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# THE BIOLOGY OF *NICOTHOË ASTACI* AUDOUIN AND MILNE EDWARDS

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(Text-figs. 1–4)

*Nicothoë astaci* is a choniostomatid copepod (Gurney, 1929) parasitic on the gills of the lobster, *Homarus vulgaris* Milne Edwards. In view of the possible effect of *Nicothoë* on the lobster, which is of considerable commercial importance in Scotland, a programme of work was instituted on the biology of the parasite.

*Nicothoë* attaches itself by means of its suctorial mouth to a gill filament of the lobster, and the wall of the filament is pierced by the sharp, styliform mandibles. The host's blood is sucked by means of a muscular gullet leading to the stomach. *Nicothoë* often occurs in groups, especially near the bases of the gills. The adult parasite is incapable of any movement except a slight lateral displacement of the abdomen and, once attached, probably remains in the same position throughout its life. Little is known of the life cycle, and all individuals so far definitely recognized have been females.

## MATERIAL AND METHODS

Specimens of *Nicothoë astaci* were collected from six samples of preserved Orkney lobsters between September 1954 and November 1955, and, in order more adequately to cover the annual cycle of *Nicothoë*, nine further samples were obtained from Bernera, Lewis, between October 1955 and November 1956. Lobsters arriving in poor condition at two merchants' premises were preserved in formalin and sent to the Marine Laboratory, Aberdeen, for examination. Living parasites were also examined, and stained sections and whole mounts prepared.

## THE ADULT FEMALE

The adult female (Figs. 1 and 2) is made up of three parts: (i) cephalothorax; (ii) thorax, which bears two large lateral expansions or wings; and (iii) abdomen, which carries two oval egg-sacs. The length to the tip of the abdomen is some 1·2 to 1·7 mm; each wing, measured from its tip to the junction of its anterior edge with the trunk, is up to some 4 mm long; the egg-sacs measure up to 3 mm.

The segmentation is set out in Table 1 and shown in Fig. 2. The appendages are not figured in detail as this has been done by previous workers (Leigh-Sharpe, 1926; Gurney, 1929).

The first two thoracic segments are fused to the head, and the next three, which are distinguishable dorsally by three rings, are concerned in the formation of the wings. Articulation is between the posterior edge of the wings and the sixth thoracic segment, the latter being fused to the first abdominal segment.

The adult female of *Nicothoë* has the full complement of segments and limbs, and is to be regarded as a modification of, rather than a degeneration from, the typical copepod form.

