Phyto-Chemical Sensitivity and Swimming Behaviour of the Free-Living Marine Nematode Chromadorita tenuis*

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ABSTRACT: Field results show that the free-living marine nematode *Chromadorita tenuis* is one of several benthic representatives inhabiting submerged macrophytes, at least during the growth period of the vegetation. In fact, *C. tenuis* is a phytal species. Laboratory experiments reveal that it is phyto-chemically attracted to submerged macrophytes; this causes the nematode to swim from the benthos to the surface of the submerged plants. Such behaviour conveys to *C. tenuis* an advantage over its benthic sister species *C. fennica* in its capacity to exploit the environment.

INTRODUCTION

Free-living aquatic nematodes are found in the sea bottom where they usually represent the most abundant group of metazoans (Gerlach, 1971; Nicholas, 1975). They are especially adapted to move in interstices (Lorenzen, 1973; Schiemer et al., unpubl.). A few studies deal with the presence of nematodes on submerged macrophytes (literature in Kito, 1975; Glowacka et al., 1976; Warwick, 1977). Although there is evidence that nematodes constitute a permanent fauna on some macrophytes (Glowacka et al., 1976; Warwick 1977), their presence was correlated with the silt content on the weeds (Wieser, 1954, 1959), suggesting that the nematodes had become dispersed by attaching themselves to the bottom material, suspended during storm (Gerlach, 1977a). Movements between the benthic and phytal nematode fauna have thus mostly been thought to be occasional phenomena not involving active nematode behaviour. Wieser (1959) proposed the term 'Schlängler Typen' for the phytal nematodes describing their poor swimming ability compared to active swimmers, such as copepods and amphipods in the seaweed zone.

A study on habitat selection of aquatic nematodes in Baltic and western European estuaries (Jensen, unpubl.) shows that an annual cycle exists in some nematodes with respect to their habitat choice between benthos and submerged macrophytes. The present paper deals with such a nematode: the epistrate-feeding *Chromadorita tenuis* and its ability to leave the sea bottom and to swim in the free water, being chemically attracted to the surface of submerged macrophytes.

MATERIAL AND METHODS

Animal and Phytal Material

Numerous specimens of *Chromadorita tenuis* (G. Schneider, 1906) (ca 1 mm in adult length) were extracted from 11 submerged macrophytes in the Tvärminne area, southern archipelago of Finland during May–October 1978 and 1979. The collecting area was described and the morphology and a differential diagnosis of *C. tenuis* were presented in a previous paper (Jensen, 1979b).

For laboratory experiments, living nematodes were obtained by shaking small amounts of the filamentous alga Cladophora glomerata (L.) Kütz in filtered sea water. This caused most nematodes and other animals to lose their attachment to the surface of the alga. The fauna was concentrated through a 45 μ m sieve and specimens of Chromadorita tenuis were picked out with a needle under a Wild M 5 stereo microscope, 10×12 magnification, and transferred to a Bovery

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dish containing filtered sea water. For each experiment, 25 specimens were used, consisting of adults and juveniles, and an amount of *Cladophora glomerata* of about 0.5 mg dry weight.

After shaking the alga in sea water, the Cladophora glomerata used for the experiments was reexamined under the stereo microscope and the remaining attached animals were removed. 100 ml of fresh sediment and its benthic animals from Krogarviken (soft bottom) were used as bottom substrate in the aquaria.

Laboratory Experiments

The aquaria used measured $10 \times 10 \times 10$ cm and were filled with artificial sea water up to 9 cm height. The phytal container was made of a PCV ring, 4 cm in diameter and 1.5 cm high, surrounded by $100~\mu m$ nylon mesh. The container was placed in the middle of the aquarium with the lower edge 2 cm below the water surface; it was held in place by a plastic-coated wire attached to the top of the container and to the side of the aquarium. The container was introduced into the aquarium 1 d after the sediment was spread out on the bottom, and suspended material had sunk to the bottom. No aeration or other water disturbance was employed during the experiments.

Each experiment was repeated 4 times: twice during July 1979 and twice during June 1980, all 4 times at a water temperature of 18 °C, as in the field. Each experiment lasted 24 h. The phytal container was fixed in 4 % formalin after each experiment and the *Chromadorita tenuis* were picked out and counted. Each container was only used once. Four different experiments were conducted in order to detect any

phyto-chemical sensitivity and active swimming of C. tenuis (Fig. 1).

Experiment 1: 25 specimens of *Chromadorita tenuis* were mixed with 100 ml sediment; the mixture was then spread evenly over the bottom of the aquarium and a filled phytal container was introduced. Question: Is *C. tenuis* attracted to *Cladophora glomerata*? If so, can it leave the sediment and swim to the plant?

Exp. 2: Similar to Exp. 1, but two empty phytal containers were introduced side by side. Question: Do *Chromadorita tenuis* swim if there are no phyto-chemical stimuli?

Exp. 3: Sediment without added *Chromadorita tenuis* was spread out over the bottom of the aquarium and a filled phytal container was introduced. Question: Does the sediment harbour *C. tenuis*?

Exp. 4: No sediment or *Chromadorita tenuis* were introduced, but a filled phytal container. Question: How efficient is the mechanical removal of *C. tenuis* from *Cladophora glomerata*? This served as a control experiment.

Since the results are self-explanatory, no statistics were applied.

RESULTS

The results of the 4 series of experiments are shown in Figure 1. The populations of 25 *Chromadorita tenuis* individuals each introduced in the sediment were mostly recovered in the phytal container after the 24-h exposure (Exp. 1), whereas nearly none were attracted by empty containers (Exp. 2). The sediment almost certainly did not harbour *C. tenuis* (Exp. 3), and Experiment 4 demonstrated a 100 % sorting efficiency.

