine littoral species not yet named, and the marine *G. locusta*. An account of the moulting of the adult mated female of *G. chevreuxi* was given in the *Marine Biological Journal* (N.S., Vol. IX, 1913, p. 550), and is quoted in full below. The process is practically the same for all, but the time taken varies in the different species, sometimes even in different individuals of the same species.

" In the case watched, the last young one of the previous brood was extruded at 2 p.m. (December 14th, 1912), while the male was holding the female.* They swam about together afterwards, stopping occasionally to seize and eat pieces of ulva.

" A periodic convulsive movement on the part of the female, increasing in frequency and violence, led up to the casting of the skin at 7 p.m. the following day. Meanwhile the male employed not only the second gnathopods, but the first and second peræopods as well in holding the female. At times the male arched itself, bringing the urosome up to rest against the fifth peræon-segment of the female, and then suddenly

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* The male usually carries the female with its second gnathopods, the claw of the right hand being inserted under the anterior edge of the tergum of the female's first peræon-segment, and the claw of the left hand under the posterior edge of the tergum of the fifth peræon-segment.

straightened out, rasping the uropods along the female's cuticle. During the whole time the male kept the lower antennæ bent over the head of the female, so touching both pairs of her antennæ. About two hours before the moult the female commenced a series of violent rapid jerks, bringing the head and urosome together, and then straightening suddenly, at intervals stiffening the body in the form of a comma, with the head bent downwards, and the body moving with a sort of convulsive tremor. Finally, the male ceased swimming, and they both lay quiet, while the female, helped by the male, freed the head from the old cuticle with the gnathopods. This process and the ensuing rest occupied not more than five minutes. Then the male suddenly arched the body as before and, in straightening again, pushed off the posterior portion of the moult with its uropods, assisted by the upward heaving of the female's body. It did not relinquish its hold for a moment. After moulting the female lay absolutely still, without even a movement of the pleopods, while the male kept up a steady current with his. In a few minutes they commenced to swim as before."

To this description a few more particulars may be added. It can nearly always be seen when a moult is imminent, especially in the young. The animal is very sluggish, keeping under the leaves out of the light, and not feeding much ; its colour becomes duller, and the whole body looks opaque. As the time of sloughing draws nearer, a thick secretion, probably lubricative in action, begins to ooze out between all the joints : in one very difficult case which was watched, the secretion was seen to ooze out of the pleon and hind peræopods first ; two hours later, out of the peræon and antennæ, by which time the body was drawn up inside, leaving the hindermost part of the cuticle empty and quite transparent. During moulting the animal lies on its side, moving spasmodically with a sort of convulsive tremor, every now and again bringing its head and tail together, and then straightening out suddenly with a jerk, apparently trying to loosen the old cuticle. It varies this by swimming rapidly in circles, with the dorsum inwards. At last the skin cracks just behind the head dorsally, the crack extending until the whole of the posterior margin of the head is free. The animal pulls vigorously at the cuticle covering its head, drawing the gnathopods down the antennæ, the body meanwhile pulsing and heaving against the dorsal crack, and so widening it. The cuticle then splits on each side along the length of the peræon at the junction of the sideplates. The final action in the very young is exceedingly rapid, taking barely a second to accomplish. The little animal gives a sudden heave, arches up its body, and squeezes out backwards through the dorsal crack, freeing the gnathopods last of all as it emerges.

In a good moult the skin comes off whole, with the appendages still in place. The sideplate attached to the first joint of each peræopod splits down its internal face, a semicircular flap of skin opens at the place of insertion of the second joint, and the six free tapering joints are easily drawn out through this opening, leaving the old cuticle intact. The sloughing of the gnathopods, however, is much more difficult. In these the terminal joints are dilated distally, and having to be pulled out through narrow constricted openings the old cuticle generally gets badly torn. Even in a "good moult" the skin of the 2nd, 3rd, and 4th joints is ripped open lengthways and that of the 5th and 6th is split; but in difficult moults the old skin of the gnathopods is torn to pieces by the animal in its struggles, the mouth-organs often being used in the effort of stripping it off. The skin on the gills is much thinner and flimsier than on any other part of the body, and is always crumpled or torn in moulting. So also is the cuticle of the broodplates of the immature female, especially of the small ones found in Moults 5 and 6 of *G. chevreuxi*, which are often pulled out like the everted finger of a glove. The broodplates in the adult, on the contrary, are very stiff with a thick chitinous cuticle.

The moulting of the older animals takes a longer time, especially in the preparatory stage. The head-portion is pulled off first with the antennæ and mouth-organs attached, as well as the lining of the œsophagus, the foregut, and the stomach with its several chambers, fringing hairs and spines. Then the body with the peræopods is drawn out of the posterior part, and lastly, the gnathopods are pulled out.

Occasionally in a delicate or unhealthy animal a part of an antenna or one or two gills will be torn off in the struggle and will be found in the sloughed skin. The antennæ are always regenerated, but I do not think the gills are. I have occasionally found deformed gills or very tiny ones present in dead animals, probably due to disease, but it appears to be hopeless to try and find out anything about the gills from the cast skins, owing to their crumpled and torn condition.

It may be as well to refer here to the difficulties encountered in getting a series of moults from one animal. It has proved impossible to obtain a complete series of perfect moults from any one individual. Over 3000 moults were collected from *G. chevreuxi* alone, and incredible as it seems, out of that number there was not one single perfect series of either male or female. One reason is that the condition and substance of the chitin varies through the animal's life, probably with its health, some moults being fairly thick and easily sloughed off, while others may be so thin in texture that they are cast piecemeal in flakes, or crumpled out of all shape. Again, moulting is sometimes very difficult, perhaps owing to insufficiency of the lubricative secretion; in such cases the cuticle of the head and of the gnathopods, particularly of the latter, will be torn to fragments by the animal in its efforts to get rid of it. But the chief cause of the difficulty lies in the fact that the *animals eat their moults* almost directly after ecdysis. Moulting, as far as my observation goes, takes place more often at night than in the daylight, and if it should happen early in the night, there will be very little, if any, of the sloughed cuticle left by the morning. The gnathopod cuticle, the last portion to be freed, is almost invariably eaten first. The males are more vigorous than the females, and more destructive of their moults, so naturally the series of male moults is more imperfect than that of the female ones.

Before passing on to describe the moults themselves, reference must be made to a picturesque legend which has grown up around *G. locusta.* It was originated by Spence Bate* in the days before the problems connected with the reproduction of amphipods were investigated, but that it still finds credence is shown by its being quoted in recent popular works on marine animals. The story which Spence Bate (l.c., p. 380) calls "one of the most interesting instances of maternal solicitude yet recorded among animals so low down in the scale of physical arrangement" is, briefly, that the mother Gammarus protects the young for some time after they are hatched until "as they grow older they obtain more confidence, and quitting, forget the anxious care that guarded them in their early hours"; that the young ones on hatching swim about keeping close to her as she moves slowly along; and that at the approach of danger, or at any alarm, *they rush back to the pouch* for shelter. The parent it was stated would then get excited and swim quickly about, and later when the threatened danger had passed, the young would emerge again and swim about as before.

Now, a moment's consideration of the structure of the pouch shows the impossibility of such a thing ever happening. The female Gammarus has 4 pairs of broodplates, 1 pair on each of the peræon-segments 2, 3, 4, and 5. The plates are fringed with long delicate hairs, which interlace and form a continuous pouch, open at both ends where the plates are separated by the width of the body. The young are very active when hatched, and can be seen moving about in the pouch, changing places, and endeavouring to push out when the mother relaxes the pressure on the broodplates. I have kept numerous amphipods of different genera under observation in the Laboratory, but I have never seen a young one re-enter the pouch after once getting clear of it. They will come partly out of the front opening, especially when the female is feeding, to share the food, but the lightest downward movement of her head sends them in again. They sometimes crawl on their sides out at the back end of the pouch on to the sternum of the 6th and 7th peræon-

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* *A History of the British Sessile-eyed Crustacea*, by C. Spence Bate and J. O. Westwood. Vol. I, p. 380; Vol. II, p. xlv. London, 1863, 1868.

segments clinging tightly with their claws, but the first beat forward of the pleopods drives them back to safety inside. Should their clutch, however, not be sufficiently firm, they will be swept off in the swirling current made by the pleopods, and after that there is no return possible. The action of the pleopods alone would prevent it, and when it is remembered that the female casts the whole of the skin and fills the pouch again with eggs within a short time of hatching the brood, the impracticability of these young re-entering will be plainly seen. In *G. locusta*, the species mentioned by Spence Bate, the process (hatching, extruding, moulting, and laying) is speedier than in most of the species, and is usually completed in a day.

Summer and Winter Broods.

Amphipods breed long before they reach the maximum size of the species. The number of growth-stages from hatching to sexual maturity appears to be different not only in the different genera, but different even in the different species of any one genus.

In *Gammarus chevreuxi* the complete series to sexual maturity numbers 7, for both the normal male and the normal female. The animals mate after the sixth moult, and the eggs are laid and fertilised after the seventh moult. From sexual maturity onwards to the maximum of growth there is very little change in the moults of the normal female, except for the increase in size and in the number of the setæ. The normal male has *two more moults* before assuming the definitive "adult male" characters, but like the female after reaching this stage it does not change except for the increase in size and in the number of setæ and coiled hairs.

The actual number of moults before the sexual characters appear in the intersex is not known, but there are apparently more than in the normal. Of the hundreds of young from the Irregular Stock set out for moults only one intersex survived the fifth moult, and this one is figured, six stages in all. The stage of development reached was not nearly as advanced as that of the normal at the sixth stage.

As *G. chevreuxi* is a species which breeds all the year round, the broods laid in the summer have been compared detail for detail with those laid in the winter. The stages of growth were found to be identical, even to the number and position of the hairs ; but, as might be expected, the summer broods reach maturity at a much quicker rate than the winter ones. They take, in fact, only about half the time, 34 to 40 days in the hot weather as compared with 74 to 99 in the cold months.

Broods kept in the Laboratory sometimes vary a good deal in the time taken to reach maturity. No two broods are alike in this respect, a later brood sometimes maturing before an earlier brood from the same parents, and kept as far as one can see under precisely similar conditions.

As a rule, all the individuals of any one brood will accomplish the first moult on the same day, and sometimes the second moults too will all occur together, but from the third moult when a great increase in activity can be noted, the strong ones go ahead and the weaker lag behind, although in the final result maturity is reached within a few days by all the members of the same brood.

The figures of the normal animals are taken chiefly from males and females of three summer broods of the F_2 generation from the Wild Stock first brought into the Laboratory. The normal female series is nearly perfect, but no complete series of any one male could be found out of all the moults of hundreds of animals which were examined. The first seven moults of the male series are from the summer broods; but the three last are from the winter broods, and were taken from two males of nearly the same age. Unfortunately K.6, the male from which the figures of the eighth and ninth were drawn, had its tenth moult during the night, and had eaten part of it before the morning examination of the pots took place. Another male a day younger, which had been compared stage by stage with K.6 and which was due to moult that day, was killed in order to prevent the destruction of the moult of this stage and the figure of Moult 10 was drawn from it. It was compared with the moult fragments left by K.6 and was found identical in every point, even to the number of setæ.

The 3 *summer broods* mentioned above were: Brood A, extruded May 26, 1913, 26 young; Brood B, extruded July 14, 1913, 17 young; and Brood C, extruded July 13, 1913, 20 young.

Of these, Brood C matured in the shortest time, 3 females surviving to mate. One female, C.4, is figured in Plates I to V.* It moulted at intervals of 5, 5, 4, 5, 4, and 6 days. On the 33rd day a male was added, but as no mating took place, it was removed the next day, and another one put in the female's bowl. Mating followed at once, and on the 36th day the female moulted and laid 10 eggs (Plate V).

The second female, C.3, had a male added on the 33rd day, mated immediately and moulted and laid eggs the day after; 16 young hatched and were extruded 10 days later, on August 26th. The pair mated again, but separated whilst the male moulted, mated once more, and on August 28th the female moulted and laid a fresh batch of eggs, the young being extruded 11 days after.

The third female, C.14, moulted at 6, 4, 4, 4, 3, and 5 days' intervals. The gonads were plainly visible on the 31st day; a male was added on the 33rd day, mated at once, and on the next day the female moulted and laid eggs. The first young one was extruded 9 days later, 15 others on the following day.

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* In these and in similar cases described in this paper the animals were examined and recorded only once in the twenty-four hours. If the *exact hour* of moulting had been known in each instance, it is not unlikely that there would have been less divergence between the different times recorded.

In Brood B, also, only 3 animals survived to maturity, 2 males and 1 female. One male, B.9, is figured in Plates VI to VIII. It became mature at the age of 40 days. The other male, B.3, lost through disease and regenerated, part of its antennæ, gnathopod 1, and the uropods. This disease is of common occurrence, and is found in the wild animals freshly brought in, as well as in the stock inbred for generations in the Laboratory. It manifests itself first as a brown mark or stain in a joint, and the joint so affected rots off In spite of the disease, B.3 matured at 38 days, and mated after this moult. It must be noted that its growth stages, except for the parts affected, were precisely the same as those figured for B.9, the normal male. This is of importance in view of the fact that an intersex appeared in this brood.

In intersexes, the growth-stages are very different from those of the normal animals, a much longer time is taken to reach maturity (that is until the distinguishing sexual characters appear), and the majority of intersexes seem to be incapable of breeding, or even of mating. The disease referred to above evidently does not delay maturity nor does it inhibit breeding.

The surviving female of this brood, B.5, had a male added on the 35th day, mated the following day, and moulted and laid eggs on the 38th day.

Brood A was not a vigorous brood, the animals were smaller than those of Broods B and C, and although more survived, the results are not of much value, owing to their propensity for eating their moults. One female, A.19, moulted at intervals of 4, 6, 7, 5, 7, 5, and 6 days. One male, A.20, is figured in Plates VII and IX. It moulted at intervals of 4 and 6 days, ate its third moult, and had the fourth on the 23rd day, then moulted at 6, 6, and 5 days. In 2 females, A.21 and A.23, the gonads were visible on the 37th and 39th days respectively.

The difference in the length of the moulting periods in winter can be shown in the *two winter broods** kept in an unheated room in which the temperature never rose above 10° C.

Brood 1, eggs laid October, 22, 1912, 34 young extruded on November 5. Six survivors reached maturity at 85, 88, 92, 93, 99, and 99 days respectively. Three moulted at intervals of 9, 13, 15, 12, 16, 17, and 17 days ; 11, 11, 14, 16, 11, 15, and 15 days ; and 10, 10, 14, 8, 11, and 14 days. One specimen, a male, moulted at the following intervals, 10, 10, 17, 10, 14, 16, 15, 17, 17, and 19 days. It reached its seventh moult, the moult at which these animals generally become mature, in 92 days, but being very small it was not seen to be a male until after its next moult, at the age of 108 days. Several females were tried with it, but it did not mate until it was 142 days old.

Brood 2, extruded on November 12, 1912, 39 in number. The 6 survivors reached maturity at 75, 81, 83, 85, 86, and 89 days respectively. The first to moult did so at intervals of 7, 9, 11, 8, 10, and 13 days ; the second at 8, 9, 11, 9, and 10 days ; another, a female, at 8, 10, 12, 12, 12, 16, 15, 14, and 17 days ; this was eaten by the male put into its bowl to test it.

The intersex, figured, C.N.397 f., is from the Irregular-eyed Stock, an F_1 from the Brood 269 in which male intersexes occurred. It was one of a brood of 10, extruded on July 30, 1921, and set out in finger bowls for observation. Only 3 of the 10 survived the third moult ; of these 2 were normals and grew quickly, the third was seen to be an intersex at the third moult, the difference in its size and swimming being very noticeable. It moulted at intervals of 6, 7, 7, 7, and 8 days, dying 14 days later from an overdue moult.

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* See p. 554 *Jour. Mar. Biol. Assoc.*, Vol. IX, No. 4, 1913.

Although hundreds of young from this Stock have been set out in the hope of getting a complete series of intersex moults, this animal is the only one, so far, which has survived the fifth moult.

Method. It is not possible to mount the moults with any degree of success, the cuticle being too thin to bear the weight of a coverglass without collapsing out of all shape. The best results are obtained by mixing glycerine and alcohol in equal parts, adding a little eosin for staining purposes, and then using enough of this mixture to float the moult fragments into the required position under the microscope. A camel's-hair brush cut down to two hairs is useful in straightening out the parts in the stronger moults, but floating is always safer, when possible.

It only remains now, before dealing with the moults themselves, to describe those parts of the body most affected externally by the modifications of growth, viz. the antennæ, the outgrowths of the cuticle or sensory armature, and the gnathopods.

THE ANTENNÆ OF *GAMMARUS CHEVREUXI*.

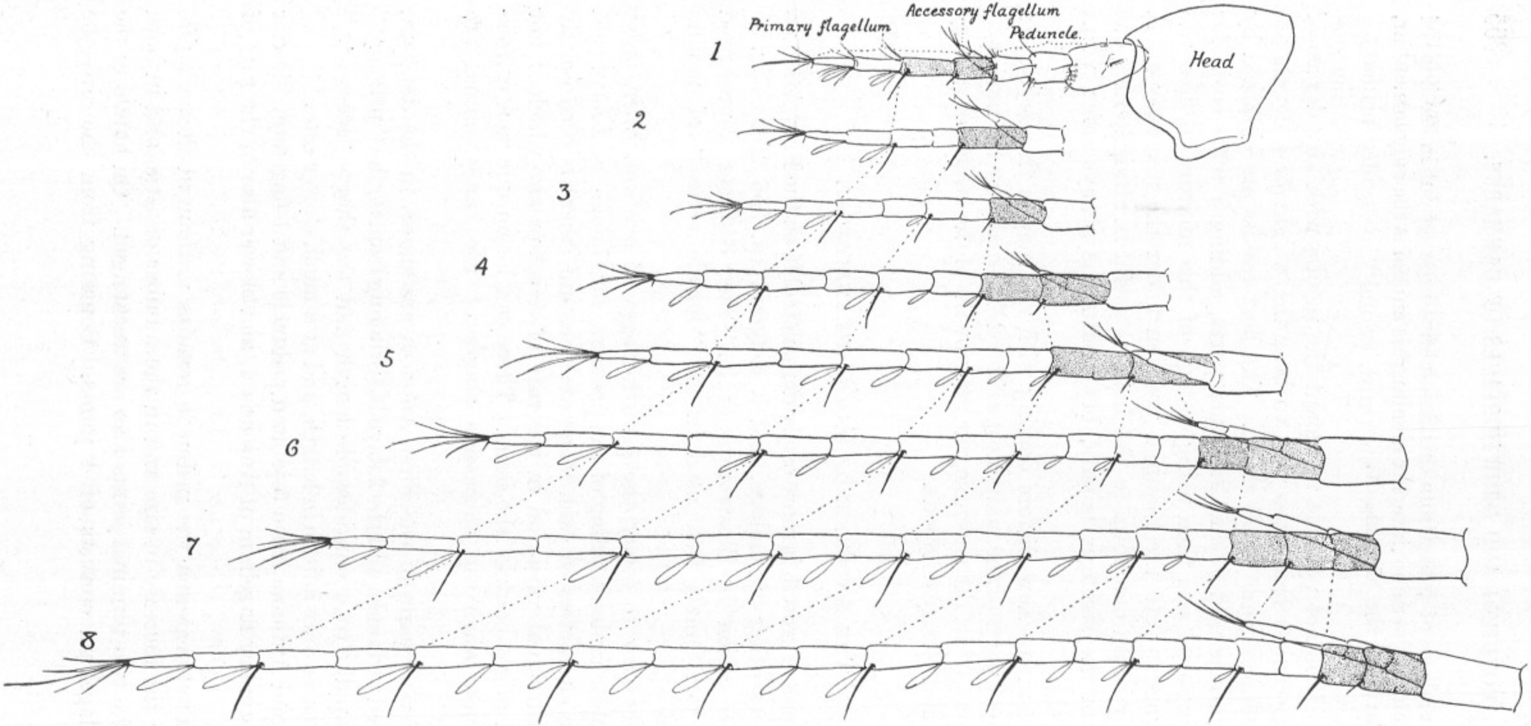
The process of growth is more easily demonstrable on the First Antenna than on any other appendage, and a diagram (p. 356, Text Fig. 2) is therefore given in illustration of it. The 8 stages represented are from the female C.4, used in the "female series" of moults (Figs. 1 to 8).

It is necessary to study the growth-stages of *one animal* in order to gain a clear understanding of the problem, for though, as I have said before, the characters of each stage are constant, there is occasionally a slight individual variation in the rate of development which if not recognised might confuse the issue. There can be no question of misinterpretation when the successive stages of the same animal are examined.

The different parts of the First Antenna are shown in the diagram, the 3-jointed peduncle, and the 2 flagella springing from it, the "primary" growing rapidly to a considerable length and the short "accessory," which increases only a little in length, and at a much slower rate.

The Second Antenna has a 5-jointed peduncle and 1 flagellum, shorter than the primary flagellum of Antenna 1, and slower also in the rate of growth.

In the First Antenna the peduncle remains unchanged through life, except for the increase in size and in the number of setæ, and in both antennæ the two terminal joints also are unchanged. On hatching the primary flagellum consists of 4 joints. Counting from the tip—the



TEXT FIGURE 2.—The progression of growth from birth to maturity as seen in the flagellum of the First Antenna. Stage 1 shows the head and First Antenna, with the 3-jointed peduncle, 4-jointed primary flagellum, and 2-jointed accessory flagellum. The dotted portion represents the growing-region or formative zone, and the new primary joints dividing off from it at successive stages. These joints subdivide later. In the Stages 2 to 8, only the outstanding bristles and sensory filaments are shown, the setæ being omitted. The 8 stages represented are all from the one animal, a female (C.4). The figures are taken from the Left Antenna, outer surface, with the exception of Fig. 5, which shows the Right Antenna, inner surface.

terminal joint; the second joint with 2 seta groups distally, one on the upper margin and one on the inner margin, with a sensory filament or æsthetasc inset in the middle; the third, a long "undivided primary" joint, carrying, in addition to the 2 seta-groups, a long outstanding stiff bristle behind the lower group on the outer side of the joint; and the fourth or proximal joint, also with an outstanding bristle.

The proximal joint is the growth-region, or formative zone of the flagellum. The process of growth is as follows:—

The proximal joint divides, usually into two portions, the distal one of which is a new joint which I have called the "*undivided primary joint.*" (Sometimes in the older animals more than one primary joint may be formed.) At the next moult this undivided primary joint elongates and itself divides into two portions, the distal part or *true primary* joint carrying the outstanding bristle in addition to the seta-groups, and the proximal portion, which may be called the *secondary joint*, developing the seta-groups, but never producing an outstanding bristle.

The process is repeated in each stage, the last-formed primary joint subdividing and giving rise to a secondary joint; the formative-zone dividing and giving off one or more undivided primary joints. In the diagram the formative zone and the undivided primary-joints are shaded.

The outstanding bristles occur only on the primary joints; the sensory filaments develop on all the joints *except the first-formed secondary joint* (see Growth-stage 2 in the diagram, Text Fig. 2).

The alternation in the armature of the joints is very characteristic in this species in both antennæ.

In the First Antenna the primary joints, easily distinguished by the outstanding bristle, carry 2 seta-groups, the upper group containing 3 setæ, 2 of which point outwards, and 1 inwards; the inner group with 4 setæ, 2 on either side of the sensory filament. The secondary joints also carry 2 seta-groups, but in the upper group the position of the setæ is reversed, 1 pointing outwards and 2 inwards, and the inner group has only 1 seta on either side of the filament. The alternation of the setæ (2, 1, 2, 1) is very striking when the antenna is viewed from the side.

In the first-formed secondary joint (joint 4 counting from the tip) the inner seta-group differs from those on the other joints, besides lacking a sensory filament. There are 3 setæ in each of its groups, in the upper group 1 seta points outwards and 2 inwards; in the inner group the position is reversed, 2 diverge outwards and 1 inwards. Sometimes, in an undivided primary joint, a seta of the secondary joint will appear at the point of division before that division takes place.

THE SENSORY ARMATURE OF *GAMMARUS CHEVREUXI.*

In this species the armature consists of sensory hairs, setæ, and strong spines, of which some remain unchanged throughout life whilst others, and these the important ones, are subject to extraordinary modification, involving even a complete change of form ; as, for example, the median serrulate-seta to a pointed-spine, and the pointed-spine in the male to a further development, the truncate-spine.

Some parts of the sensory equipment are common to the whole of the body, others again are peculiar to certain appendages ; for instance, the sensory filaments or æsthetascs (Fig. 25) are confined to the First Antenna, the serrated-hairs to the second joints of the gnathopods and the first two peræopods, the serrulate setæ and serrated-bristles to the gnathopods, and so on.

The armature of the body-cuticle consists of microscopic mobile hairs (Fig. 27) and spinules. These have not been figured, the scale at which the drawings were made not being large enough to admit of a proper representation. The hairs are scattered over the cuticle, inset sometimes singly each in a socket or pit in the skin, sometimes in rows of four to six, with the sockets coalesced and forming a small groove. Three series run down the length of the body, one along the median line and one on each side. The spinules are particularly numerous on the pleon, and are set so thickly together as to make the cuticle rasp-like to the touch ; they increase in number and size with age.

The sensory hairs, setæ, and spines may be divided into the following types, shown in Plate XV. Unfortunately the *texture* cannot be represented, nor the gradual hardening as the delicate setæ change to spines.

Hair (Fig. 26), long, thin, delicate in structure and very flexible. These develop as the animal approaches maturity, and are found generally on the under surface, e.g. on the gnathopod-hands, on the first and second joints of the peræopods of the hinder peræopods anteriorly, and in the mature female, on the margins of the broodplates.

Sensory-hair, thin, delicate, of varying lengths, with a small flagellum inserted at the tip. Found on the gnathopod-hands.

Plumose-hair (Fig. 27), short, very delicate and feathery, the flexible secondary hairs or barbs long and exceedingly fine. The shaft is slightly bulbous at the base, usually mobile and inset in a little socket. Found principally on the antennæ, the claws of the peræopods, and the telson.

Feathered-hair (Fig. 28), not as flexible as those just described, with a row of rather stiffer barbs on either side of the shaft. Found on the pleopods and third uropods.

Coiled-hair (Fig. 29), long, fine, and very flexible, the tip coiled when fully adult. Peculiar to the male and found only on the secondary sexual characters, viz. the second antenna, first and second gnathopods, first peræopod, and third uropod. The coiled-hairs do not develop in the immature male until the sixth moult is reached, and then show as long fine hairs curving but not yet coiled. The most male of the female intersexes produce a few of these "immature-male" hairs distinctly curved on the second antennæ, nearly straight on the third uropods.

Serrated-hair (Fig. 30), very long and delicate, but stronger than the hairs previously described, with the terminal portion curved and serrated on either side of the shaft. Found only on the second joints of the gnathopods, and first and second peræopods.

Seta (Fig. 31), shorter than the hair, and stouter, tapering to a fine point. There are two kinds of setæ, not distinguishable at first, the one remaining unchanged through life, the other of different structure and modified with growth. The latter is slightly wider at the base and has the tip produced into a delicate hair-like point, or flagellum. It develops into the *slender-spine* (Fig. 32), with a very long slender shaft and a small hair-like flagellum at the tip. These "modifiable setæ" are found only on the hinder peræopods.

Sensory serrulate-seta (Fig. 33), midway between the seta and the spine, stiffer than a seta, but too delicate to be called a spine. It is found only in the angle-row of the hand in both gnathopods, and forms a very important character in distinguishing the sexes, and in distinguishing the normals from the intersexes (see p. 362). The serrulate-seta has a long, slender shaft, microscopically serrulate and ridged on the upper part with a flagellum inset at the tip of the shaft. The shaft appears to be hollow, and to have an outlet, opening at the tip of the flagellum. It develops into the pointed-spine.

The *marginal-seta* (Fig. 34) of the palm of the hand appears to be similar in structure to the serrulate-seta, but it is not easy to define the distinction between them. The marginal setæ are smaller, with the shaft smooth and shorter in proportion to the flagellum. They are not modifiable.

The *bent-seta* (Fig. 35) looks like a sensory hair, but has a stiffer shaft, lightly curved or bent in the middle. It is not modifiable. Found only on the hands of the gnathopods at the commencement of the "palmar-row."

Bristle, much longer and stouter than the seta, rigid and frequently curved.

Serrated-bristle (Fig. 36) and *dentate spine* (Fig. 37), with very stout bases, and strong curved shafts tapering to the flattened sensory tip, with the upper portion deeply serrated or toothed on either side. Found only on the posterior margins of the gnathopods.

Spine (Fig. 38), short and stout, with a fine flagellum near the tip. Found on the hinder peræopods, pleon, and uropods.

Slender-spine (Fig. 32), develops from the modifiable setæ on the hinder-peræopods.

Pointed-spine (Fig. 39), develops from the serrulate-seta. The shaft widens and curves over slightly, the conical tip being on the shorter straight side. The flagellum shows as a curved tubular process, apparently open at its free end, connected with the core of the shaft. Found only on the palms of the gnathopod-hands.

Truncate-spine (Fig. 40), peculiar to the adult male. It is the spine which undergoes most modification, developing from the first serrulate-seta of the angle-row, through the pointed-spine stage to a large broad flat-topped spine. The shaft decreases in length and increases greatly in width, so that the spine frequently becomes nearly as broad as it is long. The flagellum is gradually reduced and lost, and the tip becomes a flattened disc on which rows of spinulose ridges can be seen with a high power.

Curved-spine (Fig. 41), peculiar to the adult male, found at the palmar-angle.

THE MODIFICATION OF THE GNATHOPOD-HANDS OF *GAMMARUS CHEVREUXI*.

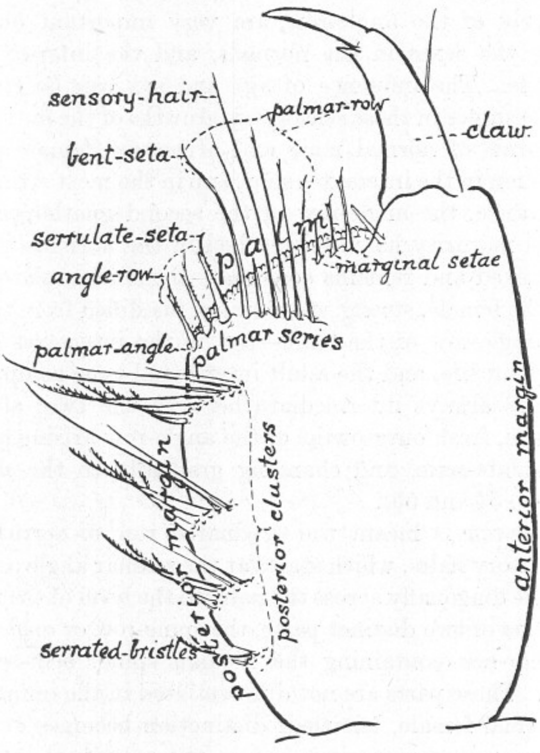
The hand is the name given to the expanded sixth joint of the gnathopods; the claw-like terminal joint closing down against the hand is often called the "finger," and these together form a powerful grasping-organ. The shape of the gnathopod hands, their size and sensory armature are of great importance in specific distinctions. Of all the parts of the body they are the most subject to modification by growth and sex, and the changes wrought are very striking, particularly in the male. As the male hands are the principal external characters used in separating the species of a genus, it follows that a correct reading of the changes undergone is of paramount importance to a clear understanding of taxonomic problems.

Figures are therefore given of the hands of both gnathopods at all the stages of growth from birth to sexual maturity, in order to show the extent of the modification up to that period (Plates XVI and XVII), whilst the fullest development attained by normal males and females, i.e. the maximum size for the species, is represented on Plates XVIII and XIX, and the development of the intersexes on Plates XIX and XX.

The principal features of the hand and the terms used in referring to them are shown in the accompanying diagram (Text Fig. 3).

The *palm* is the distal portion of the hand which extends from the insertion of the claw to the palmar angle. In the immature and the female the palm is transverse, but in the male, after sexual maturity is reached, it becomes indented and more and more oblique.

The *palmar-margin* is the crenulate distal edge of the palm. It is microscopically spinulose, and has on either side a row of the small marginal setæ running along its length and ending at the palmar-angle. In the immature and the female the palmar-margin remains unchanged, but in the mature male it begins to bend to the underside of the hand, more so in the first gnathopod than in the second, and this torsion grows more pronounced with age until eventually the palmar-angle with its two groups of spines is twisted completely underneath. The claw, which in the female is transverse and closes down against the transverse palmar-margin, bends in the male with, and to the same extent as the margin and comes at last to impinge against the under surface of the hand (see Figs. 50 and 51). In the intersexes this is reversed. The male intersex approximating to the female type has the transverse palm and



TEXT FIGURE 3.

claw of the female, and the female intersex becoming increasingly male with age develops the torsion of the palm and claw (Figs. 52 and 53).

The *palmar-angle* is the angle formed by the junction of the palm with the lower or posterior margin of the hand. It is armed with two groups of setæ or spines one on either side ; the *angle-row* on the outer surface, the *angle-group* underneath. The claw closes down between these two groups.

The structure and modification of the sensory armature of the hand, and particularly of the angle-row, are very important characters for distinguishing the sexes in the normals, and the intersexes from the normal animals. The influence of age and sex can be clearly traced through all the stages in these sensory outgrowths of the cuticle, and once the typical forms of normal male and of normal female are realised, their combination in the intersexes shows up in the most striking manner. Take, for instance, the angle-row of the second gnathopod hand. As soon as sexual maturity has been reached in the normals the definitive adult type is fixed and remains constant—slender serrulate-setæ in the angle-row of the female, strong, stout spines (modified from the serrulate-setæ) in the angle-row of the male—but in the intersexes change continues throughout life, and the adult intersexual type as opposed to the normal types is always intermediate between the two, always mixed male and female, fresh outgrowths of the angle-row arising at each stage as *female* serrulate-setæ, and changing gradually to the *male* pointed spines (see Figs. 54 and 55).

By the *angle-row* is meant the graduated row of serrulate-setæ (or spines) and sensory hairs, which starts at the palmar angle and continues in a curving line diagonally across the palm to the level of the mid-margin. It really consists of two distinct parts, the spine-row or *angle-row* proper, and the *palmar-row* containing the median spine, bent-seta and the sensory hairs. These parts are not differentiated in the immature animal nor in the normal female, but their distinction becomes evident in the male as it approaches maturity, and in the most male of the female intersexes.

In Plate XVII the gradual separation of the palmar-row from the angle-row can be seen commencing at the seventh growth-stage. At the ninth stage the sensory hairs begin to draw together from a line into a cluster, and the complete development is shown in Moult 10, where the hairs are massed together in a dense cluster behind the truncate median spine.

The order in which the different spines and hairs appear and the modifications they undergo can be traced through the moults-series (Plates XVI and XVII).

Growth-stage 1. The first of the serrulate-setæ (the median-spine of the male) is developed at birth on the hands of both gnathopods in all the animals. In the normal female it remains unchanged through life in gnathopod 2; in gnathopod 1 it becomes gradually stouter and stronger, yet never loses its setiform character. It is this serrulate-seta which changes in the male at maturity to a pointed-spine and moves away from the spine-row at the angle to the middle of the palm, and then develops into the truncate-spine peculiar to the adult male.

Growth-stage 2. The bent-seta appears, arising above the median.

Growth-stage 3. The difference between the development of the normals and intersexes is first discernible. In the normals a second serrulate-seta appears *below* the first. This one, it is interesting to note, eventually becomes the largest spine of the angle-row, and its modification differs in the female in the two gnathopods. In the First Gnathopod in all, it changes to a strong pointed-spine; so also in the Second Gnathopod in the male and intersexes, but in the female it remains unchanged through life. The first sensory-hair of the palmar-row appears *above* the bent-seta.

The new serrulate-setæ of the angle-row as they develop always arise on the lower side, and the new sensory-hairs on the upper side of the row and form a curving line across the palm.

In *Growth-stage* 6 sexual differentiation can be seen in the normal animals. The gnathopod hands, however, are still alike in the male and female; development is not so far advanced in the intersex.

Growth-stage 7, the stage before sexual maturity. There is very little change in the female, but a considerable advance in the male. In the First Gnathopod the median-spine is seen diverging from the angle row towards the middle of the palm, whilst in the Second Gnathopod it has already diverged and is in its final position.

Growth-stage 8, sexual maturity attained. The adult characters of the female are now fixed, but the male passes through two more stages before assuming the definitive adult form. The median-spine is now of the "pointed" type.

Growth-stage 9 *of the male.* In the First Gnathopod the torsion of the palm is commencing. In the Second Gnathopod the spines in the angle-row are of the male type; the median-spine is flattened at the tip, beginning the change to the truncate form; and the sensory hairs are massed together in a cluster behind it.

Growth-stage 10 *of the male*, the fully adult form. In both gnathopods the typical male curved-spines are developed at the palmar angle; the median-spine has completed the change, and is now a perfect truncate-spine.

In the female intersex there is a constant tendency to the male type.

In advanced forms (cf. Fig. 56) the median-seta not only diverges from the angle-row to the middle of the palm, but changes into a pointed spine like that of the young male in its first mature stage (Moult 8). The sensory hairs also diverge and form a cluster as in the young males. In two cases, Fig. 53 and CN 218b,* a further increase in maleness is shown in the torsion of the palm and claw of the First Gnathopod. The serrulate-setæ of the Second Gnathopod are modified into pointed-spines as in the male type, but though the change is towards increased maleness, the *intersexual type* as it may be called is always distinct, and remains intermediate between normal male and female. New additions to the angle-row arise as serrulate-setæ and change to pointed-spines, and in the typical intersex hand, either male or female, these two types will always be found together. In Plate XXI figures are given of a Female Intersex, CN. 229h., showing the hand of Gnathopod 2 at the age of 167 days and the same hand at the age of 367 days.

It will be seen that apart from size the character of the hands of the normals is practically unchanged from sexual maturity onwards, but that in the intersex a continuous modification takes place.

DESCRIPTION OF THE MOULTS OF *GAMMARUS CHEVREUXI.*

The following account gives briefly the distinguishing characters of the successive growth-stages. These stages are clearly defined one from the other, and are *the same for winter as for summer broods.* The individual variation is very slight. There is sometimes a little difference in development between the two sides of an animal, one side, generally the right, developing at a rather quicker rate than the other. The sensory armature appears to be the same on both sides, but its distribution is occasionally slightly different, e.g. one joint of an appendage may have a spine or seta more than the corresponding joint on the other side, but when this occurs it very frequently happens also that another joint of the same appendage will carry a spine or seta less than the corresponding one on the other side.

The descriptions of the moults refer particularly to the individual specimens which have been figured, but in every instance the details have been confirmed by the examination of a great number of moults from other animals of the same stage and the essential constancy of the specific characters has thus been established. *Each stage* has proved to be remarkably constant, there being extremely little variation even in the numbers and positions of the individual setæ and spines.

The left side has been figured unless otherwise stated, and the mouth-

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* *Journ. Mar. Biol. Assoc.*, Vol. XII, No. 3, p. 543, Fig. 112.

parts omitted where they would interfere with the detail of the gnathopods. The eyes are not shown in any of the figures of the moulted skins, as the cuticle extends uniformly over the cornea, and the eyes leave no impression visible in the moult.

Series I. THE NORMAL FEMALE.

Moult 1 (Female C.4, Fig. 1). The characters distinguishing Moult 1 are: primary flagella of both antennæ, 4-jointed; gnathopod-hands with 1 serrulate-seta at the palmar-angle; and third uropod with 3 spines distally on the first joint of the outer ramus.

On hatching, the young animal resembles the parents in that all the appendages are present. The difference in the proportion the various parts of the body bear to each other is, however, very marked, e.g. the head in the young is much larger in proportion, about a seventh of the total length of the body, measured dorsally, and the peræon and pleon are practically equal in length, whilst in the mature animal the head is an eleventh of the total length, and the peræon is a third as long again as the pleon.

The external characters of this stage are precisely the same in the normal male, and intersex, as in the female.

Head. The lateral and post-antennal corners are rounded; they become angular with growth.

First Antenna. On the upper side of the basal joint of the peduncle is a sensory groove with 1 delicate plumose hair inset. This groove is of great interest, as it appears to be analogous to the "auditory sac" found in many decapods (see p. 386 for description, and Fig. 27), but it has not hitherto been noted in the Amphipoda. The length of the groove and the number of the sensory hairs increase with age. On the outer side of the same joint and in a line with the groove is the group of 3 mobile plumose hairs, which is found unchanged through all the growth-stages.

The primary flagellum has 4 joints, the accessory flagellum 2.

The growth-region or formative zone in both First and Second Antennæ is at the proximal end of the flagella, the terminal joints remaining unchanged through life except for the addition of two or three setæ (see p. 355 for description and the diagram on p. 356).

Counting from the tip of the primary flagellum, the first joint has a cluster of 5 bristles, and 1 small sensory hair; the second joint carries on its inner surface a group of 4 setæ. with a long sensory-filament (*æsthetasc*, Fig. 25) inset in the middle; the third joint has a similar group of 2 setæ and a sensory filament, and in addition a strong stiff outstanding bristle behind the group; the fourth joint has a bristle of the same type, but not so far developed.

These outstanding bristles appear on alternate joints as the antennæ lengthen, and by their aid the method of growth can be traced through all the stages (see diagram).

The Second Antenna. The first of the bristle-groups of joints 4 and 5 of the peduncle is represented on each by 1 bristle at the lower distal angle. The flagellum is 4-jointed. Growth proceeds along the same lines as in the First Antenna, but not at the same rate.

First and Second Gnathopods. These form two of the principal distinguishing characters of the species, and undergo the most modification.

In both, the hands show the commencement of the angle-row, 1 large serrulate-seta (Fig. 33) being inset at the palmar-angle. This serrulate-seta develops in the male into the median truncate-spine. The angle-group of the under surface is represented by 2 very small sensory setæ.

The claw, in both gnathopods, is practically the same as at maturity, except, of course, in size ; 2 stiff setæ are inset at its insertion, and it closes down between them against the crenulate palmar-margin. The fifth joint carries 2 large serrated-bristles (Fig. 36) on its posterior distal margin.

Uropod 3. Peduncle unarmed ; 3 spines on the first joint of the outer ramus, 2 on the inner, and 1 on the outer distal margin ; and 3 bristles, 1 long and 2 short, on the terminal joint ; inner ramus only half the length of the first joint of the outer ramus, tipped with 1 long bristle.

Moult 2 (Female C.4, Fig. 2). The distinguishing characters are : flagellum of antennæ 1, 6-jointed ; of antenna 2, 4-jointed ; 1 serrulate-seta and the bent-seta in the palmar-series of the gnathopods 1 and 2 ; commencement of the first posterior-cluster on the hands, and of the sensory serrated-hair groups of the second joints of the gnathopods ; and commencement of the spine-clusters of the third uropods.

Antenna 1. Basal joint with 2 sensory-hairs in the groove ; primary flagellum with 6 joints, joint 4 (counting from the tip), the first of the new secondary-joints, never develops a sensory filament.

Antenna 2. No increase in the number of joints in the flagellum, but the proximal joint or formative zone has lengthened preparatory to division (see diagram, p. 356).

Gnathopods. On the hands in both gnathopods the bent-seta (Fig. 35), a long stiff seta with slightly bent shaft and flagellum at the tip, has now appeared on the anterior side of the serrulate-seta noted in Moult 1. This is the commencement of the " palmar row." One serrated-bristle of the first posterior cluster is found on the hands of gnathopod 2 in the female figured, C.4, but not in gnathopod 1. It is, however, present in the sister, C.14, and also in the male figured. On joint 2, in both gnathopods, the long sensory serrated-hairs (Fig. 30), peculiar to the gnathopods and first two peræopods, have appeared, 1 each side in gnathopod 1, and 1 posteriorly in gnathopod 2 in this specimen ; (1 each side in gnathopod 2 in the sister, C.14, and in the male figured). These hairs are very long and flexile, curving round at the flattened tip in the older stages, and showing long delicate hyaline serrations on each side.

Peræopods. Peræopod 2 with 1 seta on the posterior margin of joint 2 : peræopods 4 and 5 with spines developed on the mid-margin of joint 6 ; peræopod 3 with a spine on the right side, but not on the left side (which is figured).

Uropod 3. Peduncle with 2 spines distally, one at each side : outer ramus with 4 spines on the distal margin, 2 on the outer side, and 2 and 1 seta on the inner side ; 1 spine about half-way on the outer margin, the commencement of the spine-clusters.

Moult 3 (from Female C.4, Fig. 3). The distinguishing characters are : gnathopod 1, the hand with 3 in the palmar-series ; gnathopod 2, the hand with 4 in the palmar-series ; posterior clusters on the fifth joints as well as on the hands ; and 1 sensory-hair on the under surface ; 2 spines on the anterior margins of the second joints in the hinder-peræopods.

Antenna 1. Basal joint with 3 sensory hairs in the groove ; primary flagellum 7-jointed, with 3 outstanding bristles, and 3 sensory-filaments in this specimen ; but in the male (and in other specimens) the division of the formative zone can be seen, and the armature of the new secondary-joint.

Antenna 2. One bristle developed on the lower margin of joint 4, the commencement of the second bristle-row ; flagellum with the same number of joints as in Moult 2, but with the proximal joint (formative zone) lengthened considerably.

Gnathopod 1. A second serrulate-seta has appeared posteriorly in the angle-row of the right hand, but not in the left ; on both hands the first of the serrated-bristle clusters is now represented ; and, on the inner surface, 1 hair of the first sensory-hair clusters can be seen, and 1 of the small sensory marginal-setæ which border the palm (Fig. 34).

Gnathopod 2. Both hands with a row of 4 at the palmar-angle, 2 serrulate-setæ posteriorly, the bent-seta, and 1 long delicate sensory-hair. A second serrated-bristle is found in the posterior cluster, and on the under surface, as in gnathopod 1, the first of the sensory-hair clusters, and the first of the marginal-setæ are represented. The second of the posterior bristle-clusters of joint 5 has appeared on gnathopod 2, but not in gnathopod 1 in this specimen, although it has developed in the male figured.

Both gnathopods now have 3 large curved serrated-bristles in the distal row on joint 5, and 3 long serrated-hairs on joint 2.

Peræopods. Peræopod 1, 1 seta posteriorly on joint 2, and 1 seta on the posterior mid-margin on joint 6; peræopod 2, the first of the long serrated-hairs on joint 2; peræopods 3 and 5 with 1 spine on the anterior margin of joint 2 above the distal one; peræopods 4 and 5 with 1 spine on the posterior mid-margin of joint 4; all 3 hinder peræopods with spines and setæ on both sides of joint 6.

Uropod 3. On the outer side, a second spine has developed in the peduncle distal cluster, and in the spine-cluster of the outer ramus.

Moult 4 (from Female C.4, gnathopod 1, peræopods 4 and 5 from sister female C.14, Fig. 4). The distinguishing characters are: flagellum of antenna 1, 8-jointed with the 2 proximal joints undivided and very long (or in some specimens 10-jointed with the proximal joints divided and short); antenna 2, flagellum 5-jointed; 2 bristle-rows represented on joints 4 and 5 of the peduncle; both gnathopods with 4 in the palmar-series of the hand, gnathopod 1 with 1 posterior bristle-cluster represented, gnathopod 2 with 2; peræopod 1 and peræopod 2 with 1 long serrated-hair on the second joint; hinder peræopods with joints 2, 4, and 6 carrying spines or setæ on both sides.

Antenna 1. Basal joint with 4 sensory-hairs in the "auditory" groove; primary flagellum 8-jointed, with 4 outstanding bristles, and 5 sensory filaments. The 2 proximal joints, i.e. the formative zone, and the undivided primary-joint, are long; in most of the other specimens male and female, these have divided, sometimes in both antennæ, sometimes in one only. The right antenna in this female (C.4) is rather more advanced than the left.

Antenna 2. Peduncle with 2 setæ on joint 3; on joint 5, 1 bristle of the second bristle-row has appeared, making 2 each on joints 4 and 5; the long proximal joint of the flagellum has divided into 2.

Gnathopod 1 missing in this specimen. The figure is taken from the sister, C.14. The palmar series numbers 4, 2 serrulate-setæ posteriorly, the stiff bent-seta, and 1 long slender hair; the posterior bristle-cluster now contains 2 serrated-bristles; joint 5 has 1 serrated-bristle of the second posterior cluster; and joint 2 a third long serrated-hair posteriorly.

Gnathopod 2. The hand with 4 in the palmar series; 1 of the slender flexible hairs has developed in the first posterior cluster, and 1 serrated-bristle of the second posterior cluster; also a second marginal-seta on the palm, outer side; on joint 5, 1 serrated-bristle of the second posterior cluster. On the under surface of the hand, the seta at the angle is now an almost perfect pointed spine. There are, in the adult animals, 2 rows of sensory-hairs underneath; the anterior one consisting of long curving hairs, and the posterior one longer and more slender; in this stage, the first hair of the first anterior group appears.

Peræopods. Peræopod 1, the first of the long sensory serrated-hairs present on joint 2; 1 seta on the mid-margin of joint 4, making 1 each side. Peræopod 2, 1 seta, mid-margin of joint 4 on the left side, not on the right, and 1 seta, mid-margin of joint 6, both sides. Peræopod 3, a second notch on the posterior margin of joint 2; 1 seta on the anterior mid-margin of joint 4. Peræopods 4 and 5 missing in specimen C.4, and drawn from the sister C.14. Both peræopods have 2 notches on the posterior margin of joint 2, peræopod 4 with 1 spine and peræopod 5 with 2 spines on the anterior margin above the distal group; joint 4 in both is furnished with spines each side; in peræopod 5 a spine has appeared on joint 5 mid-margin, and 2 of the long distal setæ in joint 6 have developed into the long slender spines (Fig. 32) peculiar to the hinder peræopods.

Uropod 3. One sensory-hair of the first sensory-cluster is present on the under surface of the first joint, outer ramus; and 1 spine at the tip of the inner ramus.

Moult 5 (from Female C.4, Fig. 5). The gnathopods were missing from this specimen, and are therefore figured from the sister female C.14. The distinguishing characters are: Antenna 1, the flagellum either 10-jointed, with 2 long undivided proximal joints, or 12-jointed, with the 2 long joints divided into 4 short ones; gnathopods with 5 in the palmar-series; the hand of gnathopod 1 with 2 posterior-clusters, that of gnathopod 2, with 3 posterior-clusters; uropod 3, with a spine midway on the peduncle; 2 spines and 2 long bristles on the inner ramus.

This is the first moult in which the broodplates have been traced. They are microscopic in size, rounded, with no hairs yet developed on the margins, and are found on gnathopod 2 and the first three peræopods.

Antenna 1. The primary flagellum in C.4 is 10-jointed, the 2 proximal joints long, in C.14 12-jointed, the 4 proximal joints short. The growth is identical, the slight constrictions shown in the figures of C.4 (Fig. 5 in diagram) being continued across the joints as definite divisions in C.14. The latter was the more vigorous animal, and the slightly more advanced development is therefore to be expected. The armature is the same in both, 5 outstanding bristles and 7 sensory filaments. The accessory flagellum is 3-jointed in C.14, the same length in C.4 though only 2-jointed, but again the constriction is visible, which in C.14 has become a division.

Antenna 2. Peduncle with 2 bristle-clusters on joints 4 and 5 on left side, 3 on joint 4 of right side; the flagellum is 6-jointed. In the sister C.14, there are 7 joints, the 4 proximal small; in C.4 the proximal or formative zone is long, and the 2 next small, but the imminent division of the long joint is shown by the appearance on it of the bristle of the new primary joint.

Gnathopod 1. Hand of C.14; 5 in the palmar-series, another long flexile hair having arisen at the anterior end of the row; the serrulate-seta at the posterior end of the row is now a short, stout, almost perfect spine. Another marginal-seta has appeared near the insertion of the claw, and the first serrated-bristle of the second posterior-cluster. One hair of a second sensory group underneath, and 1 long seta on the outside of the hand, and 1 long seta on the outside of the fifth joint are also present.

Gnathopod 2. Hand of C.14: 5 in the palmar-series; 1 long seta on the outside of the hand as in gnathopod 1, and 1 serrated-bristle of the third posterior-cluster on joint 5 have appeared.

Peræopods. Peræopods 1 and 2, 1 seta in the mid-margin of joint 5; peræopods 3, 4, and 5 all with 2 spines on the anterior margin of joint 2, and spines in the mid-margin of joint 5. In all the peræopods of this stage the fourth, fifth, and sixth joints have spines and setæ in mid-margin, some on both sides, some on the posterior side only.

Uropod 3. One spine midway on the peduncle: setæ appearing in the spine-clusters of the outer ramus, and 1 feathered hair of the second sensory-cluster underneath, on the left side. There are 3 of these groups on the right side in specimen C.4 and on both sides in C.14. The inner ramus has 2 long bristles and 2 spines at the tip.

Telson with 2 spines at the tip, and, on the right side, 1 midway.

As this moult C.4 shows an unusual number of differences in the distribution of the sensory armature on the two sides of the animal, especially on the hinder peræopods, a list of these is given below.

Antenna 2. One bristle-cluster more on right side than on left side.

Peræopod 1. One seta less on joint 3, and 2 setæ less on the posterior margin of joint 4 on right side.

Peræopod 2. One serrated-hair on the posterior margin of joint 2, and 1 long seta of the distal group of joint 5 and the mid-marginal one less on right side.

Peræopod 3. One notch less on joint 2 on right side, but on joint 6 there are 2 spine-clusters and 2 seta-clusters on the margins represented on right side, only 1 each on left side.

Peræopod 4. One notch more on joint 2 on right side; on anterior mid-margin on joint 4, 1 spine less on right side than on left side; on joint 6, 1 spine more on right side.

Peræopod 5. On joint 6, 2 spine-clusters and 2 seta-clusters, represented on right side; only 1 of each on left side.

Uropod 1. One spine midway on peduncle right side, none on left side.

Uropod 3. Two spines in inner side of peduncle right side, 1 on left side ; 3 feathered hairs on outer ramus right side, 2 on left side.

Telson. One spine midway on right side, not on left side ; 2 spines at the insertion of the telson right side, 1 on left side.

Moult 6 (from Female C.4, Fig. 6). Gnathopod 2 from the sister female C.14 and gnathopod 1 from A.19.

The character which distinguishes Moult 6 from all the other moults in the normal female is the presence of small oval broodplates with rudiments of the fringing hairs just indicated on the margins.

Head. Lateral corners well produced, post-antennal corner subacute.

Antenna 1. Basal joint with 4 sensory-hairs in the " auditory " groove, the distal one apart from the other three. Primary flagellum with 14 joints, 6 outstanding bristles, and 9 sensory-filaments. In C.14, the left antenna has 14 joints, the proximal or formative zone long and undivided; the right antenna is 15-jointed, the proximal joint having divided. Accessory flagellum 3-jointed.

Antenna 2. Joints 4 and 5 of the peduncle each with 3 bristle-clusters represented ; flagellum 7-jointed, the formative zone lengthened, the next joint an undivided primary, showing the commencement of a division on the margin. In C.14, a more vigorous specimen, joint 4 of the peduncle has 4 bristle-clusters represented ; the flagellum on the right side has 8 joints, the formative zone long, and the next joint, a primary, divided, whilst in that of the left side the formative zone has also divided, and the joints therefore number 9.

Gnathopod 1. Missing in C.4, the figure is drawn from a smaller female, A.19, of Brood A. The palmar-series in C.14 consists of 6, 2 serrulate-setæ, the one at the angle now almost a spine, the stiff bent-seta, and 3 of the long flexile sensory-hairs : 1 serrated-bristle of the third posterior-cluster has appeared on the hand, and also on joint 5, but on the right side there are only 2 of the posterior-clusters on the hand as in A.19 ; 3 on joint 5. In the smaller specimen the development is not quite as advanced, but it will be seen that it is not possible to confuse either gnathopod 1 or gnathopod 2 with the previous stage, Moult 5.

Gnathopod 2. Left hand missing in specimen C.4, and figured from C.14 and A.19. In the right hand C.4, the palmar-series consists of 6, 2 serrulate-setæ at the angle, the bent-seta, and 3 of the flexile sensory-hairs ; in C.14 the right hand is the same as in C.4, with the addition of 1 serrated-bristle in the third posterior-cluster, but in the left hand there are 8 in the palmar-series, 3 serrulate-setæ, the bent-seta, 3 long flexile hairs in the row, and 1 crossing them in front. The fifth joint has 3 posterior-clusters in C.4 and A.19, 4 clusters in C.14. More marginal-setæ have developed, and 2 anterior and 3 posterior sensory-groups are present on the under surface. On the small *broodplates* developed on this appendage and the three succeeding ones, rudiments of the fringing hairs can be seen, but the cuticle is too thin and crumpled in all the specimens to make sure of the exact number.

This is the first moult in which the broodplates are plainly evident.

Peræopods. A great increase in the number of setæ and spines; joint 2 of peræopod 3, with 3 spines on the anterior margin, left side, 4 on the right; C.14 has 4 on the left and 5 on the right: peræopod 4 with 3, and peræopod 5 with 4 on the anterior margin, and in C.14 also.

Uropod 3. Outer ramus, 3 feathered-hair clusters represented on the under surface left side, 4 on the right side; 2 spine-clusters left side, 3 on the right side; inner ramus, spine on margin and 1 feathered-hair. In C.14, outer ramus, 4 feathered-clusters, and 2 spine-clusters; 2 feathered-hairs on inner ramus.

Telson. Spine midway on both sides.

Moult 7 (from Female C.4, Fig. 7). Gnathopods from the smaller female A.19. The principal characters distinguishing Moult 7 are the large broodplates, with numerous rudimentary or partially developed fringing hairs. The broodplates are graduated in size, the largest on gnathopod 2, and the smallest on peræopod 3.

Antenna 1. Flagellum 17-jointed, the formative zone divided into 2 short joints, the next and longer joint an "undivided primary"; 12 sensory-filaments, 8 outstanding bristles; accessory flagellum 3-jointed.

Antenna 2. Joint 4 of the peduncle with 3 bristle-clusters left side, 4 on right side; flagellum 9-jointed, 4 outstanding bristles.

Gnathopods. Hands missing in C.4, figures drawn from the smaller specimen, A.19, for the sake of comparison with the figures of the male, A.20 taken from the same Brood A.

Gnathopod 1. 6 in the palmar-series, of the 2 serrulate-setæ in the angle-row the posterior one is now a stout, fully developed pointed-spine; the seta at the angle on the under surface is also a fully developed spine, and on the right hand a second small spine has arisen beside it; 2 posterior-clusters on the left hand, 3 on the right.

Gnathopod 2. Sideplate of joint 1 with 2 setæ inset at the anterior distal angle left side, 1 on right side; palmar-series of 7, 3 graduated serrulate-setæ at the angle, the bent-seta, and 3 of the flexile sensory-hairs on the left side, 4 on the right, the fourth one in front inset across the others; 3 posterior-clusters on the left hand, 4 on the right; a great increase in the number of the serrated-bristles and sensory-hairs in these clusters. Broodplates large; 8 tiny hairs developing, in the smaller female, A.19; in C.4 the broodplate is larger, with about 14 of these hairs.

Peræopods. C.4; peræopod 1, with 5 clusters of setæ on the posterior margin of joint 4 besides the distal one; broodplate with 9 or 10 tiny hairs: peræopod 2, broodplate smaller with about 6 hairs: peræopods 3 and 4 with 4 spines on the anterior margin of joint 2; peræopod 5 with 5 on the left side, the second proximal one very small, on the right there are 4, all large; great increase in the number of spines and setæ on all the peræopods.

Uropod 2. Peduncle with 1 small spine midway on left side, absent on right side; inner ramus with 1 spine midway on right side, absent on left side.

Uropod 3. Outer ramus, 3 spine-clusters on left side and 4 feathered clusters underneath, 5 on right side; 2 more feathered hairs on the inner ramus.

Moult 8 (Fig. 8). This is the moult at which the female reaches sexual maturity. The specimen figured, C.4, laid 10 eggs.

The distinguishing characters are: the fully developed broodplates with long fringing hairs; gnathopod 1 with 2 stout spines at the palmar-angle; gnathopod 2 with a graduated row of 3 serrulate-setæ; and the armature of the hinder peræopods, particularly of the second joints.

Antenna 1. Primary flagellum with 20 joints, the long formative zone showing the commencement of the line of division; 10 outstanding bristles, and 15 sensory filaments; accessory flagellum 4-jointed. C.14, the sister, has 21 joints in the primary flagellum and 4 in the accessory.

Antenna 2. Joint 4 of the peduncle with 3 bristle-clusters left side, joint 5 with 4 clusters; flagellum 10-jointed, with 5 outstanding bristles.

Gnathopod 1. 8 in the palmar-series; of the 3 serrulate-setæ of the angle-row the first is a little stouter, the other two are now perfectly developed strong pointed-spines; the bent-seta and 4 sensory-hairs; 2 spines on the under surface of the palmar-angle; 2 posterior-clusters of serrated-bristles; and, on the under surface of the hand, 3 anterior and 3 posterior sensory-groups; on joint 5, 3 posterior-clusters. There is a great increase in the number of serrated-bristles, especially on joint 4, and in the number of long serrated-hairs on joint 2.

Gnathopod 2. Nine in the palmar-series, 3 graduated serrulate-setæ in the angle-row, the bent-seta, and 5 sensory-hairs, one in front crossing the others; 2 spines on the angle, underneath; 4 posterior-clusters with graduated serrated-bristles below, and long slender sensory-hairs above; and on the under surface, 3 anterior and 4 posterior sensory-clusters. Broodplates very large and well developed, with 24 fringing hairs (Fig. 26) on each; the posterior hairs, 6 on right side, 7 on left side, much shorter than the others.