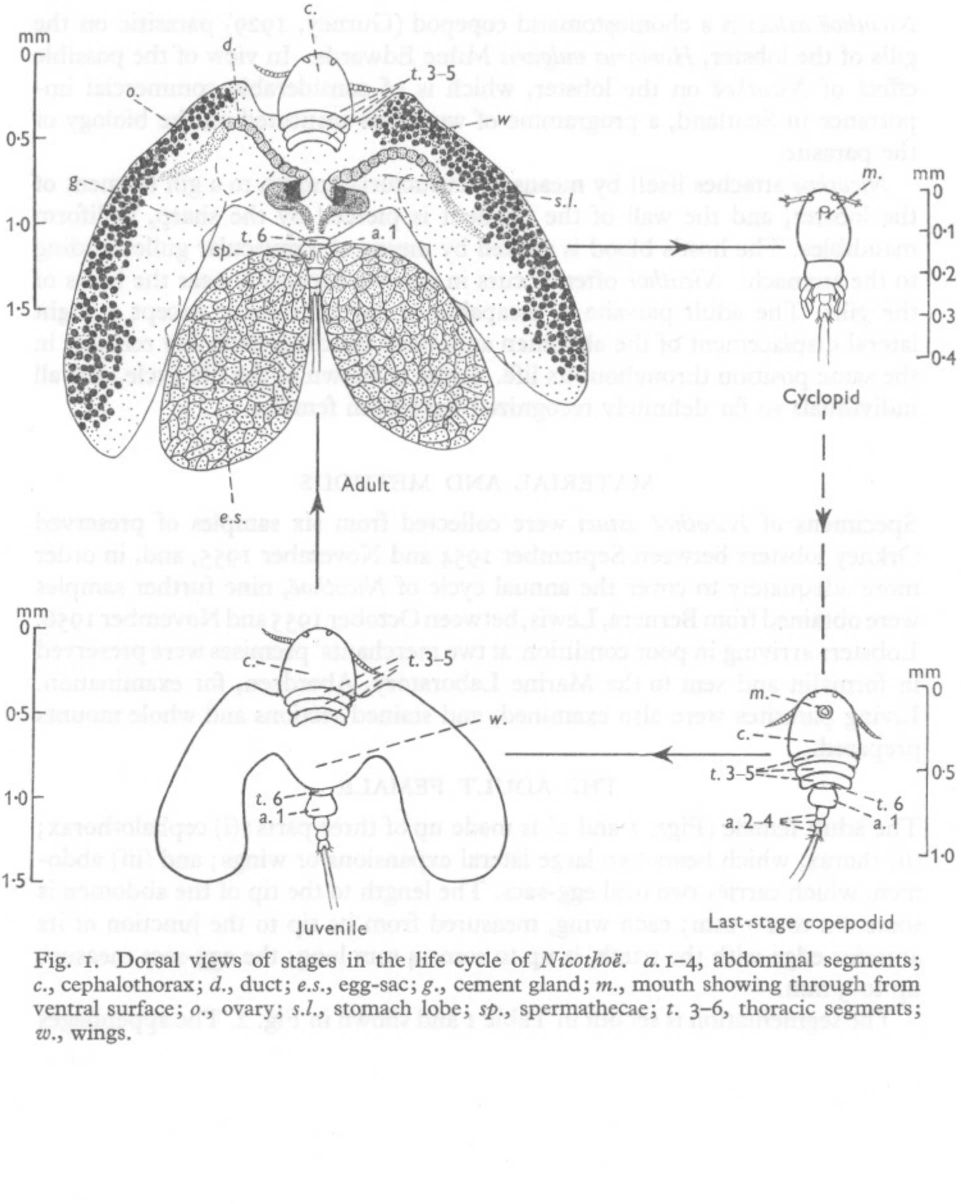


Fig. 1. Dorsal views of stages in the life cycle of *Nicothoë*. *a.* 1–4, abdominal segments; *c.*, cephalothorax; *d.*, duct; *e.s.*, egg-sac; *g.*, cement gland; *m.*, mouth showing through from ventral surface; *o.*, ovary; *s.l.*, stomach lobe; *sp.*, spermathecae; *t.* 3–6, thoracic segments; *w.*, wings.

TABLE 1. SEGMENTATION IN *NICOTHOË*

| Body region | Segment | Appendages: Name | Appendages: Form |
|---|---|---|---|
| Cephalothorax | 1. 1st cephalic | — | — |
| | 2. 2nd cephalic | 1st antennae | Long, 11-jointed, setigerous |
| | 3. 3rd cephalic | 2nd antennae | 4-jointed, flexed on themselves |
| | 4. 4th cephalic | Mandibles | Styliform, passing into mouth tube |
| | 5. 5th cephalic | 1st maxillae | 2-jointed, anterior joint tripartite |
| | 6. 6th cephalic | 2nd maxillae | 2-jointed, with a pair of lappets distally |
| | 7. 1st thoracic | Maxillipeds | 4-jointed, terminal joint small |
| | 8. 2nd thoracic | Biramous limbs | Basal joint and two 3-jointed rami, setigerous |
| Thorax (wings) | 9. 3rd thoracic (dorsal ring) | Biramous limbs | Basal joint and two 3-jointed rami, setigerous |
| | 10. 4th thoracic (dorsal ring) | Biramous limbs | Basal joint and two 3-jointed rami, setigerous |
| | 11. 5th thoracic (dorsal ring) | Biramous limbs | Basal joint and two 3-jointed rami, setigerous |
| Abdomen | 12. 6th thoracic | Uniramous limbs | Vestigial, setigerous |
| | 13. 1st abdominal. Genital | (Egg-sacs) | |
| | 14. 2nd abdominal | | |
| | 15. 3rd abdominal | | |
| | 16. 4th abdominal. Bilobed | (Each lobe has a caudal style and 4 setae) | |

## THE BREEDING CYCLE

The paired ovaries are situated one in each wing, where they cover the stomach lobes anteriorly (Fig. 1). Posteriorly each lobe is covered by a cement gland. A dorsal genital duct, which serves both ovary and cement gland, passes proximally in each wing to open on the 1st abdominal segment. The contents of the ducts, thought by Van Beneden (1850) to be eggs, are, in fact, glandular in nature. Near the looped bases of the ducts are dark bodies, thought to be concerned in the secretion of the egg-sacs. In the 1st abdominal segment, near the openings of the oviducts, is a pair of curved spermathecae.

Individuals of *Nicothoë* with small wings but without egg-sacs (juveniles, Fig. 1) are found almost entirely on lobsters which have recently cast their shells (see p. 13). As the wings grow the ovaries begin to develop; they first appear when the wings are some 1·5 mm long, and soon become ripe, generally when the wings have attained a length of 2·0–2·2 mm. The eggs are extruded with the secretion of the duct and cement glands, to form the egg-sacs. The parasites have then become adults, and have empty gonads and egg-sacs full of eggs. Development of the eggs into embryos commences at once, fertilization by sperm from the spermathecae (see p. 11), presumably having occurred before they entered the egg-sacs. The ovaries recover at the same time, and concurrent series of changes take place in the ovaries and

