

Some unsolved problems concerning copepods associated with marine invertebrates

R.V. Gotto

Department of Zoology, Queen's University, Belfast, Northern Ireland, U.K.

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Abstract

Three unsolved problems relating to symbiotic copepods of marine invertebrates are discussed: 1. The whereabouts of the unknown male of the gill parasite of lobsters, *Nicothoe astaci*. 2. The occurrence of very large and apparently post-reproductive females in the annelidicolous *Cyclorhiza megalova*. 3. The taxonomic status of certain members of the ascidicolous genus *Notodelphys*.

Résumé

Trois problèmes à propos des Copépodes associés d'Invertébrés marins sont discutés: 1. Où est le mâle inconnu de *Nicothoe astaci*, parasite de l'homard? 2. La présence des femelles très grosses du Copépode annélicole *Cyclorhiza megalova*. 3. Les espèces "classiques" du genre *Notodelphys* – sont-ils quatre espèces ou une espèce variable?

Introduction

It might reasonably be supposed that the first recognizable copepod genus to be scientifically observed would have been a large planktonic form or an obvious parasite on fish gills. Surprisingly however, the distinction would seem to belong to the notodelphyid *Doropygus* Thorell, 1859, found by Redi in 1684 within the pharynx of large ascidians (Canu, 1892). It is therefore ironic that the world of invertebrate-associated copepods to which *Doropygus* belongs, has been among the last to receive the attention which its fascination merits. Only in the

nineteen-forties was interest kindled in these symbionts by the first of Arthur Humes' many papers and, a few years later, by the sustained researches of Jan Stock. Happily, over the past four decades, such distinguished pioneers have been followed by several other workers and our knowledge of these interesting commensals and parasites has been greatly extended.

Despite this accretion of information, many gaps and puzzles still remain – copepodologists working in this field will find no difficulty in multiplying examples! Most are trivial, their appeal for attention residing only in the satisfaction derived from problem-solving. I should like here to discuss, very briefly, three such trivia, in the hope that future workers may at least obtain some pleasurable stimulation from their solution.

1. *Nicothoe* – the missing male

Nicothoe astaci Audouin & Milne-Edwards, a well-known parasite of lobster gills, was described as early as 1826. Possessing a range coextensive with that of its host *Homarus gammarus* (Linnaeus, 1758), it is widespread in European waters, infesting lobsters often in very large numbers. Being of some economic significance, it has attracted a fair degree of research. However, despite its familiarity, in the 164 years since its discovery no certain male has ever been found.

Although many of the Nicothoidae (e.g. the cho-

niostomines) have strongly transformed dwarf males, these tiny consorts invariably occur in close proximity to their females – and nothing of this sort has been observed in *N. astaci*. Moreover, a perfectly typical, though rather small, cyclopid male has been described in the related genus *Paranicothoe* Carton, 1970. Structural studies of the female *N. astaci* moreover, do not provide any evidence of a cryptogonochoric, let alone a hermaphrodite condition. Finally, even the youngest females (last-stage copepodids) established on the gills of the lobster possess spermathecae filled with spermatozoa. We must, therefore, conclude that a highly efficient “typical” male is present – but where?

Summarizing the admirable researches of Mason (1959) we can consider the following facts: Adult females release active cyclopid larvae from their egg-sacs at all times of the year, but with two peaks which coincide with the main moulting periods of the host. It is only while the gills are still soft in a newly moulted lobster that the copepodid of *Nicothoe* can pierce the gill tissue with its suckorial mouth and commence feeding on the blood. When an infected lobster moults, it sheds the outer covering of the gill along with the attached copepods, which thereupon die. Mason (1959: 15) concludes: “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 . . . 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.”

In his search for a possible intermediate host, Mason examined 28 species of invertebrates found in the vicinity of lobster beds, but without success. I believe that if such a host was involved, it would have been identified by now. Mason, however, did make one observation (1959: 9) which, in my view, may perhaps furnish a clue regarding this apparent gap in the life cycle: “When first released, the cyclopid swim actively and are positively phototrop-

ic, 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 suckorial mouths. They are easily stirred to activity again. The cyclopid are capable of crawling, drawing themselves along by means of their mouths.” This observation certainly suggests that after an initial dispersive phase negative phototaxis supervenes, directing the cyclopid to the sea bed. Here they would presumably attach themselves below pebbles, weed or other objects which might provide darkened conditions. It would not be surprising if a phase temporarily committed to so clandestine a life-style and involving larvae less than 0.5 mm in length, could well have eluded standard methods of observation and collection. During this period one or more moults must take place, since the smallest copepodids attached to the host gills are almost three times longer than the cyclopid.