Peræopod 1. Six clusters on posterior margin of joint 4. Broodplates about the same length as the gill, left side with 19 hairs, right side with 17.

Peræopod 2. Broodplates, 13 hairs left side, only 9 on right.

Peræopod 3. Four spines on the anterior margin left side, 5 on the right, the proximal one very small; 4 notches on posterior margin left side, 5 on the right. Broodplates the smallest of all, with 7 hairs.

Peræopods 4 *and* 5, with 4 and 5 spines on the anterior margins respectively.

Pleon segment 2. Three spines on the epimeron left side, 2 on the right. The cuticle of this segment and the following one is remarkably spinulose.

Uropod 3. Great increase of bristles and spines; outer ramus with 3 spine-clusters, and 4 feathered clusters on left side; terminal joint with 1 bristle, the commencement of a lateral cluster, on the inner side.

Series II. The Normal Male.

The males appear to be much more voracious than the females, cannibalism is frequent with them, whereas it is only rarely that the female turns to it. It has been found impossible to get a complete series of moults from one male, the difficulty being in the older stages, for as they grow older they devour their moults almost immediately after ecdysis. In order to get the complete series, I have had to draw certain stages from one male, fill in the missing stages from other males, and then compare this series with as many other male moults as could be obtained.

Moults 1, 2, 3, 4 are from the male B.9; it ate its fifth moult, and that stage was therefore figured from A.20; the sixth moult is from B.9; its seventh was nearly all eaten, and this stage also was figured from A.20; both B.9 and A.20 ate their eighth moults, and another male, K.6, was taken for Moult 8 and Moult 9. K.6 ate part of its tenth moult, and yet another male had to be taken, CN.444. This one, CN.444, had perfect moults of the stages 1, 2, 3, 4; the fifth moult was eaten; the sixth moult was perfect, but there was such an unusually long period between the sixth and the seventh that I feared the animal might not be healthy, and therefore did not take it to illustrate the male series. It had the sixth, seventh, eighth, and ninth moults, and was then killed to make sure of getting the tenth stage. All its moults were afterwards examined point by point with the stages here figured as well as with many other males, and were found to agree in every detail.

The only difference ever found, and that an exceedingly slight one, is in the development, a strong and vigorous animal may be rather more advanced than the weaker ones.

Moult 1 (from the male B.9, Fig. 9). This moult is precisely the same in every detail as that of the female, already described.

Moult 2 (from the male B.9, Fig. 10). This moult is practically identical with that of the female.

Moult 3 (from the male B.9, Fig. 11). This moult also is practically identical with that of the female.

Antenna 1 has 3 sensory filaments on the right side, 4 on the left.

Peræopod 4. One spine present on the posterior margin of joint 4 right side, absent from left side.

Moult 4 (from the male B.9, Fig. 12). This moult of B.9 is exactly the same as in the female figured, except for a very slight increase in the sensory armature, due apparently to the fact that B.9 was the more vigorous animal of the two.

Antenna 1. Flagellum as in the female figured, except that the 2 long proximal joints of the latter are here divided into 4 short ones. In another male, A.20, the accessory flagellum of the left side is 3-jointed, the 2 proximal joints short, right side 2-jointed with the proximal joint long, not yet divided ; and in *Antenna* 2 it has one more bristle-cluster represented on joint 4 of the peduncle on the left side than in B.9, the specimen figured.

In B. 9, *peræopod* 1 has 1 of the long sensory serrated-hairs on each side of joint 2 ; *peræopod* 2, 1 seta each side on joint 4 ; *peræopods* 4 *and* 5 with 1 spine on joint 5 on both sides, *peræopod* 3 with this spine on the left side only.

Uropod 3. A second spine-cluster on the outer ramus, both sides.

Moult 5 (Fig. 13). As the male B.9 ate the whole of its fifth moult this growth-stage has been figured from another male, A.20.

This moult is practically identical with that of the normal female.

Antenna 1. Flagellum 10-jointed as in C.4 ; accessory flagellum on the right side 2-jointed with the proximal joint long and undivided, 3-jointed on the left side with the proximal joint divided.

Antenna 2. Flagellum with 5 joints in the male A.20, 6 and 7 joints respectively in the females C.4 and C.14, but all these animals are at the same growth-stage, as can be seen on examining the flagella. In A.20, the smallest of the three, the proximal joint (i.e. the formative zone) is lengthened preparatory to division, and the next joint, an "undivided primary," carries the seta of the new secondary joint (this seta frequently appearing before the division takes place). In C.4 also the proximal joint is lengthened, but the near division and the formation of a new primary is shown by an outstanding bristle being developed ; and the "undivided primary" has divided and formed a new secondary joint, thus making 6 joints in all. In C.14, the most vigorous of the animals, the division of both the proximal joint and the "undivided primary" has taken place, making 7 joints in all.

Moult 6 (from the male B.9, Fig. 14). Sexual differentiation is first seen in this moult. The distinguishing characters are : The presence of a few curving male hairs on Antenna 2 ; gnathopod hands like the female.

Antenna 1. Basal joint with 5 sensory-hairs in the groove ; flagellum the same length as in the female figured, 16-jointed, the 2 long proximal joints of the female (formative zone and "undivided primary") are divided in this animal, and show as 4 short joints.

Antenna 2, shows the first appearance of the sensory-coiled hairs characteristic of the male (Fig. 29). On the inner surface of joints 4 and 5 of the peduncle there are 4 rows of sensory hairs, and in the 3 distal rows one or two of the longest hairs have the tips curved inwards. In the mature male these hairs are also present on the two gnathopods, the first peræopods and the third uropods.

Gnathopods 1 *and* 2. The spines in the angle-row of the hand of gnathopod 1 are much stouter than in the female. In gnathopod 2 of the female the character of the angle-row does not change through life, the serrulate-setæ remaining serrulate-setæ through all the moults, but in the male these setæ gradually develop into stout spines, and the change can be clearly seen in this stage. The right hand of gnathopod 2 has a third serrulate-seta in the angle-row posterior to the other two. The hairs of the sensory clusters of the under surface are still short.

The rest of the moult is practically the same as in the female, except for the position and increase of a few spines or setæ.

Peræopod 3. With 4 spines on the anterior margin of joint 2 ; *peræopod* 4 with 3 ; and *peræopod* 5 with 4 on the left side, 3 on the right side.

Uropod 3. Outer ramus with 3 spine-clusters represented on the left side, 2 on the right side ; in the female figured there are 2 on the left and 3 on the right. Feathered-clusters in this specimen, 5 on the left, 4 on the right ; in the female 3 on the left, 4 on the right.

Telson. Another spine has appeared on the right side, near the tip.

Moult 7 (Plate IX). The principal distinguishing characters of this stage are : the coiling of the male hairs on the Second Antenna, and the commencement of the differentiation of the palmar-series of the gnathopod hands.

The male B.9 ate its seventh moult with the exception of peræopods 3 and 4 and the third uropods ; the figures have therefore been taken from another male, the A.20, figured in Moult 5.

Antenna 1. Flagellum 16-jointed, the formative zone lengthened, but not yet divided, 11 sensory-filaments, and 7 outstanding bristles ; accessory flagellum 3-jointed. In CN.444, a larger male, the formative zone has divided, and the "undivided primary" also.

Antenna 2. Flagellum as in the female figured ; 9-jointed, peduncle with 4 bristle-groups on joint 4, 3 on joint 5, with a good many more of the male hairs developed in the clusters underneath, more coiled than in the preceding moult. In CN.444, the flagellum has 10 joints, the long proximal having divided; and one hair of another bristle-cluster is present on joint 5 of the peduncle.

Gnathopod 1. The change to the adult male type has commenced in the hands, more noticeably so in the right hand, where the differentiation of the palmar-series into palmar-row and angle-row is now clearly indicated. The second serrulate-seta of the angle-row is now a stout pointed-spine, the third and posterior one not so well developed. The first serrulate-seta has not yet been modified to a spine, but is stouter and stronger than in the last stage, and has diverged a little from the angle-row. The palmar-row in A.20 contains 4 of the long sensory-hairs in a line. In CN.444 there are 6 hairs, two very small.

Gnathopod 2 also shows the change towards the male type, more so on the right side than on the left. On the right side (see M.7 in Plate XVII) the differentiation is clearly seen; the palmar-row containing the first serrulate-seta and 5 long sensory-hairs has diverged a little from the angle-row towards the middle of the palm. The angle-row consists of the second and third serrulate-setæ (in order of development), the second and largest of the three being almost completely modified into a pointed-spine. The hand is larger in proportion than in the female, and has 4 posterior-clusters of serrated-bristles.

Peræopod 1. No coiled hairs have yet appeared; peræopod 4 in B.9 with a fifth spine on the anterior margin of joint 2, the right side as in the female C.4.

Uropod 3. The long sensory-hairs are much more numerous than in the female; in B.9 the uropods are damaged, but 5 rows can be seen on the right side, and more on the left with some of the hairs lightly coiled; some of these hairs have appeared on the inner ramus also.

Moult 8. Mature, first stage. From the male K.6 (Plate X).

This is the stage at which the males become sexually mature, but they undergo two more moults before they attain the definitive adult form.

The principal characters distinguishing Moult 8 of the male are: on gnathopods 1 and 2, the median-spine in the middle of the palmar-margin of both hands; a few coiled hairs on Antenna 2, and some lightly curved on uropod 3; those on peræopod 1 hardly noticeable.

Both the males, B.9 and A.20, figured for this series, destroyed their eighth moults; this stage and the two following have therefore been figured from K.6, a male from normal wild stock.

Antenna 1. Like that of the female; primary flagellum as in the female, 20-jointed on the right side, proximal-joint long showing the point of subdivision on the margin; on the left side this division has taken place, 21 joints being defined; 16 sensory-filaments on the right, 15 on the left, and 10 outstanding bristles in both as in the female (see diagram, Text Fig. 2), accessory flagellum 4-jointed.

Antenna 2. Peduncle, with 4 bristle-rows on joints 4 and 5, the bristles longer than in the female; and 5 rows of sensory-hairs underneath, many of the male type coiled. The flagellum is 12-jointed, but it is at exactly the same stage as in the female. The 3 proximal joints in the female are: a long growing-piece and 2 "undivided primaries"; in the male one of the primaries has divided, and the "long growing-piece" also shows a line of division. 6 outstanding bristles are present on the flagellum; there are more setæ than in the female, and on the under surface of the proximal joints clusters of sensory male hairs are developing though not yet coiled.

Gnathopod 1. Hand much larger than in the female, with the differentiation of the palmar-series complete. The angle-row contains the 2 large, strong pointed-spines; the median serrulate-seta is now transformed into a strong pointed-spine situated in the middle of the palmar-margin, with the palmar-row stretching out at an angle from it; 6 long sensory-hairs in the row, one in front crossing the others. There are 3 posterior clusters of sensory hairs and serrated-bristles, with 3 hairs and 4 bristles; 1 hair and 4 bristles; and 2 bristles respectively. On the under surface there are 2 very stout spines at the angle, the smaller one beginning to assume the typical male form, the shaft curved, flagellum reduced, and tip flattened. Seven clusters of sensory hairs and setæ are present, 3 along the anterior margin, 3 on the posterior and the first of another series developing between this one and the posterior margin. The older hairs in the posterior series have lengthened, and are slightly coiled.

Gnathopod 2. As in gnathopod 1, the hand is much larger than in the female, with the palmar-series divided. On the left hand the serrulate-setæ of the angle-row (which do not change their character in the female) have developed into almost perfect pointed-spines. The median serrulate-seta has also changed to a spine, though it is not so far advanced as those of the angle-row. It is now situated in mid-margin with the palmar-row of 5 setting out at an angle from it. On the right hand the serrulate-setæ of the angle-row are not as well developed as on the left; the median-seta, too, is less advanced, although it has commenced the change of form; it has diverged from the angle-row, but not yet reached its final median position on the palmar margin. On the under side of the angle are 2 pointed-spines, the larger one perfectly modified, the smaller not quite as much developed. There is an increase of hairs in the sensory-clusters, some are coiled, but as they are still short they do not reach beyond the margin yet; 4 posterior-clusters on the hand and on joint 5.

Peræopod 1. K.6; 1 slightly curved seta has appeared in each of the posterior clusters of joint 4.

Peræopod 3. Joint 2 with 3 spines on the anterior margin and 3 notches on the posterior left side, 4 spines and 4 notches on the right side.

Uropod 3. Both rami much more setose than in the female ; 8 clusters of sensory-hairs on the left side, several of the hairs slightly coiled ; on the terminal joint of the right side 1 bristle of a lateral cluster has appeared.

Moult 9. Mature male, second stage (Plate XI).

The characters distinguishing Moult 9 of the male are : The torsion of the palmar margin of gnathopod 1 ; the median spine with its flattened tip and small flagellum, and the group of long flexile hairs beside it, in both gnathopod hands ; and the coiled hairs on all the secondary sexual characters, antenna 2, gnathopods 1 and 2, peræopod 1, and uropod 3, most numerous on the antennæ and least numerous on gnathopod 1.

This moult is drawn from the same male K.6 as Moult 8.

Antenna 1. Primary flagellum 24-jointed, 19 sensory filaments ; accessory flagellum 5-jointed.

Antenna 2. Peduncle with a great increase in the number and length of the bristles and coiled hairs. Flagellum 12-jointed, the 3 proximal joints each with the distal hair of a new joint showing at the place of subdivision ; some coiled hairs have appeared on the inner surface of the 6 proximal joints.

Gnathopod 1. Hands much larger and more developed than in the last moult, the greatest change being in the palmar margin where the commencement of the torsion, so striking in the fully adult, can now be seen. The palmar-angle is bent in under the hand, the tip of the claw impinging against the under side. On the upper side of the angle are 2 strong pointed-spines, the smaller one of the curved-spine type characteristic of the fully adult male ; in this type the shaft is curved, the tip truncate, and the flagellum reduced or lost altogether. 2 of these small curved-spines are inset on the under side of the angle, with 1 long pointed one. The median-spine is large and stout, not tapering, the tip rather flattened and the flagellum small. The hairs in the palmar-row are now grouped in a dense cluster beside this spine, with 1 coiled hair present. The first of the 3 posterior groups also contains 2 coiled hairs. There are now 3 rows of the sensory-clusters underneath, but the hairs are still short.

Gnathopod 2. Three straight pointed-spines in the angle-row above, 2 below ; the median-spine and palmar-row have changed in the same way as those of gnathopod 1 ; 5 posterior clusters, the first containing 2 coiled hairs ; 2 rows of sensory-clusters underneath, the second one in the anterior row with 1 long coiled hair ; the first of the posterior row with 2 long coiled hairs, the second with 1.

Peræopods. Peræopod 1 with many coiled hairs developed in the posterior clusters of joints 4 and 5. Hinder peræopods very spinose, with a great increase in the number and length of the spines.

Pleon segment 2. With 3 spines in a slanting line to the margin.

Pleon segment 3. With 3 spines on the inferior margin.

Uropods 1 *and* 2. With more spines developed on the margins of the peduncle and rami.

Uropod 3. Many coiled hairs on both rami ; 4 spine-clusters on the outer ramus ; 2 bristles in the lateral cluster of the terminal joint.

Telson. With 4 spines, 2 at the tip.

Moult 10. The definitive adult stage (Plate XII). The characters distinguishing Moult 10 of the male from all the preceding moults are : the great development of the coiled hairs on all the secondary sexual characters ; the pyriform hands of the first gnathopods ; the oblique deeply indented palm and the broad truncate median-spine of the palmar margin.

The male, K.6, from which the last 2 moults were taken, ate its tenth moult with the exception of the second antennæ, 1 second gnathopod hand, part of the pleon, and a few fragments of peræopods. The male CN.444 has been figured ; it was only one day younger than K.6, and was killed the day before the tenth moult was due to take place. The new cuticle is visible, showing that the moulting was very near, but, as these males rarely ever leave their moults untouched, commencing to eat them immediately the ecdysis is completed, it was thought better not to risk losing the record. K.6 had its eleventh moult 16 days after the other, and ate the most of that.

In this stage the adult characters are established and the normal male changes very little afterwards, except, of course, for the increase in size and in the sensory armature (see Plate XVIII).

The male at Moult 10 is quite easy to distinguish from the female with the naked eye, the large gnathopods and the long hairy third uropods giving it a very different form which is especially noticeable in swimming.

Antenna 1. Flagellum 28-jointed, 14 outstanding bristles and 23 sensory filaments ; accessory flagellum 5-jointed.

Antenna 2. Flagellum 14-jointed, the proximal joints not yet divided, showing the distal hairs of the new joints at the point of subdivision ; all, except the 2 terminal, with sensory-hairs on the inner surface. This under surface on joints 4 and 5 of the peduncle and on most of the flagellum is clothed with coiled hairs.

Gnathopods. Both hands are now of the " adult male " type, pyriform, with palm oblique, particularly in gnathopod 1, and indented.

Gnathopod 1. The palmar-angle is bent completely underneath, with 1 long pointed-spine and 2 small curved-spines on each side, but the second small curved-spine of the upper side does not show from above, owing to the torsion of the margin. They are arranged in such a way that when the claw closes down there is a pair of spines (1 long and 1 short) on each side above the tip, and 1 small curved-spine each side at the tip. The median-spine is large and truncate, the flagellum reduced to nothing. Many of the bristles and long sensory setæ have developed into long coiled hairs ; on joint 5 the anterior-cluster, and 2 of the posterior-clusters have some coiled hairs in them.

Gnathopod 2. The hand is broader than in gnathopod 1 and the palm is not quite so oblique, and but little bent in underneath at the angle ; 3 stout pointed-spines, and coiled hairs as in gnathopod 1, but there are more serrated-bristles in the posterior-clusters.

Peræopod 1. With a large increase in the number of the coiled hairs on joints 4 and 5 posteriorly ; and with some anteriorly on joint 4 at the distal angle.

Uropod 3 in K.6 ; with 4 spine-clusters and 1 seta-cluster on the outer ramus ; and 2 lateral clusters on the terminal joint ; 9 sensory rows on the under surface of the left side ; and a large number of coiled hairs on both rami.

Series III. INTERSEX.

The 6 moults described below are taken from a specimen of the Irregular-eyed Stock, CN.397f., and compared with another intersex from normal stock. The two agree in practically every detail. At present these are the only two intersexes of which we have the early stages.

Moult 1 (Fig. 19).

Exactly like the normal animals.

Moult 2 (Fig. 20).

Except that it is smaller, this moult also is exactly like the normal animals.

Gnathopods. One long serrated-hair posteriorly on left side ; 1 on each margin of joint 2, right side.

Peræopod 2. No seta on the posterior margin of joint 2 ; peræopod 3, no spine on joint 6.

Moult 3 (Fig. 21).

The distinction between the normal and the intersex can be clearly seen in this stage. In size, the intersex is much smaller, and in development it is intermediate between the second and third moults of the normal animals.

Antenna 1. Flagellum 6-jointed.

Antenna 2. Flagellum 4-jointed ; no change in the armature from Moult 2.

Gnathopods 1 *and* 2. Joint 2 with 1 long serrated-hair on each side as in normal Moult 2 ; hands like those figured for the normal male at the second growth-stage (2 in the palmar-series and 1 bristle in the posterior-cluster), but on the under surface they have 1 hair of the first sensory-cluster, which in the normal is not present in Moult 2, but appears in Moult 3. On the fifth joint, too, this intermediate condition is evident : Gnathopod 1 has 3 of the serrated-bristles in the first posterior-cluster, and gnathopod 2 has 3 serrated-bristles and 1 sensory-hair (as in the normal third moult) in this cluster, but has not yet developed the second posterior-cluster.

Peræopods. All are at the same stage as Moult 2 of the normal, except peræopod 3, which carries 1 spine on the anterior margin of joint 2 (a character of the normal third moult).

Uropods 3. Exactly like Moult 2 of the normal.

The characters distinguishing Moult 3, intersex : most of the characters are those of the earlier stage of the normals, Moult 2 ; but three of the characters of the third stage are present, viz. the commencement of the sensory-clusters on the under surface of the hand ; the number of serrated-bristles in the distal posterior-cluster of the gnathopods ; and the anterior marginal spine on joint 2 of peræopod 3, the first of the hinder peræopods.

Moult 4 (Fig. 22).

Antenna 1. Basal joint with 2 sensory-hairs in the groove ; as in the normal Moult 3, flagellum 7-jointed with 3 sensory-filaments and 3 outstanding bristles.

Antenna 2. One stage behind the normal in development.

Gnathopod 1. The hand is exactly like that of the normals in Moult 2, in development as well as in size (see Plate VI) ; it has the serrulate-seta at the angle, and the bent-seta ; and 1 bristle of the first posterior-cluster. The rest of the gnathopod is like the third normal stage.

Gnathopod 2. As in the normal Moult 3 for development, but in size it is no larger than Moult 2 ; hand as in the female figured (Moult 3) with the sensory-hair on the under surface ; 1 long serrated-hair less on joint 2 than in the normal.

Peræopod 1. As in the normal Moult 3, but with a long serrated-hair developed anteriorly on joint 2 : and without the spine on the distal angle of joint 5.

Peræopod 2. Like the male figured in the normal Moult 3, but without the serrated-hair on joint 2.

Hinder peræopods. These also are at the stage of the normal Moult 3 ; peræopod 4 has a spine in the mid-margin of joint 4 on the right side.

Uropod 3. Intermediate between the third and fourth stages of the normal, e.g. the spine at the tip of the inner ramus which appears in the normal Moult 4 is present, but the feathered hair of the outer ramus which develops at the same time in the normal animal has not appeared.

The characters distinguishing Moult 4 of the intersex are: most of the characters one stage behind the normal in development; except gnathopod 1, in which the hand is 2 stages behind; and uropod 3, which has the spine at the tip of the inner ramus, as in the normal Moult 4.

Moult 5 (Fig. 23).

Antenna 1. Flagellum 8-jointed; 5 sensory-filaments, and 3 outstanding bristles; it seems to be intermediate between the third and fourth stages of the normal, not quite as advanced in development as the latter: accessory flagellum 2-jointed, proximal joint long.

Antenna 2. Also intermediate between the third and fourth normal stages; flagellum 4-jointed; it has the proximal joint (formative zone) long and the armature as in the normal Moult 3, but with the distal outstanding bristle indicative of the new primary joint, showing at the point of division. This new joint appears in the normal Moult 4, but the armature in the normal fourth stage is more advanced. The peduncle is more developed than the flagellum; it has the two posterior bristle-clusters of joints 4 and 5 represented by 1 bristle in each as in the normal Moult 4.

Gnathopod 1. The hand differs greatly from that of the normal animal of this stage; it is about 2 stages behind in development resembling Moult 3 of the normal except in the palmar-series, which here consists of 4 (as in the normal Moult 4); the serrulate-seta on the under side of the angle has become an almost perfect pointed-spine, those of the upper side of the angle are much stouter also. It is like Moult 3 also in that only 1 serrated-bristle is present in the posterior-cluster on the outer side of the hand. The rest of the appendage as in the normal third stage, except that on joint 5 the second bristle-cluster is not represented.

Gnathopod 2 is practically the same as in the normal Moult 3, except that the posterior-clusters are a little more advanced, and the sensory armature of the under side of the hand is the same as in the normal fourth stage.

Peræopods. Peræopod 1 exactly as in the normal Moult 4; peræopod 2 not as advanced as peræopod 1, like the normal male of Moult 3; the hinder peræopods are very like those of the normal male of Moult 4, but not quite as far advanced in development, particularly in the second joints of peræopods 4 and 5.

Uropod 3 is about the normal fourth stage, almost exactly like that of the normal female figured.

The characters distinguishing Moult 5 of the intersex are: most of the characters intermediate between the third and fourth stages of the normal, except in gnathopod 1, which shows some of the characters of the second stage also. The spines are longer in proportion than in the normal. The development appears to be further behind the normal than in the last moult.

Moult 6 (Fig. 24).

Antennæ. Exactly as in the normal fourth stage ; antenna 1, primary flagellum 10-jointed, 4 outstanding bristles, and 5 sensory-filaments ; antenna 2, flagellum 5-jointed.

Gnathopods. At the fourth stage of the normals in development, except the hand of gnathopod 2, in which the second posterior-cluster is not represented. The bristles and setæ are markedly longer in proportion than in the normal animals, and are more numerous in the posterior-clusters of the hand and of joint 5 of the second gnathopod.

Peræopods 1 *and* 2. As in the normal fourth stage ; peræopod 2 with 2 setæ inset on the posterior expansion of the sideplate (a character of the normal Moult 5), and with 1 seta less on joint 4 than in the normal Moult 4.

Hinder peræopods at the normal fifth stage, except the second joint of peræopods 4 and 5, which are not quite as far advanced.

Uropod 3. Left uropod damaged ; the right uropod, which is figured, was injured in Moult 2, and regenerated, but had not reached the same development as the left.

The characters distinguishing Moult 6 of the intersex are : most of the characters at the fourth stage of the normals in development, i.e. two stages behind, except the hand of gnathopod 2, which has the first bristle-cluster larger, and the second not represented ; peræopod 2 with 2 setæ on the posterior expansion of the sideplate, as in the fifth stage of the normals ; and the hinder peræopods, in which joints 3–7 are like those in the fifth stage of the normals. The bristles and setæ are much longer in proportion to the size of the animal.

This Moult 6 of the intersex has been compared in detail with the same moult in another specimen 1.B, from normal stock ; they agree in practically every particular, 1.B being slightly larger and carrying 2 or 3 more setæ.

The most important point about this moult is that the sexual differentiation which appears in the normal males and females at this stage is not shown, that is to say, neither the coiled hairs on the antennæ of the male nor the broodplates of the female are developed.

CONCLUSIONS AND SUMMARY.

The first point, perhaps, to strike an observer in examining an animal like *Gammarus chevreuxi* is the *constancy of the characters* of each successive stage of growth, i.e. the external characters of any number of individuals at any one stage of growth are practically identical to the smallest detail. Changes of temperature, changes of habitat, of salinity, or of food, or of all combined do not appear to affect the form of the cuticle, or to alter a single hair of its outgrowths. The species has been kept under artificial conditions in the Laboratory for a period of twelve years, fed on a uniform diet, and inbred for generations, yet the animals have not differed in the slightest degree as regards the cuticle and sensory armature from the wild animals freshly brought in from the open.

Changes of temperature, it is true, can shorten or prolong a period of growth, but the moult at the end of the period lasting only 3 or 4 days, for example, is precisely the same as the moult sloughed off after a period of 18 to 20 days ; it is quite as large, and quite as fully developed. Adverse conditions, also, can and do affect the *texture* of the cuticle, although the outgrowths do not appear to be altered.

The next point of interest brought out by the investigation of the moults is the *progression of growth* traceable through succeeding stages. This is, of course, demonstrable on any of the appendages, but can be more easily followed on those parts which undergo the most modification, viz. the antennæ and the gnathopods.

For the progression of growth in the *Antennæ* see p. 355 and Text Fig. 2.

The progression of growth in the *gnathopods* is best demonstrated in the "hands" (see p. 360), and can be traced in the gradual change of the palmar-margin and armature through the immature stages to the stage at which the animals become sexually mature. The differentiation of the characters stops here in the female, but in the male it is continued through two more moults to the definitive "adult form." At this point the differentiation of characters stops in the male also, and the characters now assumed by both sexes are preserved unchanged through the rest of their lives, the only alteration afterwards being in the increase of size until the maximum growth of the species is attained, and in the increase in the number of spines and setæ in the groups.

In the intersexes, however, development proceeds on different lines. It is very much slower in the early stages, but both *growth in size* (in the female intersex) and *differentiation in the characters of both male and female intersexes persist to a much greater extent than in the normal males and females*, and continue throughout life. This important fact has, I think, been conclusively demonstrated in the course of these investigations. A series of the hands of the female intersex has been figured (Plate XXI) to show the change from the normal female type of palmar armature to the male type at the early mature stage. A remarkable development in both male and female intersexes is shown, one, a male intersex hand with two truncate median spines (Fig. 57) ; and two others, female intersex hands, with two angle-rows of spines and setæ (Figs. 58 and 59).

The difference in size, too, is noteworthy; the largest male measured 14·5 mm. in length at the age of 579 days, whilst the largest female-intersex, not much more than half its age, measured 17 mm. when 310 days old.

The progression of growth, as shown in the *setæ and spines*, is also of interest. The newly hatched animal starts life with certain setæ and spines already developed on all the appendages. Some of these setæ remain unchanged through all the succeeding growth-stages, others undergo modification into spines, some to an extraordinary extent. It may be noted here that *the setæ which undergo the most modification occur on those parts of the body which are most changed by growth and sex*, viz. the hands and in particular the palms of the First and Second Gnathopods, whilst the setæ which remain unaltered occur on those parts of the body which retain their characters practically unchanged through life. One point comes out clearly in connection with the unchanged setæ, and that is: *the proximal joint and the terminal joint in all the appendages are the same in the newly hatched as in the adult*, and the bristles, or setæ, or plumose hairs present on them at birth remain unaltered through life, except for size and the addition of 1 or 2 more setæ later.

The modifiable setæ and spines are of different types, each type confined to certain appendages, e.g. the serrulate-setæ and serrated-bristles occur only on the gnathopods; the long sensory-hairs with the terminal portion serrated are found only on the second joints of the gnathopods, and the first two pairs of peræopods; and the sensory setæ which develop into the long, very slender sensory spines occur only on the hinder peræopods. The spines which appear later on the uropods, on the epimera of the second and third pleon-segments, and on the second joints of the hinder peræopods are of a different type from the spines developed from setæ. They appear on the hinder peræopods in the third moult, as already-formed small, stout spines on the anterior margin of joint 2, when the modifiable setæ at the distal anterior angle of this same joint has just changed to a spine.

The *direction of growth* is the next point to be noted. Growth takes place at the proximal end of an organ and not at the distal, e.g. the new joints which arise on appendages such as the flagella of the antennæ are formed at the proximal end of the flagellum; the new bristle-clusters of the gnathopods develop proximally, as do also the new marginal groups on the joints of the peræopods, and the spine-clusters of the third uropods.

The examination of the moults has revealed an interesting structural detail, too small to be easily detected in the living animal, viz. the *sensory groove* on the upper surface of the basal joints of the First Antenna. This groove would appear to be analogous to the "auditory sac" found in *Anaspides* and in many of the Decapoda.* It lies longitudinally, is long, narrow, and shallow, lined with exceedingly thin and delicate chitin, and is inset with very fine mobile plumose hairs, each in a little socket. One of these hairs is present on hatching, others develop as the animal grows older (Fig. 27). The groove faces towards the inner side of the joint; on the outer side and in a line with it, is a group of 3 plumose mobile hairs, found unchanged in all the moults. This groove with the accompanying group of hairs I have found in many other amphipod genera, and it probably occurs in all.*

To summarise the results of the investigations :—

1. There is a constant change in the proportions of the body from birth to maturity, e.g. the peræon which is practically subequal to the pleon in length at birth, is a third as long again at maturity.

2. The early growth-stages of the male are externally indistinguishable from those of the female, and the secondary sexual characters are not recognised until the sixth stage.

3. The male takes longer than the female to reach the "definitive adult" stage and its secondary sexual characters undergo much greater modification. This fact, hitherto unknown, is probably the cause of much of the confusion in the taxonomy of the Amphipoda, the different breeding stages being described as different species.

Another cause of confusion may be the similarity of the young immature stages of the species of a genus. If, as in the case of *Gammarus*, several closely allied species inhabit the same locality, a dredging will contain the growth-stages of various species, with more young specimens than mature. In many instances these have been described as belonging to one single variable species, and the specific boundaries enlarged to admit of the so-called "varieties."

4. In the genus Gammarus the females of some of the species, e.g. *G. locusta*, lay eggs without a male being present, although the probability is that these eggs do not develop; certain others, e.g. *G. chevreuxi* and *G. pulex*, never deposit their eggs without a male.

5. It is shown that the differences between species, even the closely allied species of the same genus, are very marked; in the number of moults to maturity, and length of moulting period, in the size and number of the eggs, the length of the incubatory period, and the time of extrusion of the young. These differences probably form an insuperable bar to cross-breeding.

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* Calman. 1911. *Life of Crustacea*, pp. 22–4. Geoffrey Smith. 1909. *Camb. Nat. Hist.*, Vol. IV, pp. 116 and 152.

6. It is at present not possible to establish specific characters which will hold good for both sexes at all stages of their growth, nor is it yet possible to distinguish the youngest stages of closely allied species by any structural character. At somewhat later stages when maturity is being approached definite differences can be seen, such e.g. as the shape of the broodplates in the immature females, or the sensory armature peculiar to the different species, though these differences have not yet been worked out in detail. The sideplates which may undergo less change than the other external parts, appear to be the most reliable characters for distinguishing the species of a genus, at least as far as *Gammarus* is concerned.

THE INTERSEXES OF *GAMMARUS CHEVREUXI.*

The appearance of intersexes in *Gammarus chevreuxi* has already been recorded (*Journ. Mar. Biol. Assoc.*, XII, 3, Sept., 1921), and a description given of the female intersexes.

These all occurred in the stock used in the Laboratory experiments, and many others have since appeared in the same stock. Male intersexes also have been recognised as such, and certain of these are now described and figured.

For the first time in the records of this species, intersexes have been found amongst the wild animals. A dredging was made in the ditches draining the salt marsh, Chelson Meadow, in February, 1922. Owing to the exceptionally dry season of 1921 the ditches were nearly empty, and the animals proved to be very scarce. After hours of work only 104 specimens were captured, but of these four were female intersexes.

I believe it will yet be found that intersexuality is not rare in the Amphipoda, and that the specimens hitherto recorded as "abnormal" in development will prove to be only abnormal in that they are intersexual and have developed some of the external characters of both male and female. Chilton, for instance, describes an ovigerous female of *Erichthonius brasiliensis* (*Dana*) with the second gnathopod of the young male,* and a female of *Corophium crassicorne* with the second antenna of the "immature male."†

A female intersex of *Tmetonyx similis* was described in *Journ. Mar. Biol. Assoc.*, Vol. XII, No. 3, 1921, p. 544.

The female intersexes previously described were characterised by having some of the characters of the male and some of the female; they

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* *Trans. N.Z. Inst.*, Vol. 54, p. 242, and figure. 1923.

† *Trans. N.Z. Inst.*, Vol. 53, p. 232. 1921.

resembled the male in general appearance, size, colour, and habit of swimming, but were provided with the broodplates of the female. The curved male hairs and the palmar-spines of the young male were present also in many of them. They appeared to vary in the degrees of intersexuality, and were divided into three groups according to the degree of development of the hairs on the broodplates, rudimentary, partially developed, or fully developed. There is probably a correlation between the development of the gonads and of the secondary sexual characters, but the exact extent of this correlation is not yet known.

The young stages had not then been observed in detail. The animals were not recognised as intersexes until they were mature, and the records previous to maturity referred chiefly to their slow development and small size.

The moult investigations have shown that the differentiation between normal and intersex becomes apparent in the second moult. The external characters on hatching are identical for normal male, normal female, and intersex. In the second moult the difference in size appears, which in the third moult is very marked. In the intersex series figured (Plates XIII and XIV) only the first 6 moults are represented, but in them it is easy to trace the difference in the rate of development as well as in size.

In the third moult the animal is intermediate between the second and third normal stages. In the fourth moult the characters are mostly one stage behind the normal with the hinder parts slightly more advanced in development. In the fifth moult the difference has become very marked, not only in size but in the rate of development which seems to be slower than before: most of the characters are now between the third and fourth normal stages.

In the sixth moult the intersex is about two stages behind the normal, but with certain distinctions which prevent the possibility of confusing it with the fourth normal stage. For example, it has the two indentations posteriorly on sideplate 4 (a character of the fifth normal moult), and parts of the hinder peræopods also are much more advanced than in the normal fourth moult. The most important point about this stage of the intersex is, that differentiation of secondary sexual characters is not yet indicated. In Moult 6, of the normal female, small broodplates are found; and in the normal male a few of the coiled male hairs appear on the second antenna. At what stage in the intersex sexual differentiation can be traced is not yet known, but experiments are still proceeding to ascertain this point.

The most striking feature in the intersex, and one which distinguishes it from the normal, is the steady progression of growth (in size in the female intersexes) and of differentiation of the characters through the whole of its life. In the normal animals sexual differentiation is complete at maturity ; growth in size continues for some time longer, until the female reaches from 7 to 8 mm. in length, and the male from 11 to 13 mm. ; then it practically ceases, the differences thereafter being hardly perceptible.

In the female intersex, on the other hand, not only does growth in size continue, but the differentiation of the characters in the " male " direction proceeds steadily on through life, although, apparently, the fully adult male characters are never reached.

In gnathopod 1 the female intersex hand develops almost exactly like that of the young male of the early mature stage (cf. the first gnathopod of CN.183m., Fig. 56, with the hand of the young male of Moult 9 in Plate XVI) ; the angle-row spines, the median pointed-spine divergent from the angle-row, and the extra spines on the under surface of the angle are all present.

It must be noted, however, that though in the female intersex the median-spine was modified into the pointed-spine of the young breeding male, the animal mated *as a female.*

In gnathopod 2 the development proceeds along the same lines as in the normal to a certain point. In the older female intersexes, as in the normal male, the serrulate-setæ of the angle-row change to pointed-spines, the first developed one of the row is modified into the median pointed-spine, and diverges from the angle-row to the middle of the palm, and even the claw moves its position and comes to impinge against the under surface of the hand as in the normal male, instead of closing down against the edge of the palmar margin as in the female. This point is the farthest towards maleness ever reached by the female intersexes, and even in these advanced specimens there is no mistaking the " intersexual type." This is best displayed perhaps in the angle-row. In the normal male the angle-row consists of spines and spines only, in the normal female of serrulate-setæ only, but in the older intersexes it is always mixed, serrulate-setæ and pointed-spines, and always changing, the serrulate-seta of one stage becoming the pointed-spine of the next.

In a specimen figured, CN.284a, the largest of the female intersexes, the various points towards maleness will be seen, the torsion of the palm, the divergence of the palmar-row, the extra spines developed on the under surface of the palmar-angle (Fig. 53), and the " intersexual type " angle-row (Fig. 49).

The hands of another female intersex, CN.229h, are also figured (Figs. 54 and 55), to show two stages of development, with six months' interval between.

The regular progression of the modification as well as the tendency always to develop more outgrowths than the normal, can be seen in each moult, the older serrulate-setæ changing to spines, and new ones arising posteriorily at the angle. This is shown in the fullest development yet found in the intersexes in two specimens, CN.289a and CN.323a (Figs. 58 and 59).* In these, a *doubling* of the angle-row seems to be taking place, more plainly evident perhaps in CN.289a, where it is just commencing. The previous moult showed only one stout serrulate-seta below the angle-row; in the moult figured there are two.

In all these female intersexes the broodplates show an increase in the number of the fringing hairs with age as in the normal female, and the number continues to increase until it becomes larger than in the normal, although the size of the broodplate itself is much smaller (see p. 392, Text Fig. 4). This is true of the fringing hairs of all the specimens, rudimentary hairs increasing in number; partially developed hairs increasing also in length as well as number in later moults.

The male intersexes are far more difficult to recognise as such than the female ones. They develop very slowly, taking some months to reach maturity. In the records kept they were noted at first as "male ? exceedingly small," or as "very small male, Antenna 2 with male coiled hairs, other secondary sexual characters not yet developed."

In normal males the secondary sexual characters appear to differentiate in the following order: Coiled hairs develop first on the second antennæ, then on the third uropods and first peræopods, and, lastly, on the gnathopods 2 and 1. In the male intersexes also these hairs appeared first on the second antennæ, and that being a male character which can be easily seen without taking the animals out of the water, led to their being marked as "male." Later, when the small size was noted as constant, they were taken out for examination of the other characters, and the intersexuality was found.

The specimens described below were all very small, about 7 mm. in length (a character of the female), and in all some of the secondary sexual characters were of the intersexual type; no broodplates were present in any of them.

CN.314b. F_3 CN.I.b. Irregular-eyed Stock (Figs. 46, 47, and 52). This specimen was one of a brood of 21 extruded on August 14, 1920; of which 5 came to maturity, four normals, 2 males, 2 females, and this male intersex. It was extremely slow in development, the normal males being fully mature on November 22, 1920, whilst this one was marked "nearly mature, exceedingly small" on February 22, 1921. In the moult of December 3, 1920, male hairs were seen on the second antennæ, but the other secondary characters were not male. On March 12, 1921,

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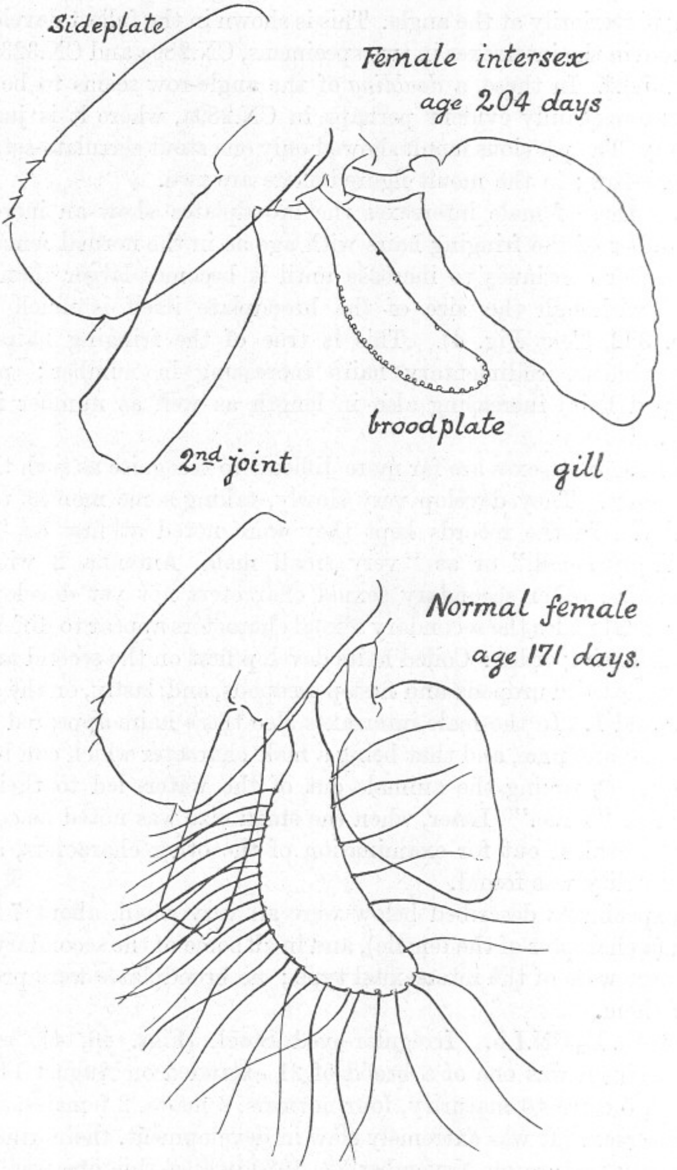
* The specimens 12 and 23 described in a previous paper, "Intersexes in *Gammarus chevreuxi*," Sexton and Huxley, *Journ. Mar. Biol. Assoc.*, Vol. XII, No. 3. 1921.



TEXT FIGURE 4.—Second gnathopod broodplates of two females from the same brood, CN.183, a normal and an intersex. The small size and rudimentary hairs of the intersex broodplate are characters of the immature normal female, but the number of the hairs is a character of the adult normal female. Drawn to the same magnification.

after a moult it was very feeble and as it was not likely to recover, it was preserved. It then measured only 7 mm.; age, 210 days.

In gnathopod 1 both hands had 3 spines in the angle-row, and the median pointed-spine and palmar-row as in the young normal male, the right hand, with 1 extra spine on the under side of the angle, not present in the left. Gnathopod 2 was of the typical "intersex" type; the palm transverse as in the female (cf. 314b gnath. 2 hand Fig. 47 with that of the female intersex 323a, Fig. 58), not, as in the normal male, oblique and deeply indented. The median pointed-spine was like that of the early mature stage of the normal male about as in Moult 8, not as advanced as Moult 9. The angle-row was typical "intersex," 1 pointed-spine and 4 serrulate-setæ in the row on the right hand; 2 spines and 2 serrulate-setæ on the left hand. On the under surface of the angle the right hand had only 1 spine; the left hand had 2, one not quite developed. Both gnathopod hands very setose, but there were only 5 posterior-clusters of serrated-bristles, i.e. at the age of 193 days the animal had no more clusters developed than the young mature male at the age of only 45 to 50 days.

The gills were very large, extending in peræopod 2 beyond the third joint.

The coiled hairs were present on the antennæ; but not on the first peræopods, nor on the gnathopods; on the third uropods a number of long fine sensory-hairs had developed, but none were coiled. The third uropods were of the intersex type, broad and spinose with about 10 sensory-clusters on the under surface of the outer ramus.

CN.289c. F_4 CN.I.b. Irregular-eyed Stock. This specimen was one of a brood of 13 black-eyed, extruded July 17, 1920, 5 of which came to maturity. None of them were normal; one, a female, had irregular eyes and no superior antennæ, mated and had young; another, a male, also irregular-eyed; the remaining three were intersexes, 2 females, one irregular-eyed, and 1 male. This specimen, also irregular-eyed, was noted as "very small" on September 8; on October 19 as "small male"; on November 24 as "exceedingly small for its age; too small to mate; antennæ with male hairs, but gnathopods appear to be of the intersex type." It died on December 3, 1920, age, 140 days; length, only 7 mm.

It is almost exactly like the male intersex just described; if anything very slightly more "male," as shown by the two or three coiled hairs on the first peræopod, and one or two more sensory-clusters on the third uropod.

The first antennæ were both broken; the second antennæ carried a few coiled hairs on both the peduncle and the flagellum.

In gnathopod 1 the hands were like those of CN.314b. (see Fig. 46). In gnathopod 2 the angle-row, typically intersex, consisted of 2 pointed-spines and 2 serrulate-setæ on each hand ; and on the under side of the angle 2 spines were present in each, one perfectly developed and one not quite fully modified ; 6 serrated-bristle clusters on each hand. All the other details exactly as in CN.314b. No coiled hairs were found on the gnathopods, but 2 or 3 were present on the first peræopod, and the third uropod carried a number of the long sensory-hairs, curving but not coiled.

CN.269d. F_3 CN.I.b. Irregular-eyed Stock. One of a brood of 29 black-eyed, extruded June 21, 1920. Two were male intersexes, this one and the next to be described, CN.269b., both normal-eyed and spotted. This specimen was almost exactly the same as the two male intersexes previously described at its death at the age of 110 days. It was then 7 mm. in length.

Fragments of its moult, on September 16 at the age of 87 days, were found and examined. The stage of "male" development then reached was about the same as that of the normal male at its seventh moult. In both the gnathopod hands the median serrulate-seta had diverged from the angle-row ; but, although broadened at the base, it was still a serrulate-seta, not a pointed-spine. Gnathopod 1 had 2 spines at the angle. Gnathopod 2 had in the right hand (the only one found) 3 serrulate-setæ in the angle-row, the first of them modified and almost a spine. By October 8, 3 spines had developed on each side of the angle on both hands of gnathopod 1. The hands of gnathopod 2 were then exactly like those figured for CN.314b. in size, shape, and armature (see Fig. 47).

This specimen, like the other two, CN.314b. and CN.289c., never developed the coiled hairs on the gnathopods. A few coiled hairs were present on the second antenna, and long fine sensory-hairs on the third uropod in the moult of September 16. At its death on October 8, coiled hairs were also found on the first peræopod ; and a number of the sensory-hairs on the third uropod were lightly curved. It was far behind the normal male in development as well as in size. In the antennæ, for example, the stage reached was about the eighth stage of the normal, 22 joints in the right primary flagellum, 21 in the left of the First Antennæ, 4 joints in the accessory flagella, and 10 joints in the flagella of the Second Antennæ.

CN.269b., the second male intersex from the brood CN.269. This specimen was slightly larger than the three preceding ones, and more "male" in its development, as shown in the pyriform shape of the hand of the first gnathopod, and in the greater number of coiled hairs.

The development of the characters can be traced through several moults. In the moult at the age of 138 days, a few coiled hairs were present on the second antenna and the first peræopod; 8 clusters of sensory-hairs, some lightly curved, on the third uropod; no coiled hairs on the gnathopods.

The hand of gnathopod 1 was more male than in the previous specimens described, pyriform, the palm oblique with the median spine just diverging from the angle-row. The hand of gnathopod 2 was of the intersex type, the median spine in mid-margin, and the angle-row composed of 3 slender spine-like serrulate-setæ.

In the moult at the age of 160 days, the number of the coiled hairs had increased on the second antenna, the first peræopod, and the third uropod; and a few had developed on both gnathopod hands.

The hand of gnathopod 1 was very like that of the young normal male of about 45 to 50 days old in the early mature stage, but not as large, the claw not much modified, and the coiled hairs and setæ much fewer. The hand of gnathopod 2 was intersexual in type, palm oblique, the serrulate-setæ of the angle-row modified into spines; only 5 posterior-clusters were present, and a very few coiled hairs.

It died on March 3, 1921, age 256 days. It had not increased perceptibly in size, nor altered much in character since attaining maturity, except that it became more intersexual rather than more male, although the number of the typical male coiled hairs had increased on the secondary sexual characters (cf. with this, the increase with age in the number of fringing hairs on the broodplates of the female intersex).

CN.199k. F_3 CN.I.b. (Fig. 57). Irregular-eyed Stock, one of a brood of 21 black-eyed, extruded April 5, 1920. Its eyes were very irregular on hatching; the right eye small, with 2 black and 1 red ommatidia, and with a long connecting thread-like white streak from the eye to a large spot over the stomach; the left eye was only a thin streak of white with 2 tiny specks of reddish black colour; it had a very large white patch on the left side over the stomach.

On June 30 it was marked as "male," but was then so small that it was considered unsafe to try and mate it, the smallest mature females being so much bigger that it was feared they would eat it if put into its bowl.

On July 1 a few coiled hairs were noted on the second antenna, 1 or 2 on the first peræopod, and the third uropod; none on the gnathopods. The hand of gnathopod 1 had 3 spines on each side of the angle; the median-spine slender, not long modified. The right hand of gnathopod 2 was the only one found in the moult; it had 1 spine and 2 serrulate-setæ in the angle-row; the palmar-row divergent, with the median-seta almost a pointed-spine; and midway between these two groups was a larger spine with a blunt tip, carrying a flagellum; 5 clusters of serrulate-bristles on the posterior margin of the hand, and 5 sensory-clusters in the posterior row on the under surface. This appearance of a *second* spine, apart from the angle-row, in the palmar-series, is the only instance yet found of such an occurrence in the male intersexes. It is comparable with the *double* angle-row of specimens CN.323a. and CN.289a. female intersexes.

The eyes were examined on July 1, and were found to have changed considerably. The right eye had developed a fairly normal shape, and was almost a Black No-white. The left eye greatly increased in size, was very large and very irregular, with several ommatidia separate from the ommateum; almost No-white.

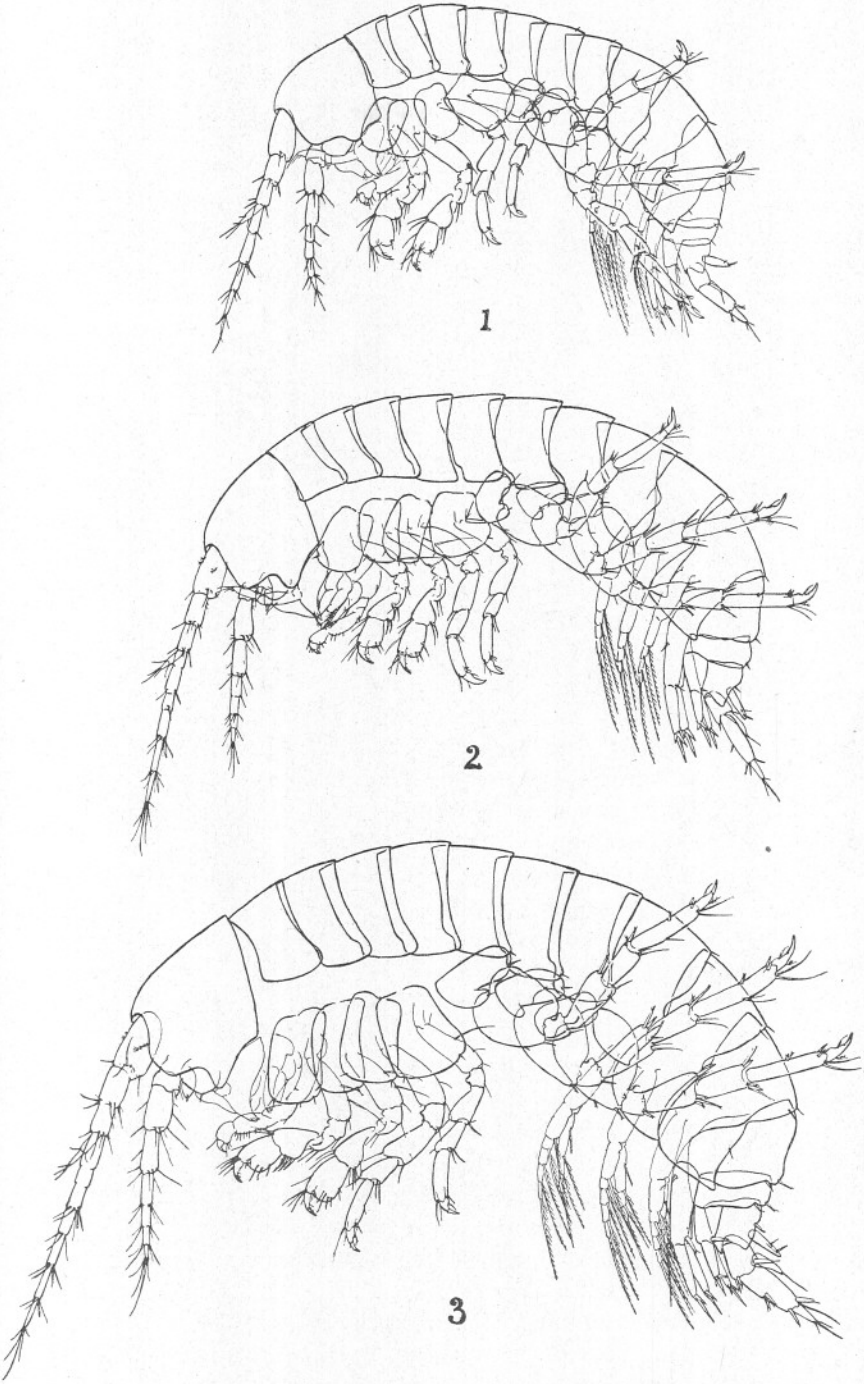
On July 26 a young fertile female was put into the bowl; mating took place, lasting till August 2. On August 5 the male intersex moulted. It mated again on August 9 for a day; the female moulted, but no eggs were laid. From August 20–24 another mating occurred, with the same result, the female moulted, no eggs laid. On August 31 it moulted once more, but did not mate again with any of the females. Its eyes remained unchanged till its death on September 16, 1920. It was only 7 mm. in length at the age of 164 days.

In the moult of August 5, gnathopod 1 had 1 median truncate-spine and 2 pointed-spines at the angle. In gnathopod 2, both hands had *two* truncate spines developed on the palmar margin, one the "median-seta" of July 1, with the cluster of sensory-hairs behind it, and the other half-way between this and the angle-row; 2 spines in the angle-row; and 7 serrated-bristle clusters. The figure given shows the hand of the second gnathopod on September 16 at the time of its death.

It will be seen that the intersexes described above begin life as males and then develop a certain degree of femaleness, or perhaps it would be better to say they are genetically males, but never attain to complete maleness, the immature (or female) characters persisting, and, in the case of the armature of the hands, combining with the partially developed male characters to produce the intersexual type. The small size reached is a female character, and so also is the shape of the gnathopod hands, and the absence of the male hairs from some of the secondary sexual characters. On the other hand, they never develop the most typical of the female characters, the broodplates, just as the female intersexes, however far advanced they may be towards maleness, never produce the typical male truncate-spines and coiled hairs.

My best thanks are due to the Director, Dr. E. J. Allen, for his help both during the course of the work and in the writing of this paper, and to Miss A. R. Clark for her assistance with the experiments.

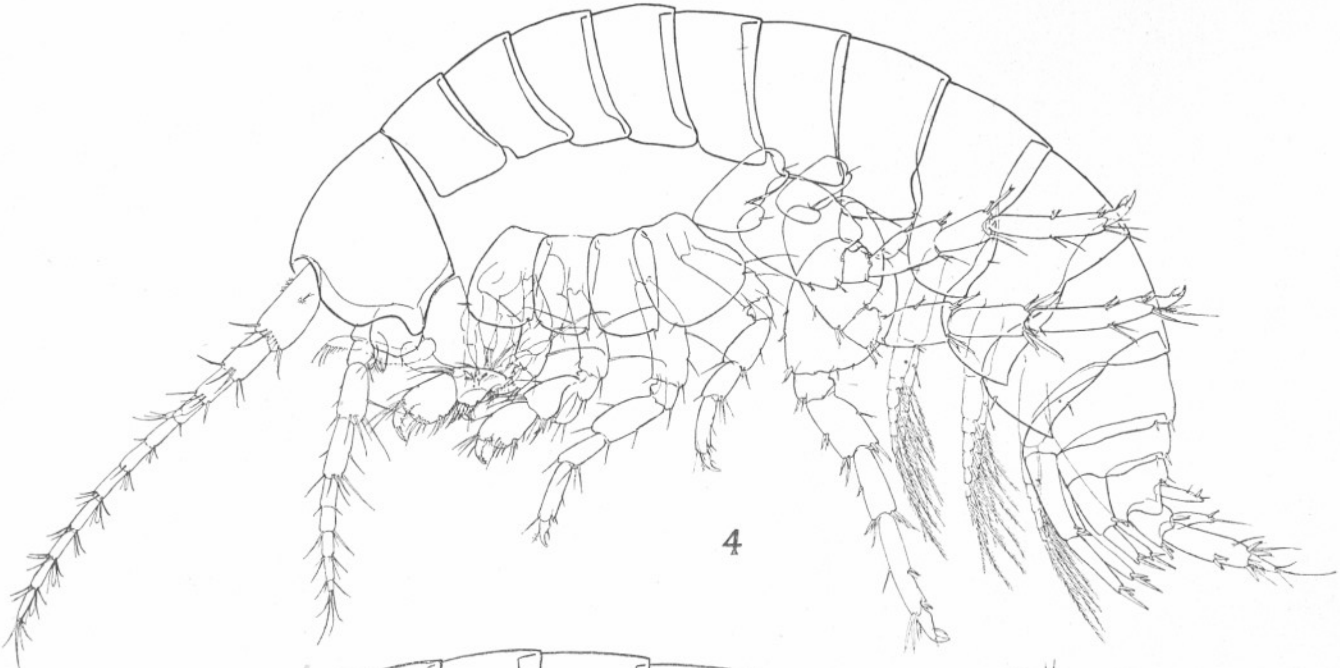
PLATE I.



E. W. SEXTON del.

Normal Female. Moults 1, 2 and 3.

PLATE II.