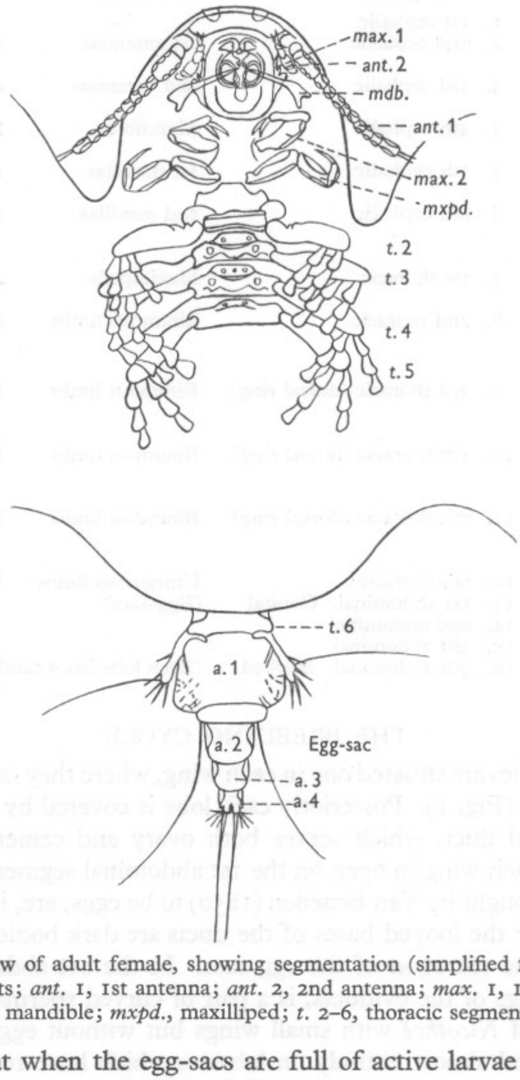


Fig. 2. Ventral view of adult female, showing segmentation (simplified for clarity). *a.* 1–4, abdominal segments; *ant.* 1, 1st antenna; *ant.* 2, 2nd antenna; *max.* 1, 1st maxilla; *max.* 2, 2nd maxilla; *mdb.*, mandible; *mxpd.*, maxilliped; *t.* 2–6, thoracic segments and appendages.

egg-sacs, so that when the egg-sacs are full of active larvae ready to be released, the gonads are again full of ripe eggs. The egg-sacs burst, releasing the larvae, the gonad spawns and new egg-sacs are extruded, and the cycle is repeated.

The series of changes in the reproductive system of the juvenile and adult *Nicothoë*, and the corresponding changes in the egg-sacs of the adult, have been divided into six stages, as follows.

*Immature* (juvenile) or *Spent* (adult). Stomach lobes occupy almost whole of wings. No sign of development of ovaries visible externally in juvenile; adult ovary appears empty or contains a few residual eggs; sections show many young oocytes, 10–12 $\mu$, each with a spherical, vesicular nucleus. Cement glands small, appear translucent externally; contain a little granular secretion, staining pale blue in haematoxylin and eosin, from glandular cells near outer wall of gland. Ducts, 75 $\mu$ wide, tapering slightly distally, appear empty, or contents sparse, but sections show that they are composed of a glandular tissue similar to that of cement glands and contain a little granular secretion. Egg-sacs contain spherical eggs, 120–150 $\mu$, or eggs which have just commenced division.

*Developing*. Ovaries become visible externally as granular, greyish bodies, but with no definite oocytes visible; sections show strings of young oocytes, 10–12 $\mu$, with a few larger ones, up to 30 $\mu$, between. A group of actively dividing oogonia on anterior edge of each wing. Cement glands larger, pale, containing more granular secretion. Glandular tissue in ducts assumes a segmented appearance, being divided up into well-defined packets, some 80 $\mu$ long, which also contain granular secretion. Larvae in egg-sacs 150–200 $\mu$.

*Half-full*. Ovaries darker, definite rounded oocytes up to 75 $\mu$ visible externally; strings of young oocytes and groups of actively dividing oogonia seen in sections. Cement glands and ducts appear darker and have similar granular contents, staining pink in haematoxylin and eosin; at centre of cement gland granules are coalescing to form small droplets of a clear fluid which stains pale pink. Larvae in egg-sacs 200–230 $\mu$, showing signs of segmentation.

*Full*. Ovaries large, full of spherical oocytes up to 95 $\mu$ in diameter, each with germinal vesicle 17 $\mu$ and nucleolus 4 $\mu$; few young oocytes; patches of oogonia present. Cement glands large, appear opaque externally, but sections show further coalescence of granules to form clear fluid which stains pale pink. Ducts darker, contents granular. Larvae in egg-sacs 230–270 $\mu$, showing rudimentary limbs.

*Ripe*. Ovaries densely coloured, pink. Eggs up to 110 $\mu$, polygonal in sections, closely packed together; some have undergone, or are undergoing, maturation, germinal vesicles break down and spindles often visible in sections. Patches of active oogonia still present, but few young oocytes. Cement glands now full of clear fluid after coalescence of granules, staining pink. Ducts also now contain clear pink-staining secretion, though some granules may persist; glandular tissue in duct now reduced to a narrow strip along one side. Dark bodies near bases of ducts also contain clear fluid, which stains pink. Egg-sacs full of active cyclopid larvae, 270–290 $\mu$, with suctorial mouth and two pairs of swimming legs. Each sac contains several hundred cyclopids. Egg-sacs of some ripe individuals have burst, releasing cyclopids, prior to spawning and extrusion of new egg-sacs.

*Spawning*. Old egg-sacs have been lost and larvae released. New egg-sacs formed and in process of being filled with spherical eggs. Outer wall of egg-sac probably composed of secretion from dark bodies which will be first secretion extruded. Ovaries patchy; matured eggs pass slowly down ducts in clear, sticky secretion from cement glands, and into egg-sacs, causing them to swell. Eggs in ducts compressed, cylindrical. Spawning results in the production of the spent individual, and the next generation of oocytes arise from the oogonia. Few individuals were seen at this stage.