If we accept the above, we can perhaps sketch a scenario along the following lines. The lobster spends much of its time in dark, sheltered crevices, especially during ecdysis. It is thus in a microenvironment attractive to the benthic, photonegative phase of a parasite. More importantly, perhaps, the actual process of moulting must create a biochemical ambience dispersing from the lobster’s shelter which could provide a directional clue to a copepodid specifically attuned to this signal. Female copepodids, homing along such a gradient, would tend to congregate at its source. Those destined to become males might, in addition, be biochemically triggered to moult for the last time. A small, highly active adult male with a very limited life-span can be envisaged, seeking out and inseminating one or more females before the latter finally establish themselves on the host’s gills. The males would then perish.

This interpretation of still problematic events is obviously speculative in the highest degree. Any attempt to substantiate it in the laboratory would clearly necessitate the provision of substrate conditions resembling those on natural lobster beds. It would also be important to sample and examine at intervals the upper layer of the substrate itself and not just the ambient water. Would some active and

inquisitive copepodologist kindly reinvestigate the biology of *Nicotohoe astaci*? Somewhere out there the missing male is waiting to be discovered.

2. *Cyclorhiza* – the fate of the female

Cyclorhiza megalova Gotto & Leahy is a much transformed siphonostome copepod belonging to the family Phyllocolididae. It was recently described from Galway Bay, western Ireland (Gotto & Leahy, 1988) where it is found as an external parasite on the phyllocid polychaet *Eteone longa* (Fabricius, 1780). In certain areas of the bay almost 20% of the worms are infested. No male has so far been found.

Ovigerous females, about 1 mm in length, are tadpole-shaped (clavate), lack all trace of legs and possess only three pairs of minute, rudimentary cephalic appendages – the antennules, antennae and maxillipeds. A buccal siphon penetrates the host skin and divides into two lengthy absorptive filaments which lie within the worm's body cavity. When the copepod reaches a length of about 0.8 mm it extrudes large eggs along with an adhesive substance which cements them into a clump resembling a bunch of grapes.

Numerous juvenile females as well as ovigerous adults have been found over an extended period. A third, much less common category was, however, also present. This comprised the occasional very large female, up to 2.8 mm in length, which had lost its "tadpole" shape and assumed a sausage-like appearance. Shrivelled remains of the egg attachment substance formed two strings which still adhered to the reproductive apertures but no new clutch of eggs had been extruded, although what seemed to be maturing ova were noticed on one occasion within the female's body. While increase in length and volume can easily be attributed to extra-ecdysial growth, the intriguing questions are these: What is the status of these relatively enormous females, and what is their ultimate fate?

It is widely accepted that parasites, once securely established on or in a host, either retain a reproductive capability as long as their host remains alive, or else die after one major reproductive effort. Does *Cyclorhiza* break these rules? On our present,

somewhat limited, evidence, it would appear that the extrusion of ova is strictly the prerogative of the smaller, tadpole-like females and that the large sausage-shaped individuals can no longer become ovigerous. Are these latter, in effect, "mothers in retirement", passively absorbing food via the nutritive filaments and continuing to grow having now fulfilled their reproductive function? Do they eventually become too great a burden on their hosts' physiological resources? Do all *Cyclorhiza* females pass into this final stage – but, if so, why are they not more frequently seen? It may be that with more time available for observations over several seasons, the answers would emerge. In the meantime, however, this little parasite certainly poses some interesting questions.

3. *Notodelphys* – one species or several?

Over 30 species are currently ascribed to the very widespread genus *Notodelphys* Allman, 1847. It is the type-genus of the family Notodelphyidae and comprises relatively large copepods possessing many basic cyclopoid features. With few exceptions they are associates of ascidians, living as commensals in the branchial sac. Their most notable characteristic is the large dorsal brood-pouch developed on adult females. Males are smaller and more active, though many females can swim and may, under certain circumstances, leave the host ascidian via the inhalant siphon.

Most *Notodelphys* species are well characterized and readily identifiable. However, several of the so-called classical species, although known for well over a century and frequently encountered along the western European seaboard, still present considerable taxonomic problems. These difficulties principally involve six forms: *Notodelphys allmani*, *N. rufescens*, *N. caerulea*, *N. tenera*, *N. elegans*, and *N. agilis*. All were originally described by Thorell (1859) from several species of large phlebobranchiate ascidians on the west coast of Sweden, and were accepted by such workers as Brady, Giesbrecht, and G.O. Sars. Due to early synonymic confusion, the exact identity of some of their recorded hosts remains uncertain, but a very significant lack of rigid host specificity is generally

apparent. It would seem that five of the species cited above can occur in most of the available phlebobranchiate hosts.