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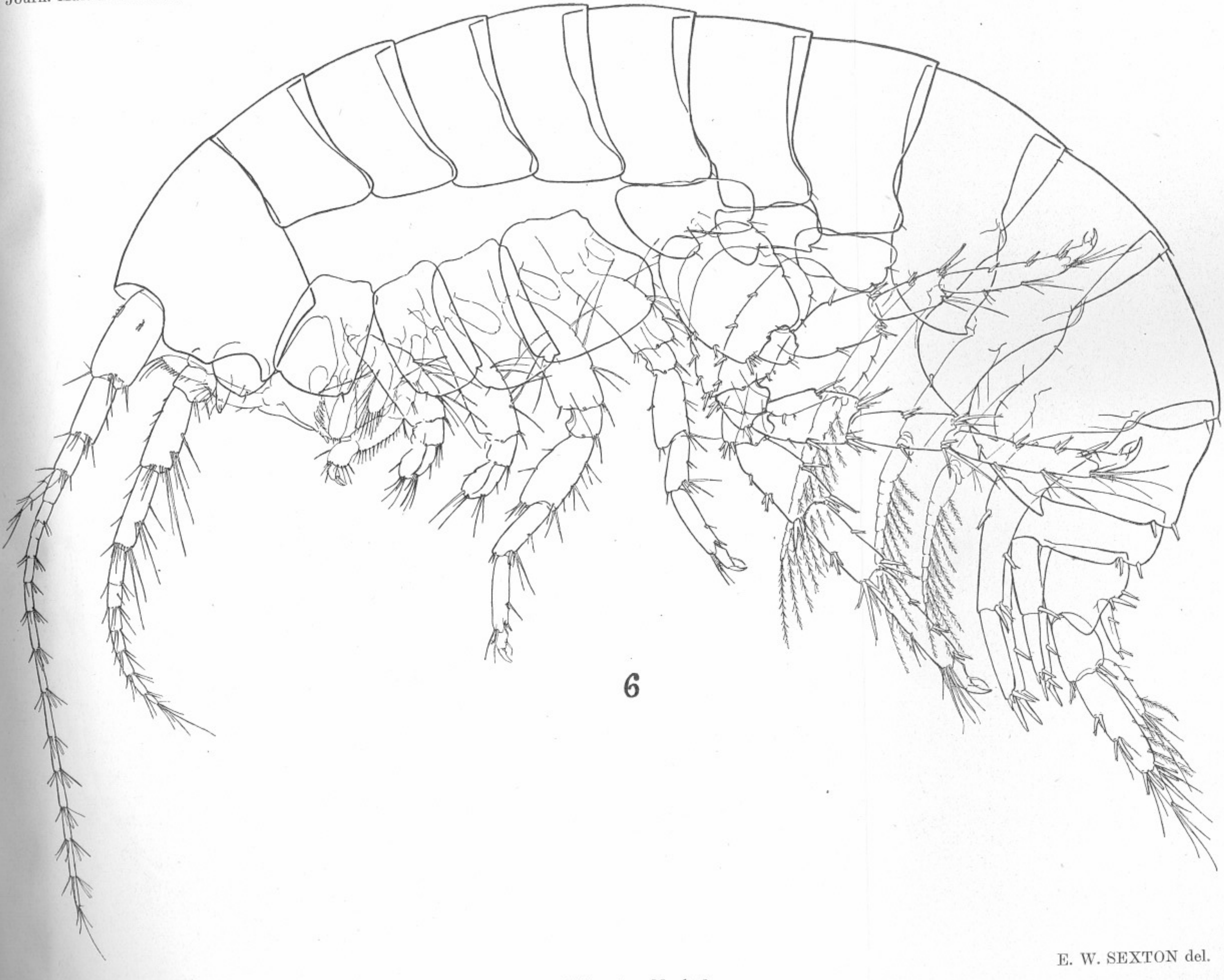

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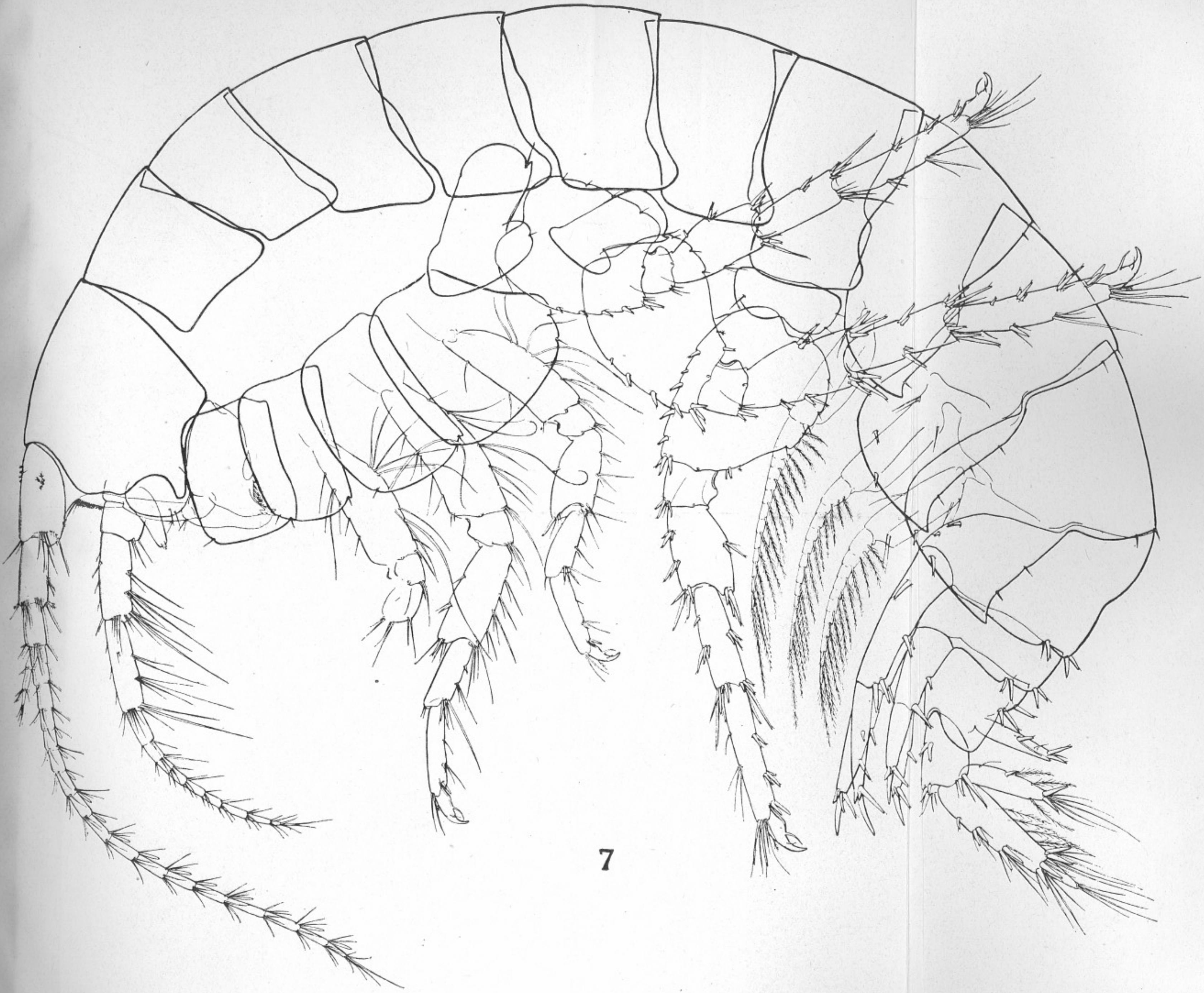
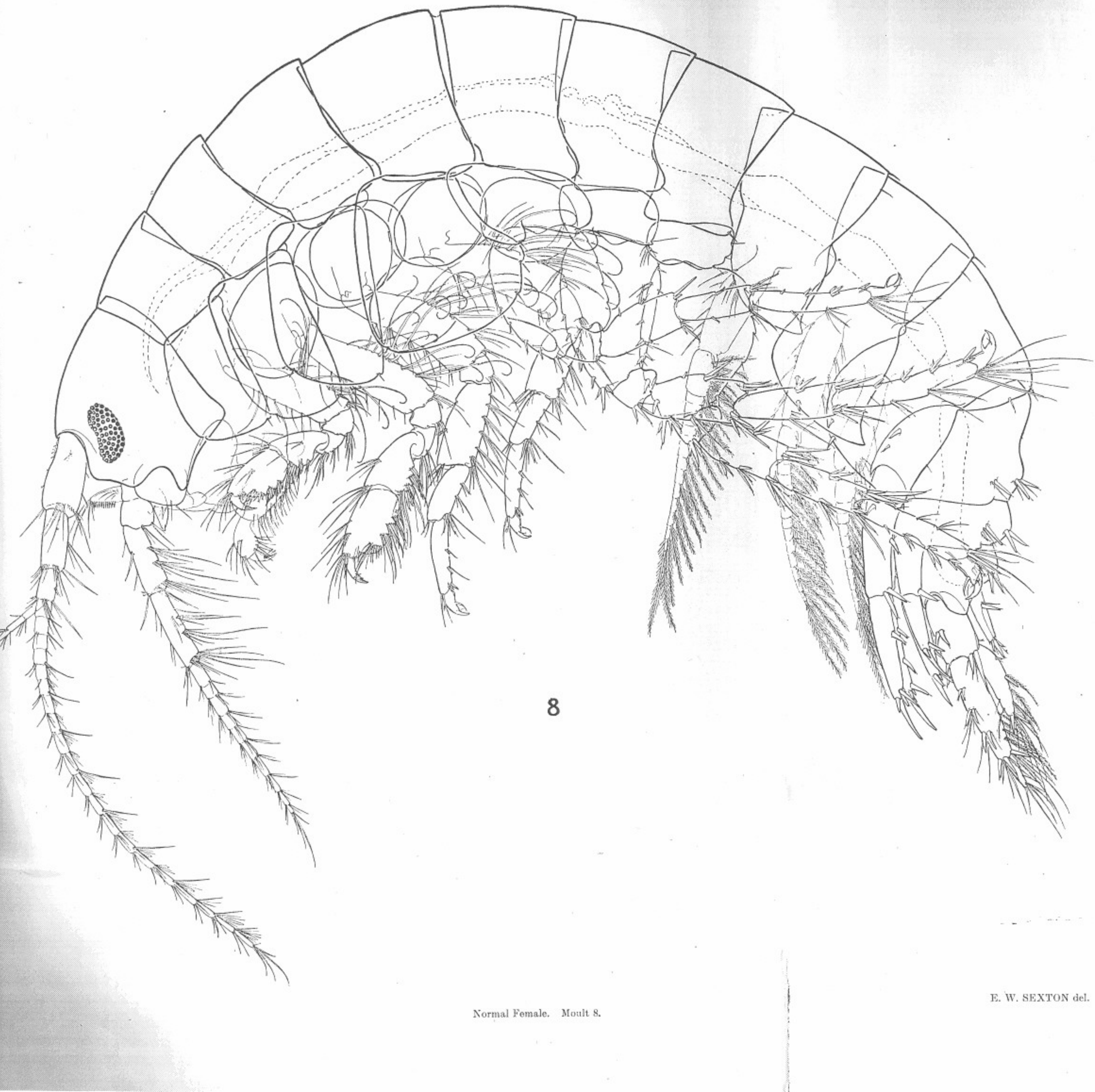
Normal Female. Moult 6.



Normal Female. Moult 7.

E. W. SEXTON del.



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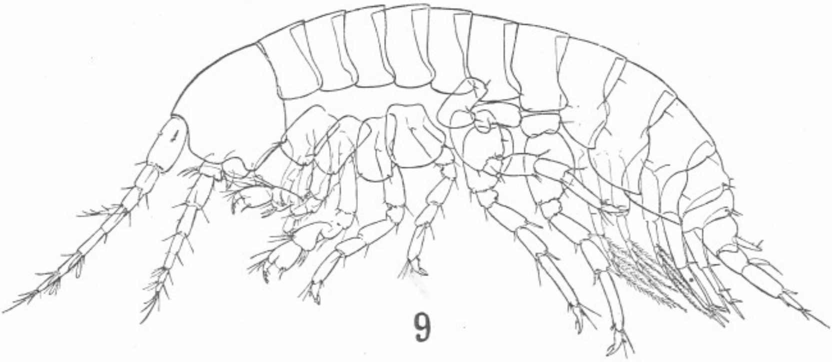
E. W. SEXTON del.

Normal Female. Moult 8.

PLATE VI.



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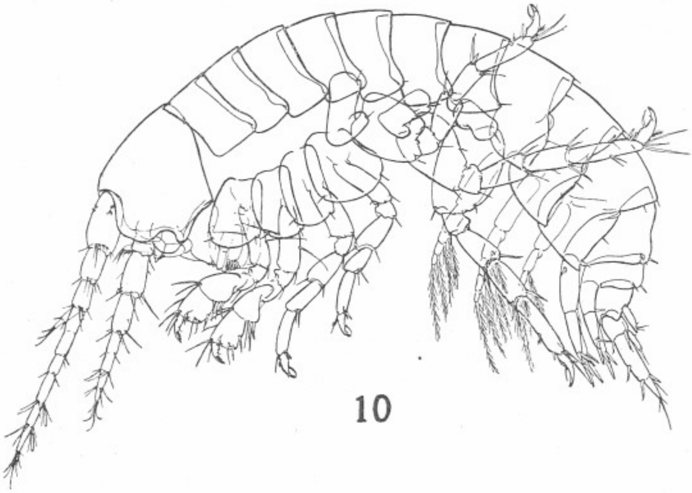

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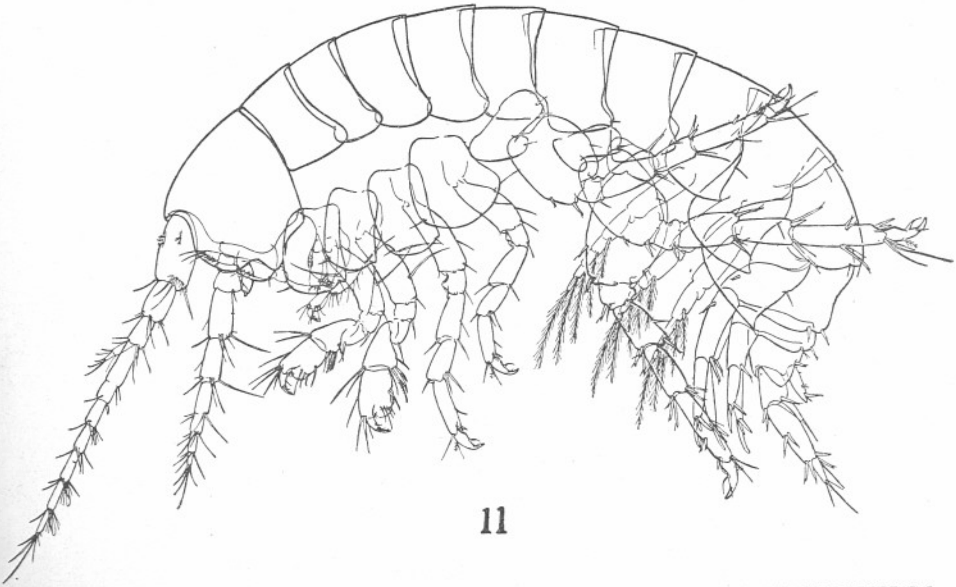
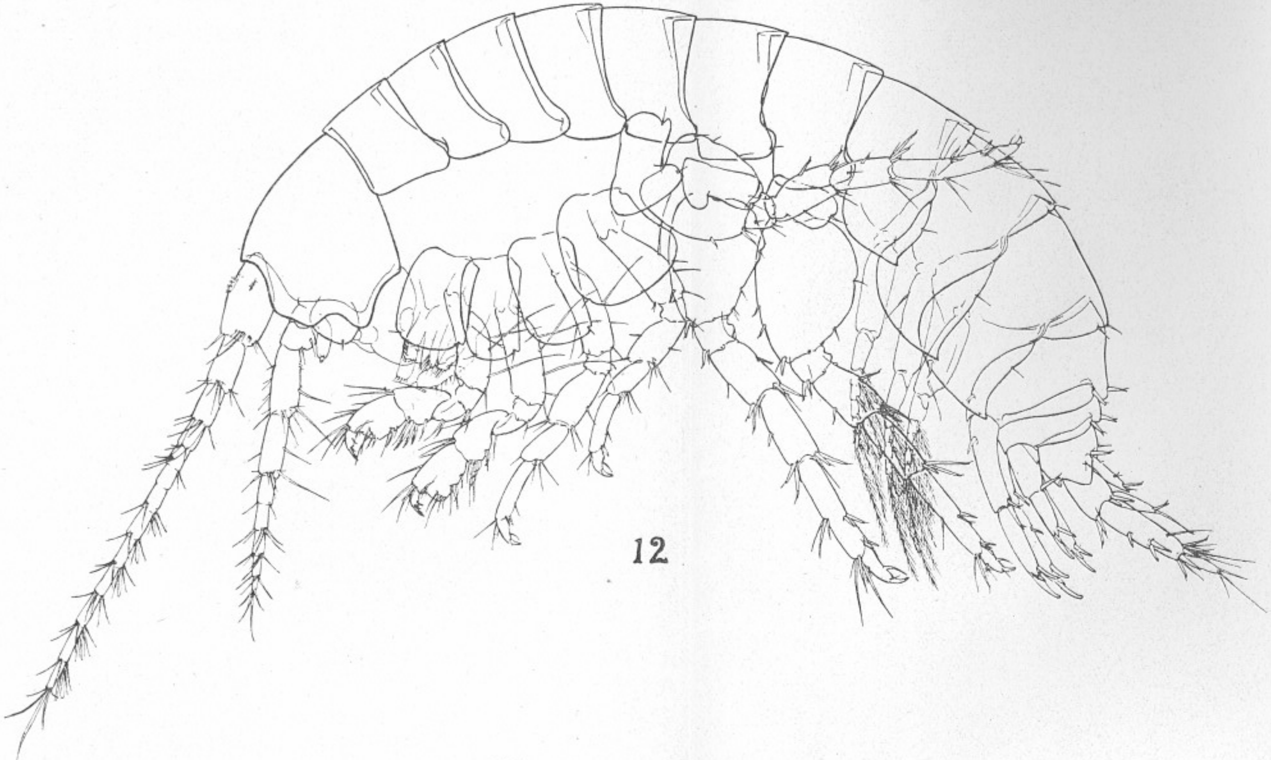


11

E. W. SEXTON del.

Normal Male. Moults 1, 2 and 3.



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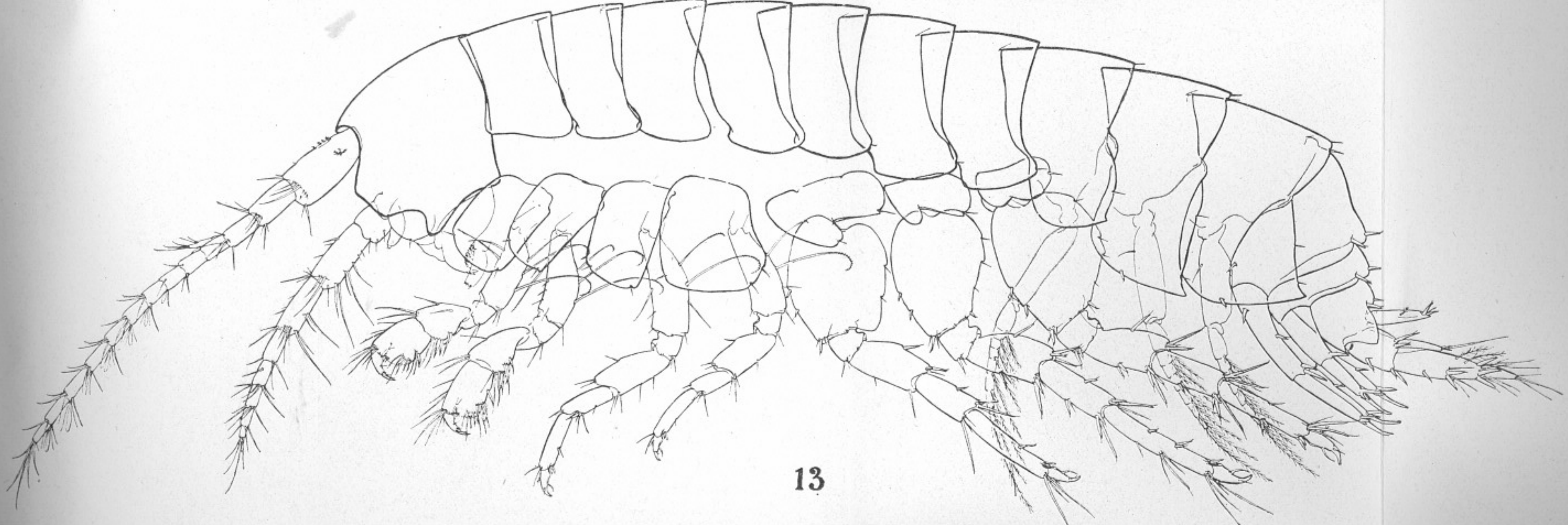

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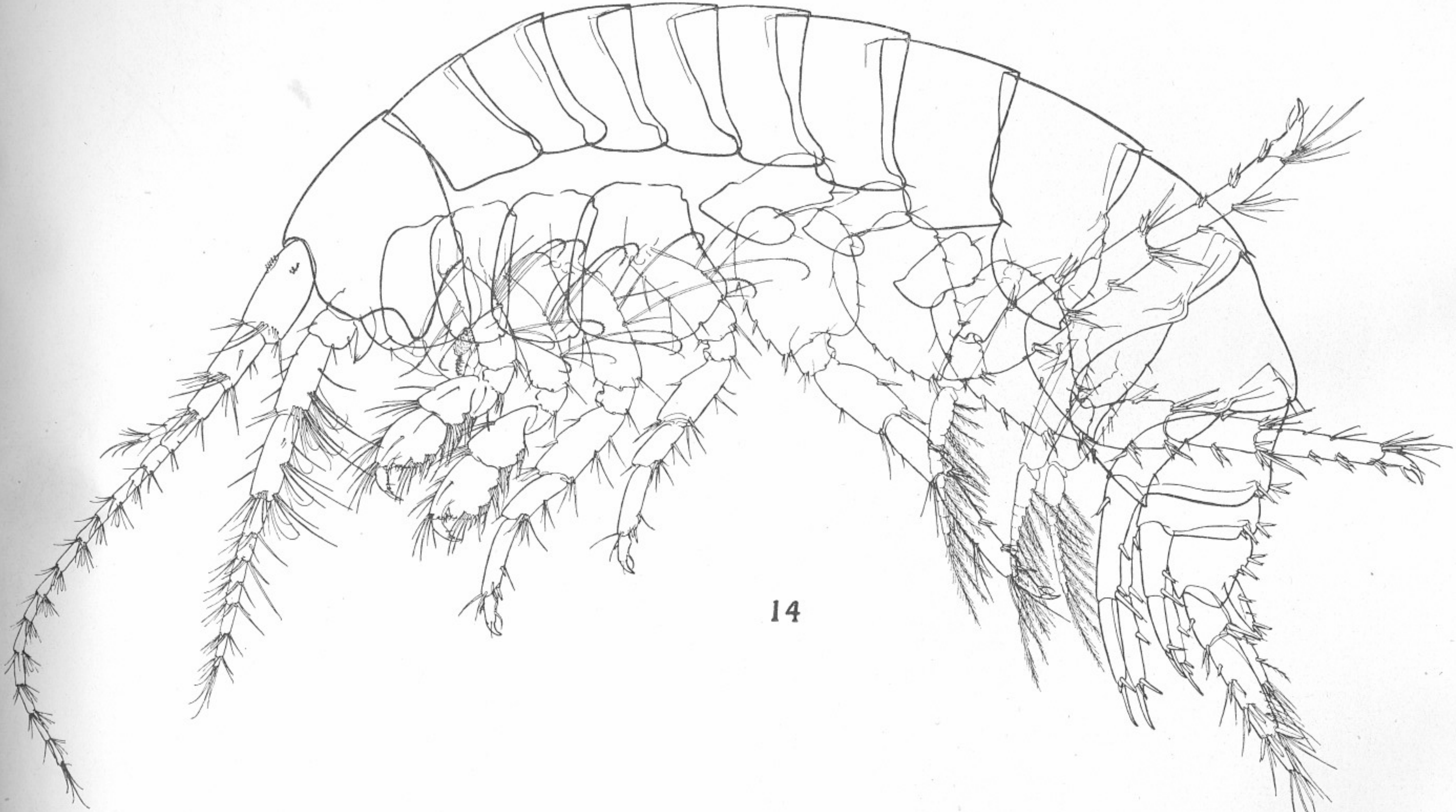
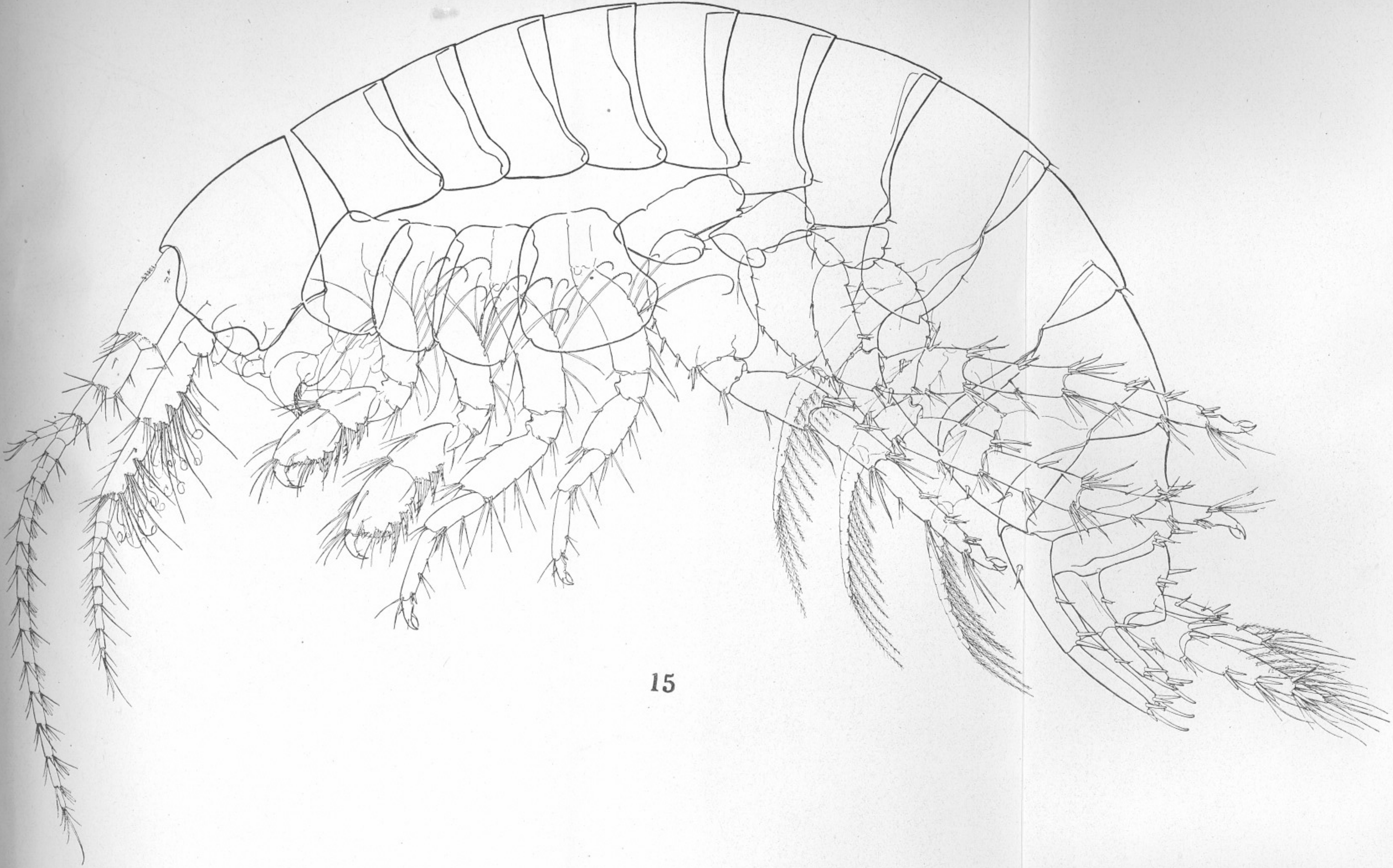


14

Normal Male. Moult 6.

E. W. SEXTON del.

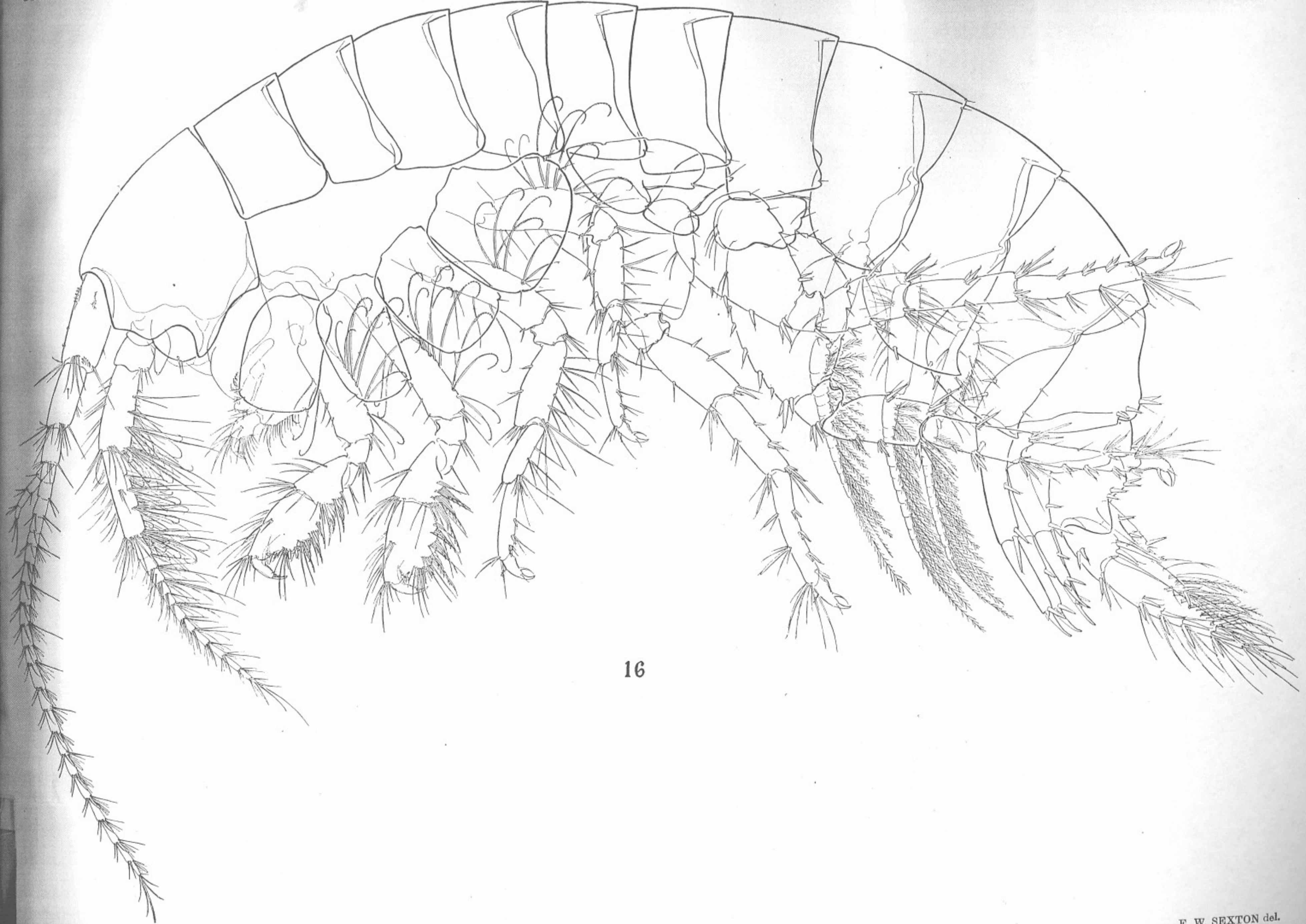
PLATE IX.



15

Normal Male. Moult 7.

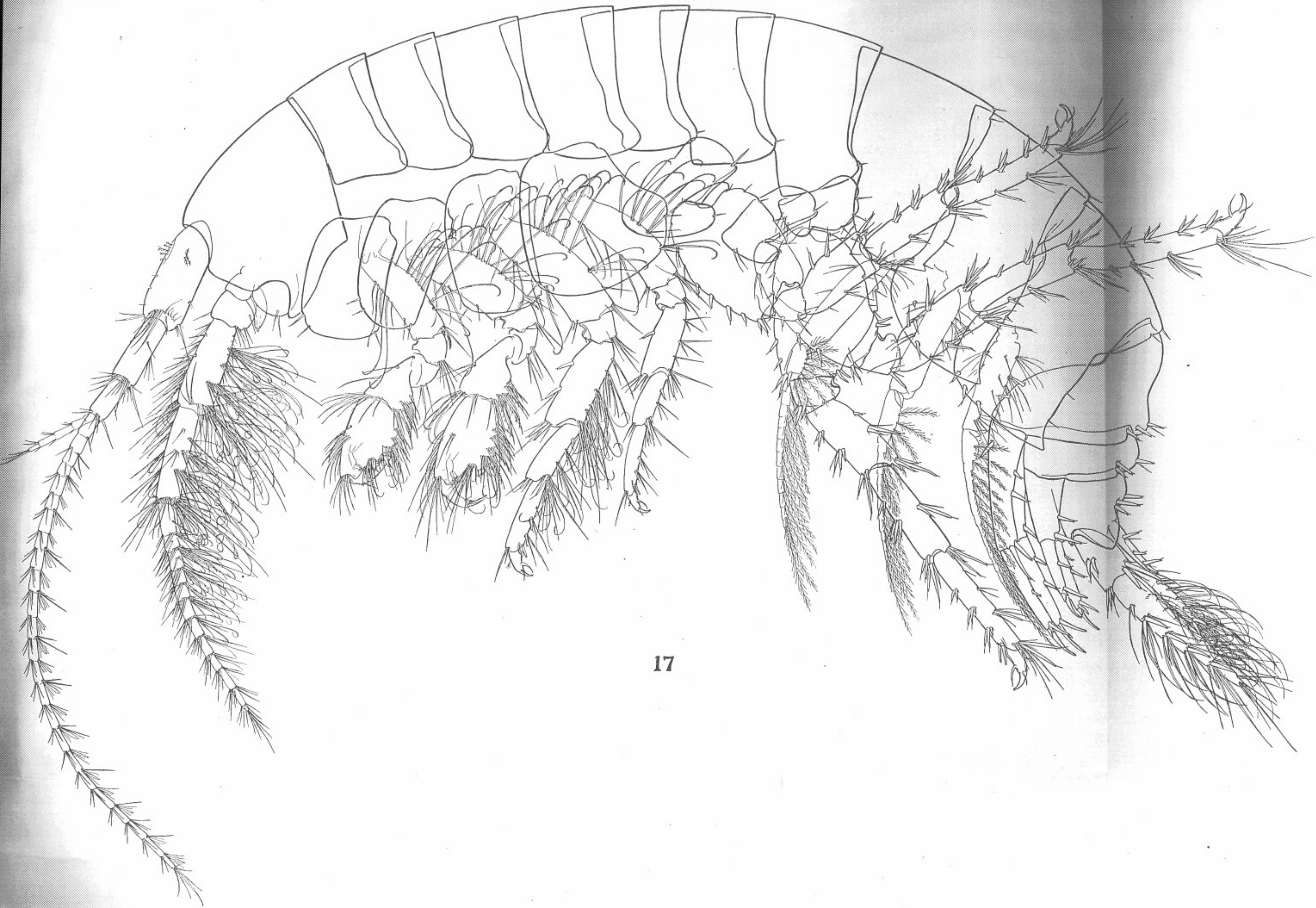
E. W. SEXTON del.



16

E. W. SEXTON del.

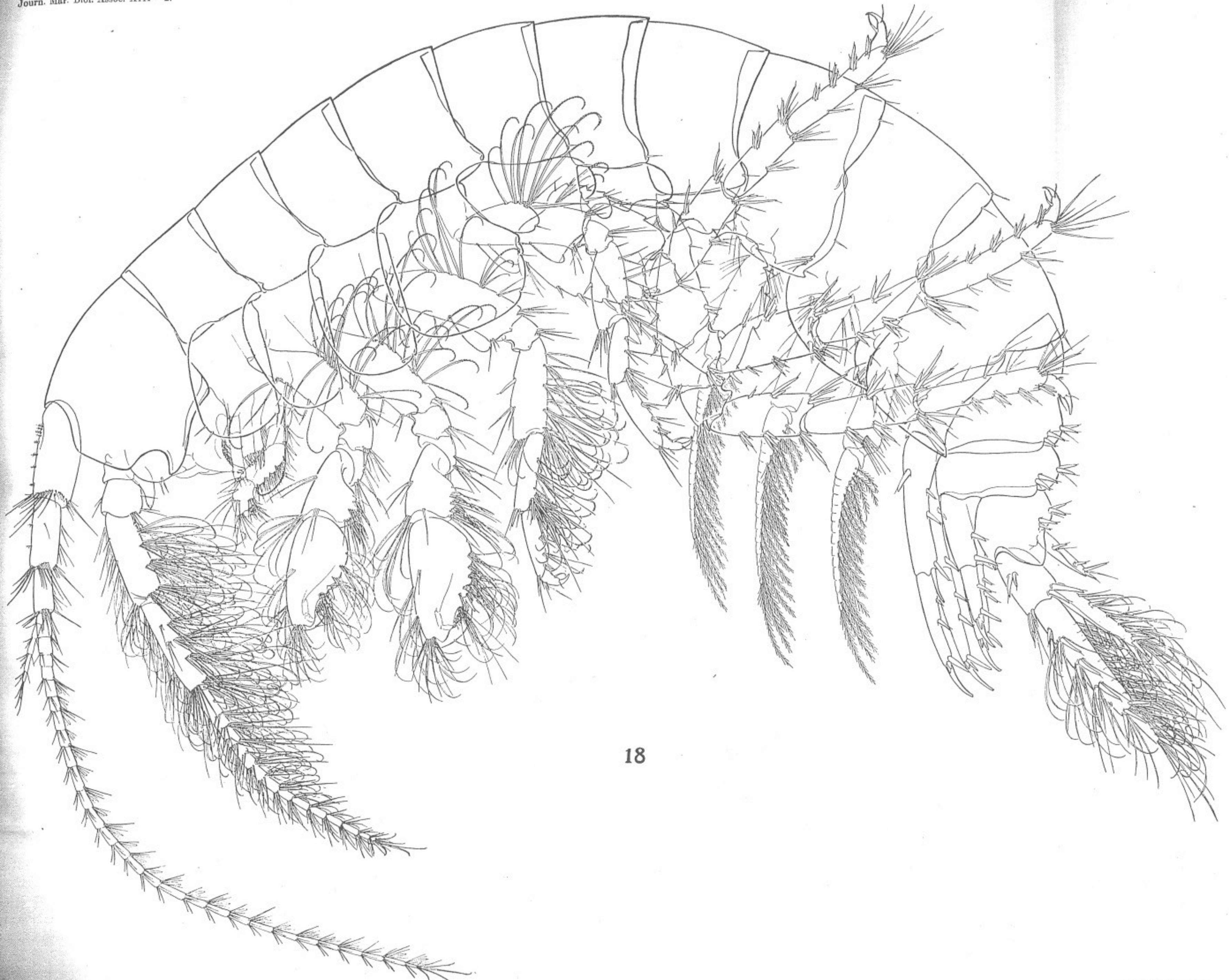
Normal Male. Moult 8.



17

Normal Male.– Moult 9.

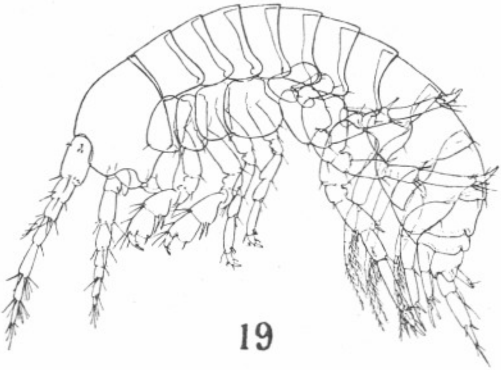
E. W. SEXTON del.



E. W. SEXTON del.

Normal Male. Moult 10.

PLATE XIII.



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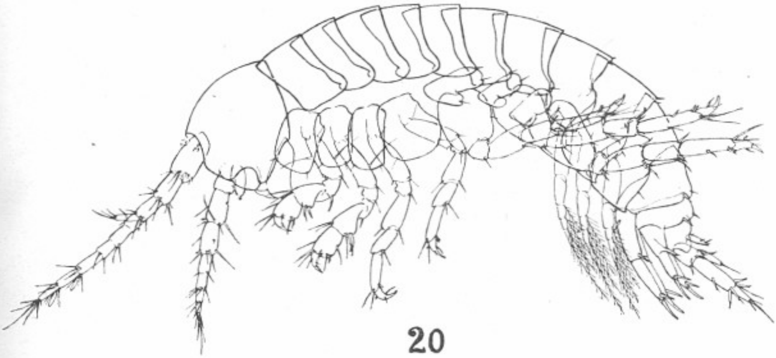

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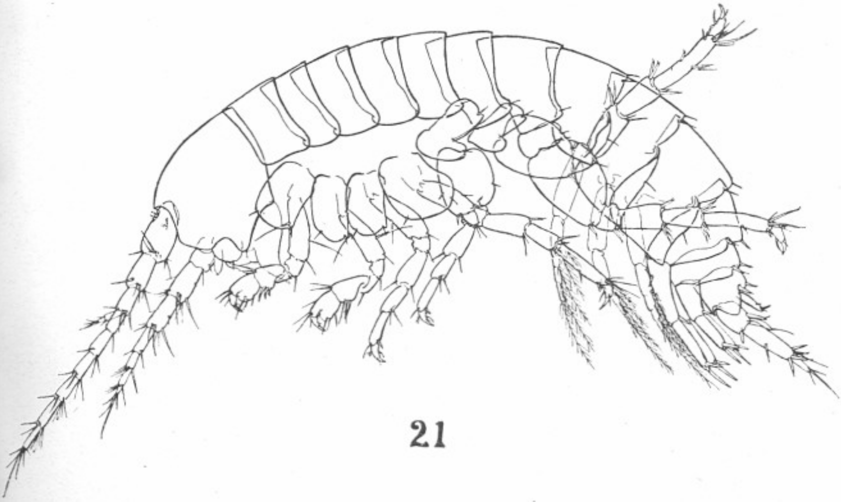
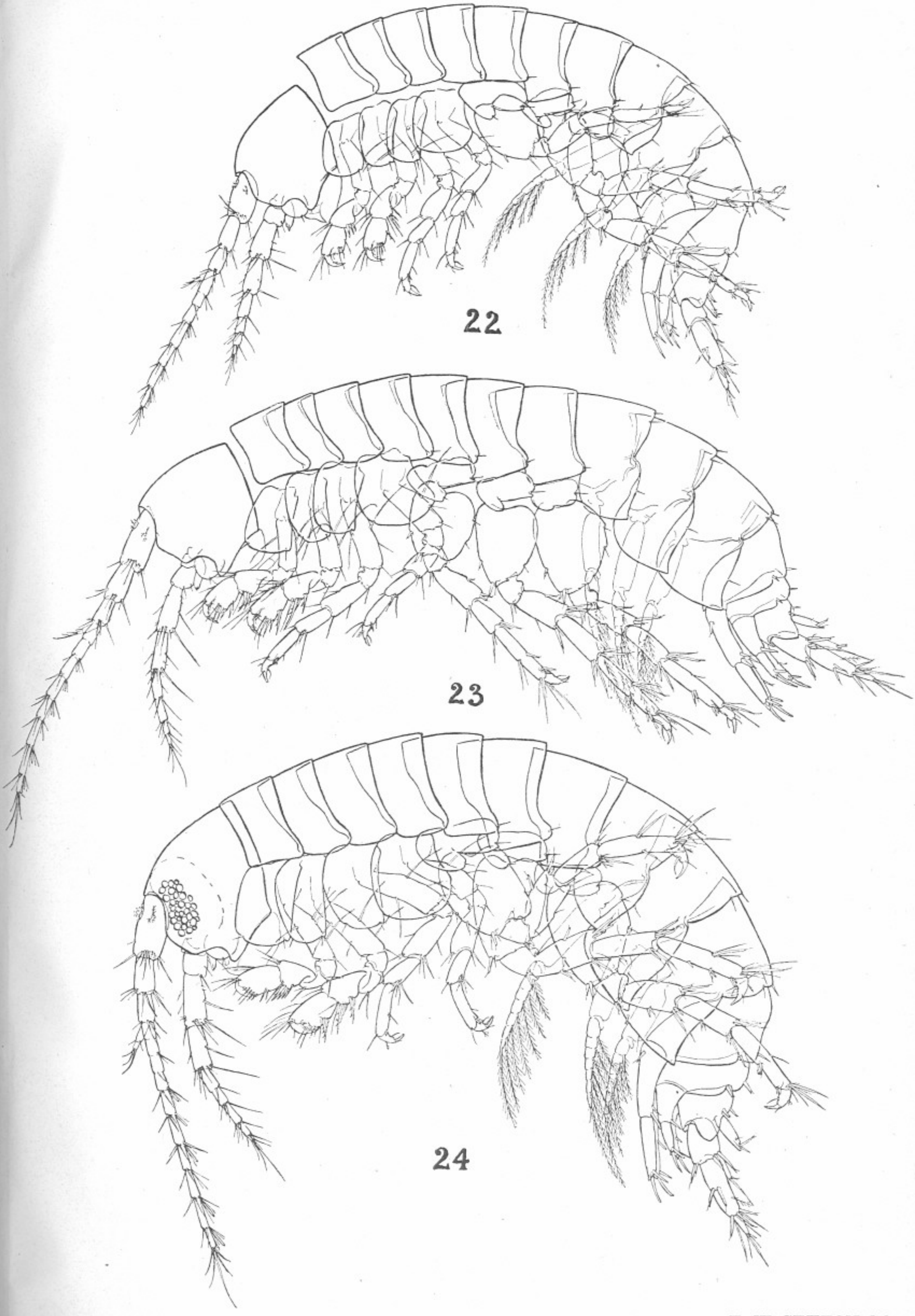


21

E. W. SEXTON del.

Intersex. Moults 1, 2 and 3.

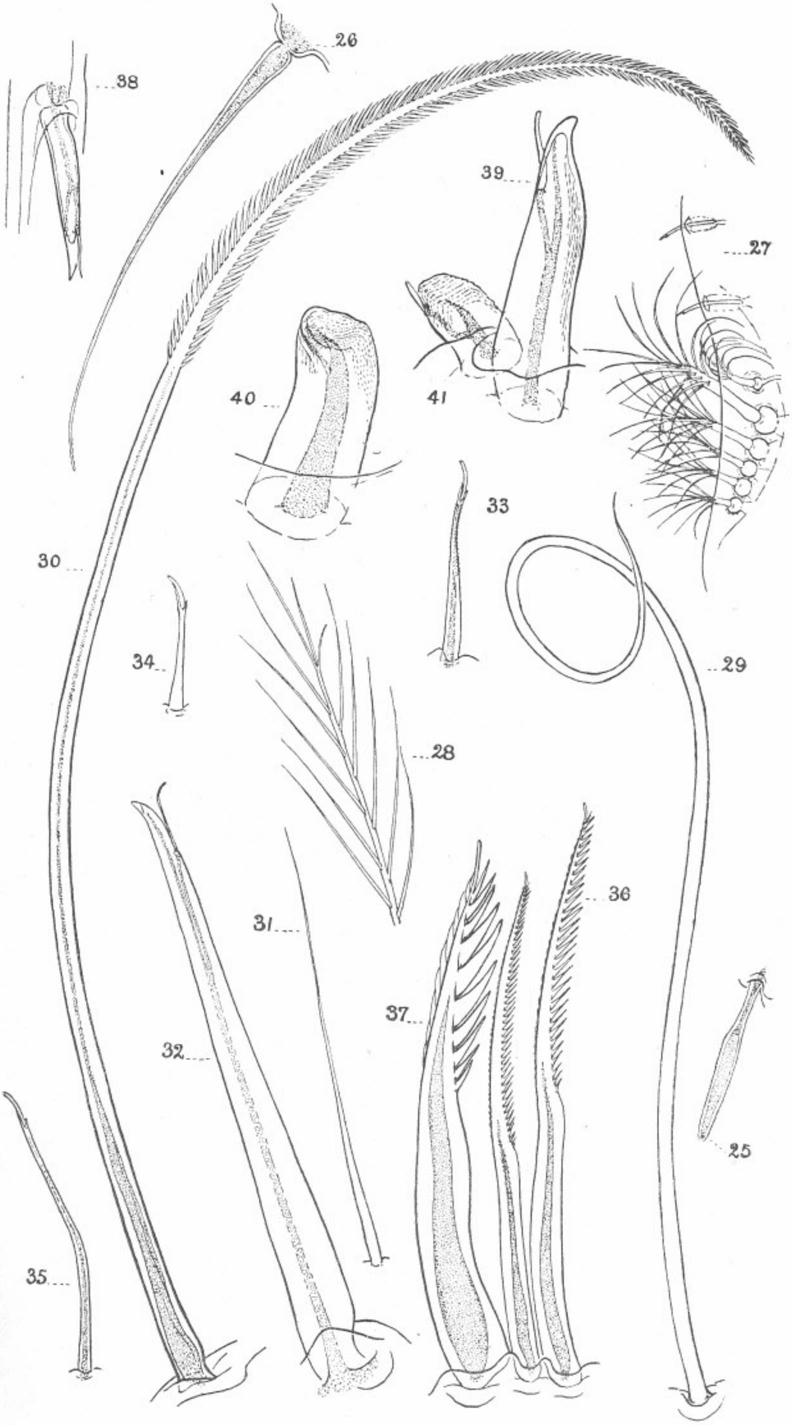
PLATE XIV.



E. W. SEXTON del.

Intersex. Moults 4, 5 and 6.

PLATE XV.



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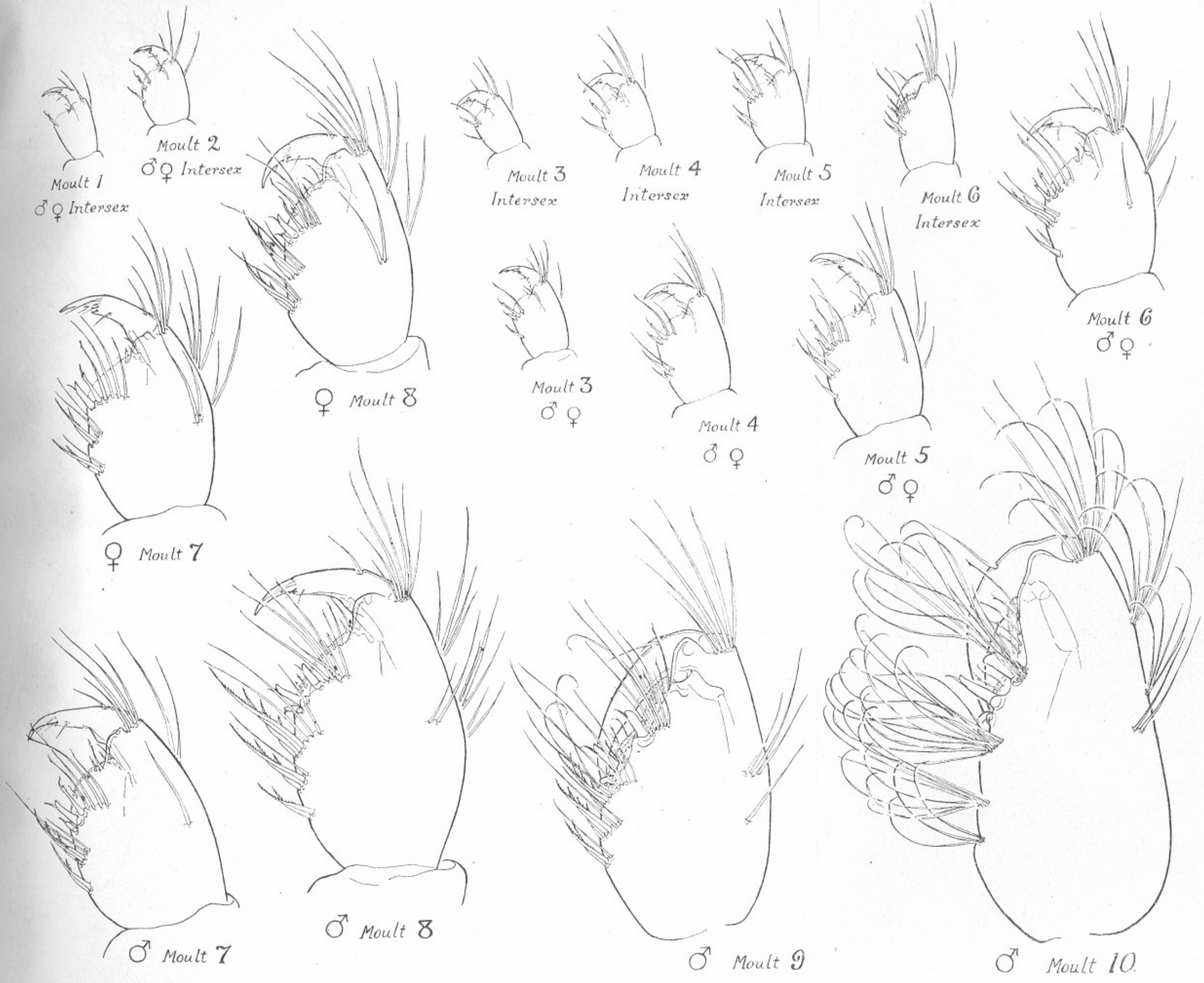
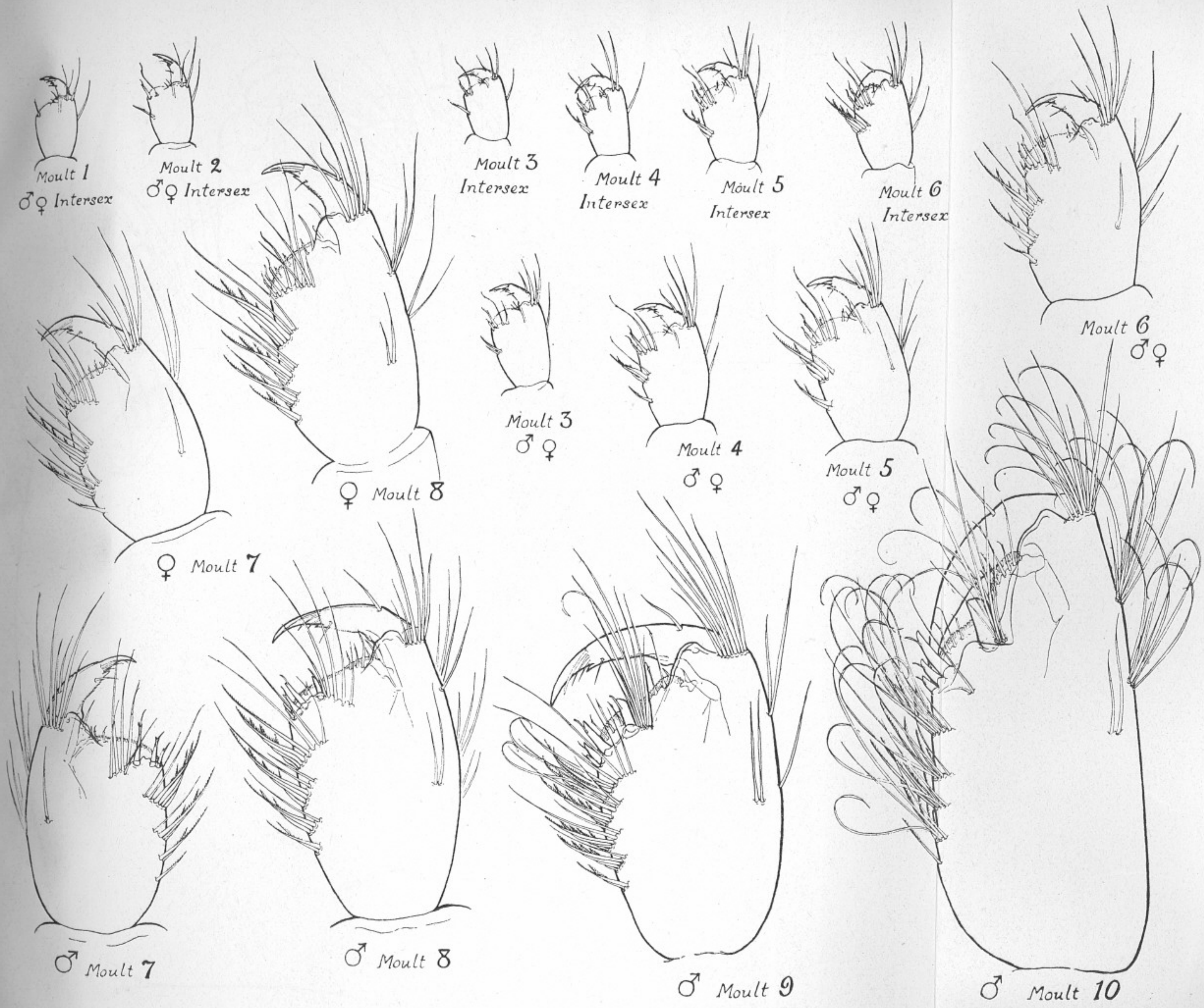


Hand. Gnathopod 1

E. W. SEXTON del.



Moult 1 ♂♀ Intersex

Moult 2 ♂♀ Intersex

Moult 3 Intersex

Moult 4 Intersex

Moult 5 Intersex

Moult 6 Intersex

Moult 6 ♂♀

♀ Moult 8

Moult 3 ♂♀

Moult 4 ♂♀

Moult 5 ♂♀

♀ Moult 7

♂ Moult 7

♂ Moult 8

♂ Moult 9

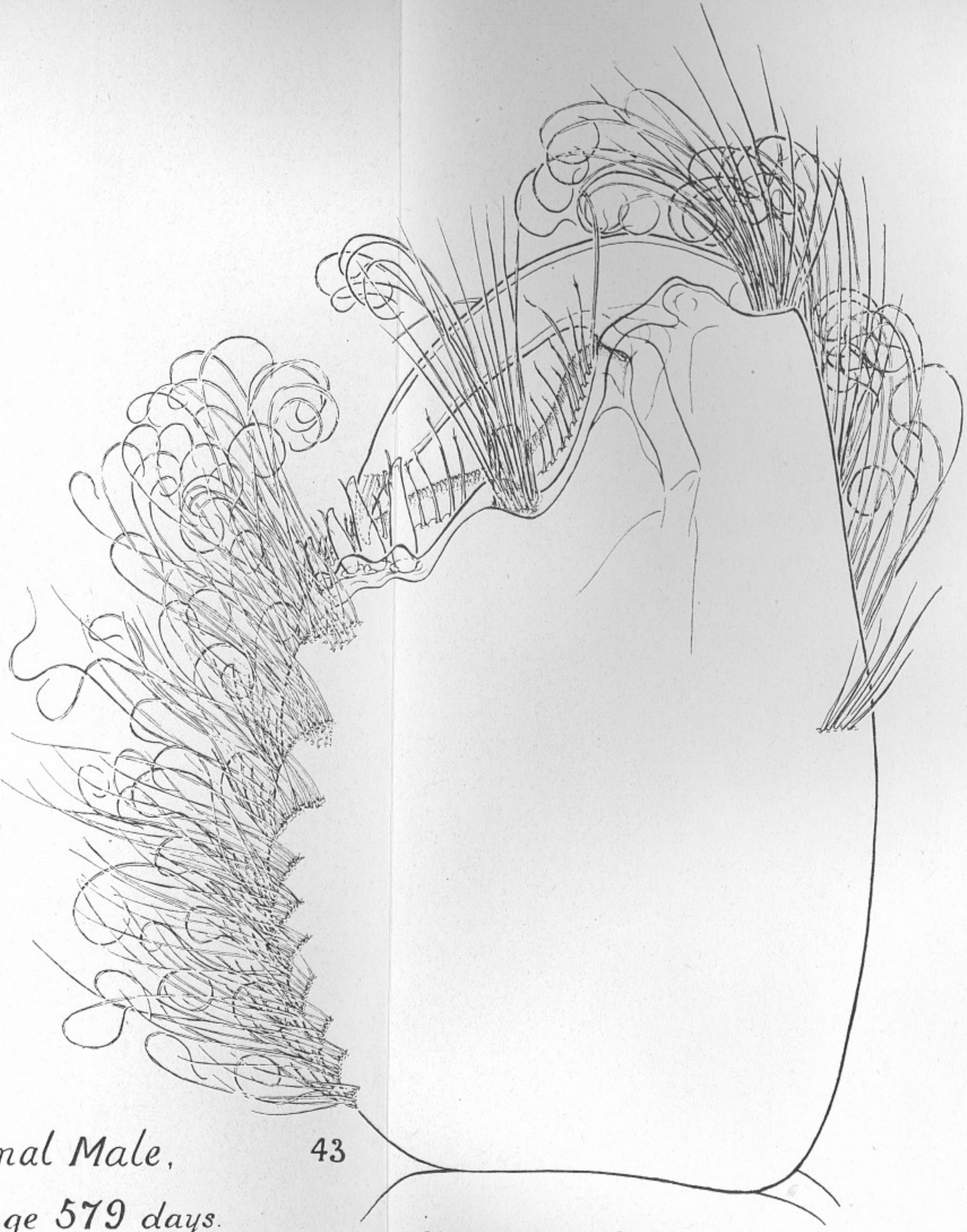
♂ Moult 10

Hand. Gnathopod 2.

E. W. SEXTON del.

42

Hand. Gnathopod 1



43

Hand. Gnathopod 2.

Normal Male,
CN.22a, age 579 days.