The development of the larvae in the egg-sacs was described by Rathke (1843) and Van Beneden (1850), and is not given here in detail.

## THE LIFE CYCLE AND GROWTH OF *NICOTHOË*

The cyclopid larva of *Nicothoë* (Figs. 1, 3), which is released from the egg-sac into the surrounding water, has been described by Gurney (1929). It is some 0·27–0·29 mm long, with a full complement of mouthparts, two pairs of legs and a rudimentary third pair. It has a suctorial mouth tube. The cephalothorax is as long as the rest of the body, and includes the segment of leg 1. The segments of legs 2 and 3 are free, and are followed by two legless segments and a pair of furcal rami.

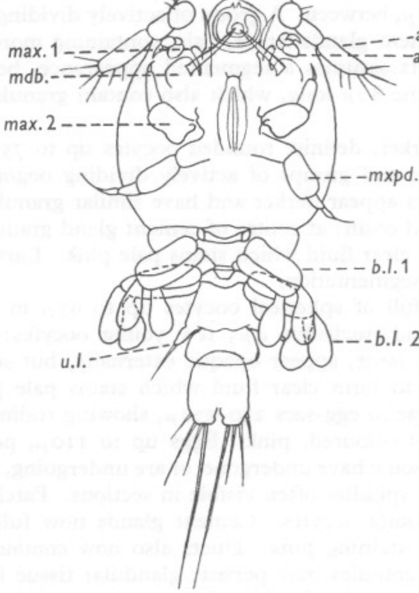


Fig. 3. Ventral view of cyclopid larva (appendages simplified). *b.l.*, biramous limb; *u.l.*, uniramous limb; other lettering as in Fig. 2.

The earliest stage of *Nicothoë* seen on lobster gills was the last-stage copepodid (Fig. 1), some 0·86–0·99 mm long, which was obtained by shaking the gills in water. It has the full complement of segments and limbs and resembles the adult in all respects except for the absence of wings and egg-sacs. Since the wings have not yet commenced development, the 6th thoracic segment abuts directly on the limb-bearing portion of the 5th. The last-stage copepodid is capable of swift, darting movements. After the last-stage copepodid is seen a whole series of stages of juveniles, showing the development of the wings, through individuals with small, bud-like growths, to those with large wings and the 6th thoracic segment well separated from the limb-bearing portion of the 5th (Fig. 1). The only increase in length after the last copepodid stage is due to the increase in size of the middle part of the wings. As growth proceeds, the gonads develop, and, usually when the wings have attained a length of some 2·0–2·2 mm (but more or less in some individuals, see Table 2), egg-sacs are extruded and the parasite becomes adult. Growth continues (the largest adult recorded had wings 4·56 mm long), and the reproductive cycle is repeated.

There is thus a gap in our knowledge of the life history of *Nicothoë*. There would seem to be a free-living stage or a phase on an intermediate host, during which one or more moults occur. There is, however, little essential difference between the mouthparts in the cyclopid and last-stage copepodid, except that, in the latter, the sucker is slightly more complicated and the 1st maxilla, whilst retaining the same form, has an extra flagellum on the anterior branch (Gurney, 1929). In both, two thoracic segments are included in the cephalothorax. The only radical changes which occur in the gap are the increase in size and the acquisition of four more segments.

Cyclopid larvae were kept for more than nine days at 11° C in filtered sea water in flasks, some with *Skeletonema costatum*, *Chlorella ovalis* or *Dunaliella primolecta* added, and some without addition. No evidence of feeding was found, and no development of the cyclopids occurred. When first released, the cyclopids swim actively and are positively phototropic, tending to congregate on the side of the container nearest the source of light. After a time they settle on the bottom of the container and become attached to it by means of their suctorial mouths. They are easily stirred to activity again. The cyclopids are capable of crawling, drawing themselves along by means of their mouths.

Other attempts to rear cyclopids were made by keeping two or three lobsters in a tank and filtering samples of surface and bottom water every 2 days. The lobsters lived for periods of from 8 to 24 days, but the larvae obtained had not developed beyond the cyclopid stage.

Plankton hauls were made over lobster beds off the west coast of Scotland and in Orkney waters between July and September. Half-metre nets, 26 or 60 meshes to the inch, were used, and hauls varied in duration from 5 to 30 min. The beds were in depths of 10–20 fathoms (18·3–36·6 m); eleven surface hauls, five midway between surface and bottom and five just above the bottom were made. Only two cyclopids were caught, both in surface hauls, and both in 26-mesh nets; neither showed any development.

In an attempt to discover a possible intermediate host, the gills and soft parts of 239 individuals representing twenty-eight species of invertebrates, and also three fish, from the lobster beds or adjacent rocky shores, were examined, mainly during the summer months. The invertebrates from the lobster beds were caught by Agassiz trawl, scallop dredge or creel. The full list of animals examined is given in an appendix. No larval *Nicothoë* were found.