In more recent times doubt has arisen as to the validity of these classic species. Bocquet & Stock (1960) obtained specimens which could almost equally be referred to either *N. allmani* or *N. rufescens*, and suggested the existence of an “*allmani-rufescens* complex”. Lejeune & Monniot (1965) collected large numbers of *Notodelphys* from Thorell’s type locality and initially concluded that all six species should be coalesced into one entity, *Notodelphys ascidicola* Allman, thus resurrecting a long abandoned name to designate what they regarded as a single variable species. In later papers, Monniot (1981, 1982) revised this opinion, but showed in a careful analysis of *N. agilis* that some variation may unquestionably exist between individuals.

At this point let us simplify matters by tentatively eliminating *N. elegans* and *N. agilis* from consideration. Both, in my opinion, possess enough stable characteristics to place their status as good species beyond doubt. However, the remaining four – *N. allmani*, *N. rufescens*, *N. caerulea*, and *N. tenera* – do seem to overlap in some supposedly diagnostic features. Justifiably, it is to these criteria which Monniot and others have objected. Thus “colour” (usually of eggs) is of dubious value, since it may depend largely on degree of development. So does “shape of brood-pouch” – though if we could always be sure that the pouch was fully distended, its final shape may be diagnostically useful. But Monniot’s main argument is against reliance on relative proportions – e.g. length/breadth ratio of caudal ramus, position of the outer edge seta of the ramus relative to the latter’s length, etc. – since he has shown that some variation in these respects can indeed occur. Moreover, fixation can result in small distortions, and he further suggests that different workers may not have used identical points between which to take measurements.

What then is the true position? Do these four forms of *Notodelphys* represent separate species or a single variable one?

Recent researches may now be shedding some light on this problem. First, Dudley (1966) revealed

the existence of male dimorphism in the notodelphyid *Doropygus seclusus* Illg, 1958. Some years later, Hipeau-Jacquotte in an outstanding series of papers (1978, 1980, 1984) studied a similar phenomenon in the related *Pachypygus gibber* (Thorell, 1859). In brief, the types of male described by these workers are either swimming or creeping forms. They are readily distinguishable by differences in size and shape, mouth structure and feeding habits, ornamentation of the cephalic appendages etc. These differences only become manifest after the second copepodid instar – the stage which infests the host ascidian. Dudley suspected the operation of a “host-factor” and Hipeau-Jacquotte provided evidence which suggested that development into one form or the other was controlled by the age of the ascidian host entered. Very young hosts promoted the development of the swimming male, older hosts that of the creeping male. It would thus seem that, in phlebobranchiate hosts at all events, structural changes in the male can be brought about by the microenvironment offered by hosts of different ages.

Now if the host environment can evoke such obvious differences in certain male notodelphyids (incontestably of the same species) similar considerations should hold for the female sex, although any alterations so produced need not necessarily be of an adaptive nature. Indeed just such a case has been reported recently by Monniot (1986) who found in Guadeloupe two distinctive phenotypes of *Pachypygus macer* Illg, 1958 occupying *Styela partita* (Stimpson, 1852) and *Microcosmus exasperatus* (Savigny, 1816) respectively. Monniot advances good reasons for supposing that the observable differences are due to the influence exercised on development by whichever host happens to be invaded.

Bearing these facts in mind, we may now return to Thorell’s four problematic species and contribute a few suggestions for consideration. I believe that the acquisition (or retention) of a second copepodid’s positive chemotactic response to a wide variety of ascidian species may be of fundamental importance in the evolution of certain *Notodelphys* populations. Differing host milieux could result in subtle phenotypic variations obser-

vable in adult females. But, if this were the only factor, we should expect a high degree of host specificity, which is not the case. However, if we take host-age into account, other possibilities become apparent. It is not difficult to imagine how an ascidian might offer an altering internal environment as it matures: gonadal development, increased endostylar production, volume of water, and incoming food processed – all must surely influence living conditions in the branchial sac, both physically and biochemically.

As a completely hypothetical example then, suppose a copepodid (the offspring of any one of our four species) enters any young, acceptable phlebobranchiate host, the resulting adult might correspond to what we know as *N. allmani*; a slightly older host might impose the *N. rufescens* pattern; older still, *N. caerulea*; finally, entering a mature host might result in *N. tenera*. At least some such mechanism might be necessary to explain the seemingly fluid evolutionary state within this genus.

At present, no positive conclusion can be reached. Monniot (1982) has suggested that if accurate and detailed analyses of enough key characters were made the discreteness of *Notodelphys* species might be maintainable. He may well be correct, but his own later work emphasizes the complexity of this problem. Hopefully some future investigator will conduct carefully controlled rearing experiments and provide us with some answers.

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