E. W. SEXTON del.

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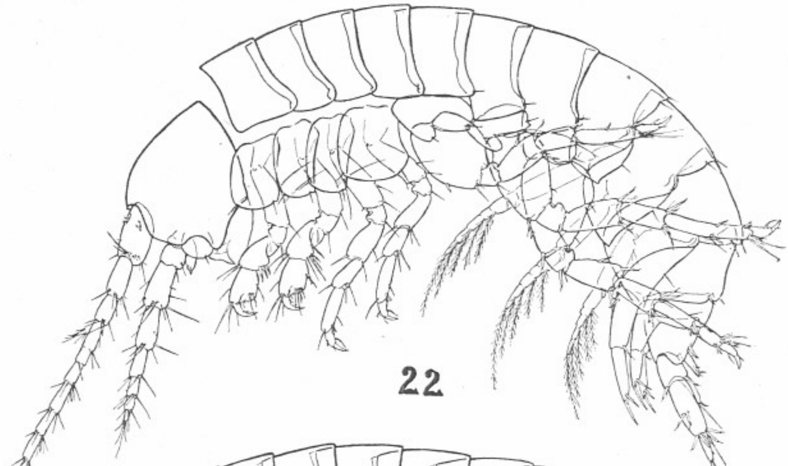

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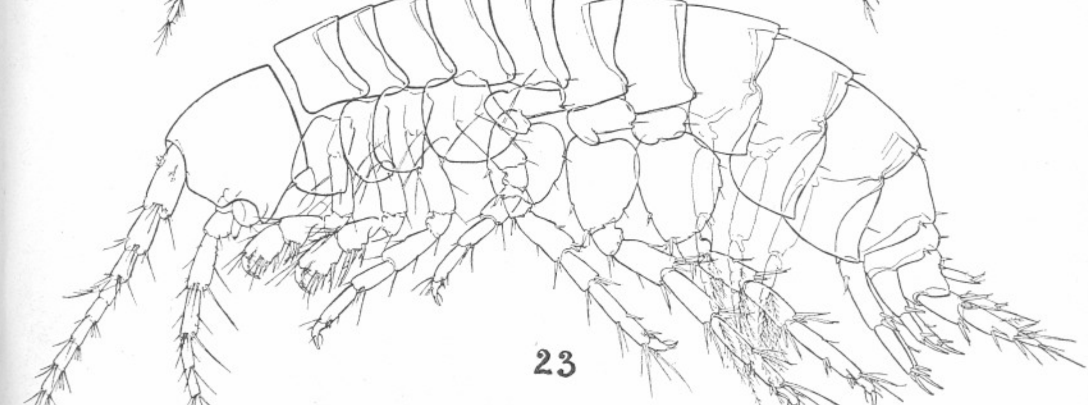

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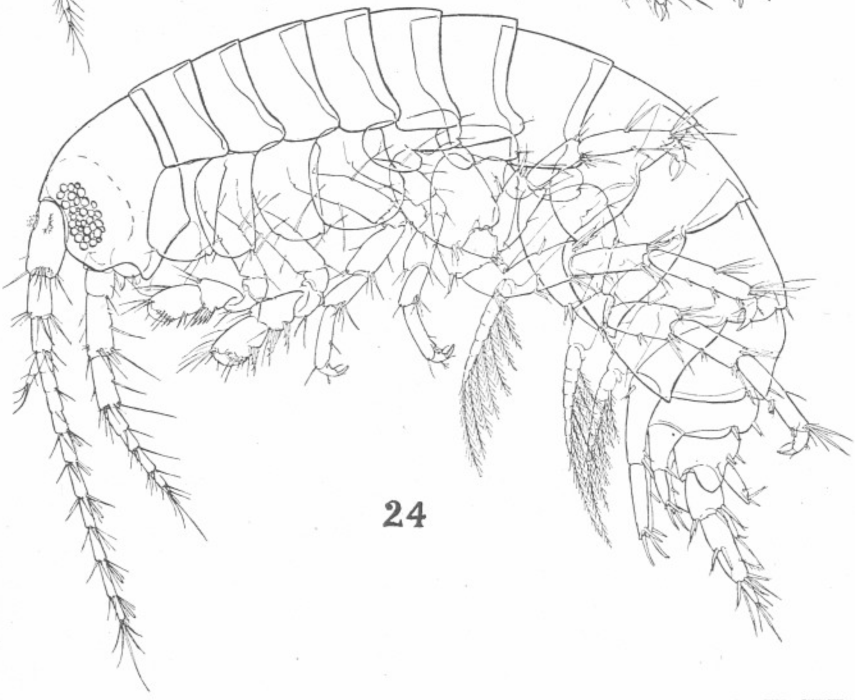
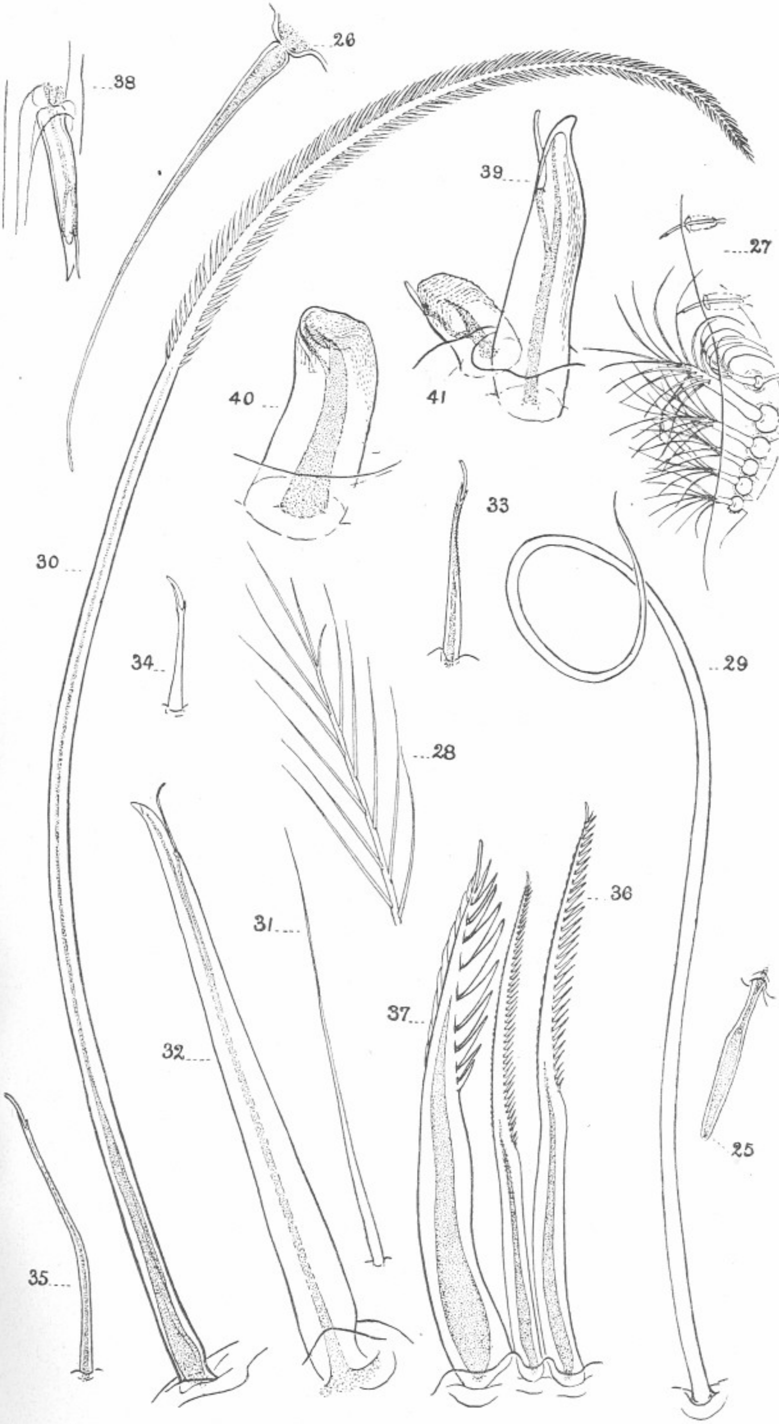


24

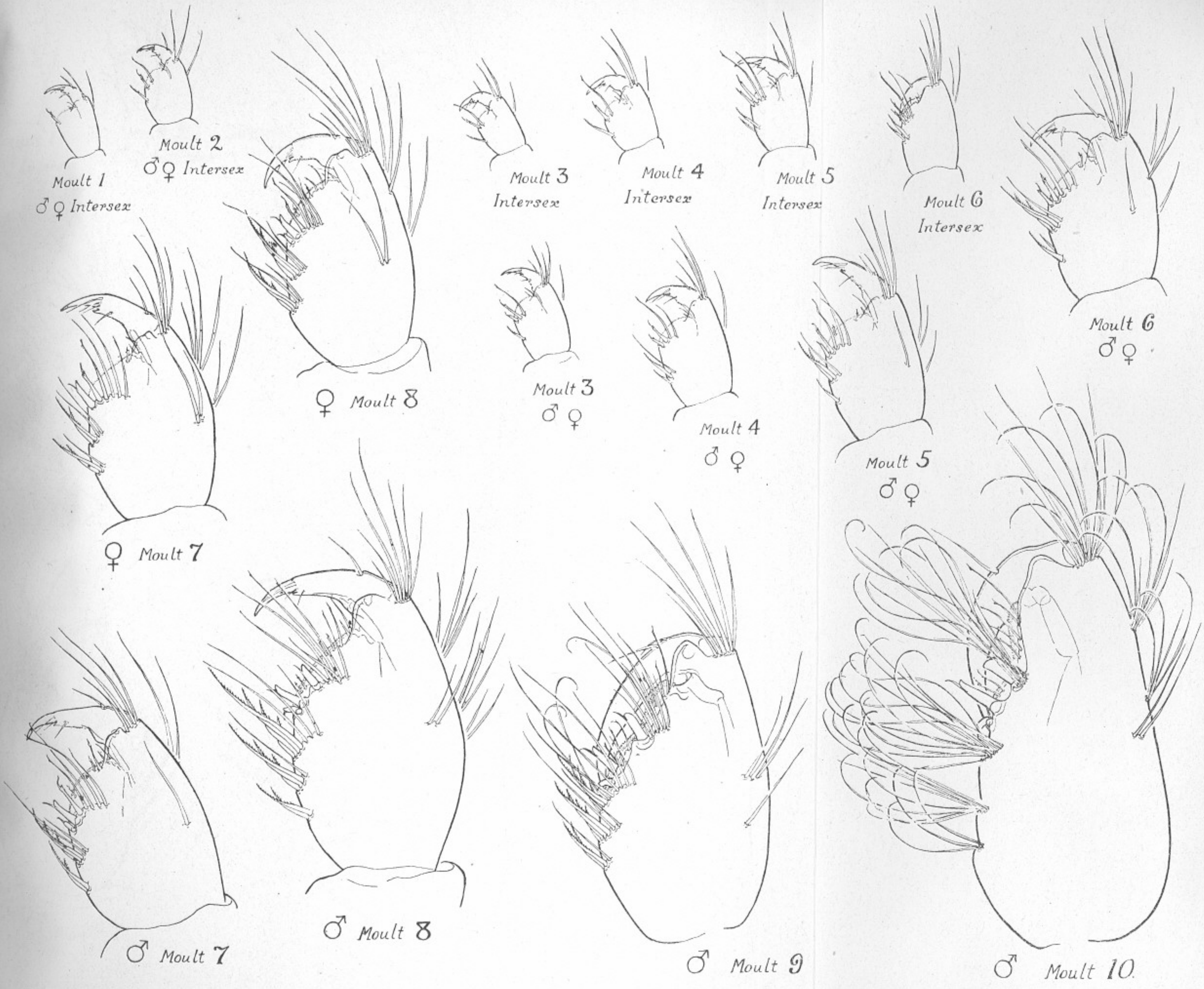
E. W. SEXTON del.

Intersex. Moults 4, 5 and 6.

PLATE XV.



E. W. SEXTON del.



Moult 1
♂♀ *Intersex*

Moult 2
♂♀ *Intersex*

♀ *Moult 8*

Moult 3
Intersex

Moult 4
Intersex

Moult 5
Intersex

Moult 6
Intersex

Moult 6
♂ ♀

♀ *Moult 7*

Moult 3
♂ ♀

Moult 4
♂ ♀

Moult 5
♂ ♀

♂ *Moult 7*

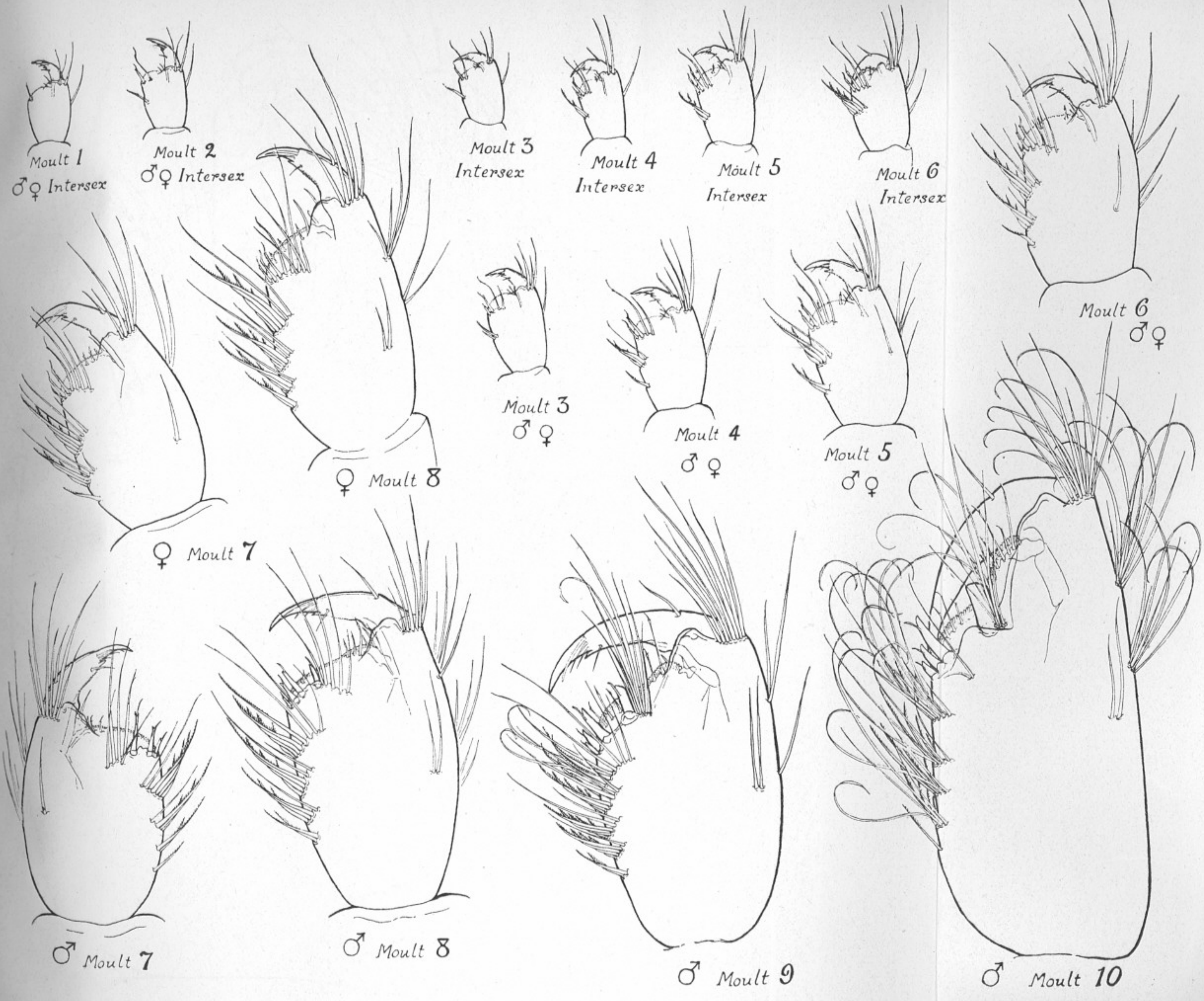
♂ *Moult 8*

♂ *Moult 9*

♂ *Moult 10.*

Hand. Gnathopod 1

E. W. SEXTON del.



Moult 1 ♂♀ Intersex

Moult 2 ♂♀ Intersex

Moult 3 Intersex

Moult 4 Intersex

Moult 5 Intersex

Moult 6 Intersex

Moult 6 ♂♀

♀ Moult 8

Moult 3 ♂♀

Moult 4 ♂♀

Moult 5 ♂♀

♀ Moult 7

♂ Moult 7

♂ Moult 8

♂ Moult 9

♂ Moult 10

Hand. Gnathopod 2.

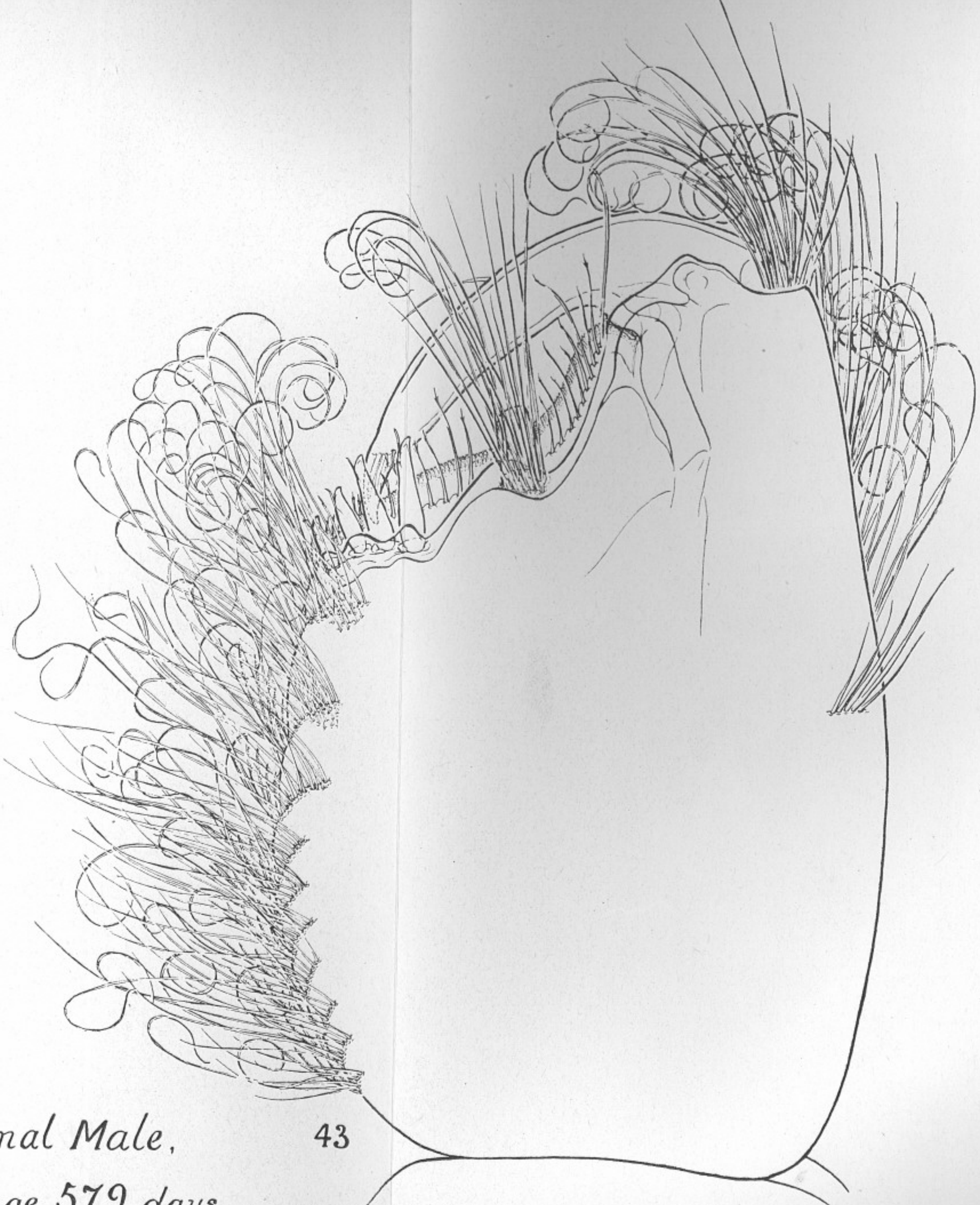
E. W. SEXTON del.

42

Hand. Gnathopod 1

Normal Male,

CN.22a, age 579 days.



43

Hand. Gnathopod 2.

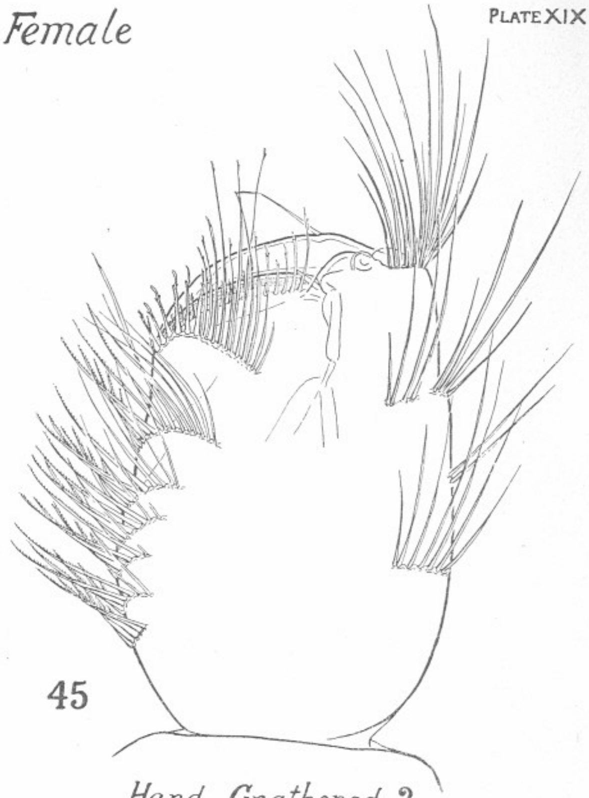
E. W. SEXTON del.

PLATE XIX

Normal Female

44

Hand. Gnathopod 1.



45

Hand. Gnathopod 2.

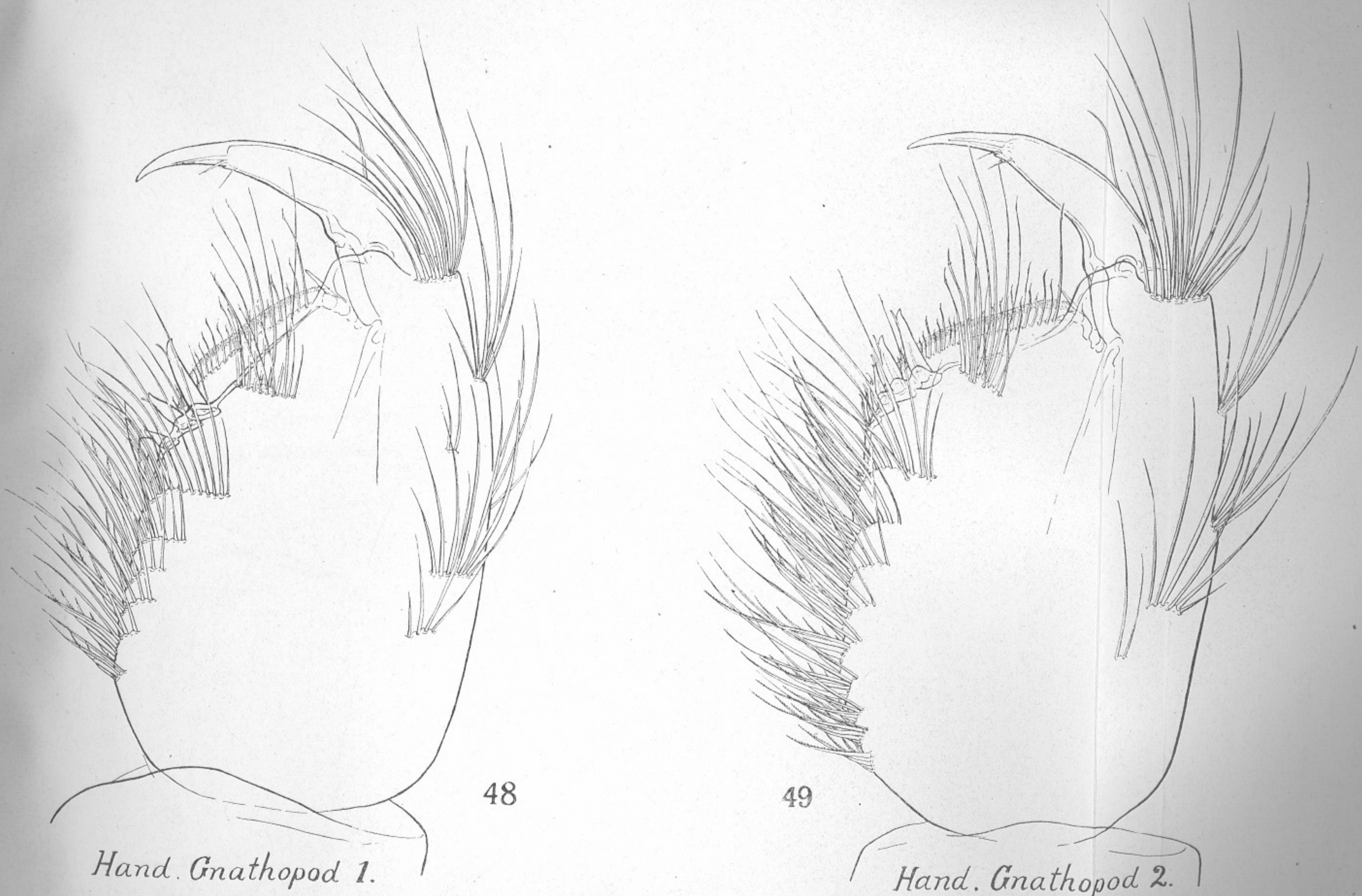
46

Hand Gnathopod 1

Male Intersex

47

Hand Gnathopod 2.



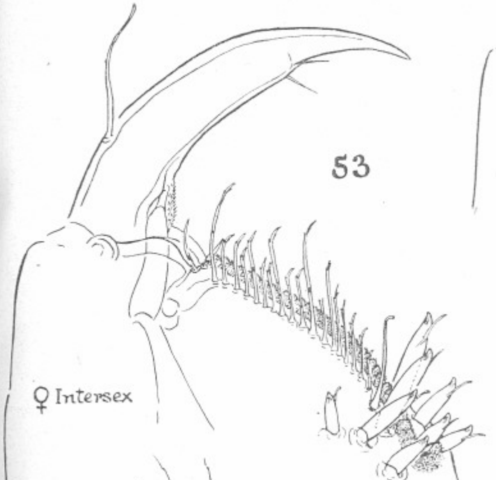
48

Hand. Gnathopod 1.

49

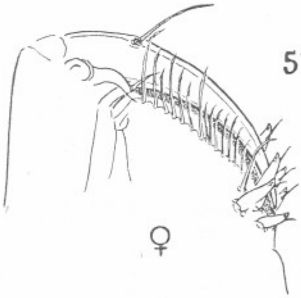
Hand. Gnathopod 2.

Female Intersex, CN284a, age 310 days.



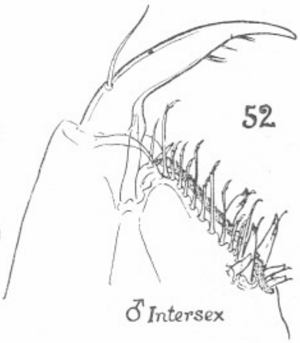
53

♀ Intersex



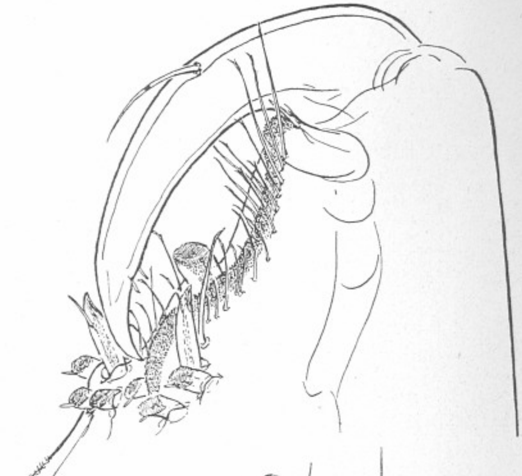
51

♀



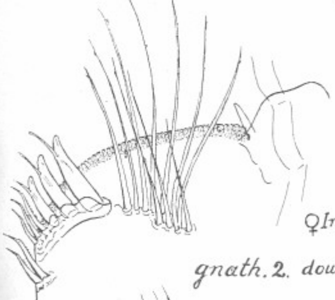
52

♂ Intersex



50

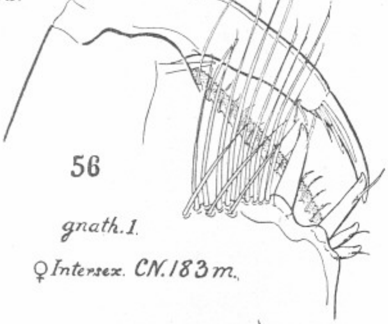
♂



59

♀ Intersex. CN. 289a

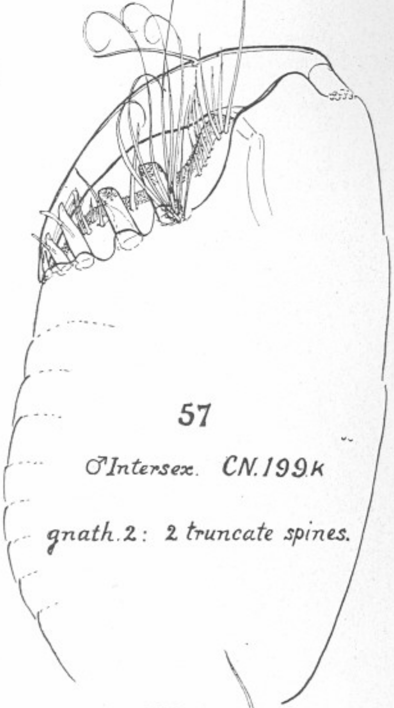
gnath. 2. double angle-row.



56

gnath. 1.

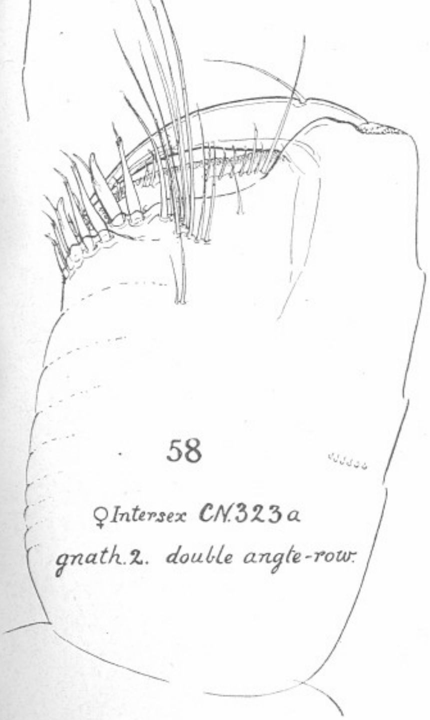
♀ Intersex. CN. 183 m.



57

♂ Intersex. CN. 199 k

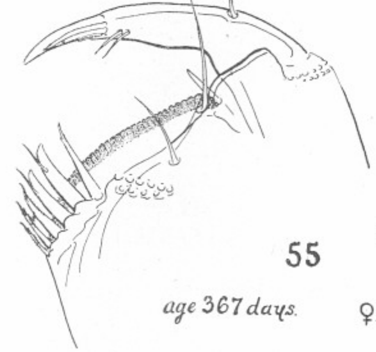
gnath. 2: 2 truncate spines.



58

♀ Intersex CN. 323 a

gnath. 2. double angle-row.

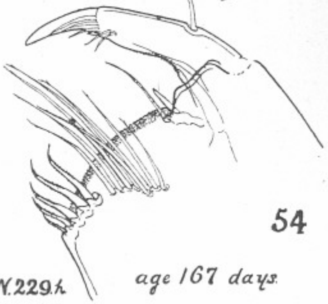


55

gnath. 2

age 367 days.

♀ Intersex CN. 229 h



54

age 167 days.

DESCRIPTION OF THE PLATES

All the figures are taken from moults except Figs. 8 and 24, which are from the animals themselves. The gills are omitted from the drawings to avoid confusion of detail.

PLATE I.

Fig. 1. Moult 1 of the normal female, C.4, age 5 days, 18 July, 1913. ×39

,, 2. Moult 2. From the same female, age 10 days, 23 July, 1913. ×39

,, 3. Moult 3. From the same female, age 14 days, 27 July, 1913. ×39

PLATE II.

Fig. 4. Moult. 4. From the same female, age 19 days, 1 August, 1913. As the first six segments, gnathopod 1 and peræopods 4 and 5, were eaten by the female, these parts have been figured from the sister female, C.14. ×39

,, 5. Moult 5. From the female, C.4, age 23 days, August 5, 1913. Six joints of gnathopod 1 and the three terminal joints of gnathopod 2 were drawn from the sister female, C.14. The first antenna, left side, was eaten, and the right antenna is therefore figured *in situ*, with the inner surface showing. ×39

PLATE III.

Fig. 6. Moult 6. From the female, C.4, age 29 days, 11 August, 1913. The gnathopod hands were eaten. ×39

PLATE IV.

Fig. 7. Moult 7. From the female, C.4, age 36 days, 18 August, 1913. Six joints of gnathopod 1 and three of gnathopod 2 were eaten. The broodplates are not shown in this figure. ×39

PLATE V.

Fig. 8. Growth-stage 8 of the normal female. C.4, after moulting on August 18, 1913, laid 10 eggs. The animal was then preserved and figured. Broodplates not shown. ×39

PLATE VI.

Fig. 9. Moult 1 of the normal male, B.9, age 8 days, 22 July, 1913. ×39

,, 10. Moult 2 of the normal male, B.9, age 12 days, 26 July, 1913. ×39

11. Moult 3 of the normal male, B.9, age 17 days, 31 July, 1913. ×39

PLATE VII.

Fig. 12. Moult 4 of the normal male, B.9, age 21 days, 4 August, 1913. ×39

,, 13. Moult 5 of the normal male. Figured from another specimen, the male, A.20, age 29 days, 24 June, 1913. ×39

PLATE VIII.

Fig. 14. Moult 6 of the normal male, B.9, age 33 days, 16 August, 1913. (This male was mature at 40 days, but ate its moult.) ×39

PLATE IX.

Fig. 15. Moult 7 of the normal male. Figured from the male, A.20, at the age of 40 days, 5 July, 1913. ×39

PLATE X.

Fig. 16. First mature stage of the normal male, Moult 8. Owing to the difficulty of getting whole moults from the males of the summer broods, this stage and the two following were taken from winter broods. The structural details are exactly the same, but the time taken in development was naturally considerably longer. The male here figured, K.6, was 74 days old, 1 December, 1921. ×39

PLATE XI.

Fig. 17. Second mature stage of the normal male. Moult 9 from the winter male, K.6, age 92 days, 19 December, 1921. ×39

PLATE XII.

Fig. 18. Third stage, the "definitive adult" normal male. Moult 10 from the winter male, CN.444, age 110 days, 6 January, 1922. K.6 moulted on 6 January, but only the second gnathopod, the second antennae, pleon, uropods, and a few fragments of peræopods were found, the rest being eaten. These fragments were compared detail by detail with the male figured, and found to agree in all particulars. ×39

PLATE XIII.

Fig. 19. Moult 1 of the Intersex CN.397f., age 6 days, 5 August, 1921. ×39

„ 20. Moult 2 of the Intersex CN.397f., age 13 days, 12 August, 1921. ×39

„ 21. Moult 3 of the Intersex CN.397f., age 20 days, 19 August, 1921. ×39

PLATE XIV.

Fig. 22. Moult 4 of the Intersex CN.397f., age 27 days, 26 August, 1921. ×39

„ 23. Moult 5 of the Intersex CN.397f., age 35 days, 3 September, 1921. ×39

„ 24. Growth-stage 6 of the Intersex CN.397f., age 49 days. Dead on 17 September, 1921. ×39

PLATE XV.

Fig. 25. *Sensory filament* or aesthetasc from the First Antenna; normal female, CN.22a. ×290

„ 26. One of the shorter *hairs* from the posterior margin of the broodplate, second gnathopod; normal female, CN.22a. ×290

FIG. 27. *Plumose hairs* from the sensory groove on the basal joint of the peduncle of the First Antenna; female intersex, CN.284a. The normal female, CN.22a., has the same number The largest hair is the one first formed. Distally two of the "*skin-hairs*" are shown. ×290

,, 28. Tip of a *feathered hair* from the first pleopod; normal female, CN.22a. ×290

,, 29. *Coiled hair* from the palmar group, First Gnathopod; normal male, CN.22. ×290

,, 30. *Serrated-hair* from the posterior margin of the second joint, First Gnathopod; normal male, CN.22. ×290

,, 31. *Seta* from the second peræopod; normal female, CN.22a. ×290

,, 32. *Slender-spine* from the fifth joint of the fourth peræopod; normal female, CN.22a. ×290

,, 33. *Serrulate-seta* from the angle-row of the Second Gnathopod; normal female, CN.22a. ×290

,, 34. *Marginal-seta* from the palmar margin of the Second Gnathopod; female intersex, CN.284a. ×290

,, 35. *Bent seta* from the Second Gnathopod; normal female, CN.22a. ×290

,, 36. *Serrated-bristles*

,, 37. *Dentate-spine*, lateral view from the distal margin, under surface of the fifth joint, Second Gnathopod; female intersex, CN.284a. ×290

,, 38. *Spine* from the anterior margin of the second joint, fourth peræopod; normal female, CN.22a. ×290

,, 39. *Pointed-spine* from the upper side of the palmar-angle, First Gnathopod; normal male, CN.22. Seen from below. ×290

,, 40. *Truncate-spine* from the middle of the palm, First Gnathopod; normal male, CN.22. Seen from the under surface. ×290

,, 41. *Curved-spine* from the upper side of the palmar-angle, First Gnathopod; normal male, CN.22. Seen from below. ×290

PLATE XVI.

Illustrates the development of the hand of the First Gnathopod, from birth to sexual maturity in the normal male and female, and in the intersex to the sixth growth stage. The left hand is figured seen from the outer surface. ×97

PLATE XVII.

The development of the hand of the Second Gnathopod. The left hand is figured, except in the seventh moult of the male, where the right hand is shown. ×97

PLATE XVIII.

FIG. 42. The hand of the First Gnathopod (right side) of the male at its fullest development is figured for comparison with the hand at sexual maturity. The oldest normal male to die a natural death in the experiments, CN.22, was 579 days old. The figure shows the oblique palm, the male truncate-spine in mid-margin, and the pointed-spine and two male curved-spines at the palmar-angle. ×97

,, 43. The hand of the Second Gnathopod (left side) of the same male, CN.22, showing the indented palm, truncate-spine, the angle-row with 4 pointed-spines and 10 posterior-clusters. ×97

PLATE XIX.

FIG. 44. The hand of the First Gnathopod of the female at its fullest development. Taken from the oldest normal female, CN.22a., from the same brood as the male above, at the age of 679 days. The figure shows the unbroken palmar-series, and the small size characteristic of the female type. ×97

„ 45. The hand of the Second Gnathopod of the same female, showing the angle-row of 6 serrulate-setæ and the unbroken palmar-series. ×97

„ 46. The hand of the First Gnathopod of the Male Intersex, CN.314b., at the age of 210 days. The intermediate character of the palmar margin of the claw will be noted, the "female type" size, and the partial male development of the palmar-series. ×97

„ 47. The hand of the Second Gnathopod of the same specimen, showing the partial male development, and the small size and transverse palm of the "female type." ×97

PLATE XX.

FIG. 48. The hand of the First Gnathopod of the female intersex, CN.284a., at the age of 310 days, the largest specimen in this case, not the oldest. ×97

„ 49. The hand of the Second Gnathopod of the same specimen. In both the large size, a male character, is noticeable. Gnathopod 2 shows the intersexual type angle-row, mixed spines and serrulate-setæ, the transverse palm of the female, the separation of the palmar-row from the angle-row and the clustering of the hairs as in the male, the claw approaching the male type, and the large number of posterior-clusters. ×97

PLATE XXI.

FIGS. 50 to 53 illustrate the difference between the full-grown normal and intersexual types as shown in the undersurface of the palm in Gnathopod 1. The figure is taken from the oldest normal male, CN.22, and shows the oblique deeply-indented palm, the torsion of the palmar margin which brings both the spine-groups of the angle to the under surface, and the character of the male spines, the truncate in mid-margin and the curved at the palmar-angle with flattened spinulose tips. ×97

„ 51. The under surface of the palm, Gnathopod 1 of the oldest normal female, CN.22a., showing the transverse slightly rounded palm, with the claw closed down against the margin, the position of the spine-groups at the angle, one on the upper side and one on the under, and the character of the spines. ×97

, 52. The same view of the male intersex, CN.314b., showing the approach to the female type, the transverse palmar margin with the claw closing down against it, the small size and the female character of the spines in the under group at the palmar-angle. ×97

„ 53. The same view of the female intersex, CN.284a., showing the approach to the male type, the large size, the torsion of the palm, bringing the two spine-groups to the under surface, the claw, bent to the same degree as the palm, and the increase in the number of the spines developed at the angle. ×97

FIG. 54. The outer surface of the palm, Gnathopod 2, of the female intersex, CN.229h., at the age of 167 days. ×97

,, 55. The same hand at a later stage, 367 days old, illustrating the development of the intersexual type of angle-row. ×97

,, 56. The palm of the First Gnathopod, in the most male of all the female intersexes yet observed in the experiments. This specimen, CN.183m., had the pointed-spine in mid-margin, which is a character of the normal male in the first mature stage, and the palmar-series separated into palmar-row and angle-row. Cf. male intersex, CN.314b., figs. 46 and 47. ×97

,, 57. This figure and the two following illustrate a remarkable development in the sensory armature of the palm, viz. a duplication of spines in the angle-row. The specimen was a male intersex, CN.199k., age 164 days, with the small size of the female type, the Second Gnathopod with the indented palm of the male type, but with *two* truncate-spines in the palmar margin. ×97

,, 58. The second instance of the duplication was in a female intersex, CN.323, age 301 days. The figure shows *two* angle-rows developed on the palm of the Second Gnathopod. ×97

,, 59. The third specimen was a female intersex, CN.289a., 362 days old. The transverse palm of the Second Gnathopod shows the usual intersexual angle-row, with a *second* angle-row developing below it. The previous moult had only one stout setiform spine in this new row. ×97

The Euphausiidæ in the Neighbourhood of Plymouth and their Importance as Herring Food.

By

Marie V. Lebour, D.Sc.,

Naturalist at the Plymouth Laboratory.

With Plates I–VI at the end.

An investigation into the euphausiids in the Plymouth waters was undertaken on account of the fact that on examining adult Herring for food it was found that *Nyctiphanes Couchii* (Bell) was of great importance, and occurred in enormous numbers in a large proportion of the Herring caught in the earlier half of the period of the Herring fishery.

Very little is known of the life-history of *Nyctiphanes Couchii*, and a detailed knowledge of its habits is wanting. In trying to elucidate the facts it was found that not only is this euphausiid extremely common, both as young and adult, but that three others new to the Plymouth waters occur abundantly at times and breed therein. These are *Meganyctiphanes norvegica* (M. Sars), *Thysanoessa neglecta* (Kroyer) and *Thysanoessa inermis* (Kroyer), the last being recorded by Norman (1906) as *Rhoda inermis*, from material received from Gough, taken once south of the Scillies, and once from Station 4, farther south. The other records are apparently new. It was thus found that the investigation involved four life-histories in order to clear up one, and it is probable that all four species are important as fish food, and therefore any new information as to their biology is of value.

In the autumn of 1923 it was decided to try to find out the food of the Herring from the beginning of its advent into the regions of the Channel near Plymouth until its disappearance after spawning. It is well known that about November these Herring enter the Channel and occur in such abundance that there is an annual fishery during the months of November, December and January. It is certain that the fish approach the coast to spawn, shedding ova from December to the end of January or into the beginning of February and then disappear. No records could be found of the food of the Herring in this locality during these months. It is a general view among the fishermen and those interested in the fishery that the Herring after spawning does not eat, or even that at this season, whether about to spawn, or during and after spawning, it does not eat. Workers in other localities, however, especially in Scotland, have shown that they may eat at all times, although usually not so much when spawning. Our own records, although based on only a few specimens on each date, show that the stomach may be full of food before, during and after spawning; but that many more empty fish occur during and after spawning, which agrees with records of other observers from different localities. The Herring were not examined from the first date they appeared (ca Nov. 1st), but examination only began on November 21st, when at first a dozen at a time, afterwards four every other day, with now and then a double supply were undertaken. The fish were procured from the local or East Country boats as they came in, and the general locality from whence they were fished was ascertained. The detailed records of the food are kept for reference.

The food was always plankton, and nearly always consisted of small crustacea. Sometimes the stomach was largely inflated by food, which generally in these cases proved to be *Nyctiphanes Couchii*. This euphausiid has lately been found in great abundance outside the Sound, one night haul taken in December during the Herring season bringing up many thousands from the surface. *Meganyctiphanes norvegica* is known to be an important food for Herrings and other plankton-eating fishes in the Irish Sea (Holt and Tattersall, 1905) and in other localities, and this and other euphausiids in the Scottish seas and lochs serve largely as Herring food. *Nyctiphanes Couchii* is found also to be of great importance as food for Mackerel and Pilchard caught with the Herring at Plymouth, all these fishes eating it in large quantities and having enormously distended stomachs full of this crustacean. Certain Mackerel had eaten young Pilchards (ca 2½–3 inches long), which themselves had eaten Nyctiphanes in numbers, so that both directly and indirectly Nyctiphanes serves as Mackerel food. So far, however, no other euphausiid has been identified inside any of these fishes from Plymouth.

Copepods come next in importance, or perhaps are equally important, or more so, although the Herring stomach is never so distended as it is with Nyctiphanes. In our samples *Candacia armata* stands out as the most frequently eaten species, and at this time of year it is the copepod most commonly taken in the Young Fish Trawl or townets in the regions of the Herring fishery, usually from the lower layers. Other copepods eaten by the Herring at Plymouth are: *Temora longicornis*, *Calanus finmarchicus*, *Pseudocalanus elongatus*, *Corycæus anglicus*, *Metridia lucens*, *Centropages typicus* and *Acartia*

Clausi. Very little food other than copepods and Nyctiphanes was seen. During spawning time a few Herring had eaten Herring ova or newly hatched Herring.

On the whole, at this season, the examination points to the two crustaceans, *Nyctiphanes Couchii* and *Candacia armata*, as the most important food of the Herring in the region of Plymouth.

It was found that out of 132 Herring examined from November to January, of which 78 were empty, out of the first 65, from November to December, about one-third were empty, whilst out of the last 67, from December to January, about two-thirds were empty. Of the 43 which contained food in the first half, half had eaten *Candacia armata* (22 out of 43) and nearly half had eaten *Nyctiphanes Couchii* (19 out of 43). Of the 19 which contained food in the second half, 8 had eaten Candacia and only 4 had eaten Nyctiphanes. It thus seems that Candacia is eaten by the greater number, but Nyctiphanes is present in enormous quantities, far greater than Candacia, when eaten.

Running females sometimes were full of food, one with newly hatched Herring, Herring eggs and Sagitta, two full of *Nyctiphanes Couchii*, two containing many *Temora longicornis*.

One spent female was full of Herring eggs, one full of *Nyctiphanes Couchii*.

One mature male contained Herring eggs.

The importance of *Nyctiphanes Couchii* as food in the early Herring season seems to be obvious, although only a few specimens were examined. It is hoped to investigate the matter further this year as soon as the Herring appear in the autumn.

An account of the detailed distribution of the euphausiids is reserved for a future occasion. In this I am having much help from Mr. O. D. Hunt, who took special night hauls. I also have to thank Mr. F. S. Russell for material sorted out from Young Fish Trawl and Metre tow-net collections. It is enough to state here that the adults and older larvæ all appear to live very near the bottom in the daytime and come up to the surface at night, although the young larvæ seem to keep near the surface, and it seems that the adult *Nyctiphanes Couchii* occurs at all the seasons in the district from beyond the Sound outwards, its young being found all the year round with a probable maximum breeding time in the spring. On the other hand, the records of *Meganyctiphanes norvegica* and *Thysanoessa neglecta* and *T. inermis* point to a habitat farther out, with a spring breeding time and a probable nearer approach to the coast during the breeding season, as larvæ are found usually much closer in than the adults.

The value of the present observations lies largely in the fact that so much has been done on the living organisms, the larvæ of *Nyctiphanes*

Couchii being reared from the parent egg-sac up to the last Calyptopis stage, and later stages being kept alive from the plankton and reared through various moults. Eggs have been obtained from *Thysanoessa neglecta* and *T. inermis*, although unfortunately the rearing of these failed, and live eggs attributable to *Meganyctiphanes norvegica*, although not obtained from the parent, were kept until nauplii emerged from them, second nauplii from these and metanauplii following. Various later stages of all these three species were kept alive and reared through several moults and series of plankton specimens were kept and preserved, so that the species could be identified. The present paper only carries these in detail, as far as the last Calyptopis stages, the two species of Thysanoessa in the three Calyptopis stages not being separated. The later stages are reserved for a future paper.

The fact that the Nyctiphanes from the surface contained more food than those from near the bottom points to their coming to the surface to feed, and as the Herrings also come to the surface at night, it is probable that they feed on the euphausiids at that time. The Nyctiphanes examined nearly always contained some dark substance in their stomachs, but in those from the bottom there was much more debris than fresh organisms, which occurred in numbers in those from the surface. The food is brought to the thoracic limbs by a current from behind, set up by the movement of the abdominal limbs, the thoracic limbs forming a sort of basket-like receptacle for the accumulated food. Although the food organisms found inside them were usually unicellular, they sometimes feed on Sagitta and crustacea. If one of their number died when in the aquarium it would very likely be eaten by the others. The commonest food organisms seen inside were the diatoms *Paralia sulcata* and *Hyalodiscus stelliger*, Paralia being the most abundant; *Coscinodiscus excentricus* and *C. radiatus* were also commonly taken and the peridinians *Prorocentrum micans* and *Exuviella perforata*. The Nyctiphanes examined for food were all from winter hauls, and these food organisms were all common in the plankton at that time.

In a sample of 50 examined from a surface night haul—December 13th, 1923, 49 contained many Paralia, in most cases together with other diatoms and peridinians. On other occasions out of 25 examined from the surface, 10 contained diatoms, chiefly many Paralia, from 25 from midwater, 18 contained diatoms, chiefly Paralia, and in 25 from near the bottom, 8 only contained diatoms (Paralia) and these singly, whilst the remainder contained sand and debris alone. From another haul near the bottom in February, 6 out of 16 contained single diatoms, the rest debris. One examined after having been kept alive in a glass jar for 5 days and given fine plankton, contained 6 *Hyalodiscus stelliger*, 2 *Grammatophora serpentina*, much debris and sand.

THE LIFE HISTORY OF *Nyctiphanes Couchii* (Bell).

It has been known ever since the species was first recognised that the female of *Nyctiphanes Couchii* carries her eggs in a pear-shaped sac, and it is figured by Bell (1853), who first described it as *Thysanopoda Couchii*. His specimens were procured from the stomach of a Mackerel caught on the Cornish coast. As Holt and Tattersall (1905) rightly observe, however, the egg-sacs are depicted in Bell's figure hanging from their narrow ends, whereas in reality they hang with their broad ends fixed as in the figure given by these authors who observed ovigerous females from 10 to 16 mm. in length, and state that in one specimen the ovisac contained naupliid larvæ, the breeding season reaching its maximum some time in May. This appears to be all the information available up to the present time on the youngest larvæ of *Nyctiphanes Couchii*, although Sars (1885), in the *Challenger* reports, figures and describes the metanauplius, three Calyptopis stages and adults of *Nyctiphanes australis*, evidently a very closely related species, the larvæ of which bear a close resemblance to those of *Nyctiphanes Couchii*. His specimens, however, are apparently all described from preserved material.

The first ovigerous female noticed in the neighbourhood of Plymouth was a dead one with egg-sacs from a surface night haul, 13.12.23. The sacs, however, were injured, and this was the only specimen seen to be breeding until April, 1924, although calyptopis stages were taken in February and March. Again in a night haul, Station E1, 10 miles S.W. of the Eddystone, 9.4.24, several females with egg-sacs were taken, two of which were kept alive, measuring 14 mm. and 15 mm. in length. One had the eggs in an early stage of development in the sacs, and this was kept alive for several days in a glass bowl, the eggs unfortunately dying. The second, which was preserved after a day, had the egg-sacs broken and the larvæ contained therein were emerging. Other specimens, 14 mm. to 15 mm. long, preserved from the same hauls, contained larvæ. The eggs are spherical and transparent, measuring from 0·36 mm. to 0·40 mm. across, the egg itself coming close up to the capsule (Plate I, Fig. 1). Unfortunately, the development of the early stages could not be studied further, owing to lack of material, but all the larvæ seen contained in the sacs of several different females were either a kind of nauplius (which, however, was unlike any known euphausiid nauplius in that its mandible consisted of a uniramous stump instead of the typical biramous swimming limb) or a stage between this and a typical metanauplius, for which I have proposed the term pseudo-metanauplius. The uniramous mandible in the nauplius is an exceedingly interesting adaptation to a long period of protection. The youngest and simplest nauplius (Plate I, Figs. 2 and 3) contained in the sac measured 0·40 mm.

to 0·44 mm. long and ca 0·32 mm. broad, of a simple oval shape, showing muscles inside the body, but no alimentary canal and having two small processes projecting behind. It has three pairs of limbs, antennules projecting forwards, simple, with three short setæ, antennæ usually projecting outwards laterally, biramous, the limbs with three and five setæ respectively, and the mandibles, which are uniramous, projecting forwards as elongated knobs. It was not possible to find an earlier stage than this, although one may be present. Apparently this simple nauplius changes inside the sac into a form like a metanauplius, but still having a thin skin over the limbs behind the mandible and covering the carapace. A later stage of the nauplius shows the abdomen formed and three limbs under the skin (Plate I, Fig. 4). It is this metanauplius-like form which I have termed the pseudo-metanauplius, and it is at this stage that the larva emerges from the sac (Plate I, Fig. 5).

On April 24th, 1924, another female, 16 mm. long, with egg-sacs, occurred from Station L4, half-way between Rame Head and the Eddystone, and this was successfully kept alive until the larvæ left the sacs. When captured there were larvæ moving in the sacs apparently in the naupliar stage, but these were not examined for fear of injury, and it was not until April 30th that the larvæ emerged. The young of *Nyctiphanes Couchii* thus does not emerge as a typical nauplius, but as an early metanauplius, which almost immediately sheds an excessively thin skin, and appears as a true metanauplius. In the absence of a proper term for the first of these two stages I suggest the name pseudo-metanauplius. The pseudo-metanauplius (Plate I, Figs. 5 and 6) measures 0·56 mm. long. It has a slightly projecting tail, which is held under the body and is armed with 4 to 8 spines, according to its age. The post-naupliar limbs, three behind the mandibles, are visible as simple rounded knobs, and in front of these are seen the rudiments of the under lip. These are all held down by a thin skin, which also encloses the true metanaupliar carapace and anterior lip. The eye is visible under the skin and also the rudiments of the ocular plates, from which the compound eyes are developed, and a striated portion each side shows the rudiments of the ocular luminous organs. The alimentary canal, liver and heart can also be seen. The antennules with three long setæ project in front, and the rami of the antennæ possess five and six setæ respectively. Almost immediately after emerging the pseudo-metanauplius sloughs a very thin skin and becomes a typical metanauplius (Plate I, Figs. 7, 8, 9). This measures 0·57 mm. long, the tail bearing 6 to 8 spines, the two second from the outside being the longest. The carapace is now free and projects at the sides. It has no teeth round the margin, which is perfectly simple, and thus resembles the metanauplius stage of *Nyctiphanes australis*, described by Sars (1885), the limbs also resembling this species with the exception of a few details in the number of setæ. The fact now shown that the larva of *Nyctiphanes Couchii* emerges from the sac at so late a stage probably accounts for the non-appearance of any stages earlier than the metanauplius in Sars' material, for the species seem to be so closely related that they would almost certainly resemble one another in their early larval stages.

All these stages of *Nyctiphanes Couchii* are quite colourless and transparent.

The metanauplii were kept alive in glass finger bowls, into which were introduced a small quantity of a pure culture of the diatom, *Nitzschia closterium*, but in no case did any of them eat. The first Calyptopis emerged from these on April 2nd and 3rd. At first these did not eat and were quite colourless, but after three days they ate Nitzschia, and immediately after eating the typical pigment appeared, consisting of two conspicuous orange-red chromatophores on the tail. Some of the bowls were kept dark and others were placed on white grounds, but the coming up of the pigment was in all cases the same. The natural food of the Calyptopis stages seem to be diatoms and other unicellular organisms, as was shown from plankton specimens.

The first Calyptopis is easily recognisable in the plankton by its distinctive coloration, and is very commonly present, especially in the early spring, and this is the earliest stage of *Nyctiphanes Couchii* so far found in the plankton, which is probably to be accounted for by the fact that such a short time is spent in the metanauplius stage. From February through March and April it may be found in abundance, usually at, or near, the surface. The adult, although living in the daytime near or at the bottom, comes up to the surface at night, and there it apparently sheds its offspring, which only go down again at a much later stage. In five days the first Calyptopis changed into the second, and this in ten days into the third, after which unfortunately all the specimens died. The larvæ were thus reared in the free state from the pseudo-metanauplius to the third and last Calyptopis, and enough was learnt from this series to make all these stages easily recognisable in the plankton. In one case a first Calyptopis, April 17th, 1924, was kept alive and changed into the second on the 19th, this to the third on the 25th, and this to the first Furcilia on the 31st, when it was killed and preserved.

The first Calyptopis (Plate II, Fig. 1) typically measures ca one millimetre in length. It may, however, be slightly longer or shorter, and enlarges after emerging from its metanaupliar skin, the size given being for one full grown and coloured. Its carapace is an elongated oval covering the ocular plates and head region and measuring 0·64 mm. in length. The abdomen is unsegmented, but in front merges into the thoracic region, the segments of which can be distinctly seen, although very narrow and without trace of limbs. The telson is square at the extremity with truncated corners, and bears twelve terminal spines besides an additional one each side below, or at the level of the chromatophores. Of the terminal spines two occupy the corners each side, eight are in a straight line terminally, the outside spines of the eight being the longest. The single dark red eye is situated in the centre of the head with an ocular plate on each side, bearing the rudiments of the ocular luminous organs. The antennules consist each of two segments with five setæ, two of which are sensory, the inner ramus barely showing and having three small setæ. The antennæ forming powerful swimming organs, one ramus with four terminal and two lateral setæ, the other distinctly jointed with seven setæ. The mandibles (Plate II, Fig. 2) are strong biting jaws with a forwardly projecting process and strong muscles. Both upper and under lips are well developed. The first maxilla (Plate II, Fig. 3) has two masticatory lobes (the first with eight setæ, the second with two strongly spined teeth with a spine in between) and two joints, the inner with six setæ, the outer with four. The second maxilla (Plate II, Fig. 4) has five small lobes on the inner side of the base, well provided with setæ, and a terminal blade with a seta on its outer base and four terminal setæ. The first thoracic limb (Plate II, Fig. 5) consists of a two-jointed base (the proximal joint with three, the distal with six setæ and a thick horn-like spine) and two rami, the inner two-jointed (the proximal joint with a seta and a thorn-like spine, the distal with four setæ), the outer of one piece with a seta at its outer base and four terminal setæ. These all are directed forwards, as shown for the second Calyptopis (Plate II, Fig. 6), their long inner spines forming a basket for the food, but the limbs also helping by their movement to bring the food towards the mouth. The abdomen in all the Calyptopis stages is capable of much movement up and down, and is extremely flexible, being usually bent at an angle with the body. The structure of the limbs is essentially the same in all three Calyptopis stages, and strongly resembles those of *Nyctiphanes australis* described by Sars.

From the first Calyptopis comes the second (Plate II, Fig. 6), which has advanced greatly in size, in segmentation and in the development of another terminal spine on the telson. It measures 1·44 mm. in length, and besides the pigment on the telson it has orange-red pigment in the mouth region and also usually near the ocular organs where the compound eyes will appear. The carapace measures 0·76 mm. long, and at the side has a small but distinct tooth which is characteristic of the adult *Meganyctiphanes norvegica,* but not present in the adult *Nyctiphanes Couchii.* It, however, persists through many larval stages. Zimmer (1909) states that this tooth is present in many young forms where it is absent in the adults. The abdomen has five segments and the telson ;

the thorax with seven, the first having a knob representing the second thoracic limb. The telson has the usual pair of orange-red chromatophores, and is armed with thirteen terminal and two lateral spines. The antennules have a three-jointed base and a biramous termination, the outer with five, the inner with three setæ. There is also a small seta at the outer base of the outer ramus, which may be double and which apparently is absent in the corresponding stage of *Nyctiphanes australis*, although present in the following stage. The antennæ are essentially the same as in the first Calyptopis but longer, the setæ reaching to the end of the carapace. The mandibles are larger, but these and the other limbs present bear a very close resemblance to those of the first Calyptopis.

A rather longer interval (ten days) takes place between the change from second to third Calyptopis than in the preceding changes, but the third and last stage has increased largely in size. This (Plate III, Fig. 1.) measures 1·92 mm. in length, the carapace being 0·96 mm. The abdomen has six segments, and there are the beginnings of uropods on the telson, which still has thirteen terminal and two lateral spines, the pigmentation being much the same as in the second Calyptopis, the compound eyes beginning and being distinctly coloured. The thorax is much the same as in the preceding stage, as are also the first thoracic limbs and those in front of it, the antennule having developed a pointed projection coming from the outside of the proximal segment of the base.

This is at present as far as it was possible to go by rearing this year with the available material. It is, however, now these larval stages are accurately known, possible to pick them out from the plankton and rear them further. In this way the second Calyptopis has been obtained from the first, the third from the second and the next succeeding stage (first Furcilia) from the third and last Calyptopis. Various other stages have also been secured, all having the typical pigment on the telson. At a small size it is possible to recognise certain adult characters in the young, *e.g.* spine over telson together with processes on the antennule, so that now at any stage it can be distinguished from other species.

The Furcilia stages are characterised by having the eyes freely exposed and no longer covered by the carapace, but they still retain the biramous swimming antennæ. The first Furcilia of *Nyctiphanes Couchii* (Plate VI, Fig. 8) has the usual characteristic pigment with the addition of a chromatophore on each side of the thorax. It measures 2·8 mm. in length, the carapace measuring 1·12 mm., and leaving the eyes fully exposed at the sides, whilst dorsally it protects their bases by a squarish shield. The lateral spine on the carapace is still present. There is a simple projection hanging down from each side of the first abdominal segment, representing the first abdominal limb, and behind under the skin a second smaller pair is seen. The second thoracic limb is longer, although still only a simple process, and behind two smaller pairs of knobs are present representing the third and fourth pairs of thoracic limbs. The eyes are very conspicuous and well developed.