Attempts were made to obtain direct infestation with cyclopid larvae of three hard and five soft (recently cast and therefore free from *Nicothoë*) lobsters in tanks of aerated sea water. The sides, but not the top, of each tank were covered with brown paper, so as to allow illumination only from above as in the sea. Active cyclopid larvae were introduced, and the lobsters were examined after times varying from 1 to 32 days. The only lobster newly infested was a soft one, left for 20 days before examination, which then carried one juvenile *Nicothoë* with wings 0·90 mm long. One isolated individual cannot be taken as indicating the successful direct settlement of a cyclopid and its subsequent moulting to a last-stage copepodid, since the lobster in question was under general circulation in the aquarium for 3 days before the commencement of the experiment, during which time it might have become infested with an intermediate larva which had been either free-living or on another host, and which had reached a stage of development at which it could moult into a last-stage copepodid. It does, however, suggest that repetition of this experiment would be valuable.

## THE MALE OF *NICOTHOË*

The only individuals definitely recognized, and described and figured by previous workers, have all been females. Van Beneden (1850) described a specimen which he called a male, but Claus (1860) said that this did not even belong to the species *Nicothoë astaci*. From the description given by Van Beneden, it was almost certainly the harpacticoid copepod *Tisbe elongata*, which is frequently found on the gills of lobsters.

Claus (1860) found an individual without wings, which, from his description, was a last-stage copepodid. He concluded, however, that since the body had a full complement of segments, it was an adult, sexually mature form, and so must be a male. He supported his conclusion by quoting Rathke (1843), who described two types of larvae as being differentiated early in the egg-sac, the wings of the female appearing at a very early stage. The present investigation has shown, however, that all cyclopid larvae are of the same type (Figs. 1, 3), all with suctorial mouths, and show no sign of wings, which first appear after the last copepodid stage. The complete series of stages, from last-stage copepodids without wings, through juveniles with small wings to adults with large wings (Fig. 1), makes it certain that the copepodids develop into females.

Quidor (1906) examined five last-stage copepodids, and said that four of them had testes in various stages of development in the thorax and genital segment. The remaining one, which had no testes, he described as an immature female. In the present study 100 last-stage copepodids, taken at various times of the year, were stained with Ehrlich's acid haematoxylin and eosin and examined microscopically, but no testes were found. On the other hand, each had a pair of curved spermathecae, full of spermatozoa, in the

1st abdominal segment. These were also seen, still containing sperm, in juveniles and adults, opening into the genital duct near its opening. It would thus appear that females are impregnated at a very early stage, before settling on the lobster, and retain the spermatozoa for fertilizing each successive generation of eggs.

The males presumably develop from cyclopids during the gap in the life history between the cyclopid and last copepodid stages, but, unlike the females, they do not settle on the lobster. In addition to the last-stage copepodids, stained preparations of cyclopid larvae from six *Nicothoë* and stained sections of thirty-five juveniles and adults were examined, but no trace of a testis was found.

## THE RELATIONSHIP BETWEEN *NICOTHOË* AND THE MOULTING OF THE LOBSTER

The most important moulting period of the lobster in Scottish waters is May–August, mature males casting every year and mature females every second year. Thomas (1958) has recently found some evidence of a subsidiary moulting season in younger lobsters in November. Observation of ten lobsters in the laboratory has shown that, at the moult, the outer covering of the gills is shed, and the parasites with it, leaving the gills clean. *Nicothoë* makes no attempt to leave the gills, but simply dies.

The preserved lobsters in each of the Orkney and Bernera samples were divided into three groups according to the state of the shell: soft (very recently moulted, free from epizoons), fairly soft (beginning to harden again, usually carries small epizoons, e.g. *Spirorbis*, *Pomatoceros*, *Balanus*), and hard (quite firm again, usually carries large epizoons). Their gills, whose outer layers are cast with the shell, are correspondingly soft, fairly soft and hard. The three groups are not represented in the samples in the same proportions as in nature; the samples contain a higher proportion of soft and fairly soft lobsters owing to the greater mortality among them than among hard ones during transit and storage.

Table 2 shows the numbers of last-stage copepodids, juveniles and adults of *Nicothoë* on the three types of lobsters in all the Orkney and Bernera samples, together with the mean lengths of their wings. The wings were measured from the tip to the junction of the anterior edge with the cephalothorax. The two wings of an individual are usually approximately equal in size, but, where this was not so, the longer one was measured. The length of the wing is the best index of growth owing to the small increase in body length after the last copepodid stage (p. 8).

Last-stage copepodids were found in most months of the year (none were found in September and no samples were obtained in March and May), and they occurred on soft, fairly soft and hard lobsters alike. Juvenile *Nicothoë*

TABLE 2. NUMBERS AND WING-LENGTHS OF LAST-STAGE COPEPODIDS, JUVENILES AND ADULTS ON LOBSTERS OF THE THREE SHELL-TYPES

(For convenience, the samples are considered as though taken in one year.)