After this much fewer specimens were seen of later Furcilia stages, only one occurring here and there. It is hoped to fill in these gaps later. Next come the Cyrtopia stages, in which the antennæ no longer serve for swimming, and these almost insensibly merge into the post-larval forms which are like miniature adults. It has not yet been possible to follow up these later larval stages in detail, but enough has been seen to show that many of the adult characters are assumed at a very small size—much smaller than any of the other local species. At 6 mm. the telson is almost like that of the adult, the antennules have fairly long filaments and the spine has appeared above the telson. The body up to this stage and longer is pellucid with the red luminous organs showing up very conspicuously in the later stages, red at the base of the telson and the proximal joints of the limbs and in the region of the mouth.

Females with egg-sacs were taken up to the middle of April, first Calyptopis stages from December to April, second Calyptopis from February to May. Later stages all through the summer and autumn. The younger larval stages, especially the Calyptopis, were nearly always at the surface or midwater, the post-larvæ near the bottom, rising to the surface at night, the usual habit of the adults.

It seems from these observations that although a few individuals may be breeding all the year round, the majority breed in the early spring, April perhaps being the maximum month, slightly earlier than in the Irish Sea. *Nyctiphanes Couchii* at some stage may be found all the year round, and apparently breeds and lives in a wide area in the neighbourhood of Plymouth, preferably in water of a depth of about 20 fathoms or more, although occasional examples may be met with close inshore, especially larval stages which have probably moved in with the tide.

It is hoped to deal with its detailed distribution in a future paper.

To sum up what we now know of the life-history of *Nyctiphanes Couchii*. This species breeds chiefly in the spring in the Plymouth waters, the female carrying her eggs in a thin-walled sac, the eggs hatching inside the sac and being retained therein for a considerable time as nauplii, which, as an adaptation to this special method of protection and unlike any known euphausiid, have no biramous mandible, but only a uniramous stump. The young escape from the egg-sac as a kind of metanauplius which has the carapace and limbs behind the mandibles still covered by a thin skin, this stage being here termed the pseudo-metanauplius. Almost directly after hatching this changes to a true metanauplius. From the metanauplius comes very quickly the first Calyptopis, which only now begins to eat, and as soon as it eats begins to have pigment—two orange-red chromatophores on the telson. From the first comes the second, and from the second comes the third and last Calyptopis. Then follow several Furcilia stages, Cyrtopia and post-larval, the adult characters arising at a very small size.

Up to the present time *Nyctiphanes Couchii* is the only euphausiid recorded from the Plymouth neighbourhood, but whilst investigating its life-history the three others mentioned above were found to be abundant at certain times of year—*Meganyctiphanes norvegica*, *Thysanoessa neglecta* and *Thysanoessa inermis*. The last, formerly known as *Rhoda inermis*, is regarded by Hansen (1911) as synonymous with *Thysanoessa neglecta*, that worker regarding the long-legged form as only a variety of the same species. Although there has not yet been sufficient time nor opportunity to go minutely into this matter, certain considerations seem to show that they are at least distinct species, although the adults are so extraordinarily similar. It is hoped to investigate these species further, but the few notes so far put together are given here, as they are certainly of some interest

THE LIFE-HISTORY OF MEGANYCTIPHANES NORVEGICA (M. Sars).

Meganyctiphanes norvegica has hitherto apparently not been recorded from the Channel, although common in many parts of Britain, especially the Irish Sea and the Clyde area. Its life-history is one of the best known, as Sars (1897) has described its eggs and early larvæ from Norway, and Brook and Hoyle (1888) have taken them in the Clyde area, although not describing them in detail. Recently Elmhirst (1923) has taken them in Millport and presumably reared them, although very little detail is given. He states that " This species seems to pass through 2 Nauplius, 1 Metanauplias, 3 Calyptopis, 6 Furcilia and 5 Cyrtopia stages before the adult form is attained."

Only one adult has been found in the Plymouth area (a male), although larval forms which must be attributed to this species are found in great abundance in the same places as *Nyctiphanes Couchii* occurs and often taken with these. For the sake of comparison with Nyctiphanes the early stages found in the neighbourhood of Plymouth are here described, although one can only infer that the eggs and younger stages belong to this species as the eggs have not been obtained from the parent. There seems to be, however, abundant evidence that these belong to Meganyctiphanes, as they are exactly similar to those described by Sars, and the later larval stages can be traced up to post-larvæ having the adult characters.

In February, 1924, eggs occurred abundantly in the plankton. These contained developing nauplii, which emerged and changed into second nauplii, these into metanauplii and the metanauplius into the first Calyptopis. Afterwards second Calyptopis came from first, and third from the second, and many Furcilia, Cyrtopia and post-larval stages were found, and could be easily recognised in the fresh state. Although the Calyptopis stages and early Furcilia closely resembled Nyctiphanes in form but not in colour, they could be separated by careful study.

The egg (oosphere as it is termed by Sars) agrees exactly with those described by him. This is, however, not exclusively characteristic of Meganyctiphanes, as eggs of *Thysanoessa inermis* obtained from the parent and described below may be exactly the same size, but it will be shown that the larvæ of Thysanœssa are quite different. The size of the egg of Meganyctiphanes is 0·67 mm. to 0·75 mm. across (Plate IV, Figs. 1–2). It is perfectly transparent, and usually contains a pinkish embryo. Most of these were developing into nauplii. In one case an egg was entangled in a piece of transparent substance looking very much like the egg-sac of Nyctiphanes. It is thus possible that Meganyctiphanes may carry her eggs for a short time, although she has never been observed to do so, and against it is the fact that Sars found it free in the one-celled stage.

The nauplius may be seen inside the egg, still of a pinkish hue, and not nearly filling the whole of the capsule, which serves as a float. On emerging the first nauplius (Plate IV, Fig. 3) measures 0·48 mm. in length, and has three pair of swimming limbs; the antennules uniramous with one long seta and the rudiments of a second, the antennæ and mandibles biramous, the antennæ with three and four setæ respectively to the rami, the mandibles with three to each ramus. The body is oval and perfectly simple with no hair-like processes behind, and is of a very pale pinkish hue. Muscles and yolk are seen inside the body, but no sign of alimentary canal. This is a perfectly typical euphausiid nauplius, and differs distinctly from the nauplius of Nyctiphanes found inside the egg-sac in that it has a biramous mandible. Almost immediately the first nauplius casts a very thin skin and becomes the second nauplius (Plate IV, Fig. 4), the same length as the first, but differing from it in having two processes at the hind end of the body, a median eye showing through the skin, the antennules with two long setæ and a rudimentary one, and the other two limbs being more fully developed. This nauplius still has a pale pinkish colour. Very soon the metanaupliar carapace and appendages can be seen under the skin of the older nauplius, and it changes by casting a very thin skin into the metanauplius. The metanauplius (Plate IV, Figs. 5, 6, 7) is 0·50 to 0·52 mm. long, having the carapace toothed all round, folded over the body ventrally and measuring ca 0·42 mm. long. A large flap, the upper lip, hangs over the mouth; the antennules bear three terminal setæ and a small lateral one, the antennæ have five and six setæ to the rami respectively, and the mandibles are reduced to a stump, which only shows traces of bifurcation. Behind the mandibles are the rudiments of the under lip and three pair of limbs show as simple knobs. The abdomen is nearly square, and bears eight to ten terminal setæ and three lateral setæ each side. When alive the two longest tail setæ and the two longest setæ on the front of the carapace stick up outside the plane of the others. The ocular plates and the rudiments of the luminous organs show faintly and certain internal organs are present, but the metanauplius does not appear to feed. The body has still a pinkish shade and differs besides this from the metanauplius of Nyctiphanes in having spines round the carapace, so that it can at once be distinguished from it. These stages from egg to metanauplius agree very well with those described by Sars (1898), as do also the Calyptopis stages. The eggs and nauplii described by Metschnikoff (1871) also bear a close resemblance. The nauplii from the eggs obtained from tow-nets in February were kept alive and turned into second nauplii and these into metanauplii, from which came the first Calyptopis, but rearing after this was unsuccessful. It was, however, possible to obtain the first Calyptopis from the tow-nets, and from it the second was secured, and the third from the second. Later stages were obtained from the plankton, and were very plentiful in spring and early summer up to late post-larval stages.

The Calyptopis stages are exceedingly like those of Nyctiphanes, differing, however, in colour and in being rather more heavily built. Later on they are much larger in the same stage of development, so that Nyctiphanes is in a post-larval stage when Meganyctiphanes of the same size is only a Furcilia.

The first Calyptopis of Meganyctiphanes is pinkish in colour with bright orange-red pigment diffusing outwards from two chromatophores in the thoracic region. Sometimes there are two pairs. Pigment is also present in the mouth region, and dorsally all along the body there is a diffuse pink shade. There are, however, no chromatophores on the telson as there are in Nyctiphanes, and by their pigmentation the species can be at once distinguished. In other respects the larvæ differ hardly at all (Plate II, Figs. 1 and 5). In the second Calyptopis the same colouring prevails, but Meganyctiphanes is slightly stouter in build, and at each successive stage the difference is more pronounced. There appears to be no important differences in the limbs of these stages in the two species.

It is hoped to work out the later stages at a future time. It is sufficient for our present purpose to note that the later Furcilia and Cyrtopia stages were present in very large quantities in certain localities, and the post-larval stages of these showing specific characters were easily recognised, so that there seems to be no doubt about the identification.

THYSANOESSA NEGLECTA (Kroyer) and THYSANOESSA INERMIS (Kroyer).

These two species are regarded as synonymous by Hansen (1911). In April, 1924, two specimens of *T. inermis* and one of *T. neglecta* were obtained from the Young Fish Trawl, and on a night trip in the same month a large number of both species were obtained together. Several of these were isolated in glass jars in order to obtain eggs from them, and eggs were shed by both species. Unfortunately it was not possible to rear these, those of *T. neglecta* not going beyond a four-celled stage, and that irregular and probably abnormal, those of *T. inermis* only reaching a spherical many-celled stage, and also usually developing irregularly. It is, however, the size of these eggs which is quite different in the two forms that primarily warrants one regarding them as distinct species. As Hansen justly remarks there is hardly any difference in the adults except for the long thoracic limbs in *T. neglecta;* but on close examination of the Plymouth specimens a distinct difference was found in the male modified first abdominal appendages, and there are apparently other slight differences which seem to be constant. A description of the adults and late larval stages is left for a future paper, but one seems to be justified in regarding these two as distinct species.

The eggs obtained from both species were shed freely into the water in the one-celled stage. Almost all the females had spermatophores attached ventrally, and these with the whole skin were cast just before the dropping of the eggs. The egg capsule of *Thysanoessa neglecta* (Plate V, Figs. 1–2) measured 0·41 mm. to 0·54 mm. across, the egg itself in the one-celled stage measuring 0·32 mm. across, clear and transparent. The egg divided irregularly and probably abnormally into two and four cells and then died. *Thysanoessa inermis* shed its eggs in the same way, the egg capsule measuring 0·73 mm. to 0·76 mm. across (Plate V, Figs. 3, 4 and 5), the egg itself measuring 0·32 mm. across, or rather more when developing irregularly, in which case no egg membrane could be seen. There is thus a very large space between egg and capsule, and the egg is very much like that of Meganyctiphanes. So far as was seen, however, it was perfectly colourless. These eggs all died after a few hours, and no more could be obtained.

There is thus shown to be a distinct difference between the eggs of *Thysanoessa neglecta* and *T. inermis*, although they are both shed freely into the water at the earliest stage and are of the same type. This is apparently the first time that the eggs of these euphausiids have been described, although Brook and Hoyle (1888) describe a small egg from the Clyde which probably belongs to *Thysanoessa Raschii* (Boreophausia). Sars (1898) states that he has "studied all phases of the larval development of a third form, probably *Thysanoessa neglecta*, the larvæ of which, especially in the more advanced stages, are easily distinguished from those of Nyctiphanes . . . by their much more slender form." Apparently, however, these descriptions were not published, as I have not been able to find them. My own observations on the larvæ show that they are, as Sars states, of a much more slender form than Nyctiphanes and Meganyctiphanes.

There is a gap in the life-history of our two species of Thysanoessa, and the nauplii and metanauplii have not been described, nor, as far as I am aware, have they been seen. The next larval stage seen at Plymouth belongs to either *Thysanoessa neglecta* or *T. inermis*, but it is impossible at present to tell which. This, the first Calyptopis (Plate VI, Fig. 9), is much more slender than either Meganyctiphanes or Nyctiphanes, the abdomen being much longer in proportion to the carapace and on the telson is a pair of crimson-red chromatophores often merging into one mass. This larva, measuring 1·3 mm. in length, is easily distinguishable from the same stage of Meganyctiphanes and Nyctiphanes, and is fairly common with them in the spring. The second Calyptopis (Plate VI, Fig. 10) measuring 2 mm in length, and the third (Plate VI, Fig. 11) measuring 2·56 mm. in length, are also easily recognisable, the crimson chromatophores now being double, one pair above and one pair below the lateral spines of the telson. The elongated form is characteristic and also the elongated narrow carapace. The first Furcilia of this form (Plate VI, Fig. 12) has no abdominal appendages. This measures 3·04 mm. in length. Several succeeding Furcilia stages were found, but it is in the Cyrtopia stage that two forms can be recognised, one with long second thoracic limbs, the other with them short, thus corresponding with *Thysanoessa neglecta* and *T. inermis* respectively. Either of these forms agrees well with the slender larvæ from which a series can be formed, and it is highly probable that both *T. neglecta* and *T. inermis* have very similar early larval stages. Their elucidation remains for future investigation. Enough has been shown, however, to prove that the slender larvæ belong to Thysanoessa, therefore as we know that a thick-set first Calyptopis closely resembling Nyctiphanes comes eventually from the egg which we have assumed to belong to Meganyctiphanes, and which is of the same size and form as the egg shed by *Thysanoessa inermis*, it seems safe to infer that we are truly dealing with the egg of Meganyctiphanes as described above, and that eventually we shall find coming from the eggs of Thysanoessa larvæ corresponding with these slender forms which can be followed up into later larval stages and shown to belong to this genus.

We are now in a position to compare the Calyptopis stages of *Meganyctiphanes norvegica*, *Nyctiphanes Couchii* and *Thysanoessa* sp. (either *T. neglecta* or *T. inermis*), and to distinguish them one from the other (Plate VI).

First Calyptopis, *Meganyctiphanes norvegica*, colour pinkish dorsally, bright orange-red in thoracic region, spreading out from two large chromatophores ; pigment round mouth (length ca 1 mm.). No pigment on telson. *Nyctiphanes Couchii*, orange-red chromatophores on telson only (length, ca 1 mm.). *Thysanoessa* sp., much more slender than the other two in both carapace and abdomen. Crimson-red chromatophores in one patch on telson (length, 1·3 mm.).

Second Calyptopis, *Meganyctiphanes norvegica*, same colour as before Rather stout build (length, 1·6 mm.). *Nyctiphanes Couchii*, same pigment on telson, a little pigment near mouth. Less robust than Meganyctiphanes (length, 1·52 mm.). *Thysanoessa* sp. Two crimson-red patches on telson. Very much elongated (length, 2 mm.).

Third and Last Calyptopis, *Meganyctiphanes norvegica*, same colour as before. Very robust (length, 2·4 mm.). *Nyctiphanes Couchii*, same colour as before. Much less robust than Meganyctiphanes (length, 2·08 mm.). *Thysanoessa* sp., same colour as before. Very slender (length, 2·56 mm.).

The first Furcilia stages have the same characteristic pigmentation, and as they grow the stages are more and more easily recognised. Detailed descriptions of these later stages are reserved for a future paper.

SUMMARY.

It is shown in these notes that *Nyctiphanes Couchii* is an important food for Herring in the neighbourhood of Plymouth, and that this euphausiid and three others are common at times, either as larvæ or adult. It has been possible to procure the eggs of all these species and to rear those of Nyctiphanes through five larval stages direct from the parent, other stages being identified from the plankton. The young of *Meganyctiphanes norvegica* have been identified from eggs to late larvæ. The eggs of both *Thysanoessa neglecta* and *T. inermis* have been obtained from the parent, and, although these could not be reared, larvæ of Thysanoessa were recognised in the plankton. The importance of these observations lies chiefly

in the fact that nearly all was done from living material, whereas in most of the researches on the subject the specimens have been preserved. The advantage of the living material is obvious, both for rearing purposes and for identification by pigment.

Much yet remains to be done, and it is reserved for the future to investigate further into the food of the Herring directly it arrives in the Plymouth waters, to deal with the detailed distribution of all species of euphausiids, both larvæ and adult, and to finish the detailed investigation of their larval stages.

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EXPLANATION OF PLATES.

PLATE I.

Nyctiphanes Couchii (all drawn to same scale).

FIG.

1. Egg from pouch of ♀, 0·36 mm. across. Station E1, surface, 9.4.24.
2. Nauplius from pouch of ♀, 0·40 mm. long. Same locality and date; dorsal view.
3. Nauplius from pouch of ♀, 0·44 mm. long. Same locality and date; side view.
4. Nauplius, later stage, with metanaupliar limbs showing through skin, 0·54 mm. long; side view. From pouch of ♀. Same locality and date.
5. Pseudo-metanauplius just emerged from pouch of ♀, 0·56 mm. long. Station L4, 30.4.24; side view.
6. The same; ventral view.
7. Metanauplius, from pseudo-metanauplius, reared in finger-bowl from ♀. L4, 24.4.24. Changed its skin 2.5.24. 0·57 mm. long; side view.
8. Metanauplius from same brood; dorsal view.
9. Metanauplius from same brood; ventro-lateral view.

PLATE II.

Nyctiphanes Couchii (all drawn to same scale).

1. 1st Calyptopsis, T.N., L4, surface, 6.3.24. 0·99 mm. long; dorsal view.
2. Mandibles of same.
3. 1st maxilla of same.
4. 2nd maxilla of same.
5. 1st thoracic limb of same.
6. 2nd Calyptopis, T.N., L4, surface, 6.3.24. 1·44 mm. long; ventral view.
7. Mandibles of same.
8. 1st maxilla of same.
9. 2nd maxilla of same.
10. 1st thoracic limb of same.

PLATE III.

Nyctiphanes Couchii (all drawn to same scale).

1. 3rd Calyptopis, T.N., L4, surface, 6.3.24. 1·92 mm. long; dorsal view.
2. Under lip of same.
3. Mandible of same.
4. 1st maxilla of same.
5. 2nd maxilla of same.
6. 1st thoracic limb of same.

PLATE IV.

Meganyctiphanes norvegica (all drawn to same scale).

FIG.
1. Egg with developing nauplius, T.N., L4, surface, 20.2.24. 0·70 mm. across.
2. Egg with later nauplius. Same locality and date.
3. 1st nauplius, from egg. Same locality and date. 0·48 mm. long ; dorsal view.
4. 2nd nauplius, from 1st nauplius. Same locality and date. 0·48 mm. long ; dorsal view.
5. Metanauplius, from 2nd nauplius. Off Knap Buoy, 22.2.24. 0·51 mm. long ; dorsal view.
6. Metanauplius ; ventral view.
7. Metanauplius ; side view.

PLATE V.

Eggs of Thysanoessa (all drawn to same scale).

1. Egg of *Thysanoessa neglecta*, shed by ♀ in glass jar. From 3 miles S.W. of Eddystone, 12.4.24, Y.F.T. 0·41 mm. across.
2. Egg of *Thysanoessa neglecta*. Same locality and date, shed by ♀ in glass jar. 0·52 mm. across.

3–6. Eggs of *Thysanoessa inermis*, shed by ♀ in glass jar. From 3 miles S.W. of Eddystone, 12.4.24, Y.F.T. 0·76 mm. across. In various stages of segmentation (3, 5 and 6 probably abnormal).

PLATE VI.

Meganyctiphanes, Nyctiphanes and Thysanoessa (all drawn to same scale).

1–4. *Meganyctiphanes norvegica* (all drawn to same scale).

1. 1st Calyptopis, from tow-nets. L4, 25.3.24. 1·02 mm. long.
2. 2nd Calyptopis. Same locality and date. 1·6 mm. long.
3. 3rd Calyptopis. Same locality and date. 2·4 mm. long.
4. 1st Furcilia. Station E1, 9.4.24 (night). 2·8 mm. long.

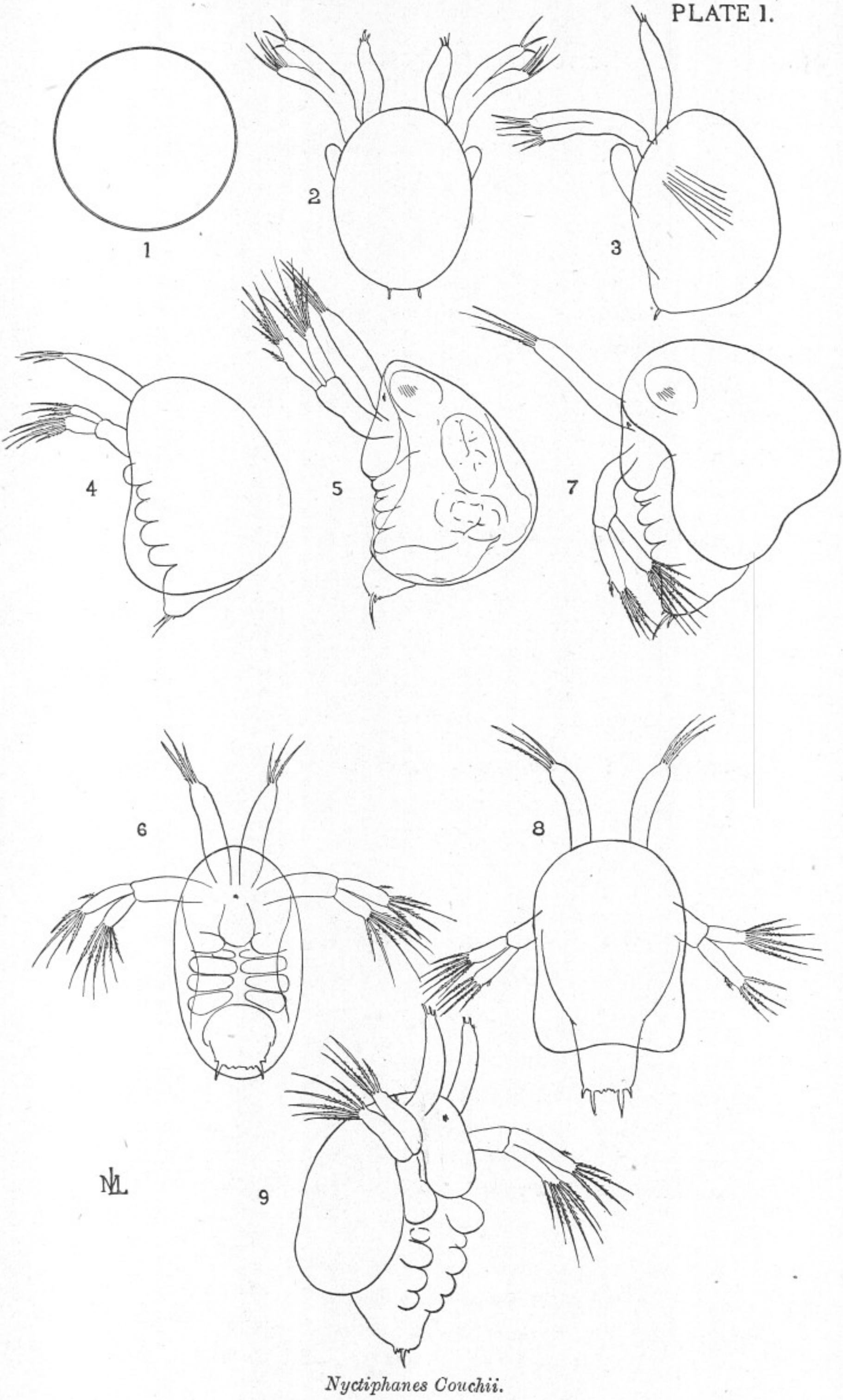
5–8. *Nyctiphanes Couchii.*

5. 1st Calyptopis, from tow-nets. L4, 9.3.24. 1 mm. long.
6. 2nd Calyptopis. L4, 6.3.24 (night). 1·52 mm. long.
7. 3rd Calyptopis. Same locality and date. 2·08 mm. long.
8. 1st Furcilia, from last Calyptopis from 2nd from 1st Calyptopis (1st from T.N. L4, 17.3.24). 2·56 mm. long.

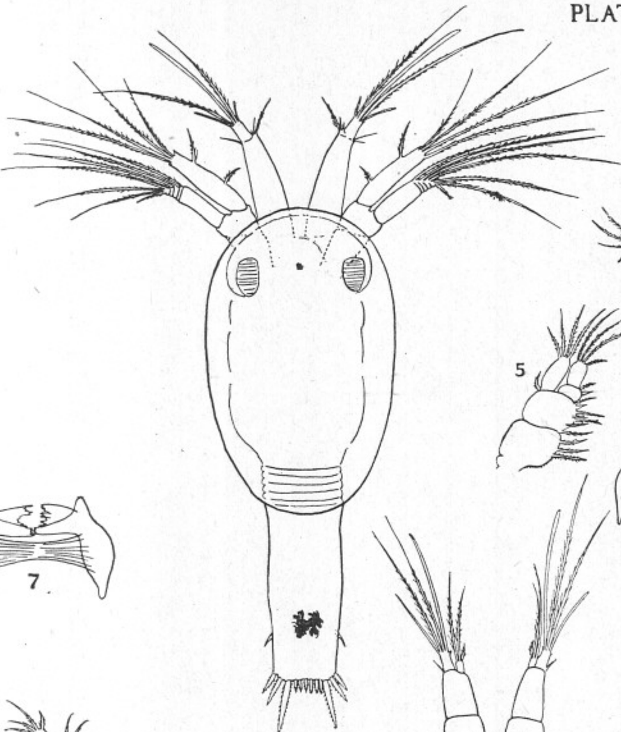
9–12. *Thysanoessa sp.*

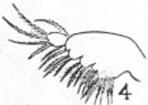
9. 1st Calyptopis. T.N., E1 (night), 9.4.24. 1·3 mm. long.
10. 2nd Calyptopis. Y.F.T., Mewstone N.E. 4 miles, 26.3.24. 2 mm. long.
11. 3rd Calyptopis. T.N., E1 (night), 9.4.24. 2·56 mm. long.
12. 1st Furcilia. T.N., E1 (night), 9.4.24. 3·04 mm. long.

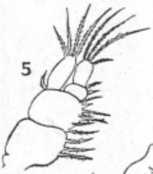
PLATE 1.

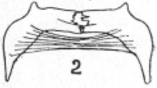


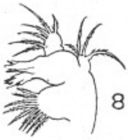
Nyctiphanes Couchii.

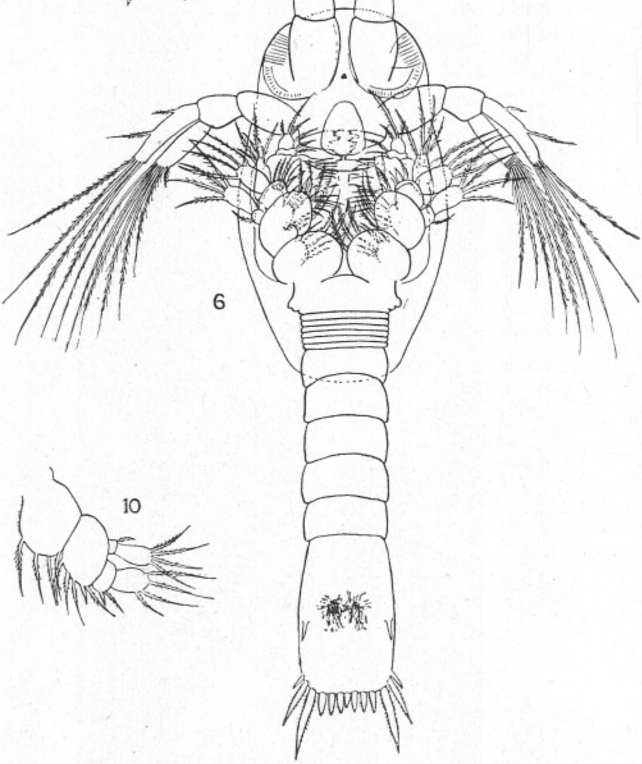












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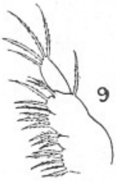
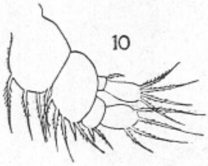
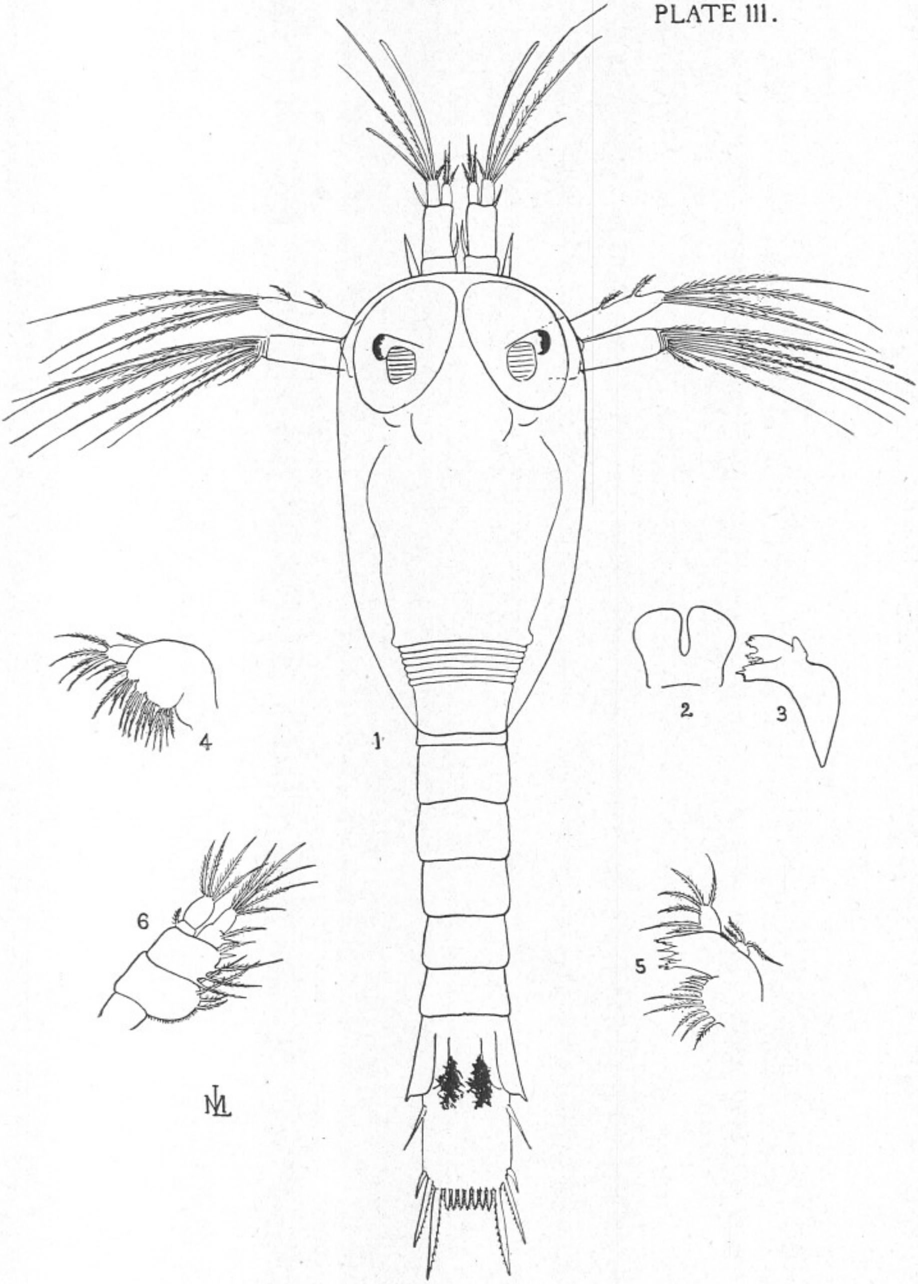




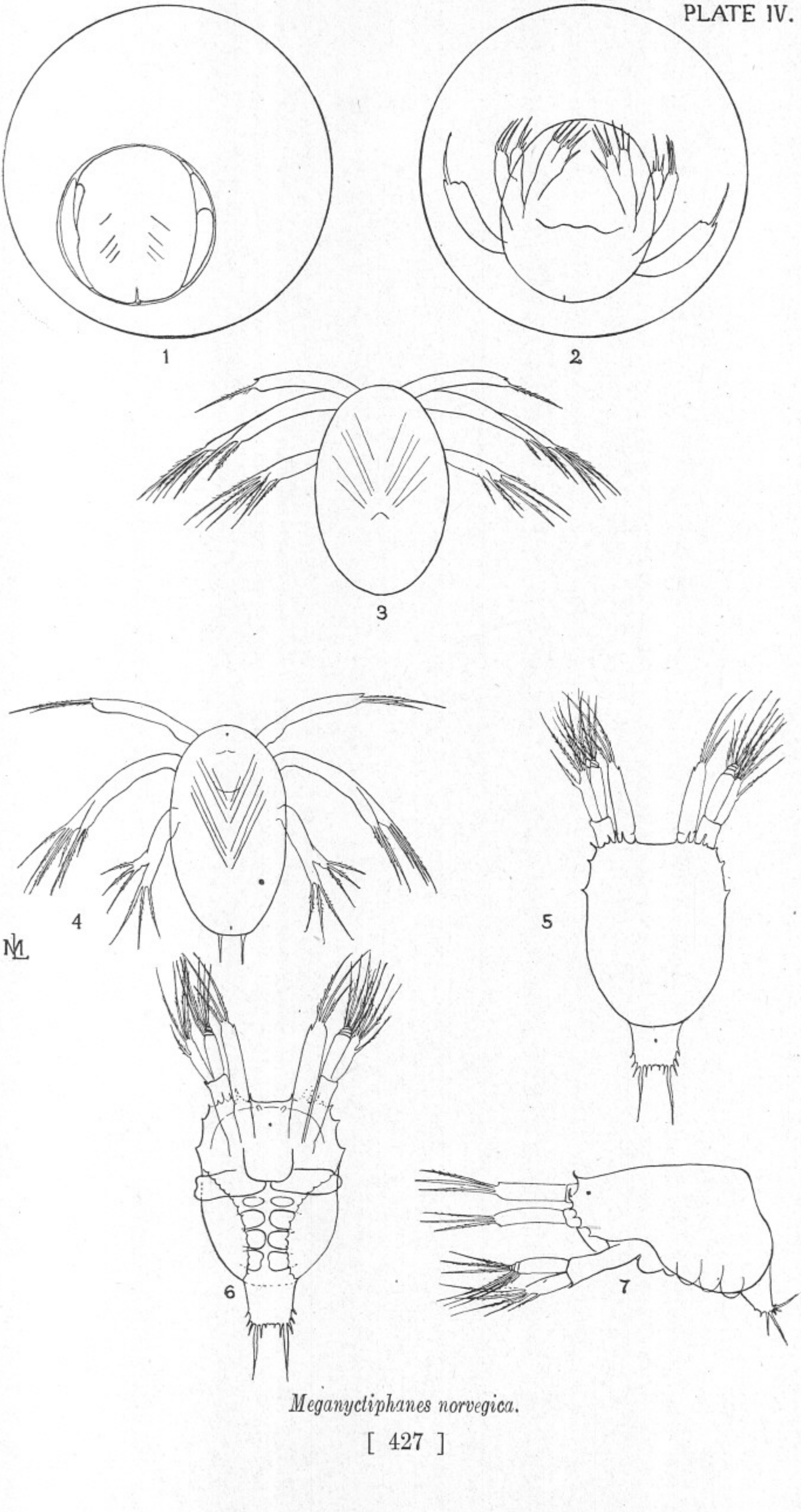
Nyctiphanes Couchii.

PLATE III.



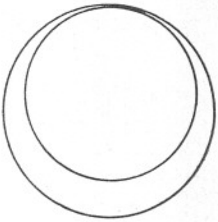
Nyctiphanes Couchii.

PLATE IV.



Meganyctiphanes norvegica.

PLATE V.



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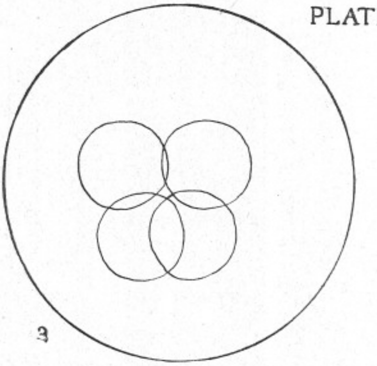

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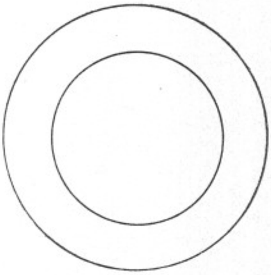

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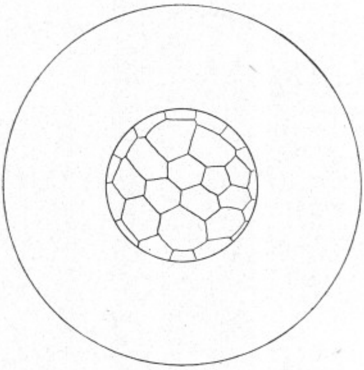

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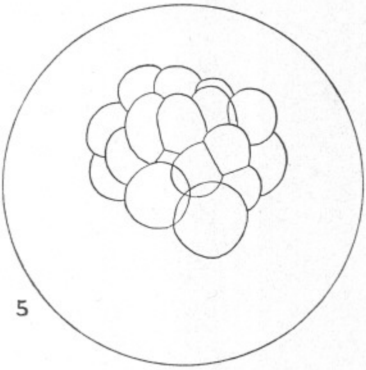

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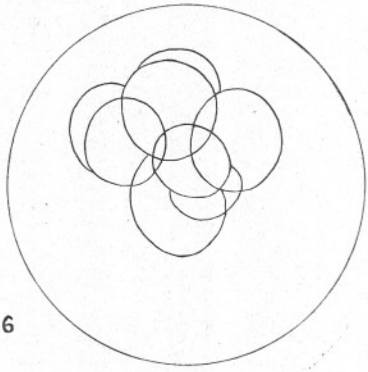

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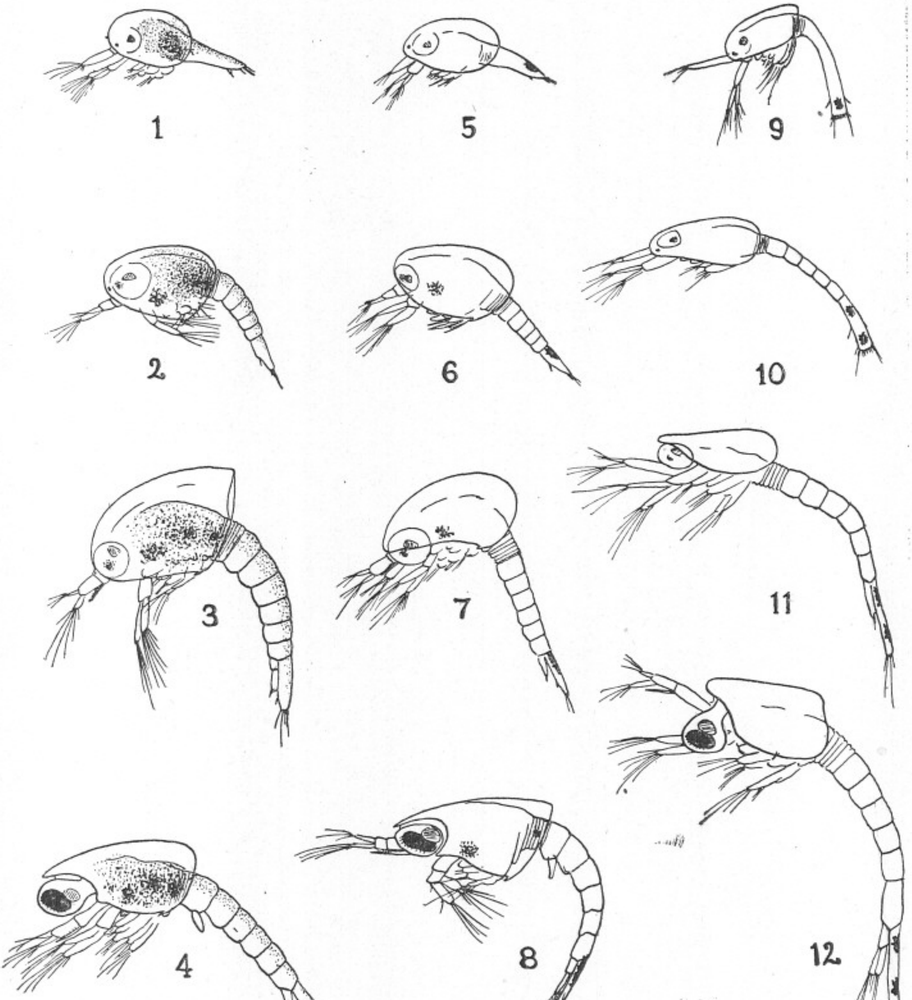
FIGS. 1–2.—*Thysanoessa neglecta*.
„ 3–6 „ *inermis*.

PLATE VI.



FIGS. 1–4.—*Meganyctiphanes norvegica.*
„ 5–8.—*Nyctiphanes Couchii.*
„ 9–12.—*Thysanoessa sp.*

The Zoea of *Eurynome aspera.*

By

Robert Gurney, M.A.

With 2 Figures in the Text.

The Zoea of *Eurynome aspera* has already been twice described—namely, by Kinahan (1857)* and Cano (1893),† but there is some discrepancy between the two accounts which an observation made at Plymouth in April, 1922, fully explains.

Kinahan observed the larva immediately on hatching and described it as having neither rostrum nor dorsal spine ; whereas Cano describes it as having both.

On April 18th, 1922, a female *E. aspera* bearing eggs was found in some material dredged from Plymouth Sound and was placed in a vessel under the circulation. At about 11 p.m. it was noticed that hatching of the eggs was in progress, and the vessel rapidly became full of actively-swimming Zoeas. Some of these were examined and found to be still enclosed in the embryonic cuticle. The following morning a large proportion of the very numerous larvæ were still in the same condition, the remainder having moulted and assumed the form shown in Cano's figure. It is evident that the larval cuticle is retained for several hours, in some cases for twelve hours or more, and that Kinahan observed the larva in this condition, a supposition already expressed by Cano.

The embryonic cuticle is usually moulted immediately after hatching, or is even cast off in the act of leaving the egg, but when it is retained for a short time, as in *Carcinus maenas*, the Zoea during that time is inactive. In the case of *E. aspera* the Zoea is almost as good a swimmer when first hatched as it is after the first moult, but its movements are, as might be expected, more erratic, and there are periods of quiescence.

The embryonic cuticle shows exceptionally well the "Protozoeal" setæ of the antennæ and telson which have been described by Faxon, Conn, and others in other species.

The telson has six very large ciliated setæ, a seventh which is short and not ciliated being placed between the third and fifth. This fourth seta contains the invaginated spine which forms the prolongation of the

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* *Ann. Mag. Nat. Hist.* (3), I, 1858, p. 233.

† *Mitth. Zool. Stat. Neapel*, X, 1893.

fork of the telson in the Zoea, and is also distinguished in the Anomura by its large size and its not being jointed off from the telson.

The first antenna bears two large protozoeal setæ which are both ciliated, while the second antenna has a large exopodite with four large setæ all springing from the same point. The endopodite is only a small knob, but the future spine is enclosed in a rather large unciliated envelope (Fig. 1). The appendage very closely resembles that of Panopæus as figured by Conn.*

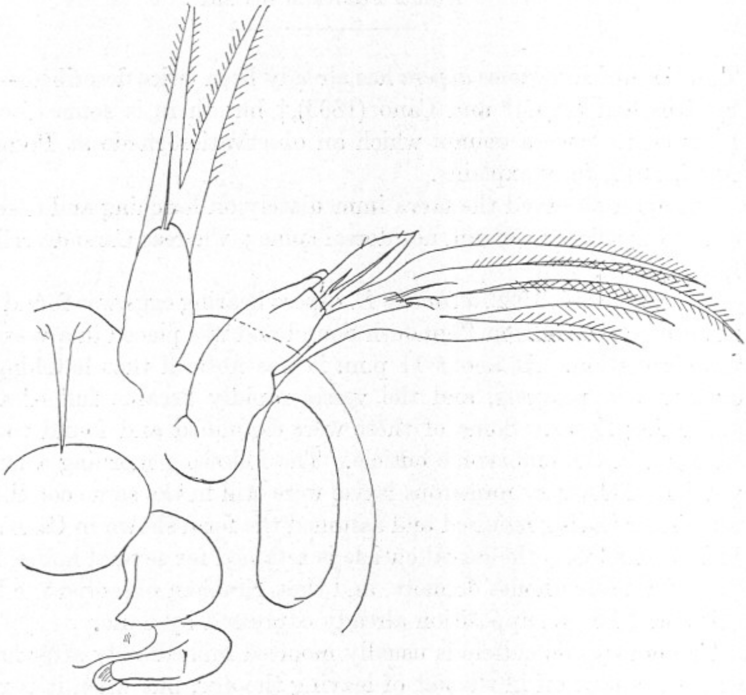

FIG. 1.—*Eurynome aspera*. Zoea before first moult. Ventral view of head.

I was not able to ascertain whether the antenna, armed with these large setæ, is used for swimming, but it seems very probable that it is so, since the swimming branches of the maxillipedes have no setæ, either embryonic or definitive.

It seems to me that the embryonic cuticle is, in fact, as Conn has suggested, a reminiscence of a Protozoea in which the second antenna was natatory, and I regard the Naupliosoma larva of Jasus which has been described by Gilchrist and by Archey as a special case of the retention in a functional condition of the appendages of this stage. In the

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* *Stud. Biol. Lab.*, Johns Hopkins Univ., III, 1884.

Naupliosoma the second antenna alone bears these provisional setæ, and it has to a very remarkable extent retained the character of a biramous appendage with a scale armed with setæ along one edge. The first antenna has no setæ. It is true that Gilchrist states that the larva moults on leaving the egg, but the general appearance of the larva as figured by him leads one to believe that, if this moult occurs, it may only be partial, and that the great setæ of the antenna are actually homologous with those of the embryonic cuticle of Eurynome and other Brachyura.

It is curious that Jasus alone apparently should have this Naupliosoma stage. It may perhaps be found later to occur in other forms, but it certainly does not occur in *Palinurus vulgaris*, of which I have been able to study unhatched and newly hatched larvæ. In this species there is no trace whatever of the natatory exopodite of the antenna.

Apparently, although the telson has in most Decapoda retained the peculiar protozoeal covering, the antennæ have lost it in all except some Brachyura and in Jasus. If, then, it has been retained in the latter and lost in all its congeners, it seems that the Nephropsidea must have branched off from the Reptant stem at a time when the embryonic cuticle still was functional in early larval life, and that in Jasus alone that function has been retained. Bouvier has ably argued the origin of the Brachyura from the Homaridea, and the fact that it is only in the Brachyura and in this one among the Nephropsidea that the natatory antenna has been preserved may perhaps be allowed to be added as a further argument in favour of the origin of the Crabs from an ancestor closely allied to the Nephropsidea, but not actually from that group. At the same time it should be pointed out that the structure of the Zoea of the Brachyura in other respects points to an origin from a primitive form of Anomuran.

As regards the Zoea itself a detailed description is unnecessary since Cano's figure (Taf. 35, Fig. 57) is quite accurate. I may, however, add that the large lateral chromatophores of the carapace and abdomen are black, with delicate yellow branches. At the base of the dorsal spine and in the stem of the second antenna is a small yellow chromatophore, while that of the posterior end of the fifth abdominal somite is red. A line of blackish pigment lies internally over the stomach.

The Zoea is in a relatively advanced condition, having rudiments of the third maxillipedes and of all five pairs of legs. The third mxp. is biramous, and the third leg is pushed in and covered by the adjacent legs.

It is rather an unusual thing to find in the first Zoea, as is the case in Eurynome, traces of the gills (Fig. 2). These are confined to the rudimentary mxp. 3 and legs 1 and 2. Mxp. 3 bears three small rudiments which no doubt represent epipodite, and two arthrobranchs. There are three quite distinct gill rudiments on legs 1 and 2, but their interpretation is a little difficult. The two rudiments on leg 1 should be by position an arthro branch and a pleurobranch ; while the single rudiment of leg 2 has the position of a pleurobranch. On the other hand, a pleurobranch is never found in the Brachyura above leg 1, the two pleurobranchs so generally found being on legs 2 and 3. The interpretation of larval gills is not an easy matter, as they are sometimes difficult to see and the limits of the appendages are ill-defined. It is therefore unsafe to attach importance to an apparent discrepancy such as this.

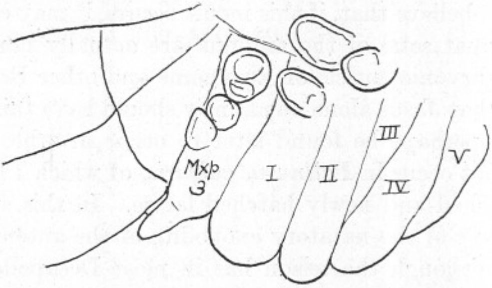

FIG. 2.—*Eurynome aspera.* First Zoea. Rudiments of thoracic appendages and gills.

The Hydrogen Ion Concentration of Sea Water in its Relation to Photosynthetic Changes.

PART III.

By

W. R. G. Atkins, O.B.E., Sc.D., F.I.C.,

Head of the Department of General Physiology at the Plymouth Laboratory.

With Figures 1–4 in the Text.

INTRODUCTION.

The present paper is a continuation of the work already published* under the above general title and should be considered in relation to the results previously recorded. The method of performing the measurements remained unchanged; xylenol blue was used to check the determinations made with cresol red in the more alkaline regions—namely, around pH 8·24. The water was tested immediately after being drawn, or within a few hours, unless otherwise stated in the tables.

The results obtained are tabulated for reference, but since the seasonal changes are in a general way similar to those of 1921–22 they have only been shown graphically in four figures, which are of interest as they illustrate the differences between the years and the variation of pH with depth.

Salinity determinations, made at the Government Chemist's Laboratory, were used to apply small corrections to the pH values of the L series where necessary, but since they are published as part of the International Hydrographic Investigations they are omitted here.

THE RELATION OF THE WATER OF PLYMOUTH SOUND TO THAT OF THE OPEN SEA THROUGHOUT THE YEAR.

In this series perhaps the most noticeable differences as compared with the previous year are the low pH values for March 12th, which extend right out to the Eddystone, L 5, instead of ceasing at the Breakwater,

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* Journ. Mar. Biol. Assoc., Vol. XII, No. 4, pp. 717–771, 1922, and Vol. XIII, No. 1, pp. 93–118, 1923.

L 2. The samples of the 14th also show this, but to a much smaller degree; while those of the 21st are normal.

The salinity determinations indicate that the effect was due to the great volume of fresh water coming down the rivers.

Unfortunately a complete series was not obtained in May, but photosynthetic activity must then have been very great, since the high values pH 8·23 were found at L 3 and L 4, both at the surface and at the bottom —namely, at 45 and 50 metres depth respectively. The E 1 depth series contains no such high values for these depths, but between Sardinia and Italy, Palitzsch records pH 8·23 at the surface and 8·21 at 100 metres.

SEASONAL CHANGES IN pH VALUES AT STATIONS L1, L2 AND E1, SURFACE AND BOTTOM, DOTTED LINE.

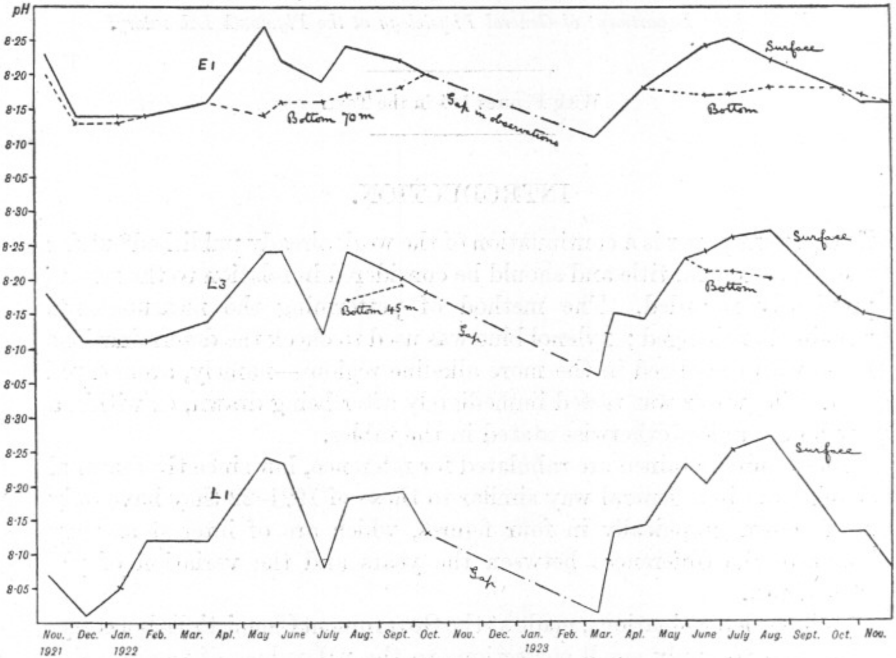

FIG. 1.

The July values for the L series are markedly different from those of the previous year. In 1922 the wet and stormy end of June caused the July pH values to be low, abnormally low it is probable, viz. pH 8·08 and pH 8·12 for L 1 and L 3, as compared with pH 8·25 and pH 8·26 respectively for 1923. This drop in July may be appreciated from a study of Fig. 1, which shows the pH values for L 1, L 3, and E 1 from November, 1921, to November, 1923, inclusive. Bottom values are shown by a dotted line. The water accordingly remained uniformly alkaline at the stations throughout the summer. The relation between this and the seasonal distribution of sunshine is shown in Fig. 4.

	March 12th.		March 14th.		March 21st.	March 28th.	
Station.	t °C.	pH	t °C.	pH	pH	t°C.	pH
L 1	8·7	8·01	8·6	7·98	8·09	9·6	8·13
L 2	8·8	8·01	8·8	8·09	8·09	9·4	8·13
L 3	9·1	—	9·0	8·09	8·12	9·25	8·15
L 4	9·1	8·01	9·1	8·08*	8·12	9·2	8·14
L 5	9·1	8·03	9·1	—	8·12	9·3	8·14
L 6	9·2	8·11	—	—	—	—	—
E 1	9·3	8·11	9·6	8·12	—	—	—

pH determined on 13th. * pH determined on 15th, rest on 16th.

	April 24th.		May 22nd.	May 31st.	June 19th.		July 10th & 12th.	
Station.	t °C.	pH	t °C.	pH	t °C.	pH	t °C.	pH
L 1	9·7	8·14	10·8	—	12·6	8·20	16·65	8·25
L 2	9·7	8·10	10·8	—	12·45	8·24	15·85	8·25
L 3	9·5	8·14	10·7	8·23†	12·35	8·24	16·7	8·26
L 4	9·7	8·13	10·4	8·23†	12·55	8·24	16·6	8·25
L 5	9·7	8·16	10·7	—	12·6	8·24	15·6	8·23
L 6	9·9	8·16	10·8	—	12·7	8·24	16·8	8·25
E 1	10·1	8·18	10·9	—	12·8	8·24	16·6	8·25

pH determined on 26th. † Same at bottom.

	August 15th.		Sept. 13th.	October.		November 7th.	
Station.	t °C.	pH	t °C.	t °C.	pH	t °C.	pH
L 1	15·4	8·27	14·8	13·0	8·13	11·0	8·13
L 2	14·5	8·26	14·6	12·8	8·14	11·3	8·14
L 3	16·3	8·27	14·4	13·1	8·17	12·1	—
L 4	16·7	8·26	15·1	13·3	8·17	12·1	8·17
L 5	16·2	8·26	14·7	13·6	8·17	12·0	—
L 6	17·0	8·22	14·6	13·6	8·18	11·9	—
E 1	16·7	8·22	15·0	13·0	8·18	12·1	8·16

pH determined on 9th.

	December 10th.		January 2nd, 1924.	
Station.	t °C.	pH	t °C.	pH
L 1	9·1	8·06	8·9	8·02
L 2	9·2	8·10	9·0	8·03
L 3	9·2	8·14	9·0	8·09
L 4	9·4	8·15	9·0	8·09
L 5	9·9	8·16	9·1	8·14
L 6	10·3	8·16	9·1	8·14
E 1	10·2	8·16	9·4	8·16

THE SEASONAL CHANGES IN THE HYDROGEN ION CONCENTRATION OF THE OPEN SEA AT VARIOUS STATIONS AND DEPTHS.

The monthly visits to E 1 were continued during 1923, but no pH values were determined for September or May. The depth series results are tabulated here and shown in Fig. 2.

When compared with 1922 the 1923 results are noticeable chiefly for the absence of the depression in July, as may be seen in Fig. 1. The results for November, 1921, which gave high values owing to the exceptionally sunny autumn, are also markedly above those for 1922 and 1923.

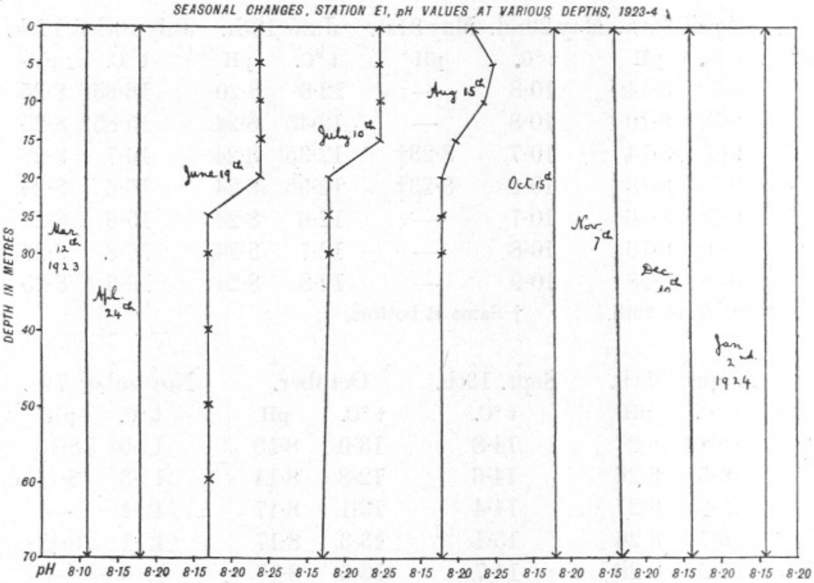

FIG. 2.

Furthermore, the 1922 maximum occurred in May, with a secondary one early in August; whereas in 1923, though June gave high values, the maximum was in July. No observations were made in May, however; but from the form of the depth series curves shown in Fig. 2 it is impossible to say whether the maximum had passed by June 19th. As in 1922, the bottom values at E 1 rose slightly during the summer to a maximum pH 8·18, at which on October 15th and April 24th the water column was uniform from top to bottom. In 1922 the October value was pH 8·20, which corresponds to a 3 per cent difference in hydroxyl ion concentration in favour of 1922.

As regards the question as to whether the July value was truly the maximum, it is of interest to note that the phosphate content at E 1 was a minimum in July, which points to the maximum algal development having occurred by that time. This does not necessarily indicate that July was also the true maximum for pH value, rather than May, but it lends support to that view.

As in 1922, the curves of the depth series, Fig. 2, are noticeably of different form during the summer months, when the more alkaline warm water is found nearest the surface, where it remains unmixed with the deeper and colder water until the autumn. This question of the mixing of the water is considered in a separate paper.

The pH values and temperatures are tabulated below, as are also similar results for stations E 2, E 3, N 1 and N 2. In Fig. 3 the pH depth series for these and E 1 is shown; the gradients at the different stations may be grouped according to position, those for the coastal stations E 3 and N 2 being nowhere steep; whereas those far from land, E 1, E 2, and N 1, are well marked.

E 1.	Mar. 12th, 1923.		April 24th.		June 19th.		July 10th.	
Depth in metres.	t °C.	pH	t °C.	pH	t °C.	pH	t °C.	pH
0	9·32	8·11	10·1	8·18	12·8	8·24	16·6	8·25
5	9·22	—	10·04	—	12·66	8·24	16·38	8·25
10	—	—	—	—	12·48	8·24	16·28	8·25
15	—	—	9·87	—	12·40	8·24	14·83	8·25
20	—	—	—	—	12·34	8·24	12·19	8·18
25	9·24	—	9·89	—	11·20	8·17	12·01	8·18
30	—	—	—	—	11·20	8·17	11·97	8·18
40	—	—	—	—	11·16	—	11·94	—
50	9·22	—	9·87	—	11·16	8·17	11·84	—
60	—	—	—	—	11·15	8·17	11·84	—
70	9·20	8·11	9·79	8·18	11·14	8·17	11·87	8·17

pH determined on 13th. pH determined on 26th.

E 1	Aug. 15th.		Sept. 13th.		Oct. 15th.		Nov. 7th.	
Depth.	t °C.	pH	t °C.	pH	t °C.	pH	t °C.	pH
0	16·75	8·22	15·0	—	13·0	8·18	12·15	8·16
5	16·52	8·25	14·98	—	13·48	—	12·34	—
10	16·28	8·24	14·32	—	13·36	—	—	—
15	12·96	8·20	13·59	—	13·38	—	—	—
20	12·70	8·18	13·33	—	13·46	—	—	—
25	12·50	8·18	13·30	—	13·43	—	12·33	—
30	12·50	8·18	13·25	—	13·35	—	—	—
40	12·50	—	13·25	—	13·35	—	—	—
50	12·46	—	13·25	—	13·35	—	—	—
60	—	—	—	—	—	—	—	—
70	12·46	8·18	13·25	—	13·40	8·18	12·32	8·17

pH determined on 9th.

E 1	Dec. 10th, 1923.		Jan. 2nd, 1824.	
Depth.	t °C.	pH	t °C.	pH
0	10·2	8·16	9·45	8·16
5	10·40	—	9·51	—
25	10·35	—	9·52	—
70	10·40	8·16	9·51	8·16
	pH determined on 11th.		pH determined on 3rd.	

E 2	March 14th, 1923.		April 24th.		July 10th.		Nov. 7th.	
Depth.	t °C.	pH	t °C.	pH	t °C.	pH	t °C.	pH
0	9·7	8·12	10·9	8·24	16·7	8·25	12·35	8·16
5	9·82	8·14	10·69	—	16·43	—	12·62	—
10	9·82	—	—	—	15·36	8·25	—	—
15	—	—	10·24	—	12·49	8·24	—	—
20	—	—	—	—	11·94	8·17	—	—
25	9·83	—	10·20	—	11·93	8·17	12·64	—
30	—	—	—		—	—	—	—
50	—	—	—	—	11·87	—	—	—
90	9·84	8·14	10·20	8·18	11·84	8·17	12·63	8·17
	pH determined on 15th.		pH determined on 26th.					

E 3	April 25th, 1923.		July 11th.		Nov. 8th.	
Depth.	t °C.	pH	t °C.	pH	t °C.	pH
0	10·3	8·19	14·43	8·24	11·15	8·16
5	—	—	13·93	—	11·85	—
10	—	—	13·69	8·23	—	—
15	—	—	12·33	8·22	—	—
20	—	—	12·19	—	—	—
25	—	—	12·14	8·19	11·85	—
50	—	—	11·81	—	—	—
75	—	—	11·59	—	—	—
100	10·39	8·19	11·57	8·17	11·85	8·17
	pH determined on 26th.					

N 1	July 11th.		Nov. 8th.	
Depth.	t °C.	pH	t °C.	pH
0	16·5	8·26	11·65	8·16
5	16·38	—	11·74	—
10	16·28	8·26	—	—
15	13·64	8·25	—	—
20	11·16	8·19	—	—
25	11·09	—	11·73	—
50	11·01	—	—	—
75	11·01	—	—	—
95	10·99	8·17	11·70	8·17
			pH determined on 9th.	

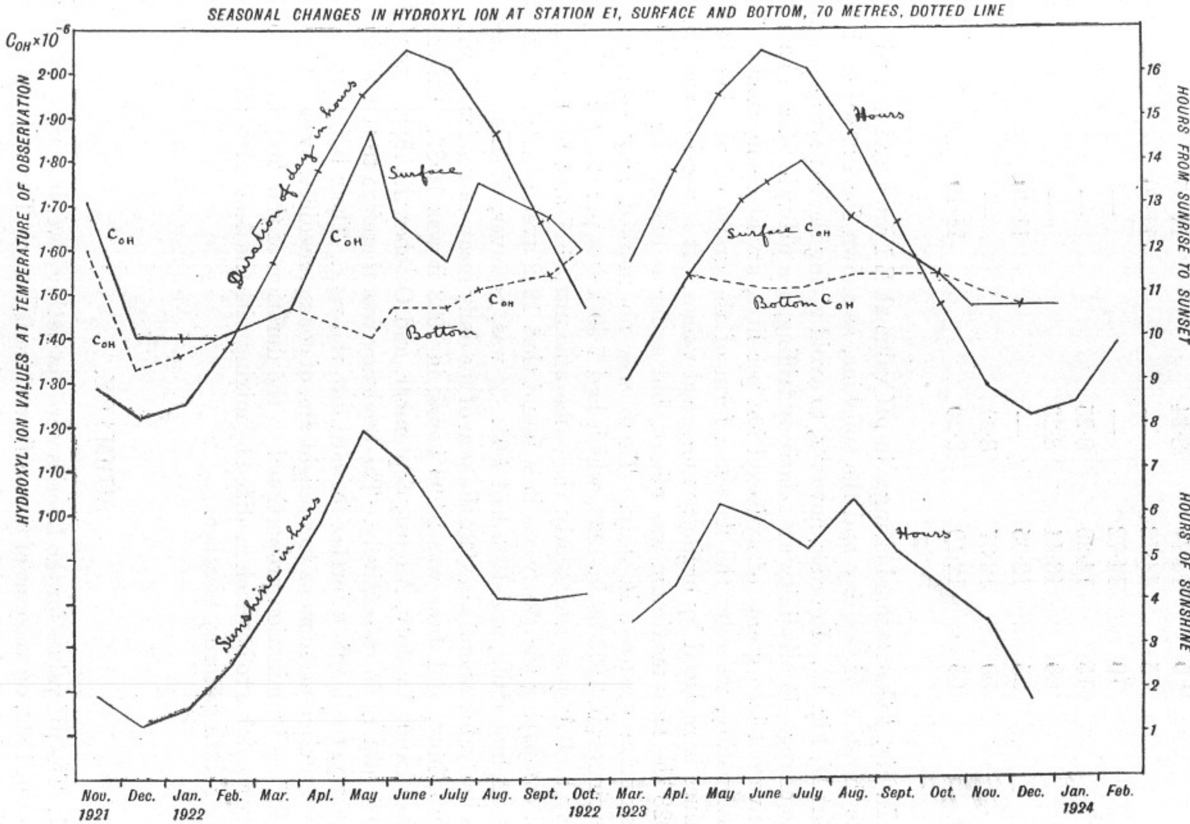
SEASONAL CHANGES IN HYDROXYL ION AT STATION E1, SURFACE AND BOTTOM, 70 METRES, DOTTED LINE
$C_{OH} \times 10^{-6}$
HYDROXYL ION VALUES AT TEMPERATURE OF OBSERVATION
2·00
1·90
1·80
1·70
1·60
1·50
1·40
1·30
1·20
1·10
1·00
HOURS FROM SUNRISE TO SUNSET
HOURS OF SUNSHINE
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
Duration of day in hours
Surface
C_{OH}
C_{OH}
C_{OH}
C_{OH}
Bottom
Sunshine in hours
Hours
Surface C_{OH}
Bottom C_{OH}
Hours
Nov. 1921
Dec.
Jan. 1922
Feb.
Mar.
Apl.
May
June
July
Aug.
Sept.
Oct. 1922
Mar. 1923
Apl.
May
June
July
Aug.
Sept.
Oct.
Nov.
Dec.
Jan. 1924
Feb.

Fig. 3.

N 2	July 11th.		Nov. 8th.
Depth.	t °C.	pH	t °C.
0	14·7	8·24	11·65
5	14·78	—	11·70
10	14·72	—	—
15	14·29	8·25	—
20	13·44	8·23	—
25	12·35	—	11·70
50	12·37	8·21	—
65	12·19	8·20	11·70

In Fig. 4 the seasonal changes in pH value at E 1 are correlated with the duration of the day and the sunshine, as shown for 1922 alone in Part II, Fig. 12. In order, however, to avoid giving the impression that the changes in alkalinity are relatively trifling, the pH values have been converted into grams of hydroxyl ion per litre, at the temperature of observation, whereby the flattened form of the graph of the log $^1/_H$ values is replaced by ordinary numerical values. It is possible that in 1923 the May maximum was missed, but as far as observations go the maximum occurred in July. There was no marked May sunshine maximum in 1923 as in 1922, which had 7·90 hours per day; in 1923 May and August had nearly the same amounts, 6·17 and 6·30 hours. On comparing the two years it is found that 1922 averaged 4·12 hours of sunshine daily, and 1923 had 4·05. It was, however, distributed dissimilarly, for whereas in 1922 the sum of the daily mean values for March, April, May, and June was 24·90 hours, in 1923 it was 19·82. On the other hand, for July, August, September, and October the figures were 17·78 and 19·65 respectively. The tendency was therefore to throw the photosynthetic effect further forward into the year. The relationship of these surface phenomena to sunlight are, of course, modified by the effect of diffuse illumination proportional to the duration of the day, and also they are liable to be much modified by mixing with the deeper less alkaline water during stormy weather.

SUMMARY.

1. The pH values for the L series were noticeably lower in March, 1923, than in 1922, on account of the outflow of fresh water. The well-marked May maximum, followed by a depression in June and July, 1922, is not found in 1923, during the summer months of which the water increased in alkalinity until August, when it slowly decreased. This appears to be due to the absence of stormy and wet weather in June and July, 1923.

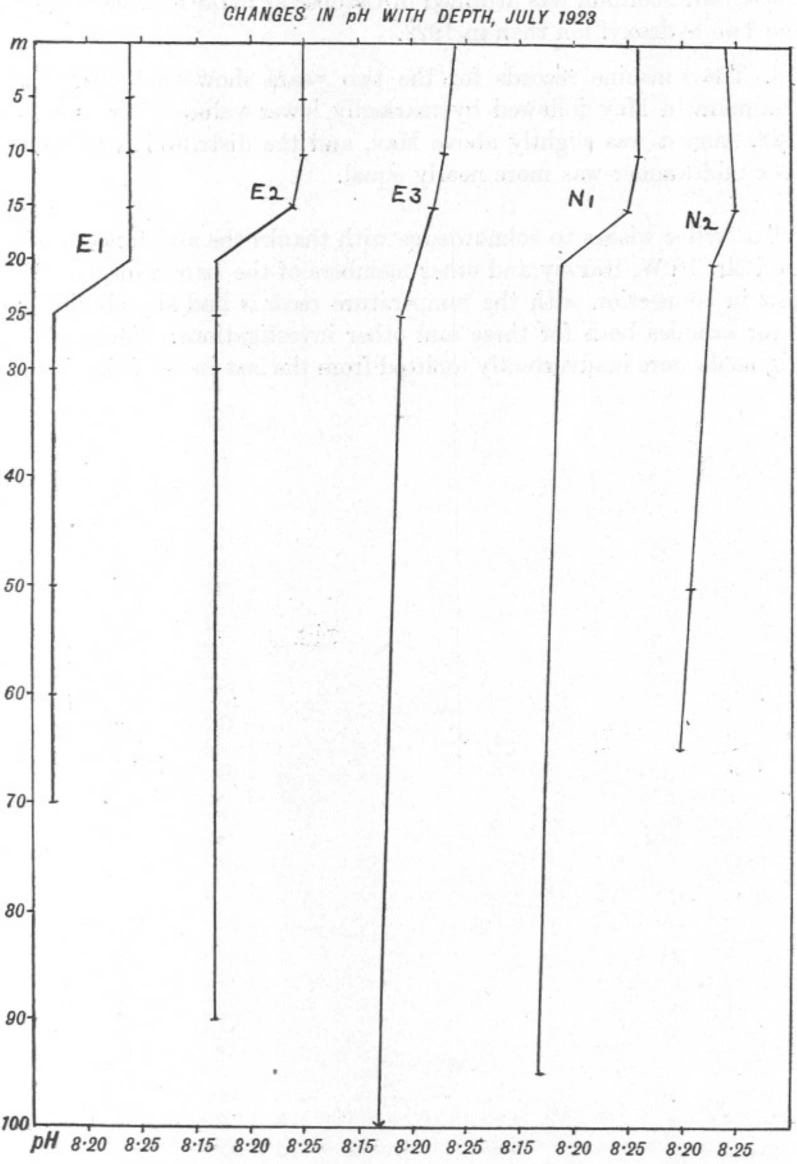
CHANGES IN pH WITH DEPTH, JULY 1923
m
5
10
15
20
25
30
40
50
60
70
80
90
100
E1
E2
E3
N1
N2
pH
8·20
8·25
8·15
8·20
8·25
8·15
8·20
8·25
8·15
8·20
8·25
8·20
8·25

FIG. 4.

2. The pH values for E 1 reached their maximum at the surface in July, but the bottom values were still low. These increased till uniformity of the water column was attained in October at pH 8·18, denoting 3 per cent less hydroxyl ion than in 1922.

3. The sunshine records for the two years show that 1922 had a maximum in May followed by markedly lower values after June. In 1923, August was slightly above May, and the distribution before and after midsummer was more nearly equal.

The writer wishes to acknowledge with thanks the assistance received from Mr. H. W. Harvey and other members of the Laboratory staff and crew in connection with the temperature records and the obtaining of water samples both for these and other investigations. Such acknowledgments were inadvertently omitted from the last issue of the Journal.

Malignant Tumours in Fishes.

By

Jas. Johnstone, D.Sc.

With Plates I and II.

THIS paper contains a general account of about forty examples of tumours, mostly "malignant," found in eighteen species of fishes, all of them marine except two, a Stickleback and a Gold-fish. In all these cases the affection was a very obvious one, attracting immediate attention from the fishermen who caught the specimens, or leading to condemnation of the fish by market inspectors. In some cases the appearance presented by the fish was grotesque, or repulsive in the extreme. I give a list of the specimens dealt with on p. 447–8 : all these represent "cancerous" affections. Many other diseased fishes, obtained in the same ways, have been seen and examined. Malformations of development, or growth ; large healing scars due to wounds ; repulsive ulcers of unknown origin ; parasitic tumours and two cases of undoubted piscine tuberculosis (in Cod) have also been examined. Here, however, I refer only to tumours which exhibit the character of malignancy.

LIST OF CASES EXAMINED.*

(1) FIBROMAS.

Plaice (3 examples) : On the head, dorsal and caudal fins (1908, 97 ; 1921, 227).

Halibut : In the body cavity (1912, 33).

Haddock : "Shelled-out" from the body muscles (1910, 39).

Pilchard : On the alimentary canal (1910, 37).

Ray : Myxofibromata in the distended mucous canals (1911, 62).

Conger : Hard nodules in the liver (1913, 50).

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* The references are to *Annual Reports of the Lancashire Sea Fisheries' Laboratory*, Liverpool, for the years cited.

(2) SARCOMAS.

Cod (3 examples): On the head near the orbit (1913, 52; 1919, 30; 1922, 88); one on the snout (1911, 55); one on the posterior part of the body (1914, 35); one on the stomach.

Haddock: On the head (1921, 227).

Ling: On the orbit (1922, 87).

Cat-fish: On the body behind the head.

Conger: On the orbit (1919, 32).

Turbot (2 examples): On the body (1922, 89; 1923, 99).

Flounder: Lymphosarcoma in the orbit with exophthalmos (1911, 57).

Gold-fish: On the body near the tail (1922, 96).

(3) MELANOTIC SARCOMAS.

Skate (3 examples): On the pectoral fins (1911, 48; 1912, 35).

Skate: Multiple tumours in the flesh (1912, 35).

Ray: On the head near the orbit (1910, 41).

Ray: Multiple tumours in the flesh (1911, 52).

Halibut: Multiple tumours in the flesh (1914, 24).

(4) CUTANEOUS PAPILLOMAS.

Halibut: Large multiple growth on the snout (1911, 67).

Turbot: Multiple growths on the body (1913, 47).

Haddock: Multiple warty growths on the body (1923, 101).

(5) EPITHELIOMA.

Whiting: On the lower jaw (1923, 103).

(6) ANGIOSARCOMAS.

Stickleback: On the cornea (1914, 41).

Mackerel: On the body (1923, 120).

Cod: On the rete mirabile of the swimbladder.

(7) OVARIAN TUMOURS.

Angler-fish: Numerous cysts on the ovary (1912, 25).

Ling: Papillary cystadenoma of the ovary (1914, 44).

(8) GOITRE.

Box vulgaris: Two large thyroid tumours in the opercular cavities (1923, 113).

SITES OF THE TUMOURS.

Later on I shall specify more particularly the tissues in which malignant growths have been observed in fishes. The general regions of the body affected are indicated in the above list. Visible tumours, identified generally as sarcomas, occur most frequently in the region of the head, particularly in close proximity to the orbits, and spreading down into the mouth and pharynx. They have been found on the body behind the head on the fins and on the tail. They occur in the body cavity as outgrowths from the peritoneum and underlying connective tissues, on the swimbladder, on the ovary and testis, on the thyroid and in the cornea and choroid coat of the eye. The skin may be affected, but it is not usually the epidermis that is the tissue that undergoes malignant growth: it is rather the underlying layer of coarse ("collagenous") connective tissue fibres that is continuous with the septa that bound the muscle segments or myotomes. In only one case have I seen what may be regarded as an epithelioma. Looking at the above list from the point of view of tissue origin we see only one case of a tumour of hypoblastic origin—that of the goitre found in *Box vulgaris*—and only one case of a tumour of epiblastic origin—the epithelioma on the lower jaw of a Whiting. This is doubtful. In all the other cases the origin is from the mesoblast. Further, they are all "pulp" tissues that have originated from the persistent mesoblastic pulp, or mesenchyme. In Adami's terminology we have to do with "hylic tumours of mesenchymal origin."

THE CRITERIA OF MALIGNANCY.

These visible fish tumours certainly belong to that kind of growths called "cancerous." Among them we find both "benign" and "malignant" tumours, and it is convenient to distinguish them in this way, though I think it would be most difficult to establish an absolute differentiation. In general a benign tumour is one which is sharply bounded from the surrounding tissues by a fibrous capsule. It grows very slowly, so slowly that its presence evokes a reaction from the adjacent tissues leading to the formation of the capsule. It grows in all its parts, peripherally and centrally. A benign tumour may lie freely (except for its stalklike attachment to the peritoneum) in the body-cavity, and such lipomas may attain a great size. It may lie in the muscles beneath the skin, and hardly at all attached to the capsule, so that on slitting open the latter the tumour may "shell-out." Biologically the very important distinction between the malignant and benign tumour is this local, *protective* reaction on the part of the normal tissues leading up to the circumscribing of the proliferating cell mass and its partial starvation, so that further growth is almost entirely arrested. It is probable that one important line of investigation, in the near future, will be the endeavour to induce the tissues round a cancerous growth to set up the reaction culminating in the formation of a bounding fibrous capsule.*

The absence of a capsule. First, it is to be noted that tumours have been studied (melanotic, multiple growths in the flesh of a Halibut) where the visible swelling was apparently sharply bounded and had an apparent capsule. But close examination of sections with a high-power lens showed that there was really a continuity between the tumour tissue and that of the adjacent parts, and that typical infiltrative (see below) growth was proceeding (see Fig. 7). The experience of surgeons is that tumours that are apparently benign may ultimately take on the condition of malignancy; the capsule may break down and rapid extension of growth may then become established. The only typically benign tumours seen, among the cases here studied, were two stalked ones (on the dorsal and caudal fins of a plaice). In man these would have been lipomatous, that is, composed mainly of fatty tissues, but in the fish they were loosely fibroid. Because of the narrow stalk by which they were attached to the host extension into the tissues of the latter was difficult or impossible.

Infiltrative growth. Highly typical of the malign tumour is the growing margin of the cell-mass (see later for details). The latter does not grow at all in its central parts, but only at its margins (where cell-division stages can be recognised). Here there is a gradual histological transition between the normal and the abnormal tissues, such that the latter insinuate themselves between, or infiltrate the healthy tissue elements, ultimately destroying the latter. *There is no protective reaction on the part of the organism*, and this is the truly sinister and biologically significant aspect of the process of malignant growth. Because of the infiltration the proliferating tissue may extend far beyond the visible limits of the tumour (say, along the lymph tracts), and so removal of the latter may not eradicate the growth with the result that recurrence may be exhibited. Thus even in removal of a carcinomatous breast, with the lymph glands in the axillæ, the furthest extensions of the roots of the growth may not be dissected away.

Generalisation with metastases. Therefore, we may have a primary growth, or focus, with secondary growths, or metastases. These metastatic tumours become established in this way: fragments of the original tumour become detached and get carried away in the blood- or lymph-vascular channels, become arrested at some place where the calibre of the vessels diminishes sufficiently and then undergo proliferation.

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* See a letter in *Nature*, Nov. 10th, 1923, Vol. 112, p. 688, by Dr. J. H. Orton.

Thus the great tendency for metastatic growths to occur in the lungs (in man).

Three examples of such multiple tumours (Skate, Ray and Halibut) are given in the list. In these the condition of metastatic growths is apparently demonstrated in a beautiful way : thus the flesh of the Halibut was simply *full* of tumours which could be felt beneath the skin all over the body. They were melanotic, and so most apparent when the flesh was cut into. Now it is not at all clear that we have, in these examples, true cases of metastatic growth, for it has been impossible to demonstrate the origin of the secondary tumours by the proliferation of detached fragments of the primary growth, carried away in the blood or lymph streams and lodged somewhere as cell embolisms. Nor is it probable that this did occur : otherwise we should expect a certain frequency of sarcomatous tumours in the gills, analogous to the frequency of metastatic growths in the human lungs. I have, so far, seen no tumour on the gills of a fish, and it would be interesting to confirm this negative result by the study of much more numerous cases of malignant growths in fishes, occurring elsewhere than in the gills, liver and kidney : in the two latter organs there are portal circulations affording the opportunities for the occurrence of cell embolisms.

Besides, close study of the growth of the tumours suggests that it is the *condition of proliferation* that extends rather than that healthy tissues become inoculated with tumour fragments : obviously some thoroughgoing experimental work dealing with the results of *implantation* of fragments of fish sarcoma in healthy fish would be highly interesting.

Considered with respect to the three principal criteria : absence of capsulation ; marginal growth with infiltration and generalisation by formation of numerous secondary growths ; the majority of the cases recorded on pp. 447–8 represent malignant tumours.

HISTOLOGICAL NATURE OF THE TUMOURS.

With five possible exceptions we have to deal with sarcomatous growths in fishes : these exceptions may be noticed at once.

(?) *Epithelioma on the jaw of a whiting.* The fish was a small one, about 9 in. in length. On the right lower jaw was a very noticeable tumour about 1 cm. in diameter. It was papillated on the surface. On cutting it open numerous small rounded bodies were seen, and one of the smaller of these is represented in Fig. 20. Here we have something in the nature of an "epithelial pearl," that is a little, spherical body consisting of a nucleus surrounded by concentric fibrous shells. The nucleus consists of round or polyhedral epithelial cells, and the concentric fibrous layers are a *stroma*, that is, a fibrous structure originating in the tissues into which the epithelial nucleus has intruded. Fig. 17 represents several of the "pearls" in situ and part of the adjacent epithelium. Fig. 14 shows a section of the epithelium where it is thickest. Very probably the tumour has originated by down-growths of epidermis. These down-growths have been pinched off, giving rise to the "pearls." This is what the structure strongly suggests, but there is no indication anywhere of the actual connection of the "pearls" with the overlying epidermis.

(?) *Thyroid carcinoma in Box vulgaris.* In a very fine work on fish carcinoma, Gaylard and Marsh describe tumours of the thyroid that (under the name of "throat disease") cause great losses of young Trout and Salmon in fish hatcheries in the United States of America. The disease has been observed elsewhere. It is endemic in some ponds and hatcheries, and it is conveyed by some agent in the water. It is characterised, at first, by simple hyperplasia—that is, numerical increase in the tissue elements (the thyroid gland acini) without any change in their physiological relationships or functions. Then there is great overgrowth of the thyroid, with departure from normal structure, the simple acini becoming converted into cords of glandular cells without normal lumina. There may be typical infiltration of this glandular tumour tissue into the adjacent tissues, with destruction of the latter. In two cases there were metastases (a thyroid tumour on the snout of one fish, and a similar growth on the anus of another). Thus we have what certainly appear to be carcinomatous tumours—malignant growths of glandular tissue elements. In all cases observed so far this carcinoma of the thyroid has occurred among fresh-water fish and such as are either domesticated or artificially reared, or with a history that suggests domestication in the parents. In the case here recorded, a *Box vulgaris* obtained by a collector of the Marine Biological Association, the fish was a typically wild marine one. The affection was a huge overgrowth of the thyroid, probably accompanied by infiltrative growth (I was unwilling to destroy an unique specimen by dissection), but yet a profound hyperplasia rather than a typical carcinoma. A section of part of the growth is represented in Fig. 12.

(?) *Cutaneous papillomas.* Three cases of cutaneous papillomas are recorded here—an Halibut, Turbot and Haddock. These growths are of the nature of skin warts, that is, irregular outgrowths of epidermis having abundant cores of connective tissue. In the Halibut the growth was about the size of a man's closed fist, and was situated on the snout. The Turbot had little slightly raised pigmented spots about 1 cm. in diameter. The entire skin of the Haddock was covered by similar warty growths—a most noticeable thing. Now in none of these cases could the covering of epidermis be recognised, and the substance of the papillomata consisted entirely of the connective tissue cores. But the epidermis of a fish may be remarkably thin and easily abraded by rough handling—especially on raised parts where there is deficient nutrition. So I think that these cases were really cutaneous warts or papillomas, though a perfectly satisfactory demonstration cannot be given.

With these five exceptions all the tumours in the list on pp. 447–8 are sarcomas.

SARCOMATOUS TUMOURS.

A sarcoma is usually a rather richly cellular tumour. The cells are of the vegetative type, and are relatively undifferentiated. They have extraordinary powers of proliferation. Typically they form interstitial cell substance, which can usually be seen in such tumours by careful staining (as by Mallory's combination).

Six tumours in the list on pp. 447–8 are called "fibromas," suggesting that fibrous tissue elements, rather than "cells," are characteristic of their histology. But we remember that all fibrous elements are really nucleated cells, and that the "fibre" is to be regarded as drawn out cytoplasmic substance, or, in some cases, perhaps, "interstitial" cell substance. Further, no fish tumour seen so far is entirely homogeneous, and while some regions may present the appearance of almost purely fibrous structure—that is, relatively few nuclei, each being surrounded with a minimal quantity of "cell-body," but with long fibrous extensions of the latter—other regions may contain spindle-shaped, or even rounded cells in fair abundance. Between the type of structure called fibromatous and the typically cellular sarcomatous type there may be insensible transitions even in the same tumour. With the five exceptions dealt with above I therefore regard all the tumours described here as sarcomas. They are essentially connective tissue neoplasms. They are "hylomas," that is, vascular pulp, or mesenchymatous formations rather than epithelial ones—the epithelial tissue, it ought to be remembered, being possibly that of epidermis, peritoneum, alimentary canal or gland.

There are varieties of sarcoma which may now be mentioned—noting that we are dealing with fish tumours. (Though all the kinds of structure represented in Figs. 11 to 22 can easily be seen in the illustrations of any good book dealing with the morbid histology of the mammal.)

Lymphosarcoma (Fig. 22). The case described is that of a Flounder showing startling exophthalmos. On dissecting the orbit it was seen that there was a large tumour of the choroid coat of the eye forcing the bulbus oculi out from the orbit, and destroying both retina and sclerotic. Obviously we have here the structure characteristic of a lymph gland: a reticulum of fibrous tissue, the meshes of which are filled with small spherical cells (of about $2\,\mu$ in diameter). This tumour occurred in just such a situation as to suggest that it had originated as a cell embolism. The efferent vessel proceeding from the pseudobranch (the ophthalmic artery) breaks up into capillaries in the choroid gland of the eye, so that cells carried in its blood stream may become arrested in the latter organ. But no traces of a tumour could be found elsewhere in the body of this fish, so that the neoplasm in the eye was probably a primary one and not a metastasis.

Myxofibroma. Like the lymphosarcoma referred to above, this is an exceptional condition. Myxofibroma is a soft "polypoid" tumour substance containing fibrous or stellate cells separated by a mucoid interstitial cell-substance with numerous capillary vessels. The case described here is that of a Ray, in which the mucous canals on the head were enormously enlarged and, here and there, expanded into cysts filled with mucus. The pores were occluded. In the cysts were polypoid bodies attached by stalks to the cyst walls. These bodies had the myxofibromatous structure described above, though it was not quite typical.

Angiosarcoma (Fig. 9). A true angioma is a tumour resulting from the proliferation of either blood- or lymph-vessels. Thus one case referred to in the list—that of a Stickleback—is probably a typical angioma. Little knots of capillaries formed "hæmorhoidal" warts, pendulous on the cornea of the eye and proceeding, of course, from the choroid layer. Two other cases of blood tumours are also recorded. One of these was a growth about as big as a hen's egg on the trunk region of a Mackerel, and the other was a large tumour in the body cavity of a Cod. The skipper of the trawler that sent me this specimen wrote about its markedly *hard* nature, but he was disappointed to find that the growth became much softer after the fish had been kept on ice before dispatch. This observation was very puzzling until, on dissection, the tumour was seen to proceed from the rete mirabile of the swim-bladder and to resemble erectile tissue in its nature.

In these two cases (the Mackerel and Cod) what immediately arrested attention was the richly vascular nature of the tumours. A typical human sarcoma is usually more vascular than a carcinoma and the vessels are thin-walled. But in the *typical* fish sarcomas described here the *bloodlessness* is a feature. It does not appear that in the growth of a "cancer" either blood-vessels or nerves are formed, and when these structures are present they probably belong to the tissues into which the carcinomatous or sarcomatous cells have infiltrated. Now in the two angiosarcomas to which I refer *the* striking feature is just the rich plexus of large and small blood-vessels. Fig. 9 has been drawn from a field that was chosen to show the *margin* of the tumour, so that the blood-vessels are not nearly so numerous as they are in the central part of the growth. Yet there is no doubt that the connective tissue elements—that is, the typically sarcomatous ones—are also highly characteristic. We have here, therefore, a very richly vascular sarcoma. Why, in these examples, a proliferation of the vascular elements should have accompanied a proliferation of the typical connective tissue ones cannot yet be explained.

Melanotic Sarcoma (Fig. 6). Sarcomatous tumours pigmented with the black substance called "melanin" are among the most malignant and rapidly growing of human "cancers." It is of interest, then, to find that such growths occur, in absolutely typical form, among marine fishes, and no fewer than seven cases in the forty quoted are of this nature. Fig. 6 shows a small nodule of actively proliferating melanoma in a Halibut, and it has been chosen to represent the first stage in the development of such a tumour. In the fully developed growths the tissue is coal-black, and the loading of the neoplastic tissues with the melanin granules is so dense that hardly any structural details can be made out. In the first stages the colour may be pink, rapidly passing into dead black.

And just as such melanomas are among the most deadly of human "cancers," so it is, in regard to them in the Skate and Halibut, that the most typical generalisation of the affection has been observed. In one of the Skates seen, and in a Halibut as well, the whole flesh of the fish was full of small and large sarcomatous nodules. (Later on I refer more particularly to the histology of these tumours.)

The forms of typical Sarcoma in Fishes. Premising that a sarcoma is an unco-ordinated (and non-adaptive) overgrowth of connective tissue,* I now proceed to note the varieties of histological structure in such tumours as occur in fishes. The typical structure is probably that represented in Figs. 15 and 18. Generally we have "fibroblasts" developing a meshwork of fibres with, at the nodes, nuclei surrounded by a minimal quantity of cytoplasm of the typical nature. I am, however, unwilling to say much about this tissue, because it has not been well investigated in fishes, and the material I have handled has not been well fixed for fine histological study: also the fact that it is morbid tissue (or, at least, physiologically abnormal) makes one cautious. However, Figs. 15 and 18 represent fairly well the general appearance of most fish sarcomas that are not referred to with some qualifying prefix. In some cases the structure of the tumour is more typically fibroid, and then we may speak of it as a "fibroma," but usually parts of the growth have the characters referred to below.

Large Spindle-celled Sarcoma (Fig. 19). This form of tissue was observed

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* The fibrosis, or overgrowth, of connective tissue round an encysted Tapeworm larva in, say, a Halibut, is an adaptation, or protective device.

in one case, that of a Ray that had a coal-black tumour on the head, near one of the eyes. The growth was very soft, and was fixed, hardened and sectioned with some difficulty. When the sections were examined it was extraordinarily hard to make out the histological structure, for not only were the cells loaded with melanin, but large granules of the pigment were crowded into the intercellular spaces. It was found possible, however, to decolourise the tissue by prolonged treatment of the sections with strong hydrogen peroxide, and Fig. 19 has been drawn from such a preparation. The cells are large (about 60 μ in length), irregularly spindle-shaped and often tapering off into fibres that seem to be continuous with a general stroma. The cell substance was loose and fragmented, and took any stains that were tried badly. The nuclei were faint and also stained badly. The cells tended, in many places, to be arranged in rows, lying side by side.

Small Spindle-celled Sarcoma (Fig. 16). The large spindle cells referred to above were only seen in the one case, but the small spindle cells represented in Fig. 16 are rather characteristic of various tumours. The case figured (that of a Halibut) was slightly melanotic, but fields could be chosen for study where the pigment did not obscure the forms and arrangements of the tissue elements. The latter, then, are spindle cells about 20 μ in length, obviously passing, at their ends, into fibrous structures. No tumour seen was wholly composed of such cells, but here and there they were characteristic of the histology. In some places the tissue elements were those called " oat-shaped " cells in the books on morbid anatomy, and always there was, in places, a considerable admixture of the fibroid structures represented in Figs. 15 and 18.

Small round-celled Sarcoma (Fig. 21). This structure is quite distinct from that illustrated by Fig. 22, where we have also a complex of small round cells. The latter are, however, of the type of " lymphocytes " ; they are markedly smaller than the cells of a simple round-celled sarcoma, and their arrangement suggests that of a lymph gland. In Fig. 21 we have a very frequent kind of sarcomatous structure : small-rounded cells about 10 μ in diameter, many of them being really the nodes in a fibrous meshwork, while others appear to lie freely in an obscure intercellular substance.

Large round-celled Sarcoma (Fig. 23). The type of structure represented here is quite exceptional. It occurred in a large tumour occupying the whole of the body cavity of a Herring (so that the fish was opened under the impression that it was a ripe female). The tumour was about 8 cm. in length and about 2 cm. in diameter. It included one testis, but the other could not be recognised. The type of structure was that of an angiosarcoma, that is, there were numerous blood-spaces and vessels, and between these lay the morbid proliferating cells. The latter were mostly about 20 μ in diameter; rounded or polyhedral, because of mutual pressure and of the type of undifferentiated epithelial cells. Their arrangement in the proximity of a blood-vessel is interesting, for they there display a marked tendency to a spindle shape, the long axes of the spindles being normal to the circumference of the blood-vessel.

Such are the common kinds of tissues that make up the fish tumours observed. As a rule, however, what the pathologists call the "mixed-cell" type is usually encountered, and the same growth may have different characters according to its degree of development.

NATURE OF MALIGNANT GROWTHS IN FISHES.

Obviously, then, we have to deal with connective-tissue tumours, or sarcomas. The two doubtful exceptions noted above hardly invalidate this conclusion, because the evidence that the growth on the jaw of a Whiting described in Figs. 14, 17 and 20 is not complete, while it would be rather straining the meaning of the facts to call the thyroid tumour represented in Fig. 12 a carcinoma. The only description of a sarcomatous tumour as occurring in a marine fish which I have encountered in the literature is that of a growth in a fifteen-spined Stickleback (see the First Report of the Imperial Cancer Institute). Apparently, then, the sarcomatous type of growth is that characteristic of malignant tumours in marine fishes.

THE MODE OF EXTENSION OF FISH TUMOURS.

The majority of the tumours described here occur in the "flesh" just underneath the skin, so that they form obvious swellings. If sections are made at the edge of the swelling it is usually possible to discover the growing, or proliferating, margin of the tumour, and so to study its mode of extension. Figs. 1, 4 and 5 represent such sections taken across the growing margin of a tumour, so that on the one side we have nearly normal tissue and on the other tissue that is in process of active proliferation.

Fig. 1 shows the growing margin of a sarcoma that was situated nearly in the middle of the coloured side of a large Turbot. In Fig. 2 the normal skin situated a few cm. away from the edge of the tumour is shown in section, the plane of the latter being nearly transverse to the long axis of the body of the fish. The parts seen are (1) the epidermis, consisting of polyhedral cells; (2) a pigmented layer; (3) a layer of "areolar" tissue containing some coarse fibres; (4) various layers of coarse fibres running in various directions ; (5) another layer of areolar tissue, and, lastly, the underlying systemic muscles. These layers are also shown, in less magnification, in Fig. 1, where it will be seen that the septa that cross the body of the fish obliquely, and provide the attachments for the "flakes" of muscles, are continuous with this sub-epidermal layer of coarse, white, connective fibres. Fig. 2 just indicates, by the stippling between the bundles of fibres, that there is another kind of tissue there : this is what we may loosely call areolar tissue, that is, it resembles the layer just below the epidermis, consisting of an open meshwork of fine fibres with small nuclei at the nodes, small "fibroblasts" and some interstitial ground substance. The coarse, white connective tissue is already specialised, is not "vegetative," and probably never takes any part in the growth of a sarcomatous tumour : it is the loosely, irregularly arranged "areolar" tissue between the fibrous bundles, or just beneath the epidermis, that undergoes active proliferation.

In Fig. 1 the abnormal tissue is represented in dead black. On the left is a region of normal skin. Below are the bundles of muscle fibres (represented by coarse stippling) separated by the connective tissue septa. Now, just at the margin of the swelling the coarse, white connective tissue fibres of the dermis are seen to fray out, so to speak, and finally disappear altogether. This is the result of the active proliferation of the minimal quantity of areolar tissue that lies between the bundles. Thus the latter are forced apart by the growth of substance in between them, are starved and finally degenerate. In the fully developed tumour tissue at a little distance to the right of the field shown in Fig. 1, the coarse fibres, and even the epidermis, would have disappeared completely. The only tissues would be those of the tumour, either bare or covered by a kind of "limiting membrane," which is not typical epidermis.

The margin, or region, of greatest proliferation is represented in Fig. 3. The lower coarsely stippled layer is that of the systemic muscles. The finely stippled region is that of the sarcoma, and this is seen to insinuate itself between the coarse connective tissue fibres and also to grow down in between the muscle fibres as little finger-shaped processes (also seen in Fig. 1).

Figs. 4 and 5 show essentially the same conditions in a Cat-fish (4) and Skate (5). In (4) the epidermis thins out and disappears, and this is also the case with the dermal fibrous layer. In (5) the tumour is situated to the right hand : in this case it had ulcerated and left an excavated sore. The large spaces are probably lymph channels, and there is also shown part of a scute. The epidermis, it will be seen, thins out and disappears, and the tumour tissue is shown infiltrating and destroying the coarse, white connective tissue layer.

Two other kinds of marginal regions are represented by Figs. 6, 7 and 9. Fig. 7 shows (under fairly high magnification) the boundary of a melanotic, sarcomatous nodule in the flesh of a Halibut : this was not visible on the surface, and was seen when the flesh was cut into. Now, the naked-eye appearance here was that of a very sharply circumscribed tumour which was apparently encapsulated : on the other hand, there were very many large and small sarcomatous nodules in the flesh of the fish, so that generalisation (whether by metastases, or otherwise) had occurred, and there seemed to be no doubt as to the malignancy of the growths. And so we see from Fig. 7 that there really was no capsule round the nodule. The tissue normal to the field consists of muscle fibres cut longitudinally, and several such are shown in the figure, some obviously undergoing degeneration. Above and below and between the fibres is the sarcomatous tissue—fibrous, but including many nuclei and some small round cells, and this is seen to be infiltrating the muscular tissue. Above is represented the fully developed sarcoma—here laden with black pigment, both in the cell bodies and between them. The capsulation is apparent only, and a typical process of infiltration is seen when the boundary of the tumour is studied under high magnification.

Fig. 9 represents the superficial part of the angiosarcoma found in a Mackerel, the field chosen being one where the tumour is thoroughly established. The epidermis has quite disappeared, the tumour being bounded by a finely fibrous layer. The pigment layer of the skin is visible, and below it is the usual fibrous layer which is being infiltrated by the abnormal tissue (shown by the fine stippling). Traces of the coarse fibres, and also some degenerating muscle fibres, are shown. The areas represented in black are sections of large and small blood-vessels.

The mode of infiltration may be examined in greater detail. Fig. 6 represents a small sarcomatous nodule (about 1 cm. in diameter) found in the Halibut mentioned above, and this was a very convenient tissue to study, because it was loaded with melanin, and so its extension was easily observable. On the upper surface (for the tumour was not visible in the intact fish) is the skin with all the normal structure. Below the skin are the systemic muscles (the sections of the fibres being shown in black). The smaller bundles are shown, and also one of the transverse body septa. The diameters of the muscle fibres are smaller just beneath the skin than they are deeper down. The densely stippled region represents the sarcoma, and the cell-like spaces were the *loci* of muscle fibres. In many of these spaces degenerating muscle fibres are still present, but others are quite empty. Between the muscle fibres, therefore, active infiltration of the sarcomatous tissue is proceeding.

Now we look at a normal part of the body where the muscles are cut transversely. This is represented in Fig. 8, the black polygonal areas being the cross sections of the fibres. A muscle septum runs obliquely across the field, and this is continuous with a very delicate reticulum, in the spaces of which the fibres are contained. In this field there were no traces of capillaries—fish flesh being relatively bloodless. There is, of course, no trace here of any abnormal tissue.

Compare such a normal part of the flesh of a fish with that represented in Fig. 10. The latter shows the conditions at the growing margin of a large sarcomatous tumour on the region of the body just behind the head in a full-grown Cat-fish (*Anarrichas lupus*). The growth was a fibrosarcoma, that is, the fibrous elements were much more prominent than were the typically cellular ones. The magnification in Fig. 10 is a little higher than that of Fig. 8, and so the muscle fibres are about the same in sectional area. Now two things are to be noted in the figure: (1) the extraordinary development of the interfibrillar connective tissue and (2) the condition that each fibre appears to lie in a space being apparently retracted away from the sheath in which it is seen to be placed in Fig. 8.

Figs. 11 and 13 show this change in the muscular tissue which proceeds upon the development of a sarcomatous tumour: these drawings represent parts of the growing margin of the angiosarcoma of a Mackerel. In Fig. 11 we have a field which is normal but for the presence of an unusually prominent capillary blood-vessel. Each muscle fibre (the stippled areas representing fibres cut slightly obliquely) lies in a sheath, and as the latter is apparently nearly always complete, no matter how the section is made, it must be made up of *sheets* of connective tissue. At the nodes of these sheaths are small nuclei, each surrounded by a minimal quantity of cytoplasmic material. Now if we were to suppose the muscle fibres completely to disappear and the connective tissue meshwork to remain intact the general form of the fish would still be retained: this may almost happen. Fig. 13 is a field from a section of the same material, only taken at the growing margin of the tumour (the fibres are cut rather more obliquely than in Fig. 11, and the magnification is a little higher). Some of the interfibrillar sheaths contain fibres, but most of them are empty, because of the degeneration of the muscle tissue. This appearance of muscle fibres lying in apparently large spaces is most characteristic of many fish sarcomas at their proliferating margins: it is shown in Fig. 6, and it would be seen very strikingly in Figs. 1 and 3 were the magnification high enough. It means that as the abnormal connective tissue grows the muscle fibres suffer in respect of their nutrition, dwindle away and finally disappear simultaneously with the development of the tumour tissue.

The proliferation of the interfibrillar tissue is also to be noted in Fig. 13.

Not only are there nodal cells in the meshwork (as in Fig. 11), but these cell nuclei have been dividing, and now there are numbers of small round cells in the space formerly occupied by the muscle fibres. Fig. 13 shows such small round cells apparently isolated from each other, but I have little doubt that a better preparation would have shown the cell bodies carrying fibrous prolongations and most of them structurally continuous with each other.

THE NATURE OF THE INFILTRATIVE PROCESS.

Further light on the precise nature of the process of infiltration of normal tissues by a fish sarcoma is only to be obtained by experimental work—particularly, it would appear, by the study of the physiology of trophic nerves going to the muscle fibres (if there are such ?), and also by tissue growth experiments. But it is difficult to resist interpreting the appearance presented by such sections as I have studied—in this way—the process of infiltration is not the extension, along certain paths, of the products of cell-division (as, for instance, we can imagine a bacterial culture to spread through the meshwork of an agar jelly). It is, rather, *the extension—along the connective tissue framework of the muscle—of the condition of malignancy.* This framework in a normal muscle (as in Fig. 8, for instance) consists of a minimal quantity of supporting tissue, and it is functionally balanced with the quantity of muscle tissue. But in the sarcomatous tumour the balance between the contractile and supporting tissues breaks down, perhaps because there is some general stimulus to proliferation to which the highly specialised muscle cells cannot respond while the relatively undifferentiated connective tissue ones do respond. So we find that in tumours of the nervous tissues it is not the neurones that proliferate, but the neuroglial supporting tissues, or it may be that something like Driesch's idea of the activities of a cell being dependent on its position with regard to other active cells may be in train—failure, in some way, of normal functioning of the muscle fibres may be the stimulus to proliferation of the connecting tissues. Something of this kind has, indeed, been suggested in the older speculations as to the causation of cancerous growths.

NECROSIS IN SARCOMATOUS TUMOURS.

Very commonly the surface of a fish sarcoma breaks through, ulcerates and gives rise to a repulsive sore. One attributes this breakdown of the growth to the rough handling of the fish during transport and capture, and, no doubt, injury is caused in this way. But there is also a process of necrosis going on from about the time when the tumour becomes an obvious growth. In the typical sarcomas described in this paper there are very few blood-vessels (and here we have a difference from the human condition where a sarcoma very often contains many thin-walled vessels). There are no nerves : at least no new ones. If we do find nerves at the growing margin of a tumour it is certain that these were present in the normal tissues into which the sarcoma has been infiltrating. There are no obvious lymphatic channels. What exists is simply the physiologically unbalanced product of proliferation of a tissue which is, elsewhere in the body, present in minimal quantity sufficient, and sufficient only, for the binding together of the other tissue-elements and organs.

The consequence is that the sarcomatous tissue is ultimately badly nourished ; there are, doubtless, excretory products which are not efficiently removed, and the cells begin to be acted upon by these toxic substances and by their own intracellular enzymes. Towards the centre of the tumour the substance becomes soft and then liquefies. Its growth still proceeds at the margins, and so a pressure is set up and the unbroken tumour becomes tense. In this state rough handling almost invariably breaks the stretched surface and a sore results, which then becomes septic.

During this process of necrotic change the minute structure of the tumour alters. In the case of the Cod mentioned in the list as having a large tumour on the body, this change was a very noticeable one. The growth was about the size of a man's closed fist and it felt liquid, yet tense. On cutting it open the contents ran out as a substance with the consistency of soft porridge. Round the margins the growth was firm, and there were solid cheesy lumps embedded in the semifluid central substance. At the margins, and in the cheesy masses, the tissue had the character of a " mixed-cell sarcoma," but the semifluid substance contained, for the most part, unrecognisable cell debris. When smears were made and stained this debris was seen to contain a great variety of cells—small round cells with large nuclei ; " polymorphic " cells ; cells with numbers of chromidial bodies, probably the result of nuclear fragmentation ; multinuclear cells ; cells containing inclusions of the nature of " Russell's bodies," etc. Fibrous elements are very scarce in such necrosed material, and this is, perhaps, a general feature of an old sarcoma : the original, normal *connecting* nature of the tissue becomes lost as the result of the cessation of functioning of the material. The cells assume very peculiar forms, which are, of course, quite aberrant, though they are doubtless responsible for many of the identifications of " cancer bodies " and parasites that have been made in the past.

In the melanotic tumours the necrosis and softening of the morbid substance proceeds even farther. Sarcomas of this kind occurring just below the skin, and so forming visible swellings, have always been broken and ulcerated. The substance remains soft, even on fixing in strong alcohol.

In the angiosarcomas the contents of the larger blood-spaces become greatly altered. The outlines of the corpuscles become obscure and finally disappear, though the nuclei may continue to stain in a typical way. Then even the nuclei disintegrate and disappear, and the blood becomes converted into a colloidal material taking extraordinary colours on staining with Mallory. The walls of the vessels break down and the colloidal contents appear to become organised, but this is due, I think, to the infiltration of the vessels by the intervascular, sarcomatous tissue. The process of thrombosis referred to above *may* be a post-mortem one, but it was too profound, I think, in some of the cases to have been established merely after the death of the fish, and it was, very probably, a process that had begun as a necrotic change during the life of the patient.

The Effect of the Tumours on the Fish.

In some cases the presence of a malignant tumour may go along with an apparently well-nourished fish, but this is unusual and indicates that the tumour is a young, rapidly growing one. Far more general is a condition of emaciation, often striking in the extreme. Thus a Ray suffering from a melanotic sarcoma on the head was so very thin and wasted that all the skeleton of the pectoral fins, even the cartilaginous radialia, could be most distinctly seen when the fish was alive. In this case the tumour was not a very large one, though it formed a deep excavation in the head, due to the ulceration of its substance. The brain, cartilage, stomach, alimentary canal and pancreas were nearly normal in appearance, and the muscles were much wasted, though not otherwise altered. The gills, spleen and liver were coal-black in colour. The liver was very soft, owing to the appearance of large lacunæ between the hepatic tubules. The cells were deeply laden with melanin, and coarse granules of this substance lay between them. On attempting to trace the structure of the liver from sections decolourised with hydrogen peroxide, no success was obtained, and the organ appeared to be in a state of considerable disintegration.

It is not possible yet to make a " clinical history " with regard to a sarcomatous fish. As a general rule the diseased fish comes to us from a market or from an official of the Ministry of Agriculture and Fisheries,* and it is not always even in a fit condition for exact histological study.

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* Here I may express indebtedness to many correspondents (market inspectors, collectors of fishery statistics, and naturalists) who have most kindly taken much trouble to forward interesting specimens.

In only two cases has an opportunity occurred for observation of a living fish bearing a sarcomatous growth. In one such case Dr. Orton, of the Marine Biological Association, obtained a large Turbot with a tumour near the dorsal fin. All possible care was taken to keep the fish alive in the Aquarium tanks, but it died, after a few days, and the result was due to the inevitable troubles of captivity in a tank in the case of such a large fish.

In the other case a small Goldfish, about 7 cm. in length, had a tumour about the size of a hazel-nut on the body near the root of the tail. The patient was kept in a small aquarium jar in the Laboratory; the water was changed frequently; the jar cleaned; the fish fed with "ant-eggs" and all reasonable care was taken to keep it alive. We had it for several months, during which time the tumour increased in mass perceptibly. The skin over it became tense and the scales dropped off, though their scars were still recognisable. There was, during the time that the fish was under observation, no evident change in its appearance, and it seemed to be plump and well-nourished. It was ultimately found dead (previously to which its movements in the jar had become more and more languid). It was at once preserved in 10 per cent formalin solution, and still appeared to be normal in its condition—apart from the presence of the tumour, of course. The parts of the body containing the sarcoma and the other regions were cut out and decalcified and dehydrated, and then the tissues collapsed in an amazing way, the body becoming almost ribbon-shaped. When sections were made it was seen that everywhere throughout the body the muscle fibres were degenerating. In the neighbourhood of the tumour they had disappeared and were being replaced by the usual sarcomatous tissue, but even at the other end of the body they were much smaller than normal, while the connective tissues round them had not increased. Even in this degenerate condition the cross-striation of the fibres was still very marked—more so, perhaps, than in the normal state.

We may conclude, then, that the presence of a sarcomatous tumour is detrimental, and that this is so because of the diffusion, through the blood and lymph channels of toxic products resulting from autolysis of the malignant tissue. This is, of course, the justification for condemnation of fish that exhibit abnormal growths: the flesh, in such cases, cannot be regarded as the normal food material that the buyer desires. As to the communication of disease to the person consuming such a diseased fish, there can be no possibility, so far as we know, but just as one rightly refuses to buy a fish that is stale because of incipient putrefaction, so we do not choose to buy a fish the flesh of which is wasting because of the presence of substances that prevent proper nutrition. Nor ought such a fish to be sold as an article of human food.

General Remarks.

First, as to the incidence of malignant disease among marine fishes : Unfortunately no generalisation can yet be made. Nevertheless, it has taken over ten years to collect the forty or so cases referred to in this paper, and the importance of noting the occurrence of "cancerous" growths in fishes has been in the minds of many observers who are highly skilled in respect of the characters of normality and abnormality in these animals. My colleagues and I must, for instance, have actually *handled* many thousands of Plaice, Herrings and Cod during these years, and it is quite certain that no fish displaying a visible swelling could have been overlooked. So also with other naturalists and inspectors, who must have seen very large numbers of fishes. The inspectors, in particular, have abundant opportunities of detecting unwholesome and diseased fish ; they are mostly aware of the importance, or at least the interest, of such conditions that are spoken of here, and it is their job to prevent unhealthy or stale fish from getting into the retail shops. Yet they have seen very few cases of malignant disease. Again, fairly large numbers of living fish are being watched in the various aquaria throughout this country, and the occurrence of animals exhibiting tumours would be sure to be noticed. On the whole we seem forced to the conclusion that malignant disease in marine fishes is very rare—far more rare than it is among men and women.

We ought, however, to note that "cancer" is a disease of mature, or old age. It is certain that the death-rate (or at least, the incidence) must continue to rise in civilised human populations, simply because the tendency of private and public medicine is ever to minimise the occurrence of, and the mortality from, preventable disease. Since we must all die there must be diseases that are not to be avoided or survived, and so the future of medicine must see the postponement of mortal illness until old age—an age, further, which will always tend to increase. As the theory and practice of medicine become more and more scientific and successful, so the incidence and death-rate of *most* affections must decrease, while the incidence and death-rate of a few such diseases as arterial sclerosis, cerebral hæmorrhage and (perhaps) "cancer" will continue to increase.

So as malignant disease may be characteristic of mature or old age we may not have the best of opportunities of observing it among marine fishes, for the most of those that are captured for the public markets are rather young animals. (Was it the case that among the very old Plaice that were taken when the Iceland and White Sea grounds were first exploited, there were many diseased individuals ? That has been asserted, and it would have been interesting if the occurrence of malignant tumours had been noticed.) It is significant that animals which are relatively short-lived (mice and even dogs) seem to be rather susceptible to cancer, while very few (if any) cases of true malignant tumours have been observed among reptiles, which probably live much longer than our experience of these animals in captivity suggests.

Here I must note the prevalence of "carcinoma of the thyroid" in domesticated Trout and other fresh-water fish in the American experience. But it cannot yet be taken as thoroughly established that this affection is quite similar to what we call carcinoma in the mammalian animal, or even that it is a quite typical form of malignant tumour. Many features suggest that the American "throat disease" ought, in the meantime, to be placed in a category by itself: it is endemic in certain cultural establishments; it is epidemic, and the causal agent is contained in the water supply; it can be favoured by some kinds of food and made to regress by other kinds; it can be arrested by adding such substances as contain mercury or arsenic or iodine to the water, and it displays a certain resemblance to epidemics of goitre that occur among the inhabitants of villages in Northern India. If we could find examples of the same kind of illness among truly wild marine fishes some kind of correlation might be set up between habits, food, etc., and the illness; but, so far, the only case of tumour of the thyroid recorded from a marine fish is that of the *Box vulgaris* mentioned above. And I hesitate to describe this as a case of malignant disease in the typical sense.

The causation of Piscine Sarcoma. The number of cases recorded is, of course, far too few to enable us to make any suggestion as to causation. Nevertheless, one cannot help remarking on certain negative results. Perhaps the most widely held opinion among physicians, at present, as to the cause of "cancer" is that the condition of malignancy is initiated because of chronic irritation of some kind or another. Thus there is work on gastric cancer said to be due to irritant parasites; the epithelioma that is said to be due to the use of clay pipes; malignant skin disease among workers in paraffin oil refineries; cancer of the rectum set up by chronic constipation, etc. Now there are beautiful examples of chronic irritation among marine fishes: the parasites *Lernea* (fixed in the ventral aorta) or *Lerneonema* (fixed in the eyes of Sprats); persistent tapeworms in Turbot and Cod; copepod parasites on the gills, in the nasal cavities and on the skin of many fishes, etc. Here we have what appear to be competent causes of malignant growth—if irritation is to be accepted as such a cause. Yet nothing suggests that a sarcoma originating in the skin of a fish has come about as the result of parasitic irritation and no tumour of the gills, or other region of the body specially prone to parasitic irritation, has been observed.

As to the ways in which a piscine sarcoma generalises nothing can be said. In man such a growth forms metastases, and the latter are initiated by fragments of the primary tumour that become detached and are then carried in the lymphatic and blood streams : so much seems to be quite certain. But in fishes we do not (so far) appear to find metastatic growths in the gills—where cell embolisms would be very prone to establishment. As to the possible spread along the lymph tracts I can say nothing, since these are so very imperfectly known in fishes that observations are difficult just yet.

As to the association of malignant disease with the food, habits, etc., of fishes nothing can be said. The data are far too few even for rough and tentative correlations.

SUMMARY.

1. About forty cases of malignant growths have been recorded from British marine fishes.

2. These tumours are nearly all sarcomata. One doubtful epithelioma and a doubtful carcinoma are mentioned.

3. The types of malignant tissue growth are entirely similar to those recorded from man and other mammals. Spindle-celled, oat-celled, round-celled, mixed-celled and fibrous sarcomas are described. Typical melanolic sarcomas are frequent in occurrence.

4. The tumours may generalise, but (apparently) not by the formation of typical metastases.

5. No species or even family of fishes seems to be exceptionally prone to malignant disease.

6. The sites of the tumours are (usually) the dermis and the intermuscular connective tissues.

7. Carcinomata are very rare, though at least one case is on record (but not in the present collection).

8. No suggestion is made as to causation, but it appears that chronic irritation as a competent cause of malignant growth is not probable in marine fishes.

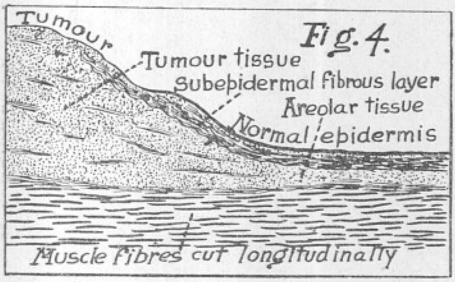
9. There is need of sustained investigation and record so that correlations may be made. As to causation there is need of experimental work.

PLATE I.

Figures 1–10.

1. The growing margin of a Sarcoma in a Turbot; the tumour tissue is black. Mag. 6 dia.
2. The same: the normal skin near the region of active cell proliferation. Mag. 45 dia.
3. The same: the marginal region. The tumour tissue is lightly stippled; the muscle fibres are coarsely stippled. Mag. 45 dia.
4. The growing margin of a Sarcoma in a Catfish; the tumour tissue is lightly stippled. Mag. 40 dia.
5. The growing margin in a Sarcoma from a Skate. The tumour tissue (on the right) is lightly stippled; the epidermis coarsely stippled; the tumour has ulcerated. Mag. 50 dia.
6. A small nodule of melanotic sarcoma in the muscles of a Halibut. Muscle fibres black; the tumour tissue stippled and shown growing in between the muscle fibres, which are degenerating. Mag. 25 dia.
7. Marginal region in a nodule of Sarcoma in the flesh of a Halibut. Muscle fibres striated; tumour tissue fibrous below and densely melanotic above. Mag. 100 dia.
8. Normal muscle tissue in a Turbot, the fibres being cut transversely. Mag. 50 dia.
9. Marginal region in an angiosarcoma from the Mackerel. Blood-vessels black; sarcomatous tissue stippled. Mag. 50 dia.
10. Region of active infiltration in a Sarcoma from the Catfish. Muscle fibres black; tumour tissue fibrous. Mag. 50 dia.

Fig. 4.



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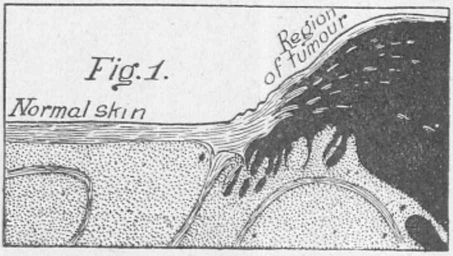

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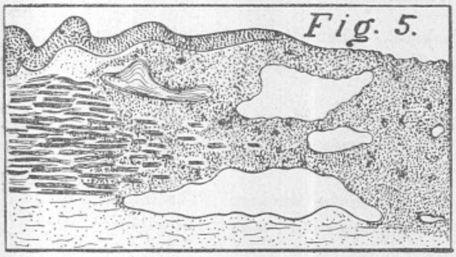
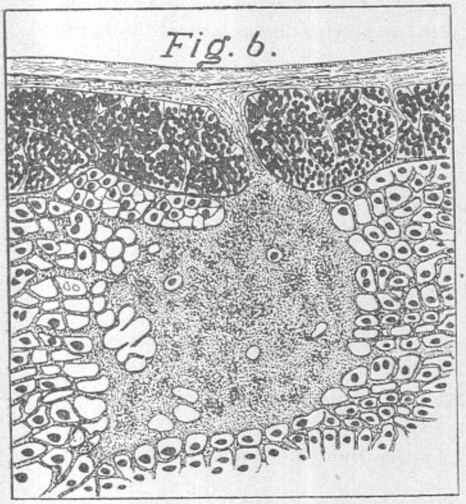


Fig. 2.

Fig. 3.

Fig. 6.



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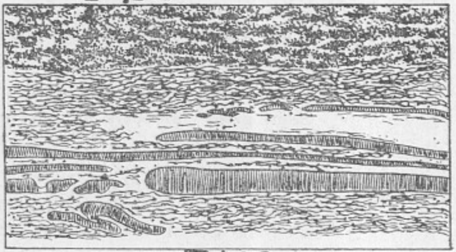

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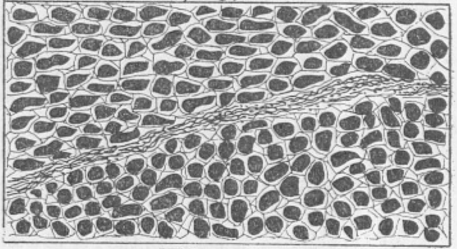

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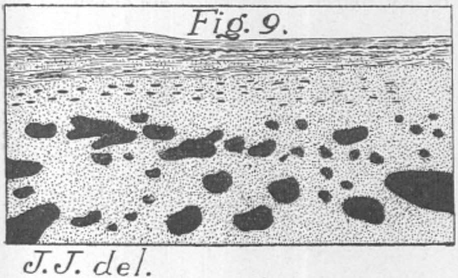

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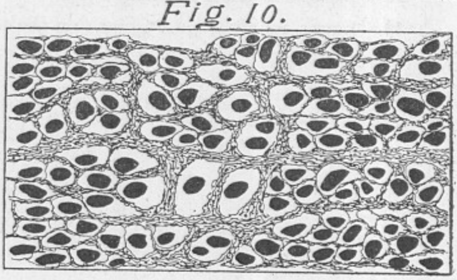


J.J. del.