| | | | Mean nos. per lobster | | | Length of wings: Juveniles | | Length of wings: Adults | |
|---|---|---|---|---|---|---|---|---|---|
| Month | State of shell | No. of lobsters | L.-s. copeps. | Juvs. | Adults | Mean length | Size range | Mean length | Size range |
| | | | A. Orkney, 1954–55 | | | | | | |
| April | Soft | — | — | — | — | — | — | — | — |
| (26. iv. 55) | Fairly soft | 1 | — | 10·0 | 4·0 | 1·94 | 1·20–1·49 | 2·12 | 1·94–2·41 |
| | Hard | 10 | 1·7 | 0·5 | 167·6 | 1·70 | 1·38–2·11 | 2·82 | 1·51–4·04 |
| June | Soft | 1 | — | — | — | — | — | — | — |
| (7. vi. 55) | Fairly soft | — | — | — | — | — | — | — | — |
| | Hard | 14 | 3·1 | 2·9 | 49·6 | 1·64 | 0·09–2·15 | 2·74 | 1·72–4·30 |
| August | Soft | — | — | — | — | — | — | — | — |
| (2. viii. 55) | Fairly soft | 6 | 0·7 | 60·8 | 0·5 | 1·72 | 0·04–2·71 | 3·11 | 2·80–3·40 |
| | Hard | 16 | — | 0·2 | 31·1 | 2·05 | 1·94–2·15 | 2·80 | 1·81–4·13 |
| September | Soft | 7 | — | 29·0 | 0·9 | 2·00 | 1·03–2·67 | 2·16 | 1·81–2·37 |
| (21. ix. 54) | Fairly soft | 12 | — | 1·8 | 3·4 | 1·97 | 0·99–2·58 | 2·55 | 1·72–3·40 |
| | Hard | 6 | — | — | 23·7 | — | — | 2·66 | 1·63–3·70 |
| November | Soft | — | — | — | — | — | — | — | — |
| (8. xi. 55) | Fairly soft | 14 | — | 1·0 | 9·9 | 2·12 | 1·72–2·37 | 2·96 | 1·81–4·09 |
| | Hard | 5 | — | 1·3 | 80·8 | 1·58 | 1·51–1·98 | 3·29 | 2·11–4·47 |
| December | Soft | — | — | — | — | — | — | — | — |
| (14. xii. 54) | Fairly soft | 3 | — | 0·3 | 25·7 | 1·42 | 1·42 | 2·79 | 2·37–3·48 |
| | Hard | 9 | — | — | 20·0 | — | — | 2·66 | 1·76–3·66 |
| | | | B. Bernera, 1955–56 | | | | | | |
| January | Soft | — | — | — | — | — | — | — | — |
| (26. i. 56) | Fairly soft | 5 | 0·2 | 1·8 | 9·2 | 1·85 | 0·95–2·32 | 2·59 | 1·85–3·48 |
| | Hard | 3 | — | — | 103·7 | — | — | 2·81 | 1·85–3·87 |
| February | Soft | — | — | — | — | — | — | — | — |
| (8. ii. 56) | Fairly soft | 3 | 0·3 | 23·7 | 24·3 | 1·97 | 1·28–2·58 | 2·53 | 1·59–3·83 |
| | Hard* | 8 | 0·5 | 2·0 | 81·2 | 1·44 | 0·43–2·36 | 2·74 | 1·55–4·13 |
| April | Soft | 3 | — | 10·7 | 4·0 | 1·88 | 0·90–2·32 | 2·31 | 1·89–2·32 |
| (12. iv. 56) | Fairly soft | 3 | — | 26·0 | 171·3 | 2·06 | 1·46–2·75 | 2·78 | 1·72–3·87 |
| | Hard | 2 | — | 1·0 | 4·0 | 1·26 | 0·77–1·76 | 2·71 | 2·15–3·48 |
| June | Soft | 1 | 6·0 | 4·0 | — | 1·06 | 0·73–1·33 | — | — |
| (19. vi. 56) | Fairly soft | 4 | 0·2 | 41·0 | 15·5 | 2·12 | 0·82–2·92 | 2·45 | 1·98–3·05 |
| | Hard | 5 | 1·6 | 0·4 | 112·2 | 1·66 | 1·63–1·68 | 2·99 | 2·28–4·56 |
| July | Soft | 1 | 9·0 | 180·0 | — | 1·05 | 0·09–1·89 | — | — |
| (24. vii. 56) | Fairly soft | 6 | 4·8 | 47·2 | 46·0 | 1·63 | 0·04–2·80 | 2·52 | 1·72–3·66 |
| | Hard | 2 | — | 1·5 | 266·5 | 1·99 | 1·59–2·58 | 2·94 | 2·02–4·30 |
| August | Soft | — | — | — | — | — | — | — | — |
| (24. viii. 56) | Fairly soft | 6 | 0·2 | 3·2 | 122·7 | 2·03 | 1·16–2·49 | 2·57 | 1·29–4·00 |
| | Hard* | 5 | 0·8 | 0·6 | 83·2 | 1·91 | 1·51–2·15 | 2·65 | 1·63–3·70 |
| October | Soft | — | — | — | — | — | — | — | — |
| (4. x. 55) | Fairly soft | 8 | 2·2 | 22·5 | 38·4 | 1·15 | 0·09–2·32 | 2·49 | 1·38–3·66 |
| | Hard* | 3 | — | 0·3 | 90·7 | 0·22 | 0·22 | 2·88 | 1·94–4·21 |
| November | Soft | — | — | — | — | — | — | — | — |
| (2. xi. 56) | Fairly soft | 10 | 0·4 | 9·9 | 55·6 | 2·06 | 1·16–2·75 | 2·77 | 1·36–4·47 |
| | Hard | 3 | — | 5·0 | 174·7 | 1·76 | 1·20–2·75 | 2·68 | 1·59–4·26 |
| December | Soft | — | — | — | — | — | — | — | — |
| (7. xii. 55) | Fairly soft | 15 | 17·9 | 9·3 | 19·0 | 1·67 | 0·09–1·76 | 2·85 | 1·89–4·26 |
| | Hard* | 4 | 3·8 | 1·5 | 122·2 | 0·77 | 1·29–2·24 | 3·07 | 2·32–4·21 |

Each sample marked * excludes one hard lobster with badly damaged gills, which carried more than the usual numbers of juvenile *Nicothoë*, as below (see text):

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| February | Hard | 1 | — | 10 | 390 | 1·87 | 1·68–2·06 | 2·69 | 1·72–3·74 |
| August | Hard | 1 | 2 | 14 | 508 | 0·88 | 0·22–1·89 | 2·70 | 1·85–3·78 |
| October | Hard | 1 | 1 | 40 | 288 | 1·69 | 0·69–2·11 | 2·93 | 1·72–3·87 |
| December | Hard | 1 | 16 | 44 | 756 | 1·95 | 1·29–2·24 | 3·07 | 2·32–4·31 |

were found in all samples, but, with only four exceptions, were present in numbers only on lobsters which had recently moulted (soft and fairly soft). Hard lobsters had the most, and also the largest (adult) *Nicothoë*. It appears probable that the last-stage copepodid cannot pierce a gill filament if the latter is hard. If, on the other hand, the gills are soft, the parasite attaches itself by its suctorial mouth to a filament, which it pierces by means of its mandibles. Feeding on the host's blood then results in the growth of the wings and development, through the juvenile, to the adult state.

TABLE 3. PERCENTAGE OF INDIVIDUALS OF *NICOTHOË* IN EACH STAGE OF DEVELOPMENT—HARD LOBSTERS

(For convenience, the samples are considered as though all taken in one year.)

| Month | Gonad stage: Empty | Developing | Half-full | Full | Ripe | Spawning | No. examined |
|---|---|---|---|---|---|---|---|
| | A. Orkney, 1954–55 | | | | | | |
| April (26. iv. 55) | 46·1 | 13·9 | 3·1 | 11·0 | 23·5 | 2·4 | 1185 |
| June (7. vi. 55) | 18·5 | 25·6 | 15·8 | 15·7 | 23·1 | 1·3 | 671 |
| August (2. viii. 55) | 15·1 | 33·0 | 23·0 | 13·0 | 15·9 | — | 339 |
| September (21. ix. 54) | 26·1 | 22·5 | 21·8 | 25·4 | 4·2 | — | 142 |
| November (8. xi. 55) | 12·4 | 27·2 | 14·8 | 15·1 | 28·0 | 2·5 | 404 |
| December (14. xii. 54) | 15·0 | 8·4 | 16·1 | 52·2 | 7·2 | 1·1 | 180 |
| | B. Bernera, 1955–56 | | | | | | |
| January (26. i. 56) | 3·9 | 31·5 | 28·0 | 21·2 | 13·2 | 2·2 | 311 |
| February (8. ii. 56) | 11·7 | 25·5 | 21·0 | 22·5 | 19·3 | 0·1 | 1040 |
| April (12. iv. 56) | 4·8 | 16·1 | 28·2 | 27·4 | 23·0 | 0·6 | 522* |
| June (19. vi. 56) | 20·9 | 24·4 | 11·2 | 13·5 | 30·0 | — | 561 |
| July (24. vii. 56) | 32·3 | 15·2 | 13·7 | 17·1 | 21·7 | — | 533 |
| August (24. viii. 56) | 27·7 | 20·4 | 5·4 | 21·6 | 22·2 | 2·7 | 924 |
| October (4. x. 55) | 47·5 | 18·0 | 5·9 | 16·3 | 12·1 | 0·2 | 560 |
| November (2. xi. 56) | 23·7 | 18·1 | 12·0 | 14·1 | 31·1 | 1·0 | 524 |
| December (7. xii. 55) | 27·0 | 20·6 | 15·4 | 15·4 | 21 4 | 0·2 | 1245 |

* Includes two lobsters not quite hard.

The four exceptions referred to above, lobsters with hard shells which carried respectively 10, 14, 40 and 44 juvenile *Nicothoë*, all had badly damaged gills. It is probable that the last-stage copepodids became attached, and the damage to the gills permitted them to suck the host's blood without the necessity of penetrating the filaments.

One lobster, caught in December 1955, was noteworthy in that, while the shell was hard, and the gills on the left-hand side were hard and greeny brown, those on the right-hand side were soft, clean and white. The left-hand gills carried 100 adult *Nicothoë* and no juveniles, while the right-hand gills carried no adults and 23 juveniles.

There is a seasonal rhythm in the release of cyclopid larvae of *Nicothoë*. Table 3 shows the percentages of adult *Nicothoë* in each of the six stages of gonad development (p. 7). Since lobsters of the three shell groups are not present in the same proportion as in nature, only hard ones, which are in the majority in nature even in the moulting season, were considered. Adults in the ripe and spawning stages indicate the release, or impending release, of cyclopid larvae. Since these stages were present in all samples taken, release of larvae occurs throughout the year. Two peaks were shown in the release of cyclopid larvae in both Orkney and Bernera lobsters (Fig. 4). The first peak, in May or June, occurred at the beginning of the main moulting period, and the percentage remained relatively high throughout this period, while the second peak, in November, coincided with the subsidiary moulting period.