Sarcomata in Fishes:
growing margins of the tumours.

PLATE II.

FIGURES 11–22.

11. Almost normal muscle tissue from a Mackerel. There is an unusually prominent capillary blood-vessel. The muscle fibres are cut rather obliquely and are stippled. Oil-immersion lens.

12. Tumour of the thyroid in a *Box vulgaris.* The figure shows sections of the gland acini. The other tissue resembles that occurring in inflammatory conditions. Mag. about 10 dia.

13. The region of active infiltration in a Sarcoma from the Mackerel. The interfibrillar connective tissue is proliferating, forming small round cells. The muscle fibres are degenerating. Oil-immersion lens.

14. pidermis (probably proliferating) from the skin of the lower jaw of a small Whiting. A sense organ is showing, also part of the underlying fibrous layer of the dermis. Oil-immersion lens.

15. Sarcomatous tissue from a Halibut. Fibrous tissue with rounded cells 5 μ in dia. Some giant cells. Oil-immersion lens.

16. Sarcomatous tissue from a Halibut. Small spindle cells about 20 μ in length.

17. Epithelioma from the lower jaw of a Whiting. "Epithelial pearls" shown in the tumour tissue beneath the epidermis (which is coarsely stippled). The black area is a section of one of the bones of the lower jaw. The epithelium faces the cavity of the mouth. Mag. 25 dia.

18. Ordinary sarcomatous tissue of the fibrous type. A small blood capillary is shown. Oil-immersion lens.

19. Melanotic Sarcoma from a Ray. The tissue was decolourised with hydrogen peroxide. Large spindle-cells about 60 μ in length.

20. Epithelioma from the lower jaw of a Whiting. Details of structure of one of the "epithelial pearls." Oil-immersion lens.

21. Small round-celled sarcomatous tissue from the Halibut. Round cells about 10 μ in dia.

22. Lymphosarcoma from the eye of a Flounder. Small lymphocytes about 2 μ in dia.

23. Large, round-celled Parcoma on the testis of a Herring. Cells about 2 μ in dia.

Fig. 11.

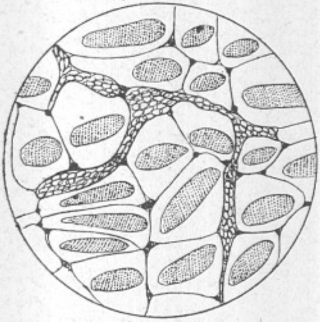
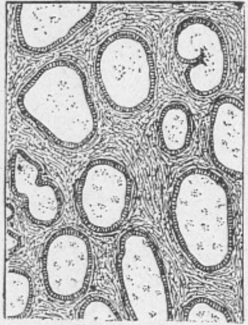


Fig 12



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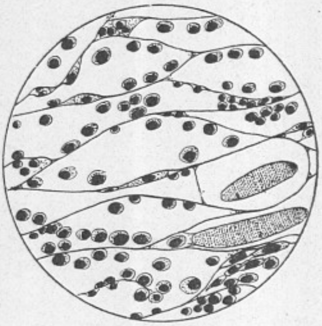
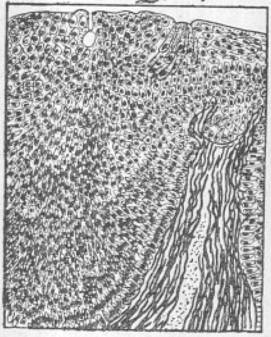


Fig. 14.



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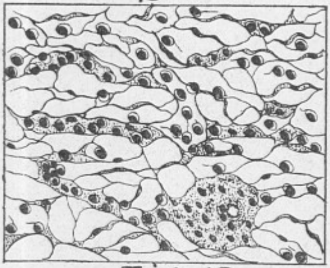

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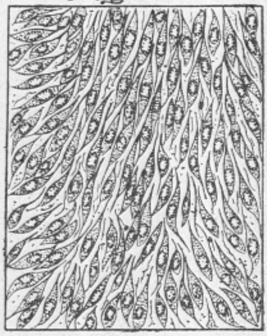

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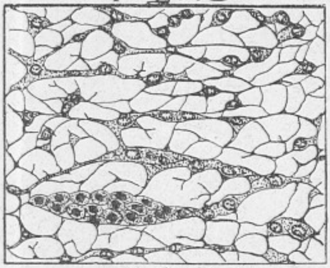

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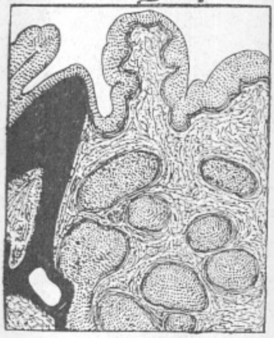

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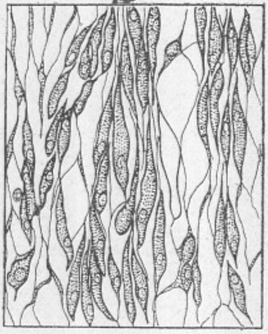

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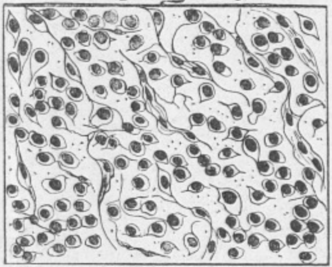


Fig. 20

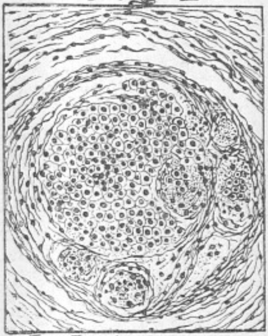
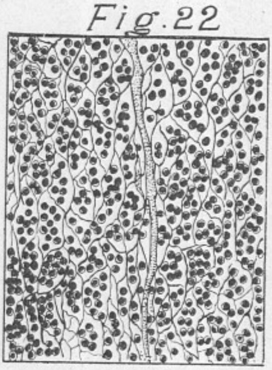


Fig. 22



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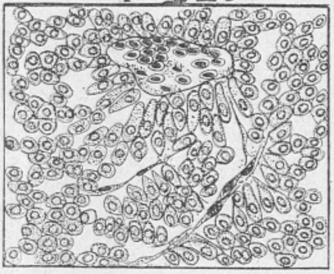

J. J. del.

Sarcomatous and other Tumours in Fishes: details of the tissues.

The Food of *Calanus finmarchicus* during 1923.

By

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With 1 Figure.

In view of the importance of *Calanus* as a food for fish, and especially for the Herring, its food and feeding habits have been kept under examination throughout the course of the year.

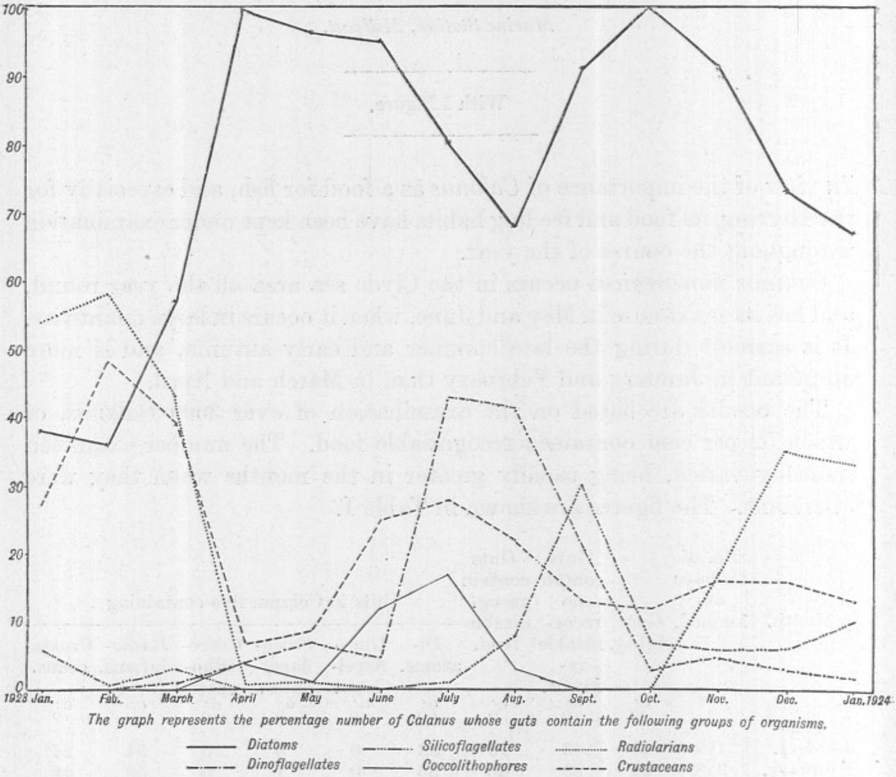
Calanus finmarchicus occurs in the Clyde sea area all the year round, and has its maximum in May and June, when it occurs in large quantities. It is scarcest during the late summer and early autumn, and is more abundant in January and February than in March and April.

The results are based on the examination of over 3000 *Calanus*, of which 52 per cent contained recognisable food. The number examined monthly varied, being usually greater in the months when they were abundant. The figures are shown in Table I.

Month.	No. of *Calanus* examined.	Guts empty.	Guts contain no recognizable remains.	Guts contain recognizable food.	Guts in Column five containing					
					Diatoms.	Dinoflagellates.	Silicoflagellates.	Coccolithophores.	Radiolarians.	Crustaceans.
		%	%	%	%	%	%	%	%	%
1923										
January.	179	38	43	19	38	0	6	0	54	27
February.	328	24	30	46	36	0	1	0	58	48
March.	135	27	15	58	57	1	3	0	43	39
April.	268	28	7	65	99	4	0	4	1	7
May.	256	27	7	66	96	7	0	1	1	9
June.	241	28	9	63	95	5	0	12	0	25
July.	141	21	13	66	80	43	1	17	0	28
August.	120	22	16	62	68	42	8	3	0	22
September.	130	21	10	69	91	21	30	0	0	13
October.	155	28	2	70	100	3	7	0	0	12
November.	257	31	19	50	91	5	6	0	17	16
December.	336	41	29	30	73	3	6	0	35	16
1924										
January.	188	31	36	33	67	2	10	0	33	13

Table I.—The last six columns show the percentage number of feeding Calanus (those in column five) whose guts contain specimens of the various groups.

The guts were, as a rule, examined fresh, for it was found much easier to identify the remains when fresh than when preserved. In cases where this could not be done the *Calanus* were preserved in weak formalin. It was found that after leaving them alive in the jar for several hours, all the guts were filled with copepod remains, and so the *Calanus* were all either preserved or examined within an hour or two of capture. Most of the food was in the form of fæcal pellets at the hind end of the gut, and it is most probable that this had been taken in before capture.



The graph represents the percentage number of Calanus whose guts contain the following groups of organisms.

FIG. 1.

The method adopted was to cut off the head of the *Calanus* about the level of the mouth, so as to free the front end of the gut, and then to draw out the latter with its contained food pellets, from the hinder end. The guts were then removed to a drop of clean sea water, the food pellets teased up, and examined with an oil-immersion.

A certain proportion of the guts, generally 20 to 30 per cent, was always empty, and a certain proportion always contained small quantities of unrecognisable brownish or greenish debris. The latter proportion varied very much, from between 30 to 40 per cent in winter to 2 per cent during the autumnal diatom maximum in October. The surprisingly small proportion of *Calanus* feeding in winter was later found to be due to the habits of the copepod. In winter they cease almost entirely to feed during the day and feed instead at night. From November onwards few of the *Calanus* contain any recognisable food until an hour or two after dark, and they stop feeding again whenever it becomes light. Even bright moonlight seems to have a deterrent effect. As spring comes on and the diatoms increase in number the proportion feeding by day grows larger, and in summer, records from the day and night differ little, although the percentage feeding is always higher in summer than in winter, even at night. The reason for this change of habit is not apparent. There are, as a rule, larger numbers of copepods, and crustacea generally, present at the surface during the day than during the night, and this holds good for summer as well as winter. The surface is probably richer in their food than the lower layers, but this does not explain the difference between summer and winter, nor the fact that moonlight seems to act in the same way as daylight.

The food consists mainly of diatoms, which confirms the previous work on the subject (Dakin, 1901; Esterly, 1916; Lebour, 1922). When diatoms are scarce other organisms are eaten instead. During the winter minimum a species of Radiolarian, *Acanthonia mülleri*, is common in the plankton, and this forms an important part of the diet, along with the winter diatoms, *Coscinodiscus* and *Biddulphia*. The winter 1923–4 was not so good for Radiolarians as the previous winter, and the proportion eaten was smaller.

As spring comes on, diatoms bulk more and more largely, and during the spring maximum in April almost every gut contains numbers of *Skeletonema* with *Thalassiosira* a close second. These two diatoms changed places in May, and in this month and in June *Thalassiosira* was eaten oftener than *Skeletonema*, this change corresponding with conditions in the tow-nets. Various species of Naviculids were common in April, May and June, and *Fragilaria* in long bands was common in the guts in the end of May and in June.

In July diatoms were still the most important food, but the species eaten this month was *Rhizosolenia fragillima*, a small form very abundant in the tow-nets for about three weeks. In August *Rhizosolenia* was still important, but (again corresponding with changes in the plankton) the species this month was *R. shrubsolei*, and *Chætoceros* was eaten more freely than *Rhizosolenia*.

A group which is of importance during the summer months is the

Peridiniales. Gymnodinians are probably eaten much more than the records show, since they will disintegrate very rapidly. The exploded nematocysts of *Polykrikos* were found in one gut in September, and in July and August a small yellowish Peridinian was common. *Peridinium* itself was most abundant in August and September, the species most commonly eaten being *P. pellucidum,* although it was often impossible to identify the species. *P. depressum* was the species commonest in the tow-nets, and had its maximum at the end of July and beginning of August. Considering the abundance of *Ceratium* in August one would have expected it to be used as much as *Peridinium*, but such is not the case. I did not find it in any gut, nor has it been recorded by other workers. *C. tripos* is recorded from the gut of *Centropages typicus* (Lebour, 1922). *Dinophysis* and *Phalacroma* also occurred occasionally. *Prorocentrum* was found by Esterly to be common, but was rare here.

In the latter half of September and the beginning of October occurred the autumnal maximum of diatoms, consisting like the spring maximum of *Skeletonema* and *Thalassiosira* and the *Calanus* guts were again full of these diatoms. The numbers eaten decreased after this, although *Thalassiosira* remained of importance throughout the winter. *Coscinodiscus* and *Biddulphia* appeared in the guts in November, as did *Acanthonia.*

The Silicoflagellates are eaten in small quantities, most frequently during the *Distephanus* maximum in September. *Dictyocha* is rare, and was found only once or twice, but *Distephanus* is occasional throughout the winter, and *Ebria* throughout the summer.

Pontosphæra huxleyi was eaten during the summer (April to August), but although it occurred in 17 per cent of the guts in July it was never present in large numbers, and cannot be looked on as an important constituent of the food. The same may be said of the Silicoflagellates. Esterly, however, found some guts of *Calanus* packed with coccoliths, probably those of *Pontosphæra huxleyi.*

A certain proportion of the *Calanus* are always to be found eating Crustacea. These are not often recognisable, sometimes only bristles or hairs being present, but other copepods were occasionally identified. Most were eaten in winter, and at their summer maximum.

Remains of other organisms, such as molluscan larvæ, cœlenterate nematocysts (possibly ingested on other Crustaceans), Tintinnoids (*Tintinnopsis ventricosa* and *Tintinnus subulatus*), bits of algæ and so on are occasionally found, but are of little importance.

In addition to the recognisable fragments, usually the indigestible chitinous or siliceous tests, there is always a mass of greenish or brownish debris. Part of this must be due to the contents of the diatoms or other food, but part is possibly due to soft-bodied organisms which leave no recognisable remains.

The food in any one gut is generally mixed. Some individual records are given below to illustrate this :—

January. (1) Masses of *Coscinodiscus*, some *Biddulphia sinensis*, many Radiolarian spines and bits of copepod.

(2) Five Acanthometrid centres and spines, and copepod remains.

April. (3) Much *Skeletonema*, some *Thalassiosira* and a bit of *Coscinodiscus*.

(4) Much *Skeletonema*, a *Navicula*, a bit of *Biddulphia* and several *Ditylium brightwelli*.

June. (5) Several Naviculids, a *Synedra*, a *Peridinium pellucidum* and several *Pontosphæra huxleyi*.

July. (6) About fifty cells of *Rhizosolenia fragillima*.

(7) Masses of *R. fragillima*, a little *Chætoceros*, several *Navicula* and bits of other diatoms, a *Tintinnus* case, a *Pontosphæra huxleyi*, numerous Gymnodinians and crustacean remains.

August. (8) Masses of *Chætoceros* and a *Distephanus*.

(9) Remains of at least nine *Peridinium* (mostly *P. depressum*) and two *Gymnodinium*.

September. (10) Bits of *Chætoceros, Skeletonema, Coscinodiscus, Rhizosolenia*, Naviculids, a *Tintinnus subulatus*, a *Peridinium*, and eight nematocysts of *Polykrikos*.

(11) A little *Skeletonema*, a good deal of *Thalassiosira*, a *Distephanus* and an *Ebria*.

November. (12) Enormous quantities of *Thalassiosira*, bits of *Coscinodiscus*, a large Naviculid and a *Dinophysis*.

December. (13) An *Acanthonia*, some *Coscinodiscus* and *Biddulphia*.

The last two records were from night tow-nettings.

Table I shows the number of copepods examined, and the number feeding. The other columns show the percentage of feeding *Calanus* whose guts contained specimens of the various groups of organisms. Fig. 1 expresses the same results graphically. It will be seen that the highest point on each curve corresponds to the time when the group was at its maximum.

The contents of the gut of *Calanus* are thus seen to reflect fairly accurately the progressive changes in the microplankton. Diatoms are undoubtedly the most important constituent, at least of those recognisable. In view of Pütter's calculations, estimating that to satisfy its food requirements a *Calanus* would need to take in daily an amount corresponding to 15,800 *Coscinodiscus*, or 9,750,000 *Thalassiosira nana*, it has sometimes been supposed that the greater part of the energy was derived from naked flagellates, ciliates, etc., which were quickly absorbed, leaving no trace. My material was examined fresh, and although there were, especially in summer, a certain number of flagellates recognisable, yet the number was not so great as to suggest that they formed the most important part of the food supply. It is not known how long the process of digestion takes in copepods, but the numbers of diatoms counted in any one gut are very far below Pütter's figures. It is difficult to estimate the number exactly, but in the case of *Rhizosolenia fragillima* the number is often over sixty, and in the case of *Skeletonema* it is very much higher. The larger diatoms, *Coscinodiscus*, *Biddulphia* and larger species of *Rhizosolenia* are always broken, but the number is much lower.

No particular preference is shown for any one type of diatom. The small round forms, *Skeletonema*, *Thalassiosira* and small *Coscinodiscus*, are certainly by far the most abundant, but this is probably due to their abundance in the plankton. Organisms with long spines (e.g. *Chætoceros*, *Acanthonia*), such as might have been supposed to afford them some protection, are eaten quite freely. When an *Acanthonia* is found in the gut the spines are usually broken off short, and the solid central portion remains compact, with the broken bases sticking out round it.

A few observations were made on some of the other copepods, *Pseudocalanus elongatus*, *Temora longicornis*, *Acartia clausi*, *Centropages hamatus* and *Anomalocera patersoni*. Conditions here were much the same as in *Calanus*. Diatoms formed the chief part of the food in most cases, although *Temora*, *Centropages* and *Anomalocera*, as Lebour found at Plymouth, are crustacean feeders to a greater extent than the others. *Temora* appears to be the most voracious. Its gut is practically always full and it eats a large variety of organisms.

Undoubtedly the most important diatom in the Clyde sea area, as regards food, is *Skeletonema costatum*. In spring, and again in autumn, it occurred in enormous quantities, and every crustacean gut examined, from Mysids and Euphausids to copepods, contained it, often in large numbers. It was also eaten by planktonic larvæ, Polychætes, *Mitraria*, *Cyphonautes*, by Appendicularians (*Fritillaria furca* and *Oikopleura dioica*) and by Ciliates and Gymnodinians.

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Notes on *Haliotis tuberculata.* I.

By

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CONTENTS.

I. INTRODUCTION.

Haliotis tuberculata, the "ormer" (from *oreille de mer*) of the Channel Islands, is, as is well known, used as an article of food, both in those islands and elsewhere. Of recent years a marked decrease in its numbers has been observed in Guernsey, and in order to devise suitable legislation for checking this decrease, the States of Guernsey undertook to finance a short investigation of the mollusc during the summer of 1923. I undertook this investigation, and spent three months in Guernsey in connection with it. I must here record thanks not only to many helpers in Guernsey, and to the States of Guernsey for the facilities placed at my disposal, but also to Prof. Watson for the loan of apparatus, and to Dr. Orton and Prof. Fleure for advice. In addition I wish to acknowledge help in the actual work given by my wife, which made it possible to get through far more in the time.

It was impossible, of course, to make more than an outline-investigation in so short a time, but we aimed at clearing the ground. If the investigation should be continued later, the notes offered here could be largely extended; and we hope ourselves to add to them later, especially by working out the life-history of *Haliotis* in detail, for which purpose material has been preserved. But as further work must be postponed for the time being, the present paper aims at adding something to our general knowledge of the bionomics of an interesting species.

In addition to the shortness of the time, we were necessarily somewhat incompletely equipped, since *Haliotis* is an animal which cannot be kept in captivity save under conditions available only at a biological station.

There seems to be no doubt about the actual diminution of *Haliotis* in Guernsey (although it is not by any means dying out yet), and the diminution seems to have been quite marked. Estimates of the period which it has covered, however, vary from ten to about thirty-five years, the mean estimate being over twenty years. M. Joubin, of the Museum d'Histoire Naturelle, who has studied *Haliotis* in France, tells me he has heard of no such diminution in Brittany.

II. BREEDING-TIME AND AGE, ETC.

Sizes of the Young Ones. *Patella* and *Crepidula* can attain a length of 2 cm. in a year, and in special circumstances much more (Orton). If *Haliotis* were a winter breeder, one would expect specimens a few *millimetres* long to occur during the summer, on the analogy of these other molluscs; if it were a summer breeder, the next summer one might expect specimens 2–3 *centimetres* long. On our collecting expeditions we searched carefully for any very minute ormers; but although minute animals of other sorts were clearly visible, we never found an ormer smaller than 9 millimetres long, and this was exceptional. We measured nearly 100 young specimens, ranging from ·9 to 3·95 cm. in length. This in itself suggests that summer is the breeding time, and that these are mostly one-year-olds. The majority would be between 1·5 and 3·5 cm. and a good many under 3 cm. The few tow-nettings we were able to take did not help much in fixing on the breeding-time; at any rate, we obtained no young *Haliotis* we could certify as such, though a few of the veligers may have belonged to it.

Development of the Gonad. In determining the sex of young ormers, it was found that females are recognisable from a gonad sample at as small a size as 1·85 cm., the young eggs being very clear; the youngest male we were able to determine was 2·8 cm. long. Sometimes samples from a young specimen would be indecisive as to sex. It does not follow that a specimen, the sex of which can be determined by a sample, has a gonad sufficiently developed to be visible as a whole to the eye. In fact, the smallest female with a gonad visible as such was 2·55 cm. long; the smallest male with visible gonad being ca. 3·3 cm. long.

If the shell is removed from a young ormer, there is often no visible gonad at all; but a more or less distinct tinge of green or yellow on the conical cæcum* of the visceral hump, or at its base, or on the cæcum and neighbouring parts, often suggests the beginning of the gonad: this tinge is not invariably present. In sufficiently developed specimens

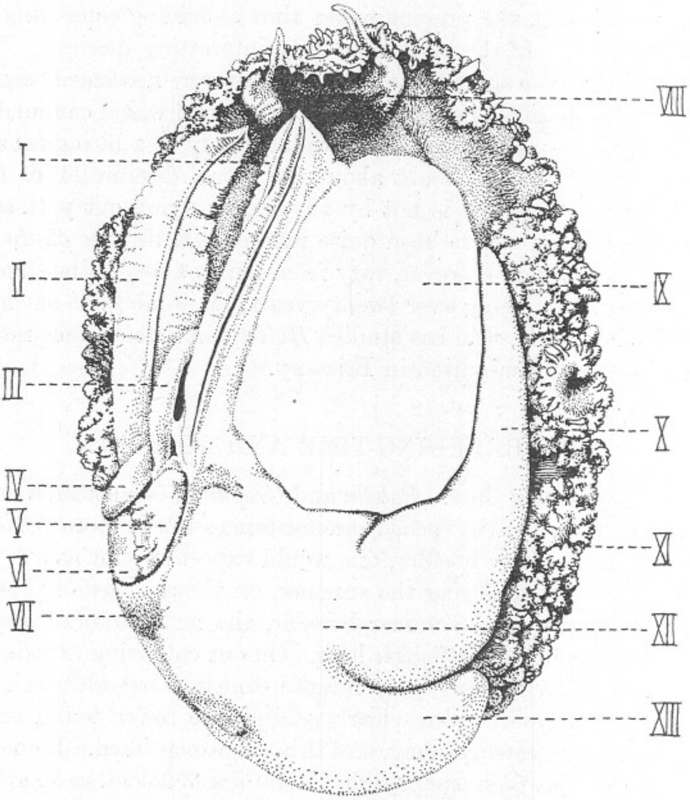

Fig. 1.—A preserved specimen of *Haliotis*, slightly dissected, to show general arrangement of parts. The roof of the branchial cavity has been removed, so as to expose the gills, rectum, and left kidney. The roof of the pericardium is also removed, and so are parts of the mantle.

I: Right gill. II: Left gill. III: Rectum. IV: Left kidney. V: Right auricle. VI: Left auricle (the two auricles cover and hide the ventricle in their present state of dilation). VII: A small portion of the liver, which is not covered up, as most of it is, by gonad. VIII: Head, with two pairs of tentacles, the eyes borne on the hinder pair. IX: Large shell-muscle. X: The conical cæcum of the visceral hump, containing a core of liver surrounded by gonad. XI: Epipodium. XII: Gonad (covering most of the surface of the visceral hump). XIII: The part of the visceral hump, which is lodged in the spiral tip of the shell.

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* "Conical cæcum"—the conical extension of the visceral hump which stretches forward on the right-hand side of the large shell muscle (see Text Fig. 1). It contains a core of liver surrounded by a layer of gonad, in the adult.

the actual gonad is just visible as a thin creamy or greenish film, which may be uneven in thickness, and may cover about half the upper surface of the visceral hump, or more, and may be thickest on the conical cæcum; one specimen had a slight creamy film on the conical cæcum only.

It is difficult to estimate the time which these specimens with just-visible gonads would need for the ripening of their sex-products. A female 3·3 cm. long on June 16th had some of its eggs reaching small medium size and getting opaque; one, 3·95 cm. long, on July 1st had also some of them beginning to be opaque. But judging from older specimens, it would take individuals of this sort a good while to ripen; perhaps one could not expect it for another year, when they might be two years old. It is certain, however, that a female 5·55 cm. long can spawn, since we actually witnessed it (see below)—this at an estimated age of two or three years. A male can have active sperms at as small a length as 2·8 cm., when it is presumably about a year old; and could probably effect a fertilisation during its second summer of life, if not before, in some cases at any rate.

Summarising, one may say that in the female the sexual products may be clearly differentiated before the animal is 2 cm. long, and the gonad visible before it is 3 cm. long; and that it can spawn at 5·55 cm. It is probable that the gonad becomes visible during the second summer of life and that maturity is reached the third or fourth summer, i.e. at two or three years old. In the male the gonad may be differentiated before the animal is 3 cm. long, visible before it is 4 cm. long, and certainly ripe at 5·5 cm. (we saw one spawn at this length) if not before; and a male could perhaps spawn at a year, almost certainly at two or three. For comparison, *Patella* can breed as a male certainly at an age of a year, and as a female almost certainly, in many cases, at two years (Orton).

Progress of the Gonads. Gonads and gonad samples were examined at intervals during June and July, with a view to finding out when ripeness occurs. The following notes apply to "adult" specimens, i.e. specimens over 4 cm. long.

Females. None of the specimens examined in June seemed to be ripe or very near to ripeness. Eggs in several stages would be present in the samples: the eggs were inclined to be irregular in shape (and though some would be round and regular they were perhaps under size), the large ones especially tending to be crushed looking. Not many eggs would wash out in water, and samples would be murky and apt to contain a good deal of tissue. In July a fair number of specimens were judged to be approaching ripeness, though there would be others still far from ripe. There would be more free eggs in the samples, and less tissue, and in the best cases plenty of free eggs washing out easily, clean, round and regular in shape, and little tissue. The gonad of a fully ripe female exhibits a perfectly characteristic appearance with even, regular, loose eggs of uniform size. Artificial fertilisations were made (twenty-seven attempts) as a control, from the beginning of June onwards. In June no results were gained or expected ; the same is true of July, although there seemed more chance of results then ; but on August 1st a small proportion of embryos were obtained from the eggs of females sampled the day before ; on August 2nd a female laid eggs in formalin while being preserved ; and on August 3rd a male and female spawned of their own accord, in observation vessels. Notes of the actual extent of the gonads, made from June 18th onwards, show that in the great majority of cases the gonad spreads over three-quarters (or oftener more than three-quarters) of the area of the upper side of the visceral hump, at this time of year. Sections taken through the conical cæcum, at the same time, about half an inch from the tip, showed that the layer of gonad in that region was usually thick, so thick sometimes that the cæcum consisted of almost solid gonad. The gonad would often be extremely plump.

Males. In all males examined after June 18th, the gonad was similar in distribution to that of the female. The gonad would usually run milky when cut, though sometimes very slightly. In every living male examined during the summer *active* sperms were present.

Conclusion. These observations are not enough in themselves to fix the extent of the breeding-time in detail, and are of the kind which need confirmation by observations made at other times of year. But as far as they go, they suggest that the eggs are ripening gradually during June and July, and prove at any rate that the beginning of August falls within the breeding-time. Taken together with the sizes of the young specimens collected, they render it probable that *Haliotis* is a late-summer breeder ; and there is no indication so far of a second breeding period in early spring, such as would leave young specimens a few millimetres long behind it, during the summer. These conclusions are further strengthened by a later observation. Nine ormers sent by post from Guernsey were examined on December 13th, 1923. They varied in length from 4·1 to 5·2 cm. In these the gonads were in a reduced condition as compared with those examined in the summer, having become thin and patchy, and not even opaque save at certain spots in given cases ; sometimes barely visible at all. They seemed to be gonads which had died down after spawning.

Sex-change. We had not time to get any evidence as to whether sex-change occurs in *Haliotis*. No *very* young specimens were available. All that can be said is that young ones estimated as last year's spat are often females.

III. METHOD OF SPAWNING: FERTILISATION: DEVELOPMENT.

Method of Spawning. The actual process of spawning was witnessed in both a male and a female, during the evening of August 3. A male 5·5 cm. long, which was alone in a glass jar, began puffing out clouds of sperm through the holes in its shell. At about 7·15 p.m., while the male was still discharging, a female, 5·55 cm. long, alone in another glass jar, shot out a cloud of eggs from the holes in its shell; they quickly sank to the bottom, and made a pale green carpet there. The eggs are perfectly circular, pale green, each enclosed in a transparent shell. The gonads of these two ormers were examined afterwards; that of the female was yellowish, and looked speckled by reason of ripe eggs, with transparent patches where eggs had gone; the male gonad looked much as usual, but rather patchy, and ran very milky when cut. The age of these specimens, as far as the data we have will allow us to estimate, would be two or three years. On August 2nd a female laid eggs in formalin as she was pickled. We find it difficult to reconcile these details with the account given by Mr. Sinel (Guernsey *Star*, May 7th, 1923) of some data collected by a naturalist in Herm about 1890. According to this account a female ormer was obtained in the act of depositing the eggs, of which about 1000 were laid, and they were deposited in a thin gelatinous mass in May or early June. In the case we witnessed there was no question of any gelatinous mass. Our specimen probably laid something like 10,000 eggs at one puff, all free from one another. It is not impossible that in the case recorded by Mr. Sinel, the accidental proximity of an ormer and the egg-mass of another mollusc may have led to a mistake.

Fertilisation. In the case of the two individuals which spawned on August 3 some of the details of fertilisation were seen. Sperms were introduced into the vessels containing the eggs (some of which had been removed into finger-bowls from the original jar) at 7.35 p.m. In samples examined just afterwards many sperms could be seen with their heads up against the egg-shell, the long axis of the head being at right angles to the surface of the shell; they were quite motionless as far as one could see, but the tails were not visible. Sometimes a single sperm could be seen apparently penetrating the egg-shell, and sometimes a single sperm within the shell which seemed to be entering the egg. The birth of a polar body was witnessed in one case, and polar bodies were visible in other cases.

Development. To follow up the fertilisations made on August 3, from the spawning individuals, first—at fourteen to fifteen hours after the introduction of sperm, there were large numbers of active young ones, at an early trochophore stage with a clearly visible prototroch, some of them revolving in the egg-shell. We were unfortunately unable to make prolonged examinations of the young at any point, because they were developing just as we were obliged to make preparations for leaving the island; but a number were preserved, and we hope to work them out later. At forty-four to forty-six hours after introduction of sperm, a considerable number of larvæ had escaped from the egg-shell, and were swimming actively about at various levels in the water, other embryos being still within their shells at the bottom. The swimmers were plainly visible to the naked eye. These larvæ were much more advanced than at fourteen to fifteen hours, and from the condition of oval masses with a belt of comparatively short cilia, had changed to a stage with a body and a prototrochal crown separated from it by a constriction. The cilia of the crown were very numerous, long and powerful, and seemed to be held typically in such a way that some projected upwards and others curved down over the edge of the crown, which had a narrow transparent rim outlining its denser central portion. At sixty to sixty-two hours after introduction of sperm the larvæ seemed little different in general form from those at forty-four to forty-six hours, and further than this our observations could not be carried, as we were obliged to leave.

Apart from the larvæ just described, the first fertilisations which produced any result were made on July 31st, in the morning, from eggs and sperm extracted from living gonads. In the evening a few two-cell stages were seen. Samples examined during the next two days showed a certain number of segmentations, though the majority did not develop. Two- and four-cell stages were to be seen, as well as stages with a distinction of cells into macro- and micromeres, but nothing further; and even these embryos gave the impression that they were developing rather abnormally.

In the supposed case of *Haliotis* development mentioned above, and recorded by Mr. Sinel, hatching occurred in seven to twelve days, and the veligers began to swim then. L. Boutan (*Arch. de Zool.*, VII, 1899, p. 270) has given an illustrated account of the young stages of *Haliotis*, but has not been able to determine at what age the swimming larvæ begin to creep. The larvæ doubtless swim in the sea as they do in captivity. In confirmation of this there is a note of Mr. Sinel's, to the effect that he has found ormers in pools nearly at high-tide limit, on a reef near St. Heliers; a locality where larvæ might settle but which adults would be less likely to seek out. Dr. Orton has also found ormers in pools high up.

In our attempts at rearing *Haliotis* and certain other mollusc eggs which we got as far as veligers, we used the finger-bowl method and also a plunger jar. The sterilisation of vessels and instruments, and the filtering of the water, had to be less meticulous than we could have wished, because of the conditions under which we were working; but we gained the impression that apart from this, *Haliotis* larvæ may need a better water supply than these methods give, if they are to be reared all the way through.

IV. METHOD OF FEEDING.

Samples of stomach-contents from twenty-two living *Haliotis* gave a certain amount of information as to its food materials. The things most clearly recognisable were, a good many chips of coarse brown weeds, some of them of considerable size (e.g. 5·5 mm. long); remains of small crustacea; sand, sometimes a good deal of it; spicules and parts of spicules, including triradiates and presumably belonging, many of them, to sponges; diatoms; foraminifera; remains of polyzoa; and filaments of confervæ. A good deal of the refuse seemed to be of a vegetable nature, and much of it one could not identify.

Boutan (*Ann. des Sci. Nat., Zool.*, VI, 1923, p. 59, etc.), in speaking of *Haliotis*, states that it is herbivorous, and that if kept in glass aquaria with small green algæ lining the sides, it makes these its food, and browses with the radula in such a way as to leave sinuous tracks devoid of algæ on the glass.

We witnessed the feeding-process more than once. In one case a specimen fixed on to the vertical side of a glass jar began feeding at about 6 p.m., everything being clearly visible through the glass, by aid of a lens. The end of the snout was spread out either very close to or actually pressed against the glass, and was rounded in outline. On the opening of the slit-like mouth in the centre of this area, the end of the radula came out, with curled-in edges, licking the glass like a tongue. Bits of dirt and slime, stuck to the glass, were licked off and swallowed. The animal did not walk very straight up the vertical side of its jar, it would go from side to side or even turn round and go down again. A piece of *Fucus* held near the mouth was seized by wrapping the snout round it, and several pieces were bitten out of the edge of it. Carmine and plankton were placed just in front of the mouth, and portions of both were swallowed when they came within pull of the lips and tongue, but the animal did not seem to seek out the plankton provided, if anything the reverse, eating it only if it came his way.

A number of experiments were made in the hope of finding out whether *Haliotis* gains part of its food supply from plankton, after the manner of *Crepidula*.

If the shell be removed from a living *Haliotis*, and it be pinned out under water, it will often settle down quite well and expand, the heart beating actively and the tentacles waving. (It can live for months after shell removal, see p. 490). If carmine (or plankton) be then scattered on the gills, it passes off them by ciliary action, to a groove along the right side of the left gill, whence it follows a definite diagonal track* across the back of the head and into another groove formed by the right half of the epipodium. Ultimately it floats or falls off the edge of the epipodium quite close to the mouth. This experiment was repeated a good many times, and always the particles (apparently tangled in a cord of slime) followed the same route, sometimes moving steadily and rapidly. The direction they follow is the general direction of the row of holes in the shell. Sometimes odd particles will fall of their own weight into convenient crevices, but this track is the normal direction taken by the bulk of them. In no case did the animal make any attempt to eat the plankton thus provided, although it could have reached it. Sometimes it would get rather excited and feel about with snout and tentacles, or would simply jerk about, when the foreign matter reached the edge of the epipodium. Waste from the rectum was seen to follow the same path.

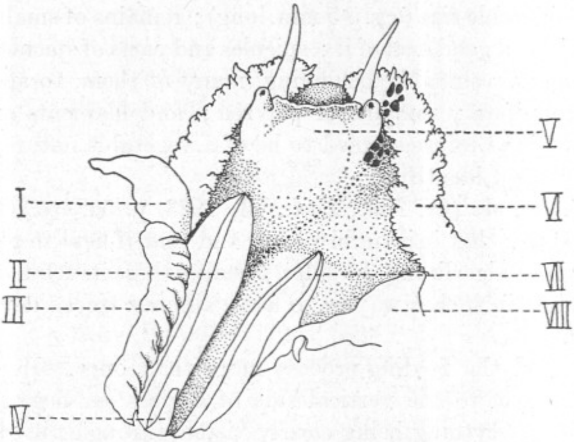

Fig. 2.—Diagram of the fore part of *Haliotis*, sketched from a living specimen after removal of shell. To show the direction of the track followed by particles of carmine, plankton, etc., when scattered on the gills. This track is dotted in heavily, and masses which have collected at its front end are shown on the right side of the head. I, VIII : Flaps of the mantle curled back. II : Left gill. III : Left mucous-gland curled back. IV : Rectum. V : Head. VI : Epipodium. VII : Right gill.

In other cases plankton or carmine were introduced into the branchial cavity of a *Haliotis* with the shell still on. In these cases the plankton would come out in a worm, fairly rapidly from under the edge of the shell ;

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* The direction of this track may be understood from Text Fig. 2.

but there was no attempt to eat it. Some of the looser particles would be puffed out, via the holes in the shell sometimes, before the main stream came out from under its edge.

Another experiment was made by leaving ormers in baskets sunk in the sea in a place inhabited by other ormers, but providing them with no food save what could be extracted from the water. After six weeks the baskets were recovered, and although they were tightly tied and all the lashings were intact, some of the ormers had escaped, despite the absence of any visible crevice or mesh of the baskets through which they could have done so. It was possible, however, to identify those remaining accurately, to the best of our belief; and not one showed any measurable increase in size whatever. Inside the baskets were trochi, young crabs, and in particular young scallops had settled there and had attained a length of about half an inch in the six weeks—so there must have been a supply of food in the water for animals which could use it. The *Haliotis* were quite healthy.

These experiments were unfortunately not conclusive. But at least they suggest that Haliotis does not use plankton much; so far as they go they give no sign of it. The ciliated track in branchial cavity can be understood in connection with the normal removal of the heavier part of the rectal waste, and perhaps also of sand which must sometimes intrude. It is at least definitely proved that *Haliotis* is a browser, can eat fairly coarse as well as fine materials, and is fairly omnivorous.

V. GENERAL NOTES.

During the summer about 250 living specimens passed through our hands altogether (estimated), and the sizes of those measured varied between 9 mm. and 12·3 cm. Of 127 examined for sex, 50 were males, 71 females and 6 (young ones) did not give decisive information, in the absence of sections. The male gonad is usually white or cream, greenish white or greenish cream, rarely pale yellow or salmon. The female gonad may be bright or dull green, various shades of grey-green, grey, fawn and brownish; it may be creamy when very young; in a specimen which had just spawned the spent gonad was yellowish. The sex of an ormer can usually be determined without making any incision or removing the shell, if the animal is not too small (but the observations above recorded are made after removal of shell and sampling the gonad). The underside of visceral hump and conical cæcum are visible at the back end of the animal, if foot and epipodium be turned down; the gonad colour is then usually perceptible through the skin at a given point on the inner side of the curve and close to the large shell-muscle, although partially masked by pigment in the covering skin.

Occurrence. *Haliotis tuberculata* occurs on the coast of France from Barfleur southward, as well as in the Channel Islands. We collected it in Herm and several parts of Guernsey and received specimens from Sark. In our experience it occurs chiefly beneath stones not embedded in sand, in clean places. It is found typically only in the Laminarian zone (and is only available in quantity at low spring tides), but occurs at higher levels in a certain number of pools and lagoons which never dry. The species tends to occur in colonies, and chooses its localities with some exactness ; for instance, one small shallow bay in an off-shore reef which we visited, was known locally as a special resort of young ormers ; and certainly we found more of them there than elsewhere. The depth-range of the species is uncertain ; according to M. Joubin it extends only " some few metres " below low water of spring tides. A diver working from St. Peter Port obtained two ormers from a rock at a depth of not more than about 35 feet of water at low water of springs. Probably the main home of the species is in fairly shallow water close to low-water mark of spring tides.

Habits. *Haliotis* is probably not a homing mollusc like *Patella.* It is difficult to watch a marked specimen, because the creature is so active. It walks very rapidly, surprisingly so—Sinel estimates the pace at not less than 5 or 6 yards a minute, and we have seen it go at a similar rate. It adheres very firmly to its stone (so that sometimes the shell will come off rather than the animal) ; but if one fails to remove it at the first pull, it does not necessarily adhere all the faster for an indefinite time, like a limpet ; often after a minute or two it runs away, if left alone. Again, when an ormer is removed from a stone, so far as we have seen it never leaves behind it a distinctly marked-off area as a limpet often does ; the surface from which it was detached is quite indistinguishable from the rest of the stone ; the ormer may have been covering anything, for instance an incrusting animal, and the foot may bring away some of the incrustation with it. Three ormers which had settled in our tank one evening were noticed and all had gone elsewhere by morning ; we believe this to be usual. These things are only hints, but do not suggest a homing habit.

When *Haliotis* is healthy the foot is very active, strong and mobile. If the animal is laid on its back it can, at best, pick itself up wonderfully quickly by attaching the tip of its tail and rearing itself up vertically thereon. The foot is pale yellowish or creamy on its underside, and very conspicuous ; but can fold up longitudinally, so that the upper side is exposed, and this is of dull greenish and greyish shades, dark and inconspicuous.

If the shell be removed from *Haliotis,* the animal remains quite lively and creeps about as usual. Boutan has kept *Haliotis* for months after shell removal (see *Ann. des Sci. Nat., Zool.,* VI, 1923, p. 59, etc., and *Comptes Rendus de l'Acad. des Sci.,* 127, 1898, p. 828), and finds that the shell is regenerated ; but the new shell is abnormal and falls off very easily, after which yet another will be secreted. Boutan has also succeeded in producing pearls in *Haliotis* by the introduction of foreign bodies in a suitable manner.

According to Sinel, *Haliotis* is nocturnal in habits.

Conditions demanded by Haliotis. It is evident from the works of Boutan that *Haliotis* can be kept for long periods in captivity, and will acclimatise themselves easily, provided they can be supplied with well-aerated water in sufficient quantity. But the grade of aeration required is high, and involves a supply of water under pressure from a reservoir. In Guernsey we were unable to obtain these conditions, and found it almost impossible to keep ormers in a tank or other vessel of still water, even by changing some or all of the water each day ; although the water was aerated also in some degree and was kept clean ; and we had to keep our stock of specimens floating in the sea in a basket, which keeps them lively, but is inconvenient. Sometimes specimens would live a few days in a tank, and a few small ones lived as long as a month ; but these were exceptions and usually one dare not leave them in a tank even overnight. Many animals could have been kept in health easily with the facilities at our disposal. An old experiment by Beudant (see Flattely and Walton, *The Biology of the Seashore,* p. 81), in 1816, showed that *Haliotis* will not stand lowering of the salinity of its water as well as some other animals. All this makes it clear that *Haliotis* demands high conditions ; and sometimes even if kept in a tank with new sea water flowing constantly through it, will not live long, to judge from Mr. Sinel's experience.

VI. *HALIOTIS* FROM AN ECONOMIC STANDPOINT.

It does not seem suitable to give an extensive account here, of the various possibilities which have to be considered in connection with the shortage of *Haliotis* in the Channel Islands, but a summary of the question may be of interest. A fuller report has been sent to Guernsey.

It was not possible within three months to follow up the various lines of inquiry laid before us, in much detail. We think it fair to say, however, that if legislation can check the disappearance of *Haliotis,* suitable regulations can probably be made on the basis of the knowledge now at our disposal. They could be modified as time goes on should further investigation make it needful.

In trying to find out the cause of the shortage, we were naturally obliged to rely partly upon information gained by word of mouth in the island. There are a good many ideas current about the shortage. The outstanding points may be summarised as follows :—

1. There is universal agreement as to the actual diminution in the number of ormers available. Reliable estimates give former catches at as much as ten to fourteen dozen per head, now three dozen is reckoned a good catch for one man. The quality of the ormers is not thought to have deteriorated. The decrease has been going on for some years, the mean estimate being over twenty.

2. During our work we have found the ormers apparently in excellent health. They are clean, plump and active, showing no obvious signs of disease or parasitisation. " Sick " ormers are known, though we did not actually see any ; they occur, however, in very small proportion. We examined 100 shells, but found nothing to suggest that these were suffering enough from outside attacks to affect the general health of the animals. Seventy per cent of them were practically perfect.

3. *Natural Enemies.* It seems established that octopus, starfish and oyster-catchers will attack *Haliotis.* There is evidence that the ormer forms, at any rate, a small part of the normal food of *Octopus.* There is nothing to show that any steady increase in the numbers of starfish or octopus has occurred recently, comparable to the decrease in ormers. *Octopus* is nevertheless regarded in some quarters as the villain of the piece. The extent to which any one of these enemies can account for ormers is not clear. Beyond the possibility that a heavy octopus year (octopus varies much from *year to year*) and a poor ormer year may coincide, there is no sign that natural enemies have anything to do with the ormer scarcity as a main cause.

4. *Climatic conditions.* It was suggested that some kind of change in the Gulf Stream had taken place and had led to a local cooling of the water, and this to fatalities among the ormers. An enquiry has been made into this question, but is not yet complete. It promises to be interesting, but any change involved would be very slight, and the effect of it on the ormers difficult to estimate. The Channel Islands, however, are the northern limit of the species, and there if anywhere a very slight temperature change might affect it. In any case this question would not affect corrective legislation, since the temperature of the sea is uncontrollable !

5. *Contamination, etc.* So far there has been no evidence pointing to contamination from oil, petrol or sewage forming any serious source of trouble. Nor does there seem to have been silting-up of suitable habitats upon any large scale ; certain temporary silting has been noticed.

6. *Frost.* It is said that "all that is needed to bring the ormers up is a good frost," the shortage being put down to lack of such. The details collected in connection with this idea certainly do not lead to the conclusion that there is any explanation of shortage here.

7. *Food supply and overfishing.* As far as our study has enabled us to judge, we think the main answer to the question lies here. It is evident that the ormers' food supply forms a low growth on rocks and stones, in the main, unless it can strain out plankton from the water also, which so far seems doubtful. A certain proportion of this food supply, perhaps a large proportion, is the growth found underneath clean stones and boulders which are not embedded in sand—and where the ormers themselves are mainly found. Some section of this part of the food supply is very easily upset. During ormering the stones and boulders will get turned over to an enormous extent, with the result that a good deal of animal food (polyzoa, sponges, larvæ, eggs, etc.) is doomed to die of exposure. These boulders cannot be expected to recover a growth as rich as they originally had for some time, perhaps for a year or so. It is clear that if the beaches get disturbed on a wholesale scale too often, this could interfere with the food supply in the disturbed area, apart from the taking of too many ormers and of too small ones, which would help to spoil the fishery. If this did nothing else, it might in time place the upper limit of the zone inhabited by ormers a little lower down than before, and this would make them no longer available for fishing, since they cannot be got at in more than a few feet of water.

It is not easy to find out whether more people actually go after ormers than formerly; opinions are very conflicting. The most widely held view is that the number of those who fish has increased very much; and it is significant that the population of the island of Guernsey is now nearly twice what it was one hundred years ago. Jersey has to be considered separately in this matter of ormers; the conditions there may be different; but Guernsey is the headquarters of the species, with its neighbouring islands of Sark and Herm.

8. *Conclusions.* If ormers are more fished than formerly, and the beaches consequently more disturbed (and it is possible to disturb them very badly), we need probably look no farther for a main cause of shortage. It does not follow that there are not other subsidiary causes. If this is *not* the cause, it may well be a matter of natural fluctuation spread over a period of years, and possibly reversible. If it is due to overfishing, suitable legislation may hope to check it; if to natural fluctuation, that would be revealed by the failure of legislation. Natural fluctuation would be connected with some cause or causes not yet evident, and possibly involving some connection with changes in food supply not

brought about by man, or with temperature. We suggested a total suspension of the fishery for two years, followed by further biological investigation. After the two-year period a detailed set of more permanent regulations can be worked out. The two-year period of suspension has been adopted by the States of Guernsey. The question of artificial breeding of ormers has been considered, but it is difficult to see how it could be made a sound scheme economically. The difficulties of keeping the active *Haliotis* captive and of supplying it with sufficiently extensive browsing grounds, make it a problem very different from that of the sedentary current-feeding oyster.

SUMMARY.

1. Eggs may be clearly differentiated in a female specimen of *Haliotis* before a length of 2 cm. is reached by the animal, and the female gonad visible before 3 cm. is reached. The female may spawn at 5·5 cm. In the male, active sperms with tails may be differentiated before a length of 3 cm. is attained, and the gonad visible before 4 cm. is reached. The male may spawn at 5·5 cm., if not before.

2. It is estimated that specimens up to about 3·5 cm. long are a year old or less. If so, male and female can both spawn at three years old at any rate, more likely at two years.

3. The first week in August certainly lies within the breeding season. The range of that season is not known, but evidence points to its being late summer.

4. The male gonad is typically white or cream-coloured, or with a tinge of green in addition; rarely salmon or pale yellow. The female gonad varies more, various shades of green, grey-green, brownish grey, etc., are found. These data refer to specimens observed in June and July.

5. Of 127 specimens examined for sex, 50 were males, 71 females, 6 young ones not giving decisive evidence.

6. A male and female were seen spawning. The male puffed out successive clouds of sperms. The female puffed out one cloud of eggs through the holes in the shell, perhaps 10,000 of them. They sank rapidly. They were visible to the naked eye, pale green and quite free from one another. Each was enclosed in a transparent shell.

7. Fertilisation took place after the eggs were laid. The young had reached an early trochophore stage at fourteen to fifteen hours after introduction of sperm. At forty-four to forty-six hours many had left the egg shell and were swimming actively, being then at a decidedly more advanced trochophore stage. How long it is before they settle down and end the larval stage is not known.

8. The food supply consists of algæ (both coarse ones and confervæ, also diatoms), polyzoa, sponges, small crustacea, foraminifera, etc. A good deal of sand is taken in with it.

9. *Haliotis* is certainly a browser and uses the radula as a licking tongue. Experiments were made to ascertain whether it can extract plankton from the water as part of its food as *Crepidula* does. The results were interesting (see p. 487), but not conclusive, pointing to inability to use plankton.

10. There is no evidence to show that *Haliotis* is a homing mollusc like *Patella*, what there is pointing the other way. It is an exceedingly active species.

11. *Haliotis* demands the highest possible conditions of aeration in its water. Given these it is hardy, and will even live for months after removal of its shell, secreting one or more new ones (Boutan).

12. In the attempt to find out why *Haliotis* is getting scarcer in Guernsey and the neighbouring islands (leaving Jersey out of account), it was concluded that this could probably be brought about by overfishing, and by a too ruthless disturbance of the beaches, leading to a certain diminution of the food supply over the area within which *Haliotis* is available for fishing. If this is not the main cause, some kind of natural fluctuation may account for it ; contamination, natural enemies, etc., not appearing to be main factors. The fishing of *Haliotis* in Guernsey has consequently been totally suspended by the States for a period of two years. At the end of that time more permanent regulations will be devised.

Abstracts of Memoirs

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY.

Abstracts of Papers by W. R. G. Atkins, O.B.E., Sc.D., F.I.C. some with Miss M. V. Lebour, D.Sc., and one with Mr. E. W. Fenton, M.A., B.Sc., Seale-Hayne Agricultural College.

THE hydrogen ion concentration of any chemical compound or mixture of compounds is an important factor, inasmuch as it is related to the solubility of substances of low solubility, to the activity of enzymes and to the state of aggregation and chemical behaviour of many other colloidal substances. The series of papers abstracted here constitutes an attempt to trace these relationships as affecting a number of biological problems. The papers dealing with applications to marine biology have been printed in full in this Journal.

1. Relation of Hydrogen Ion Concentration of the Soil to Plant Distribution.

By W. R. G. Atkins.

Nature, 1921, *Vol.* 108, *p.* 80, *Sept.* 15*th.*

2. Some Factors affecting the Hydrogen Ion Concentration of the Soil and its relation to Plant Distribution.

By W. R. G. Atkins.

Sci. Proc. Roy. Dublin Soc. (*N.S.*), 1922, *Vol.* 16, *pp.* 369–413, *and Notes, Bot. School, Trinity Coll., Dublin*, 1922, *Vol.* 3, *No.* 3.

3. The Hydrogen Ion Concentration of Plant Cells.

By W. R. G. Atkins.

Loc. cit., pp. 414–426, *and loc. cit, No.* 3.

4. Note on the Occurrence of the Finger and Toe Disease of Turnips in relation to the Hydrogen Ion Concentration of the Soil.

By W. R. G. Atkins.

Loc. cit., pp. 427–428, *with Bibliography for the three papers, pp.* 429–434, *and loc. cit., No.* 3.

5. The Hydrogen Ion Concentrations of some Indian Soils and Plant Juices.

By W. R. G. Atkins.

Agric. Research Institute, Pusa, 1922, *Bull. No.* 136, *pp.* 1–12.

6. Some Physical and Chemical Factors which affect Plant Distribution.

By W. R. G. Atkins.

Ann. Rep. of Brit. Assoc., 1922, *Sect. K.*

The soils studied lay between pH4·1 and pH9·0, peaty soils being at the acid and the calcareous silts of Behar, India, at the alkaline end. The reaction of the natural waters of the districts studied varied from pH5·0 for the amber water of a bog pool to pH9·7 for a pond containing calcium and magnesium salts during the active photosynthesis of abundant algæ. Calcium carbonate in the absence of free carbon dioxide or of bicarbonate produces a reaction of pH9·0, whereas for magnesium carbonate the value is phH10·0. Soil alkalinity of over pH10, due to sodium carbonate, may be reduced to pH8 by the addition of gypsum, and thus a reaction which is injurious or destructive may be converted into one that is favourable to most plants.

Records given for the hydrogen ion concentration of the habitats of over a hundred plants show that many plants are limited to a short range of pH values. Others, with a wider range, occur mainly in one portion of it, but some plants grow well at widely different soil reactions.

Adjacent fields of similar clay soil were found to be badly infested with and free from finger and toe disease in the turnip crop. It was found that they contained, respectively, 0·17 and 0·40 per cent of calcium, calculated as oxide. The hydrogen ion concentrations were respectively 0·25 and $0{\cdot}20 \times 10^{-6}$ grams per litre, or pH6·6 and 6·7 or slightly over. An adjoining garden at pH7·8 was also free from the disease, though treated with farmyard manure infected from turnip feeding.

In addition to the measurements on the sap of algæ (this Journal, 1922, **12**, 785), which were found to lie between pH6·3 and 7·3, determinations were made on a number of land plants. The greatest concentration, pH1·4, was found in an unidentified berry, like a gooseberry, produced by a large Indian tree. All the tissues examined lay on the acid side of neutrality, parenchyma being often about pH6 and the xylem more acid as seen in cross-sections stained with appropriate indicators.

The transpiration stream was found to be almost neutral, but digestive secretions, such as those of *Sarracenia*, *Nepenthes* and *Drosera*, may be more acid than pH5. The hydrogen ion concentration met with in a tissue was, in the cases studied, usually near, but slightly less than, the optimum for the activity of the characteristic enzyme at air temperature. This ensures that the acidity does not destroy the enzyme at such higher temperatures as may be experienced by the plant under natural conditions.

7. The Hydrogen Ion Concentration of Natural Waters and some Etching Reagents in relation to Action on Metals.

By W. R. G. Atkins.

Trans. Faraday Soc., 1923, *Vol.* 18, *pp.* 310–317.

8. The Hydrogen Ion Concentration of the Soil in relation to the Flower Colour of Hydrangea hortensis W., and the Availability of Iron.

By W. R. G. Atkins.

Sci. Proc. Roy. Dublin Soc., 1923, *Vol.* 17, *pp.* 201–210, *and Notes, Bot. School, Trinity Coll., Dublin*, 1923, *Vol.* 3, *No.* 4.

Attention is drawn to the possible utility as etching reagents of buffer mixtures and of acids of relatively low hydrogen ion concentration, since the hydroxides of the metals begin to be precipitated at different pH values, as for example, copper pH5, ferric iron pH3·5, ferrous iron pH5·1, the precise value being largely affected by the concentration of the metallic ion.

Ferrous salts in solution become more acid on standing, with precipitation of ferric hydroxide. The latter is completely precipitated before ferrous hydroxide, as the solution is made more alkaline. These facts are considered in relation to the rusting of iron. The precipitation of ferrous hydroxide is incomplete even at pH7·1, hence a trace of acid suffices to attack iron, and the hydroxide produced through hydrolysis is oxidised and precipitated. The hydrolysis equilibrium is thereby upset and acid is regenerated. Thus provided oxygen is available the cycle is again begun, but in its absence the acid is not regenerated and further corrosion ceases. These precipitation limits for ferrous and ferric salts have a direct bearing upon the formation of iron pan in soil, since the iron in solution percolates into the less acid subsoil, and is there precipitated, the ferrous hydroxide becoming in time oxidised.

The common hydrangea acts as a guide to the amount of iron in solution in the soil water, since it produces blue flowers in soil at about pH5·7 to 6 or over, and pink flowers at and above pH7·5, with mixed blue and pink and intermediate shades in between. The blue flowers are richer in iron than are the pink, as shown by quantitative analysis and by Macallum's hæmatoxylin test. The difference in the colour of the flowers is not due to the natural pigment acting as an indicator, since blue and pink flowers from the same plant were both at pH4·2.

9. The Hydrogen Ion Concentration of the Soil in relation to Animal Distribution. By W. R. G. Atkins.

Nature, 1921, *Vol.* 108, *p.* 568, *Dec. 29th.*

10. Measurements of the Acidity and Alkalinity of Natural Waters in their Biological Relationships. By W. R. G. Atkins.

Salmon and Trout Magazine, 1922, *pp.* 184–198, *Sept.*

11. The Hydrogen Ion Concentration of Soils and Natural Waters in relation to Animal Distribution. By W. R. G. Atkins.

Rep. British Assoc., 1922, *Sect. D.*

12. Soil Reaction, Water Snails, and Liver Flukes.

By W. R. G. Atkins and M. V. Lebour.

Nature, 1923, *Vol.* 111, *p.* 83, *Jan.* 20*th.*

13. The Hydrogen Ion Concentration of the Soil and of Natural Waters in relation to the Distribution of Snails.

By W. R. G. Atkins and M. V. Lebour,

Sci. Proc. Roy. Dublin Soc., 1923, *Vol.* 17, *pp.* 233–240.