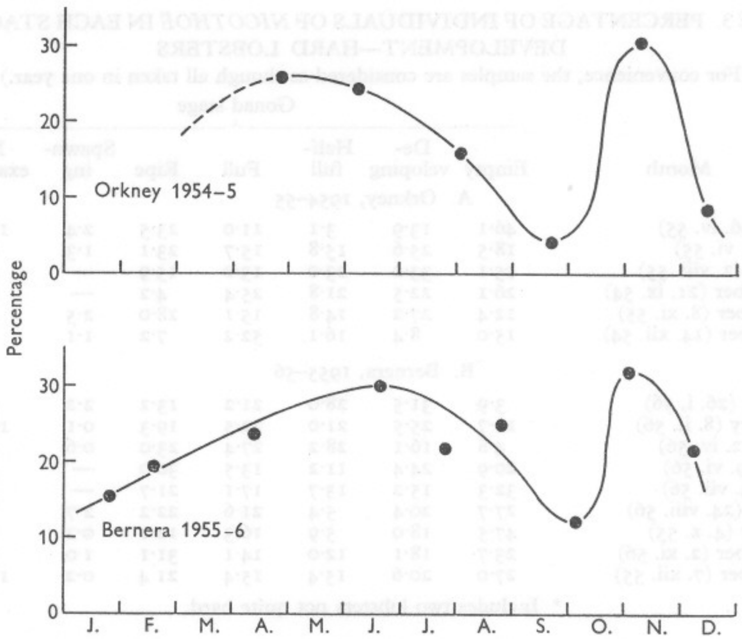


Fig. 4. Percentages of adult *Nicothoë* in ripe and spawning stages: Orkney, 1954–5; Bernera, 1955–6. See Table 3.

It appears, then, that *Nicothoë* can infest only recently cast lobsters, but it can do so at any time of the year. Most infestation will, however, presumably occur during the main moulting periods, when the highest proportion of soft lobsters is present, and when most cyclopid larvae are released.

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## SUMMARY

The only individuals of *Nicothoë astaci* so far definitely recognized have been female.

Concurrent series of changes take place in the ovaries and egg-sacs, so that when the gonads are full of ripe eggs, and are ready to spawn, the egg-sacs either contain active cyclopid larvae or have just released them. After the release of the cyclopid into the sea there is a gap in our knowledge of the life cycle, the next stage known being the much larger last-stage copepodid on the gills of the lobster. From this a series of changes can be traced, with the appearance of wings and the development of gonads, through juveniles (which have never spawned) to adults with egg-sacs. All attempts to bridge the gap have failed; cyclopid larvae kept alive for up to 9 days showed no sign of development, and no intermediate stages have been found, either free-living in the plankton or parasitic on the lobster or other animals. Attempts to parasitize lobsters by means of cyclopid larvae have failed with one exception whose significance is doubtful.

Individuals described as males by previous workers either belonged to another genus or were almost certainly last-stage copepodids. All last-stage copepodids examined had spermathecae containing sperm, and must have been impregnated at a very early stage, the male presumably developing in the gap between cyclopid and last-stage copepodid, though all the cyclopids were of one type. The sperm are retained and fertilize successive generations of eggs.

When the lobster moults the *Nicothoë* are shed with the old shell and die, and re-infestation by settlement of last-stage copepodids can only occur in significant numbers shortly after the moult, before the gills become hard again. There is a seasonal rhythm in the release of cyclopid larvae by the adult females, there being two peaks, of which one coincides with the lobster's main moulting season (May–August) and the other with a subsidiary moulting period of younger lobsters (November).


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## APPENDIX

*Animals examined for intermediate stages of* Nicothoë

| | | No. examined |
|---|---|---|
| Porifera | *Halichondria panicea* | 4 |
| Coelenterata | *Aurelia aurita* | 1 |
| | *Actinia equina* | 9 |
| Annelida | *Nereis pelagica* | 6 |
| Crustacea | *Balanus* sp. (from lobsters' shells) | 30 |
| | *Gammarus* sp. | 7 |
| | *Pandalus montagui* | 8 |
| | *Palaemon serratus* | 2 |
| | *Crangon vulgaris* | 1 |
| | *Nephrops norvegicus* (trawled nearby) | 10 |
| | *Munida bamffica* | 1 |
| | *Eupagurus bernhardus* | 4 |
| | *Portunus puber* | 39 |
| | *Carcinus maenas* | 17 |
| | *Cancer pagurus* | 22 |
| | *Hyas araneus* | 1 |
| | *Inachus dorsettensis* | 2 |
| Mollusca | *Patella vulgata* | 7 |
| | *Gibbula cineraria* | 2 |
| | *Littorina littorea* | 10 |
| | *Nucella lapillus* | 12 |
| | *Mytilus edulis* | 8 |
| | *Chlamys opercularis* | 10 |
| Echinodermata | *Astropecten irregularis* | 1 |
| | *Porania pulvillus* | 4 |
| | *Asterias rubens* | 11 |
| | *Ophiura texturata* | 2 |
| | *Psammechinus miliaris* | 8 |
| Pisces | *Zoarces viviparus* | 1 |
| | *Cottus bubalis* | 2 |