14. The Habitats of Limnæa truncatula and L. pereger in relation to Hydrogen Ion Concentration. By W. R. G. Atkins and M. V. Lebour.

Loc. cit., 1924, *Vol.* 17, *pp.* 327–331.

Since many animals, especially insects, are associated with particular plants, it is obvious that since the pH value may limit the distribution of the plant it may also do the same for the animal. Apart from this, however, an increase in acidity may in itself exert a harmful effect upon an animal, as for example, in the case of trout, where Rushton has shown that flood water from bogs causes death through coagulation of the mucus of the gills. The distribution of fish food also appears to be regulated by the pH value, both directly by that of the water and indirectly by that of the banks—for land-bred insects form a considerable proportion of the food of fresh-water fishes.

The distribution of snails is largely affected by soil reaction, and they occur in greatest number from pH7–8. The number of species of snails found in the districts studied increases from pH5 four species to pH7 twenty species, falling at pH8 to fourteen out of the total twenty-seven species collected. Snails with hyaline shells may be found in any portion of the range, but those with calcareous shells are limited to the more alkaline end. Granite and quartzite regions have few species, basaltic districts have a more numerous fauna, and in limestone areas both species and numbers of individuals give high values.

There remain over a number of puzzling cases in which, within an area of two square miles, certain species are altogether absent from one locality, though abundant in others, in spite of similarity in pH value, salt content of soil, and aspect. A difference only of exposure to wind could be noted.

The habitats of *L. pereger* and *L. truncatula* appear to differ in the fact that whereas the former is truly a water-snail, and can endure even somewhat stagnant water, the latter is amphibious, and can live either in shallow, well-aerated water or on moist land, or even on cliffs in a region of high humidity.

The observed ranges for the two species are almost identical as regards reaction and salt content of the water (as shown by electrical-conductivity), those for *L. pereger* being pH6·6–7·7 and $C=72-227\times10^{-6}$ at 0°C., and for *L. truncatula* pH6·4–7·8 and $C=59-294\times10^{-6}$. It is noticeable that the records include neither upland waters of very low salt content with conductivity $20-30\times10^{-6}$, nor regions of high acidity.

15. The Differentiation of Boiled and Unboiled Water. By W. R. G. Atkins.

Nature, 1921, *Vol.* 108, *p.* 339, *Nov.* 10*th.*

16. The Hydrogen Ion Concentration of Natural Waters in relation to Disease. By W. R. G. Atkins.

Journ. of State Medicine, 1923, *Vol.* 31, *pp.* 223–226.

17. The Hydrogen Ion Concentration of the Soil and Natural Waters in relation to Diseases other than Bacterial. By W. R. G. Atkins.

Parasitology, 1923, *Vol.* 15, *pp.* 205–210.

Boiling drives off free carbon dioxide and decomposes bicarbonates, so water is more alkaline after boiling than before, as may readily be shown by an appropriate indicator. It is therefore possible to keep a check upon whether or no orders as to boiling drinking water have been carried out.

With the exception of bog waters and those abnormally rich in metallic salts it seems that naturally occurring waters are at pH values favourable to the continued existence of the *Vibrio choleræ* and bacilli of the typhoid group. The suggestion is made that water may be rendered safe for drinking purposes by rendering it as alkaline as pH10·5, or thereabouts, by adding ash derived from vegetable matter, which is rich in carbonates of potassium and sodium. Temperatures should also be stated when limiting, and optimal pH values are given for the growth of various organisms.

Facts known as to the relation between pH values of soil and water may possibly be applied to explain the distribution of malarial fever, as illustrating insect-borne disease, and that of some of the numerous Trematode infections, afflicting man and other animals, in which snails act as intermediate hosts, viz. bilharziosis, the Japanese skin disease "kabure," liver fluke disease, the disease in fish due to *Lissorchis fairporti* Magath., and that in the human lung occasioned by *Paragonimus westermani.*

18. Seasonal Changes in Water in relation to the Algal Plankton.

By W. R. G. Atkins.

Rep. Brit. Assoc., 1923, *Sect. K.*

This is a brief account of the changes in pH and in phosphate content, as already published in full in this Journal.

19. The Hydrogen Ion Concentration of the Soil in relation to the Distribution of Pasture Plants. By W. R. G. Atkins and E. W. Fenton.

Rep. Brit. Assoc., 1923, *Sect. M.*

Following the lines of Nos. 1 and 2 of these abstracts provisional results are given for the pH values at which species of grasses and clovers occur and are most abundant. Since in practice species sown are usually crowded out in a few years by others native to the soil, such an investigation appeared to be desirable. It was ascertained that wild white clover might occur in sites as acid as pH5·6, whereas *Medicago maculata* was found from pH6·7–7·8. A few values for grasses are also recorded.

W. R. G. A.

Haplosporidium nemertis nov. sp. By P. Debaisieux.

C. R. Soc. Biol., Paris, T. LXXXII, 1919, *pp.* 1399–1400.

The author describes the existence of a new Sporozoan, *Haplosporidium nemertis*, in *Lineus bilineatus* MacIntosh. The parasites are extremely abundant in the infected hosts. The spores are protected by an ovoid membrane which is differentiated into a movable valve at one of its poles; they contain a single nucleus, comparatively large. The life-history of the parasite is briefly described, and allows the species to be placed among the Haplosporidia.

P. D.

Quelques Protozoaires parasites des Chitons et des Patelles.

By P. Debaisieux.

C. R. Soc. Biol., Paris, T. LXXXII, 1919, *pp.* 1400–1402.

In the molluscs, Chitons and Limpets, certain stages of sporozoa have been known for some time. Their study has led several authors (Ray Lankester, 1891; Labbé, 1899; Mrs. Pixell Goodrich, 1915) to interpret in different ways the systematic position of these parasites. The careful study of different stages observed in molluscs found in the neighbourhood of Plymouth has enabled the author to distinguish clearly several species, *Pseudoklossia chitonis* nov. sp. and an *Eimeridea* in *Acanthochiton fascicularis* L.; *Haplosporidium* (*Minchinia*) *chitonis* in *Craspidochilus cinereus* L.; *Pseudoklossia patellæ* nov. sp. in *Patella vulgaris*.

P. D.

Haplosporidium (Minchinia) chitonis Lank., Haplosporidium nemertis nov. sp., and the group of Haplosporidia. By P. Debaisieux.

La Cellule, T. XXX, fasc. 2, 1920, *pp.* 291–313. 2 *Figures.*

In this work the detailed study of two Haplosporidia discovered at Plymouth is given, the one in *Lineus bilineatus*, the other in *Craspidochilus cinereus*. Both species have young stages, which are intracellular and generally binucleate; by nuclear division these parasites give rise to large plasmodia in which the paired nuclei increase considerably. These nuclei divide by a very characteristic mitosis, with a very marked intracellular spindle, with an intranuclear corpuscle (Karyosome ?) separating off and dividing at the moment of anaphase. The large nuclei divide a certain number of times without increasing in size, so that finally the plasmodium contains a number of small nuclei; the protoplasm fragments and the plasmodium splits up into spores. The author endeavoured to interpret the significance of all the observed stages and to establish the life-history of the species studied. He discusses at length the affinities of the genus and attaches it to the Microsporidia. He extends the discussion to the whole group of Haplosporidia, considerably diminishes the importance of the group, and finally reduces it to a few species about which little is known.

P. D.

Note sur deux Coccidies des Mollusques: Pseudoklossia (?) patellæ et P. chitonis. By P. Debaisieux.

La Cellule, T. XXXII, fasc. 2, *pp.* 231–246. 1 *Plate.*

In this work the author undertook the cytological study of two Coccidia found in Limpets and Chitons (*Acanthochiton fascicularis*). He establishes the differences, chiefly in size, existing between the two species and then describes their life history. True schizogony appears to be lacking, but it is replaced by an asexual multiplication into successive halves. Gametogenesis (macrogametes and microgametes) was observed, but not the development of the spores; it probably occurs outside the body of the host. With this gap in the knowledge of the life-history of these two Coccidia it is impossible to classify them definitely. Meanwhile what we know of their development allows us to place them very near to, and probably in, the genus Pseudoklossia of Léger and Dubosq.

P. D.

Nuclear Division in the Dinoflagellate, Oxyrrhis marina Duj.

By J. S. Dunkerly, B.Sc.

Proc. Roy. Phys. Soc. Edin., **20**, 1921, *pp.* 217–220.

Nuclear division as seen in *Oxyrrhis marina*, which occurred plentifully in tank material from Plymouth grown in Allen and Nelson culture medium, is of the type known as promitosis, with a karyosome acting as a division centre, massive chromatin plates with numerous threadlike chromosomes and clear polar caps to the division spindle. The division figures resemble those of other Dinoflagellates, e.g. *Ceratium*, with the important difference that the karyosome does not appear to act as division centre in *Ceratium*. *Oxyrrhis*, therefore, is of a more primitive type, as regards nuclear division, than other Dinoflagellata, and is in this respect intermediate between them and the Euglenoidina.

J. S. D.

Rhabdamœba marina gen.n. et sp.n. By J. S. Dunkerly, B.Sc.

Proc. Roy. Phys. Soc. Edin., **20**, 1921, *pp.* 220–221.

A very small (7·5μ diam.) amœboid form with minute spiny projections on the pseudopodia was found in preparations made of the surface film organisms in a culture of *Oxyrrhis marina* in sea water with Allen and Nelson medium. No details of its life-history were made out, but its form distinguishes it as a new type of organism, while its small size and extreme transparency may explain its previous non-discovery.

J. S. D.

Fish Myxosporidia from Plymouth. By J. S. Dunkerly, B.Sc.

Parasitology, **12**, 1921, *pp.* 328–333.

An examination was made of the Myxosporidia found parasitic in marine fish, especially of the forms inhabiting the gall-bladder of their host. Three hundred and twenty fish belonging to forty-six species were examined. Of these, eighty-three individuals belonging to fifteen species proved to be infected with Myxosporidia, of which fifteen species were identified, five of them being described as new. A further paper dealing with some of the results of this work has now been prepared.

J. S. D.

The Preparation of Dogfish for Market. By E. Ford, A.R.C.Sc.

Fish. Board, Scotland, 1923.

This pamphlet, written for the Fishery Board for Scotland, provides an account of the preparation at Plymouth market of dogfish for sale as Flake. The market arrangements for the employment and payment of gutters and for the disposal of the large amount of offal, are dealt with, and the descriptions of the successive stages in the operations of gutting, skinning, beheading and packing, are accompanied by text figures.

E. F.

An Investigation into the Cause of the Spontaneous Aggregation of Flagellates and into the Reactions of Flagellates to dissolved Oxygen.

By H. Munro Fox.

Parts I and II, Journ. Gen. Physiol., III, 1921, *pp.* 483–511.

Methods of studying the Respiratory Exchange in small aquatic organisms, with particular reference to the use of Flagellates as an Indicator of Oxygen Consumption. By H. Munro Fox.

Journ. Gen. Physiol., III, 1921, *pp.* 565–573.

A flagellate, *Bodo sulcatus*, forms aggregations in regions where the concentration of dissolved oxygen has a certain value. This value is less than the saturation concentration of oxygen dissolved in water under atmospheric partial pressure. The flagellates move out of regions where the oxygen concentration is above or below the optimum to gather into the optimal regions. They are positively chemotactic to a certain concentration of dissolved oxygen.

This behaviour of the flagellates can be made use of to indicate changes in the concentration of dissolved oxygen due to the respiration of an aquatic organism present in the water. For if the organism under investigation be kept motionless in a suspension of the flagellates in water with oxygen at the atmospheric partial pressure, the flagellates will collect into those regions where the oxygen concentration is lowered through the respiratory activity of the organism. The sizes of the aggregations of flagellates thus formed will show the relative amounts of oxygen absorbed by the different parts of the surface of the organism.

H. M. F.

The Genus Polysiphonia Grev., a critical Revision of the British Species, based upon Anatomy. By Lily Batten, M.Sc., Ph.D.

Linnean Society's Journal, Botany, Vol. XLVI, April, 1923, *pp.* 271–311.

Species of British Polysiphonia may be classified according to their anatomical differentiation. The thallus consists of a central siphon, surrounded by four or more pericentral siphons. In the corticate forms, external cells are also present which do not extend individually for the complete length of an articulation. Protoplasmic continuity is present throughout the plant in the young stages, although later some of the connecting pits may become closed. The form of the attachment organ varies with the species, and is influenced by the nature of the substratum. Four types may be distinguished :—

1. The ecorticate plant is originally attached by rhizoids which are developed from siphons by longitudinal proliferation. Later, siphons of

procumbent branches also develop rhizoids, the tips of which may be modified in various ways.

2. Species which show the elementary aggregation of the rhizoids to form a large disc.

3. *P. fruticulosa*, which is originally attached by a number of longitudinally developed rhizoids, and later certain stunted procumbent branches function specially in the formation of the attachment organ.

4. Species with an upright habit, which do not branch near the base, develop a large disc-like expansion at the base of the thallus.

A classification and description of the individual species follows, together with a key for identification.

L. B.

On a new type of Teleostean Cartilaginous Pectoral Girdle found in young Clupeids. By E. S. Goodrich, F.R.S.

Journ. Linn. Soc. Zool., Vol. 34, *pp.* 505–509.

In the young of *Clupea sprattus, C. harengus* and *C. pilchardus* about 20–30 mm. in length, the right and left coracoid regions fuse to a solid cartilaginous ventral bar, which becomes bent and again subdivided in later stages. This fusion is probably a specialisation to strengthen the support of the pectoral fins before the complete development of the dermal bones of the pectoral girdle.

E. S. G.

The Spore of Thelohania. By H. L. M. Pixell Goodrich, D.Sc.

Arch. Zool. Exp. et Gen., Vol. LIX, Notes et Revue, No. 1, 1920, *pp.* 17–19.

A prawn, *Leander* (*Palaemon*) *serratus*, from the tanks at Plymouth Aquarium had opaque white muscles, and seemed obviously infected with *Thelohania octospora*. The spores, however, were all provided with three long tails as well as a polar capsule. This, the first recorded instance of a tailed spore occurring among true Microsporidia, furnishes a point of resemblance between these parasites with minute spores provided with a polar filament and the family Haplosporidiidæ, many members of which have tailed spores, but never a polar filament.

H. L. M. P. G.

Some Notes on Leander longirostris M. Edwards, and other British Prawns.

By R. Gurney, M.A., F.L.S.

Proc. Zool. Soc., 1923, *pp.* 97–123.

Some account is given of the specific characters, distribution and breeding periods of the British Palaemonidæ. To the four species recorded as British a fifth, *L. longirostris* M. Edw., may now be added. This species, which has recently been redescribed by De Man,* is common in Dutch estuarine waters and also in the Norfolk rivers Waveney, Yare and Bure, which discharge into Breydon Water. It has not been found elsewhere in Britain. It is a river prawn, equally at home in salt or in fresh water, but it goes down to salt water to hatch out its larvæ which are never found in the rivers. De Man has now† separated the Dutch form (with which the Norfolk prawns agree), as a new variety *robusta*, from the typical form of Milne Edwards.

L. serratus differs from all the other species in its breeding period, which begins in the winter, larvæ being found from December onwards. Any Leander larvæ taken before June may confidently be referred to this species for this reason alone.

The pleopods of the female undergo certain changes at the time of oviposition in all the species, developing peculiar ovigerous setæ which are absent at other seasons.

In *L. squilla* and *L. longirostris* there appear to be two broods produced during the breeding season, but it is doubtful if there is more than one as a rule in *Palæmonetes varians.*

R. G.

A Note on the Physiology of the Shipworm (Teredo norvegica).

By C. R. Harington.

Biochem. Journ., Vol. XV, 1921, *pp.* 736–741.

Preliminary experiments *in vitro*, to determine the toxicity to *Teredo* of different substances which might conceivably be used in the impregnation of timber, showed that certain aromatic nitro-compounds were highly toxic ; promising results were also obtained with carbazol and with an arsenic derivative of diphenylamine. A series of sea-tests was started to determine the efficacy of these various substances under the conditions of actual use.

C. R. H.

Report on Work done at the Marine Biological Station, Plymouth, July 1st to September 18th, 1920. By C. R. Harington.

Dept. Scient. and Industrial Research. Deterioration of Structures in Sea-water.
Second (*Interim*) *Report of the Committee of the Inst. C.E.*, 1922, *pp.* 35–42.

A series of experiments was carried out in relation to various aspects of the physiology of *Teredo* which might have a bearing upon the protection of timber against its attacks. It was attempted to rear *Teredo* from

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* *Tijdschr. Ned. Dierk. Vereen* (2), *XIV*, 1915–1916.

† *Ibid.* (2), *XIX*, 1923.

the larval stage in the Laboratory; although these experiments failed in their primary object, they showed that the duration of the free-swimming stage may be at least as long as a fortnight. The study of the larvæ during their free-swimming existence brought to light the fact that they were strongly attracted towards wood; further investigation of this phenomenon showed that this power of attraction was shared by ethereal and alcoholic extracts of sawdust and also by pure malic acid. This suggests the probable mechanism by which the larvæ are led to settle upon timber.

In order to throw some light upon the nutrition of the animal, the enzymes of the digestive gland were briefly investigated. It was found that extracts of the gland possessed marked amylolytic activity, and also were apparently capable of hydrolysing the hemi-cellulose of wood to glucose; so that *Teredo* would appear to be capable of deriving at least part of its nutriment from the wood-borings which pass through its alimentary canal.

C. R. H.

Further Studies on Restitution-bodies and free Tissue-culture in Sycon.

By Julian S. Huxley.

Q.J.M.S., Vol. LXV, 1921, *pp.* 293–322.

Confirmation is given of the fact that calcareous sponges can reorganise themselves after their tissues have been dissociated in various ways. Reorganisation consists mainly in the sorting-out of the cells of the two primary layers; thus in this form of regeneration fate is not a function of position, but position a function of nature.

By various methods an excess of either collar-cells or dermal-cells can be obtained. In the former case hollow spheres of collar-cells may be formed, or segments of spheres protruding from a mass of mixed cells. In the latter case, similar segments of spheres entirely composed of one layer of dermal-cells may be formed. No complete spheres composed of dermal cells were observed. There appears to exist a definite attraction between dermal-cells.

Spontaneous segmentation of restitution masses into smaller masses may occur, simultaneously with the secretion of a gelatinous covering.

A peculiar small finger-shaped amœbocyte is described.

J. S. H.

Dedifferentiation in Echinus larvæ, and its relation to Metamorphosis.

By Julian S. Huxley.

Biol. Bull., Vol. XLIII, 1922, *pp.* 210–234.

In very weak toxic solutions (KCN, $HgCl_2$), dedifferentiation of Echinus larvæ occurs. This results in the loss of the arms, the closure of mouth and anus, and the final attainment of a spherical state in which the internal organs are reduced to a few vesicles with a packing of mesenchyme. The hypothesis is advanced that normal metamorphosis in Echinoids is initiated by the weight of the Echinus rudiment pulling the larva down to the bottom, which is unfavourable to the larval tissues. These then start to dedifferentiate, and are resorbed in favour of the developing adult tissues.

It is pointed out that tissues with large cell-surface are especially sensitive to agents causing dedifferentiation.

In dilute solution the toxic effect of mercury salts is shown to depend upon the total amount present as well as upon the concentration.

J. S. H.

Studies in Dedifferentiation. IV. Resorption and Differential Inhibition in Obelia and Campanularia.

By Julian S. Huxley, M.A. and G. R. de Beer, B.A., B.Sc.

Q.J.M.S., Vol. LXVII, 1923, *pp.* 473–494.

Details are given of the process by which the hydranths of various hydroids disappear under unfavourable conditions. It is shown that the disappearance is initiated by a true dedifferentiation, which is followed by resorption into the stolon, the cells of the hydranth tissues migrating individually into the cavity. This confirms and extends the work of Loeb, Thacher and others.

Dilute toxic solutions quantitatively accelerate the process. Phagocytosis of nematoblasts and other cells appears to occur, after they have migrated into the cavity.

Resorption is regarded as the natural result of dedifferentiation when there are adjacent cavities into which the cells can migrate. In higher forms it has been largely replaced by phagocytosis.

J. S. H. AND G. R. DE B.

Report on the Life-History of Hemiurus communis Odhner.

By M. V. Lebour, D.Sc.

Parasitology, Vol. XV, 1923, *pp.* 233–235.

A larval Trematode was twice found emerging from *Acartia clausi* taken from tow-nets, one inside and the other outside the Sound. This was identified as *Hemiurus communis,* Odhner, a common species in these regions. Both specimens were in an intermediate stage between cercaria and adult with male organs fully developed and female organs incomplete. The adult worm lives inside various fishes, especially gadoids, including *Gadus luscus*, *G. merlangus*, *G. minutus* and *G. pollachius*, and is one of the commonest marine trematodes. So far this is all that is known of its life-history.

M. V. L.

The Comparative Morphology of the Secondary Sexual Characters of Elasmobranch Fishes—the Claspers, Clasper Siphons, and Clasper Glands.

By W. H. Leigh-Sharpe, M.Sc.

Memoir I. Journ. Morph., Vol. 34, 1920, *pp.* 245–265.

The muscular sac called the siphon in *Scyllium*, etc., is homologous with the sac containing the clasper gland in *Raia*. Experiments are given in support of the view that the siphons are normally full of sea water and surrounded by powerful muscles by which spermatozoa already in the clasper grooves are injected into the female and rotated by a fan-like structure. It is the purpose of this and succeeding memoirs to compare together on these points all Elasmobranchs obtainable. Parasiphons are present in *S. catulus*. The histology of the siphon wall, a description of spermatozoa, and some new details of the clasper gland of *Raia* are given, together with remarks on the peculiarities of the striped muscle attached to the clasper gland.

W. H. L.-S.

Memoir II. Journ. Morph., Vol. 35, 1921, *pp.* 359–380.

The claspers function as penes and should be called such, and while it is beyond doubt that both are inserted together, it is possible that on occasions one may be inserted at a time. The siphons of *Galeus* and *Mustelus* are enormously developed. *Lamna* possesses a peculiar clasper gland unlike that of *Raia*, while the clasper gland of *Rhina* is a mucous gland, as is also the labial " organ." The clasper glands are developed in the same way as prostatic glands, and are homologous with them. The claspers with siphons have strong skeletal supports, and are roughened with denticles to prevent elision, and do not depend upon erection. The claspers with accessory glands are smooth, have much erectile tissue, and but feeble skeletal support, the large rhipidion preventing elision. It is suggested that some part of the gland, or more probably its muscular wall, secretes a metabolite capable of causing vasodilation. Thus the glands are physiologically similar to prostatic glands. The rectal gland is not a mucous gland, but probably excretory.

W. H. L.-S.

Note on the Systematic Position and Distribution of the Actinian Sagartia luciæ. By J. Playfair McMurrich, C.M.Z.C.

Proc. Zool. Soc., London, 1921, *pp.* 729–739.

A study of the anatomical characters of *S. luciæ* indicate that it possesses a well-defined fosse, that there is complete absence of a mesoglœal sphincter, and that it possesses only sixs pairs of perfect mesenteries which are also sterile. It therefore belongs to the sub-family Metridiinæ, in which the Aiptasias should be included, but differs generically from any form at present included in that sub-family.

The species has been recorded from the coast of Massachusetts and from Plymouth. Record is now made of its occurrence also on the coast of Vancouver Island, where, as is shown by unpublished drawings made by Mr. Alex. Agassiz, it was observed in 1859. This suggests the possibility of a former circumpolar distribution. Attention is drawn to the great probability of *A. chrysosplenium*, described from Cornwall by Mr. Cocks in 1851, being identical.

The species cannot be assigned to the genus Sagartia, of which *S. effœta* L. should be taken as the type. Gosse assigned *A. chrysosplenium* to a subgenus Chrysoela, and, assuming the identity of the forms known as *S. luciæ* with Mr. Cocks' species, they should be known as *Chrysoela chrysosplenium* (Cocks) Gosse.

J. P. McM.

On the Physiology of Amœboid Movement, II. The effect of Temperature.

By C. F. A. Pantin, B.A.

Brit. Journ. Exp. Biol., 1924, *Vol. I, No.* 4, *pp.* 519–538.

The velocity of two kinds of marine amœbæ varies with the temperature in the manner characteristic of many other biological processes. Movement is reversibly inhibited near 0°C. There are respective optima temperatures (20°, and 22°–25°) above which activity falls rapidly. This fall ends in irreversible inhibition.

Above the optimum some part of the mechanism, possibly an enzyme, is progressively destroyed by the heat: the rate of destruction rises rapidly with the temperature above the optimum. Below the optimum the velocity rises with the temperature. Were it not for the destructive effect the velocity would continue to rise with the temperature above the optimum. The rise in velocity with temperature is probably general for all forms of amœboid activity.

The mechanics of amœboid activity are considered. It is conceivable that the energy of amœboid activity might be derived *directly* from a chemical reaction. But if this were so the velocity of the reaction would control the rate at which work was done and not the velocity of locomotion. Calculation of the rate of doing work shows that its temperature coefficient is very high and unlike that found in most biological processes.

On the other hand, the rate at which the protoplasm can change its state from endoplasm (sol) to ectoplasm (gel) may directly control the velocity of an amœba. If temperature affects the rate of change of state as it does the rate of many other biological processes, we have an explanation of why the *velocity* of an amœba is affected by temperature in the same way as other processes.

It is therefore suggested that the velocity of an amœba is not directly controlled by the velocity of a chemical reaction supplying the energy necessary for activity, but that it probably is controlled by the rate at which the protoplasm can change its state.

The temperature coefficient of the velocity indicates that the rate at which the protoplasm can change its state is itself possibly controlled by a chemical reaction. Amœboid activity would then ultimately depend on this reaction, but only indirectly.

C. F. A. P.

The Structure and Function of the Liver of Teredo (the Shipworm).

By F. A. Potts, M.A.

Proc. Cambridge Philosophical Society (*Biol.*), *Vol. I*, *pp.* 1–17, *Pls. I and II.*

The alimentary canal of this wood-boring form has been described in its morphology and development by Sigerfoos, who does not, however, give any account of the remarkable histology of the "liver." This gland communicates by wide ciliated ducts with the stomach, and its lumen is always filled with fragments of wood. In many of the lobules of the liver the epithelial cells are phagocytic and take up large numbers of these fragments: the lumen is also full of free phagocytes, which are derived from the epithelium. These constitute the "digestive" part of the liver. In other lobules the epithelial cells contain large quantities of highly refringent, resistant granules of unknown chemical nature. These lobules make up the "excretory" part of the liver, which is yellow or brown in colour. The stomach, cœcum and liver contain no recognisable organic material other than wood. In the intestine occasional diatoms are found, but to the author it seems that the histological evidence points to the conclusion that the food of the shipworm is almost entirely wood. Other evidence is given to show the practical independence of this animal of plankton organisms, though the gills of *Teredo* constitute a mechanism by which solid suspended particles can be forwarded to the mouth.

F. A. P.

Note on the British Species of Anomia. By R. Winckworth, M.A.

Proc. Malacological Soc., Vol. XV, pp. 32–34, *Plate I,* 1922.

The shell characters of the species grouped under *Anomia* are very variable, while young individuals are specially difficult to place, as the muscular scars are then very faint. This paper recommends examination of the gills as an aid to discriminating the species, for which purpose a good lens is sufficient. The author recognises four species :—

Anomia ephippium (L.). Upper or left valve with three distinct muscular scars. Gill W-shaped in section, with a depending membranous flap of the outer ascending lamella.

Monia patelliformis (L.). Two distinct muscular scars. Gill W-shaped, without the flap : there are also intermediate ciliary junctions, one in the ascending filaments, two in the descending filaments.

Monia squama (Gmelin)=*Anomia striata* Lovén. The scars of the shell adductor and byssal adductor adjoin one another in the upper valve. Gill similar to that of the last species, but the filaments are finer, and the number of ciliary junctions more numerous ; there are typically two rows on the ascending filaments and three on the descending filaments, but there may be more, as the rows are often irregular.

Heteranomia squamula (L.), including the spinous form *Anomia aculeata* Müller. Two muscular scars in the upper valve, small adjacent but distinct, not radially furrowed as in *Monia*. The gill lamellæ have descending filaments only, each gill being therefore ∩-shaped in section.

All four species occur off Plymouth : material was also obtained from other parts of England and from Scotland.

R. W.

Marine Biological Association of the United Kingdom.

Report of the Council, 1923.

The Council and Officers.

Four ordinary meetings and one special meeting of the Council have been held, at which the average attendance was thirteen. The thanks of the Council are due to the Royal Society, in whose rooms the meetings have been held.

A Committee consisting of six members of the Council visited and inspected the Plymouth Laboratory in April.

The Plymouth Laboratory.

The engines and pumps have been maintained in good working order, and the Aquarium tanks have been exceptionally well stocked with fish, which have lived in a healthy condition, a good circulation of both air and water being provided.

The boiler used for heating the building, which had been in use since the Laboratory was opened in 1887, collapsed early in the year, and has been replaced by a new one of somewhat greater power and efficiency.

A portion of the drainage system has been opened up and put in a state of repair.

The new building for the use of the Easter Class was completed in the spring, in time for use by the class. It is situated behind the main Laboratory building, its dimensions are 40 ft. by 16 ft., the walls are of brick and the roof covered with ruberoid. The internal fittings are simple and adequate, and electric light is installed. It affords accommodation for 20 students at one time. When not in use by the class, the building makes a very useful research laboratory.

A Guide Book for sale to visitors to the Aquarium has been provided. The book has been written by Mrs. E. W. Sexton, and illustrated by Mr. L. R. Brightwell, to both of whom the thanks of the Council are due for the labour which has been freely given to its preparation.

The Boats.

The steam trawler-drifter *Salpa* has continued to work successfully. A detailed survey of the machinery and boiler was made in October and everything was found to be in first-class order. The small laboratory, which was built on deck last year, has been of great value, and makes it possible to do much more effective work on the ship.

A motor-boat, the *Gammarus*, 25 ft. long and 8 ft. beam, built to our own design and fitted with two 3 h.p. Kelvin engines, was completed in August, and has since been in daily use for inshore work.

The sailing boat *Anton Dohrn* is also still available for collecting in the Sound.

The Staff.

Mr. R. S. Clark left at the end of August on appointment as Senior Naturalist at the Aberdeen Laboratory of the Fishery Board for Scotland. Mr. E. Ford has been promoted to take Mr. Clark's place on the Laboratory staff, and Mr. F. S. Russell, Assistant-Director of Fisheries under the Egyptian Government, has been appointed an Assistant Naturalist. Mr. Russell will devote his time especially to the study of fishes.

Occupation of Tables.

The following naturalists have occupied tables at the Plymouth Laboratory during the year :—

Miss D. ATKINS, London (Polyzoa).
Dr. J. BARCROFT, F.R.S. } Cambridge (Hæmoglobin in Arenicola).
H. BARCROFT }
G. BATESON, Cambridge (Commensals of Synapta).
Miss L. BATTEN, London (Gracilaria).
N. J. BERRILL, Bristol (General Zoology).
Dr. R. A. BUDINGTON, Oberlin, U.S.A. (Embryology).
G. S. CARTER, Cambridge (Fertilization of Echinus Eggs).
J. T. CUNNINGHAM, London (Ciona and Sacculina).
W. DE MORGAN, Plymouth (Protozoa).
Miss FAULKNER, Edinburgh (Pontobdella and Filograna).
Miss M. G. FORDHAM, Liverpool (Echinus).
Miss S. GARSTANG, Oxford (Development of Botrylloides).
A. S. GILLESPIE, Bath (Ecology).
E. R. GUNTHER, Cambridge (General Zoology).
C. R. HARINGTON, London (Teredo).
L. A. HARVEY, London (General Zoology).
Prof. E. NEWTON HARVEY, Princeton, U.S.A. (Pholas and Noctiluca).
C. C. HENTSCHEL, London (Gregarines).
G. HERKLOTS, Leeds (Plankton and Cephalopoda).
Dr. W. T. HILLIER, Birmingham (Osteology of the Herring).
A. D. HOBSON, Cambridge (Development of Polychætes).
Miss KEHOE, Plymouth (Platyhelminths).
Prof. HARALD KYLIN, Lund, Sweden (Algæ).
A. G. LOWNDES, Marlborough (General Zoology).
P. D. MURRAY, Oxford (Innervation of Striated Muscle).

H. G. Newth, Birmingham (Holothuria).
Miss A. M. Philip Smith, Cambridge (Protozoa).
F. A. Potts, Cambridge (Teredo and Pomatoceros).
Miss L. Russell, London, Ray Lankester Investigator (Nudibranch Metamorphosis).
Mrs. E. W. Sexton, Plymouth (Gammarus).
Miss E. S. Smyth, Bristol (Chromatophores in Red Algæ).
T. A. Stephenson, London (Zoantharia).
C. C. Stockman, Cambridge (Respiration in Invertebrates).
Prof. D. M. S. Watson, F.R.S., London (Turbellaria).
J. F. G. Wheeler, Bristol (Formation of Yolk in Teleosteans).
Miss E. Worsnop, Plymouth (Oysters).
L. R. Wormold, Leeds (Pycnogonida).

The usual Easter Vacation Course in Marine Biology was conducted by Dr. J. H. Orton, and was attended by forty students from Oxford, Cambridge, London, Manchester, Birmingham and Aberdeen, the number of students attending being limited by the accommodation available.

Mr. E. W. Shann brought a class of six boys from Oundle School, and Mr. A. G. Lowndes a class of twelve from Marlborough College.

A joint meeting of the Challenger Society and representatives from Marine Laboratories, under the Development Commissioners' scheme, was held at the Plymouth Laboratory on July 3rd and 4th. In addition to the staff and workers at the Laboratory the following attended the meeting: Messrs. J. O. Borley, R. E. Savage and Miss D. Thursby-Pelham (Lowestoft Laboratory), Mr. Spicer (Irish Fisheries Department), Mr. A. Scott (Piel), Mr. W. C. Smith (Port Erin), Mr. R. Elmhirst (Millport), Prof. Hindle (Cairo Medical School), Messrs. J. Needham and A. C. Gardiner (Cambridge), and Mr. R. A. Todd, H.M. Inspector of Fisheries, S.W. Area.

General Work at the Plymouth Laboratory.

During the first half of the year Mr. R. S. Clark continued his work on the distribution of the young of the principal marketable and other fishes. This work will not be lost in consequence of Mr. Clark's removal to Scotland, as he hopes to combine it with similar studies made in northern waters, and to publish one comprehensive account dealing with the young stages of British fishes as a whole. His work on the hake, which had made good progress, he hopes to treat in a similar way.

An account of Mr. E. Ford's work on the distribution of the animals forming the food of bottom-living trawl fish is published in the current number of the Journal. The work has been done by employing the Petersen grab, which takes from each spot on the sea-floor where it is used a definite sample of the soil with the animals living in and upon it, which can be treated in a quantitative way. Several important feeding banks have been explored and their limits determined. The work is supplemented by a study of the food actually eaten by the fishes by an examination of the contents of the alimentary canal.

Dr. J. H. Orton has continued his general studies on marine bionomics, and various short publications of results have been made pending extensive treatment. He delivered a series of three lectures on these subjects at King's College in February at the invitation of the University of London. Dr. Orton has also revised and prepared for press, in a slightly shortened form, the final report on the Oyster Mortality investigations, which he carried out for the Ministry of Agriculture and Fisheries and the Oyster Planters' Association. A summary of this report is published in the Journal of the Marine Biological Association.

A good deal of field work has been done by Dr. Orton in connection with experimental investigations on the rate of growth and sex-change in Crepidula and the oyster, and especially in following up sex-changes and growth in isolated oysters of known sex at a given time. It has been proved for the first time that male oysters change into females and that a few oysters female in 1922 or early 1923 were female again later in 1923. More than 200 cases of immediate change of sex of female oysters to male after spawning have been accumulated. The West Mersea experiment of 1922–23 was spoiled by mud accumulation, but the prospects for 1924 are promising. Ninety-five per cent of oysters operated upon in July, 1923, and found to be males were doing well in October and had mostly put on a remarkable growth of shell. It is hoped to obtain spawn from a good proportion of them next late spring.

Observations on the conditions correlated with shell-growth in the oyster, mussel and cockle, and with the condition of the gonad in the oyster, Crepidula and other animals are being continued. In this respect a short note on the experimental production of " rings " on the shells of Cardium has been published, in view of the importance of this result in the interpretation of the growth-periods of molluscs taken in the grab, and its possible importance in problems connected with periodical growth in fishes.

In addition to the above studies Dr. Orton has been engaged on experimental work on Anti-fouling Paint Compositions, which was begun in 1919, and a short account of the results was given at the Challenger Society meeting at Plymouth. He has also attended the meetings of the Devon and Cornwall Sub-committee on River Pollution, and with Prof. W. H. Lewis has prepared a memorandum on the methods of approaching problems of river pollution.

Dr. Lebour has continued to study living plankton in the plunger jars, with very similar results to those obtained last year. The medusa Chrysaora was specially watched, and although two individuals in the same jar would never attempt to eat each other they eagerly devoured Aurelia of the same size. Fishes nearly as long as the umbrella were also frequently eaten, besides many other plankton organisms. Several other medusæ were seen to eat fishes. *Rathkea octopunctata*, so common in the early part of the year, proves to be a great enemy of the larval herring, and eats larvæ many times its own size. Further enemies of the larval herring were shown to be Sagitta and Tomopteris, many

Sagitta having eaten the herrings. Pleurobrachia is also fond of larval herring having its stomach sometimes full of them, and some specimens of the same animal from a cruise of the *George Bligh* contained larval plaice and plaice eggs.

Further work has been done on the food of different animals of the plankton, confirmatory of last year's results, and tow-nettings have been regularly examined. The very fine tow-nets and centrifuged water were specially made use of for the study of Peridinians. Several interesting plankton animals were reared in the plunger jars, including the larva of Peachia, formerly recorded as Halcampa, which as a young larva clings to the medusa Phialidium.

An account of the Northern Peridinians is finished and ready for publication, entitled *The Dinoflagellates of Northern Seas.*

Mr. O. D. Hunt has been studying the food and methods of feeding of bottom-living animals, chiefly from the trawling grounds, by a systematic examination of stomach contents, supplemented by observations and experiments on feeding in aquaria. Broadly speaking, two types of feeding can be recognised, for whilst some animals are carnivorous, feeding on other animals of relatively large size, others consume chiefly the mud, which forms the surface layer of the soil of the sea-floor, and the many minute organisms which live in that mud. In the case of many of the species which have been studied, it is becoming possible to trace the chain of food relationships to these minute organisms, especially to the microscopic algæ amongst them, which seem, in this neighbourhood at any rate, to be of more importance than the dead and decaying organic matter in the mud itself.

Amongst the carnivorous animals the majority seem to have a restricted diet, feeding upon one or two species only, but there are a few which are more miscellaneous feeders. Thus the starfish, Astropecten, which lives on the trawling grounds, consumes large numbers of young bivalve molluscs and of the echinoderm, *Echinocyamus pusillus*, its diet in this respect being similar to that of the dab with which fish it must be a strong competitor for food. The closely allied but larger starfish Luidia, on the other hand, preys mainly on other echinoderms, devouring numbers of Asterias, as well as large Spatangids and *Thyone fusus*.

Hydrographic stations were worked by Dr. W. R. G. Atkins and Mr. H. W. Harvey in the *Salpa*, including five cruises to Ushant and thence to the Bristol Channel. The data obtained are being sent to the International Council and to Dr. Le Danois of the French Fishery Department for co-ordination with the French and Irish results. Dr. Le Danois is publishing from time to time a review of the hydrographical conditions in the English Channel and on the Atlantic slope.

Dr. Atkins has determined hydrogen ion concentrations of the water samples taken and has followed the variations in organic content of the waters from the acidity produced in the samples on standing. His work is further referred to below.

The hydrographic data obtained monthly at the Station E1 (22 miles S.W. of Plymouth) during the three years 1921, 1922, and 1923 are beginning to show promise of correlating the duration and strength of the north-easterly drift of the Gulf Stream into the English Channel, with the general climatic conditions of the autumn and early winter.

Mrs. E. W. Sexton has continued her experiments on the Mendelian inheritance of eye-colour in *Gammarus chevreuxi*. The Red eye mutation occurred once in 1912, and has never since appeared until this year, although many hundreds of experiments have been closely followed, and at least 50,000 wild specimens examined. It has now reappeared in the stock which is being employed in experiments on the influence of temperature. This stock was brought in from Chelson Meadows in September and October, 1922, and the red eyes occurred in the offspring of the first generation of those which were being kept at the ordinary temperature of the Laboratory, and in the second generation of those kept at a higher temperature in an incubator. Other mutations have also been found in the same stock. These mutations are now being tested, in order to see if they are of exactly the same genetic constitution as those previously used in the experiments. Large samples of Gammarus from the particular ditches where the above stock was taken have been examined, without finding any with abnormal eyes.

Mr. W. De Morgan has completed a paper on the protozoan, *Foettingeria actiniarum*, parasitic in Anemones, in which the nuclear changes during reproduction are described. The paper is being published in the Quarterly Journal of Microscopical Science.

Mr. J. F. G. Wheeler, who worked at the Laboratory until September, with a grant from the Department of Scientific and Industrial Research, has completed a paper on the histology of the developing eggs of fishes, which is now in course of publication.

Department of General Physiology.

During the year the space available was taxed to its utmost, and would have proved altogether inadequate were it not that workers visiting the Laboratory were accommodated in the new Easter Class Building and in the main general laboratory over the tank room. As shown by the list of workers the subjects studied were of a varied nature. In the light of the requirements of visitors some additional apparatus is being purchased.

Dr. Atkins has continued his work on the hydrogen ion concentration of sea-water, and minor differences between the years 1921, 1922 and 1923 were noted. The data are now nearly complete for making a revision of the estimate of the minimum value of the plankton crop by the alkalinity method.

During the year the phosphate content of sea and estuarine water has been studied, as has also that of certain fresh waters. The results for sea-water are in close agreement with those obtained in 1915–16 by

D. J. Matthews. It has further been established that the surface water well out to sea is entirely denuded of phosphate during the summer, the change being such as to lower the concentration very markedly right down to the bottom. The diminution in phosphate is due to the development of the algal plankton, and was studied in the Laboratory on insolated sea-water and on a culture of Nitzschia. Assuming that the plankton contains 0·15 per cent of P_2O_5, reckoned on its wet weight, the observed change from March to July suffices to produce 1·4 kilograms of algal plankton per square metre in a column 70 metres in depth, or 1,400 metric tons per square kilometre. With a certain assumption as to the percentage of carbohydrate in this plankton the figure just given is in good agreement with that obtained by the alkalinity method.

Estimations have also been made of the silica in solution in sea and fresh water, and it has been shown that the latter may vary considerably in silica content, but is as a rule far richer than is sea-water.

The estimation of the oxidisable organic matter in sea-water necessitated a modification of the standard method owing to the high chlorine content. Seasonal changes have not as yet been studied.

A few exposure tests were made with young fish trawl and silk plankton nets, and it was found that sunlight appears to be a far more potent agent than are bacteria in causing deterioration, especially in the case of silk. Formalin neutralised with borax was tried as a preservative, and was found to be injurious, as was also a daily rinsing with fresh water. Rapid drying followed by storage in the dark is recommended.

Mr. C. F. A. Pantin has continued at this Laboratory work started with Mr. J. Gray at Cambridge upon the physiology of amœboid movement. He has traced the effect of hyper- and hypotonic solutions upon the rate of motion. The changes in the form and consistency of the amœba have also been studied, as well as its changes in reaction as demonstrated by intra vitam staining with indicators. This is believed to be the first instance in which such a change in reaction, accompanying motion, has been demonstrated in a single cell.

Published Memoirs.

The following papers, the outcome of work done at the Laboratory, have been published elsewhere than in the Journal of the Association :—

ALLEN, E. J. *Scientific Research in Relation to the Fisheries, including the Work of the Independent Institutions.* Assoc. Brit. Fisheries, Vol. I, No. 3, App. "G," 1923. Also Fish Trades Gazette, Vol. XLI, 1923, No. 2089, p. 33.

ATKINS, W. R. G. *The Hydrogen Ion Concentration of Natural Waters in Relation to Disease.* Journ. of State Medicine, Vol. XXXI, 1923, pp. 223–226.

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The Library.

Both the general library and the special physiological library have continued to increase during the year, and the collection of books dealing with the science of the sea is now one of the most complete in the country.

The thanks of the Association are again due to numerous Government Departments, Universities and other Institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library. Thanks are due also to those authors who have sent reprints of their papers to the Library.

Vice-Presidents, Officers, and Council.

The following is the list of gentlemen proposed by the Council for election for the year 1924–25:—

President.

Sir E. RAY LANKESTER, K.C.B., LL.D., F.R.S.

Vice-Presidents.

The Duke of BEDFORD, K.G.
The Earl of STRADBROKE, C.V.O., C.B.
Viscount ASTOR.
Lord MONTAGU OF BEAULIEU.
The Earl of BALFOUR, K.G., F.R.S.
The Right Hon. Sir ARTHUR GRIFFITH-BOSCAWEN.
The Right Hon. AUSTEN CHAMBERLAIN, M.P.
G. A. BOULENGER, Esq., F.R.S.
W. B. HARDY, Esq., SEC.R.S.
Sir ARTHUR STEEL-MAITLAND, Bart., M.P.
Prof. W. C. MCINTOSH, F.R.S.

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Prof. W. GARSTANG, D.Sc.
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J. A. ROBERTSON, Esq.
Prof. D'ARCY THOMPSON, C.B., F.R.S.
Prof. D. M. S. Watson, F.R.S.

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Hon. Treasurer.

GEORGE EVANS, Esq., 1 Wood Street, London, E.C.2.

Hon. Secretary.

E. J. ALLEN, Esq., D.Sc., F.R.S.,
The Laboratory, Citadel Hill, Plymouth.

The following Governors are also members of Council:—

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E. T. BROWNE, Esq.
OWEN HUGH SMITH, Esq., (Prime Warden of the Fishmongers' Company).
W. T. BRAND, Esq. (Fishmongers' Company).
GEORGE EVANS, Esq. (Fishmongers' Company).
His Honour Judge CHAPMAN (Fishmongers' Company).
LOTHIAN D. NICHOLSON, Esq. (Fishmongers' Company).
Major NIGEL O. WALKER, O.B.E. (Fishmongers' Company).
Prof. G. C. BOURNE, D.Sc. F.R.S. (Oxford University).
Sir ARTHUR E. SHIPLEY, G.B.E., D.Sc., F.R.S. (Cambridge University).
Sir WILLIAM A. HERDMAN, C.B.E., D.Sc., F.R.S. (British Association).

List of Annual Subscriptions

Paid during the Year, 1st April, 1923, to 31st March, 1924.

	£	*s.*	*d.*
Dr. W. M. Aders	1	1	0
E. J. Allen, Esq., D.SC., F.R.S.	1	1	0
G. L. Alward, Esq.	1	1	0
Prof. J. H. Ashworth, D.SC., F.R.S.	1	1	0
J. R. Baker, Esq.	1	1	0
Prof. W. Bateson, F.R.S. (1923 and 1924)	2	2	0
Sir W. Maddock Bayliss, D.SC., F.R.S. (the late)	1	1	0
W. J. Bazeley, Esq.	1	1	0
Lieut.-Col. T. T. Behrens	1	1	0
Mrs. M. G. Bidder	1	1	0
E. J. Bles, Esq., D.SC.	1	1	0
H. H. Bloomer, Esq. (1922 and 1923)	2	2	0
H. Moss Blundell, Esq.	1	1	0
Mrs. H. Moss Blundell	1	1	0
L. A. Borradaile, Esq.	1	1	0
E. G. Boulenger, Esq.	1	1	0
Prof. Gilbert C. Bourne, F.R.S.	1	1	0
Col. Henry Bowles	1	1	0
Dr. A. Bowman	1	1	0
Sir J. Rose Bradford, K.C.M.G., M.D., D.SC., F.R.S.	1	1	0
Brighton Public Library	1	1	0
H. H. Brindley, Esq.	1	1	0
Carried forward	25	4	0

	£	*s.*	*d.*
Brought forward	25	4	0
L. W. Byrne, Esq.	1	1	0
Dr. W. T. Calman, F.R.S.	1	1	0
H. Graham Cannon, Esq.	1	1	0
Prof. C. Chilton	1	1	0
Dr. J. Clark	1	1	0
J. F. Coonan, Esq.	1	1	0
L. R. Crawshay, Esq., M.A.	1	1	0
H. H. Dale, Esq., C.B.E., M.D., F.R.S.	1	1	0
Commander G. L. C. Damant, R.N.	1	1	0
Prof. Otto V. Darbishire	1	1	0
Dr. W. Cameron Davidson	1	1	0
W. C. De Morgan, Esq.	1	1	0
Prof. A. Dendy, F.R.S.	1	1	0
Director of Agriculture and Fisheries, Travancore, S. India	1	1	0
F. A. Dixey, Esq., F.R.S.	1	1	0
C. C. Dobell, Esq., F.R.S.	1	1	0
F. Martin Duncan, Esq. (1922 and 1923)	2	2	0
J. S. Dunkerly, Esq., D.SC.	1	1	0
Howard Dunn, Esq.	1	1	0
Major E. V. Elwes	1	1	0
George Evans, Esq.	1	1	0
G. Herbert Fowler, Esq., B.A., PH.D. (1922 and 1923)	2	2	0
Dr. E. L. Fox	1	1	0
Prof. F. W. Gamble, D.SC., F.R.S.	1	1	0
Prof. J. Stanley Gardiner, F.R.S. (1923 and 1924)	2	2	0
Prof. E. S. Goodrich, F.R.S.	1	1	0
J. Gray, Esq.	1	1	0
Carried forward	56	14	0

	£	s.	d.
Brought forward	56	14	0
Robert Groome, Esq.	1	1	0
Sir Eustace Gurney	1	1	0
Wilfred Hall, Esq.	1	1	0
A. C. Hardy, Esq.	1	1	0
Prof. Sydney J. Hickson, D.SC., F.R.S.	1	1	0
Prof. J. P. Hill, F.R.S.	1	1	0
W. T. Hillier, Esq., M.R.C.S.	1	1	0
T. V. Hodgson, Esq.	1	1	0
Capt. G. C. L. Howell	1	1	0
P. Hoyte, Esq. (1922 and 1923)	2	2	0
J. S. Huxley, Esq.	1	1	0
J. J. Judge, Esq.	1	1	0
Sir Frederick Keeble, C.B.E., SC.D., F.R.S.	1	1	0
R. Kirkpatrick, Esq.	1	1	0
J. J. Lister, Esq., F.R.S.	1	1	0
Prof. E. W. MacBride, D.SC., F.R.S.	1	1	0
Stanislaus Makovski, Esq.	1	0	0
D. J. Matthews, Esq.	1	1	0
Capt. W. N. McClean	1	1	0
J. H. Midgley, Esq.	1	1	0
Milford Haven Trawler Owners and Fish Salesmen's Association, Ltd.	1	1	0
W. S. Millard, Esq.	1	1	0
P. Chalmers Mitchell, Esq., C.B.E., D.SC., F.R.S. (1922 and 1923)	2	2	0
Major A. R. Moncrieff (1923 and 1924)	2	2	0
C. C. Morley, Esq.	1	1	0
H. G. Newth, Esq.	1	1	0
Carried forward	87	2	0

	£	s.	d.
Brought forward	87	2	0
Charles Oldham, Esq.	1	1	0
G. W. Paget, Esq. (1922 and 1923)	2	2	0
Enrique Pascual, Esq.	1	1	0
Plymouth Corporation (Museum Committee)	1	1	0
Plymouth Corporation (Education Committee) (1922 and 1923)	2	2	0
Plymouth Proprietary Library	1	1	0
Port of Plymouth Incorporated Chamber of Commerce	1	1	0
Mrs. H. Porter (1922 and 1923)	2	2	0
W. P. Pycraft, Esq.	1	1	0
Major G. Raymond	1	1	0
J. A. Robertson, Esq., J.P. (the late)	1	1	0
E. S. Russell, Esq., D.SC.	1	1	0
J. T. Saunders, Esq.	1	1	0
R. E. Savage, Esq.	1	1	0
F. W. Schiller, Esq. (1922 to 1924)	3	3	0
Edgar Schuster, Esq., D.SC.	1	1	0
W. L. Sclater, Esq.	1	1	0
L. E. Sexton, Esq. (the late)	1	1	0
Miss Lilian Sheldon	1	1	0
W. Eric Stoneman, Esq. (1922–1924)	3	3	0
H. H. Sturch, Esq.	1	1	0
S. Takeda, Esq.	1	1	0
Prof. W. M. Tattersall	1	1	0
Sir H. F Thompson, Bart.	1	1	0
Sir John Thornycroft, F.R.S.	1	1	0
Lieut.-Col. H. J. Walton, I.M.S., M.D., F.R.C.S.	1	1	0
Sir Nicholas Waterhouse, K.B.E. (1921–1923)	3	3	0
Carried forward	124	18	0

	£	s.	d.
Brought forward	124	18	0
Arthur W. Waters, Esq.	1	1	0
A. T. Watson, Esq. (the late)	1	1	0
Mrs. Weldon	1	1	0
W. A. Willes, Esq.	1	1	0
Ronald Winckworth, Esq., M.A., F.R.G.S.	1	1	0
Total	£130	3	0

Special Donations for Easter Class Building Fund

For the Year, 1st April, 1923, to 31st March, 1924.

	£	s.	d.
E. T. Browne, Esq.	25	0	0
T. T. Barnard, Esq.	10	0	0
Prof. J. Stanley Gardiner, F.R.S.	10	0	0
Dr. W. M. Aders	5	0	0
F. Balfour Browne, Esq.	5	0	0
Prof. F. W. Gamble, F.R.S.	5	0	0
J. H. Orton, Esq., D.SC.	2	2	0
Total	62	2	0

Donations for 1922–23	214	13	6
Donations for 1923–24	62	2	0
Total	£276	15	6

THE MARINE BIOLOGICAL ASSOCIATION

Dr.

Statement of Receipts and Payments for the

GENERAL

	£	s.	d.	£	s.	d.
To Balance from 31st March, 1923 :—						
Cash in hand	10	15	9			
Cash at Bank	327	8	0			
Balance from Easter Class Building Fund	153	10	0	491	13	
,, Grants :—						
,, Ministry of Agriculture and Fisheries Grant from Development Fund	9,000	0	0			
Fishmongers' Company	757	10	0			
British Association	25	0	0	9,782	10	0
,, Subscriptions				130	3	0
,, Composition Fees				31	15	0
,, Donations				42	10	6
,, Sale of Specimens (*less* Purchases)				880	10	6
,, ,, Fish (*less* Expenses)				59	10	6
,, ,, Nets, Gear, and Hydrographical Apparatus				338	6	1
,, Table Rent (including Trustees of the Ray Lankester Fund), £20 ; Oxford University, £52 10s. ; Cambridge University, £25 ; Bristol University, £25 ; London University, £50 ; Leeds University, £10 10s.				299	4	0
,, Tank Room Receipts				306	1	1
,, Interest on Investments :—						
4% War Stock	3	2	8			
4% New Zealand Stock	12	14	8			
Deposit Account	9	2	8	25	0	0
,, Royalties on Films produced by "British Instructional Films, Ltd."				386	10	0
,, Final Dividend from Naval Bank				1	2	5
				£12,774	16	10

The Association's Bankers hold on its behalf:—
£410 14s. 8d. New Zealand 4% Stock, 1943–63.
£78 9s. 4d. 4% War Loan, 1929–42.
£51 War Savings Certificates.

SPECIAL

	CAPITAL		
	£	s.	d.
To Balance from 31st March, 1923 :—			
Cash at Bank	550	18	9
	£550	18	9

EASTER CLASS

	£	s.	d.
To Donation	62	2	0
,, Sale of War Savings Certificates	94	1	2
	£156	3	2

MOTOR BOAT

	£	s.	d.
To Sale of War Savings Certificates	£350	1	2

OF THE UNITED KINGDOM.

Year, 1*st April*, 1923, *to* 31*st March*, 1924. **Cr.**

FUND.

	£	s.	d.	£	s.	d.
By Salaries :—						
Director	912	10	0			
Physiologist	840	0	0			
Naturalists	2,544	3	4			
Hydrographer	478	6	8	4,775	0	0
,, Laboratory Wages (including National Insurance and Pension)				1,523	7	6
,, Annual Upkeep of Library				331	10	2
,, Scientific Publications :—						
Journal, Vol. XIII, No. 1	370	7	7			
Less Sales	35	12	11	334	14	8
,, Annual Upkeep of Laboratories and Tank Rooms :—						
Buildings and Machinery	453	8	9			
Electricity, Gas, Coal, and Water	234	3	0			
Chemicals and Apparatus	481	7	11			
Rates, Taxes, and Insurance	84	0	1			
Travelling	57	14	8			
,, Challenger Society Meetings	23	10	8			
Stationery, Postages, Telephone, Carriage, and Sundries	364	14	7	1,698	19	8
,, Annual Maintenance and Hire of Boats :—						
Wages (including Diet Allowance, National Insurance, and Casual Labour)	1,512	6	8			
Coal and Water	669	10	5			
Maintenance and Repairs, with Nets, Gear, and Apparatus	830	8	4			
Boat Hire and Collecting Expeditions	32	8	3			
Insurance	363	1	0	3,407	14	8
,, Interest on Loan				3	5	9
,, Balance :—						
Cash in hand	12	12	9			
Cash at Bank	687	11	8	700	4	5
				£12,774	16	10

FUND.

EXPENDITURE.

	£	s.	d.
By Outfitting Steam Drifter	244	15	9
,, Physiological Library	105	14	11
,, Lords Commissioners of His Majesty's Treasury (Repayment of Loan and Balance on Capital Account)	200	8	1
	£550	18	9

BUILDING FUND.

	£	s.	d.
By Balance from 31st March, 1923 :—			
Amount due to General Fund	153	10	0
,, Expenditure on Building	2	13	2
	£156	3	2

ACCOUNT.

	£	s.	d.
By Expenditure in Building Boat	£350	1	2

Examined and found correct,
(Signed) N. E. Waterhouse.
Geo. P. Bidder.
J. O. Borley.
Edward T. Browne.

3 *Frederick's Place,*
Old Jewry, London, E.C. 2.
29*th April*, 1924.

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Journal of the Marine Biological Association of the United Kingdom.

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OBJECTS

OF THE

Marine Biological Association

OF THE UNITED KINGDOM.

THE ASSOCIATION was founded at a Meeting called for the purpose in March, 1884, and held in the Rooms of the Royal Society of London.

The late Professor HUXLEY, at that time President of the Royal Society, took the chair, and amongst the speakers in support of the project were the late Duke of ARGYLL, the late Sir LYON PLAYFAIR, the late Lord AVEBURY, the late Sir JOSEPH HOOKER, the late Dr. CARPENTER, the late Dr. GÜNTHER, the late Lord DALHOUSIE, the late Professor MOSELEY, the late Mr. ROMANES, and Sir E. RAY LANKESTER.

The Association owes its existence and its present satisfactory condition to a combination of scientific naturalists, and of gentlemen who, from philanthropic or practical reasons, are specially interested in the great sea fisheries of the United Kingdom. It is universally admitted that our knowledge of the habits and conditions of life of sea fishes is very small, and insufficient to enable either the practical fisherman or the Legislature to take measures calculated to ensure to the country the greatest return from the "harvest of the sea." Naturalists are, on the other hand, anxious to push further our knowledge of marine life and its conditions. Hence the Association has erected at Plymouth a thoroughly efficient Laboratory, where naturalists may study the history of marine animals and plants in general, and where researches on food-fishes and molluscs may be carried out with the best appliances.

The Laboratory and its fittings were completed in June, 1888, at a cost of some £12,000. Since that time investigations, practical and scientific, have been constantly pursued at Plymouth. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council; in addition, naturalists from England and from abroad have come to the Laboratory, to carry on their own independent researches, and have made valuable additions to zoological and botanical science, at the expense of a small rent for the use of a working table in the Laboratory and other appliances. The number of naturalists who can be employed by the Association in special investigations on fishery questions, and definitely retained for the purpose of carrying on those researches throughout the year, must depend on the funds subscribed by private individuals and public bodies for the purpose. The first charges on the revenue of the Association are the working of the sea-water circulation in the tanks, stocking the tanks with fish and feeding the latter, the payment of servants and fishermen, the hire and maintenance of fishing-boats, and the salary of the Resident Director and Staff. At the commencement of this number will be found the names of the gentlemen on the Staff.

The purpose of the Association is to aid at the same time both science and industry. It is national in character and constitution, and its affairs are conducted by a representative Council, by an Honorary Secretary and an Honorary Treasurer, without any charge upon its funds, so that the whole of the subscriptions and donations received are devoted absolutely to the support of the Laboratory and the prosecution of researches by aid of its appliances. The reader is referred to page 4 of the Cover for information as to membership of the Association.

CONTENTS OF NEW SERIES, Vol. XIII., No. 2.

NOTICE.

The Council of the Marine Biological Association wish it to be understood that they do not accept responsibility for statements published in this Journal excepting when those statements are contained in an official report of the Council.

TERMS OF MEMBERSHIP.

		£	s.	d.
Annual Members	per annum	1	1	0
Life Members	Composition Fee	15	15	0
Founders		100	0	0
Governors		500	0	0

Members of the Association have the following rights and privileges: they elect annually the Officers and Council; they receive the Journal of the Association free by post; they are admitted to view the Laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the Laboratory for research, with use of tanks, boats, &c.; and have access to the books in the Library at Plymouth.

All correspondence should be addressed to the Director, The Laboratory, Plymouth.