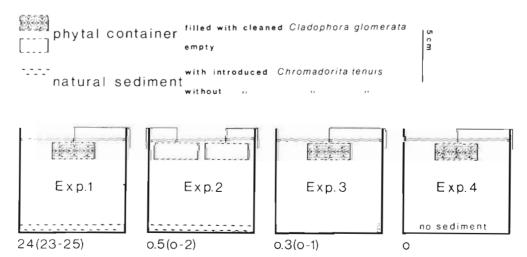


Fig. 1. Chromadorita tenuis. Graphic representation of 4 experiments testing phyto-chemical sensitivity and swimming behaviour. Each experiment lasted 24 h and was repeated, with fresh nematodes, 4 times. Numbers on bottom: mean numbers (min.-max.) of individuals recovered in phytal container after each set of experiments

DISCUSSION AND CONCLUSIONS

Chromadorita tenuis has up to now been regarded as a member of the benthos. However (Jensen, unpubl.), it is a permanent member of the phytal community in shallow mesohaline waters, where it feeds and reproduces during May-October, when submerged macrophytes with their epiflora are present. During winter, C. tenuis lives on the sea bottom in detritus originating from decaying macrophytes. Where algae are present throughout the year, the nematode is found on the algae.

The present study clearly shows that Chromadorita tenuis prefers a phytal habitat to a benthic one. It further demonstrates that both adults and juveniles are able to follow the seasonal alternation between growing and decaying submerged plants by swimming to the macrophytes. This can be correlated neither with the silt content on the macrophytes nor the texture of the macrophytes (Jensen, unpubl.). The only explanation for the nematodes' activity seems to be the release of chemical compounds from the macrophytes (which are known to attract plant-parasitic nematodes, see review by Croll, 1970) or from the epiflora (their food resource), or from both. Plastic panels submerged for collection of epiflora in the Tvärminne area show C. tenuis to be present, indicating that the chemicals released from the epiphytes attracted the nematode. Furthermore, samples of young, 4-cm high pond weeds Potamogeton perfoliatus, which had just penetrated the soft bottom in Krogarviken at the end of May 1980, also harboured C. tenuis, although no epiflora was visible under the microscope. Finally, since I have found C. tenuis on several different submerged macrophytes under various environmental conditions in northwestern European waters, it is most likely that the attractive chemical compounds are correlated with the photosynthetic process, independent of the species of

The location of the postulated chemosensory receptor(s) of the nematode is unknown. Candidate organs are the amphids (a pair of laterally positioned sense organs on the head), papillae or pores on the body, all of which may be involved in the reception of released material (reviews by Coomans, 1979; Croll, 1977; Lee and Atkinson, 1976; McLaren, 1976). However, neither the external morphology nor the shape of the body indicates that Chromadorita tenuis is advanced in terms of chemo-reception or swimming behaviour, compared with its sister species C. fennica Jensen, 1979, which lives permanently in the benthos (Jensen, 1979a). The average swimming speed of *C. tenuis* was determined to be ca 5 cm min⁻¹ in a Petri dish with phytal material; in contrast, C. fennica did not swim, even when placed together with its original substrate

material or algae. At best, individuals were able to propel themselves over a short distance.

The present findings are the first to suggest that phyto-chemical sensitivity may initiate swimming behaviour in a free-living marine nematode. Presumably, many so-called benthic nematodes behave in a similar way (Jensen, unpubl.). Meyers and Hopper (1966) showed experimentally that the large nematode *Metoncholaimus scissus* Wieser and Hopper, 1967 was strongly (chemically) attracted to cellulose mats inocculated with marine fungi, and Gerlach (1977b) used a decaying fish to attract numerous specimens of the benthic *Sabatieria migrans* Jensen and Gerlach, 1977. The swimming ability of these two nematodes is, however, unknown.

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LITERATURE CITED

Coomans, A. (1979). The anterior sensilla of nematodes. Revue Nématol. 2(2): 259–283

Croll, N. A. (1970). The behaviour of nematodes; their activity, senses and responses, Edward Arnold, London

Croll, N. A. (1977). Sensory mechanisms in nematodes. Ann. Rev. Phytopathol. 15: 75–89

Gerlach, S. A. (1971). On the importance of marine meiofauna for benthos communities. Oecologia (Berl.) 6: 176–190

Gerlach, S. A. (1977a). Means of meiofauna dispersal. Mikrofauna Meeresboden 61: 89–103

Gerlach, S. A. (1977b). Attraction to decaying organisms as a possible cause for patchy distribution of nematodes in a Bermuda beach. Ophelia 16: 151–165

Glowacka, I., Soszka G. J., Soszka, H. (1976). Invertebrates associated with macrophytes. In: Pieczynska, E. (ed.) Selected problems of lake littoral ecology. University of Warsaw, pp. 97-122

Jensen, P. (1979a). Nematodes from the brackish waters of the southern archipelago of Finland. Benthic species. Ann. Zool. Fennici 16: 151–168

Jensen, P. (1979b). Nematodes from the brackish waters of the southern archipelago of Finland. Phytal species. Ann. Zool. Fennici 16: 281–285

Kito, K. (1975). Preliminary report on the phytal animals in the Sargassum confusum region in Oshoro Bay, Hokkaido. J. Fac. Sci. Hokkaido Univ. Ser. VI, Zool. 20: 141–158

Lee, D. L., Atkinson, H. J. (1976). Physiology of nematodes, 2nd ed., The Macmillan Press, London

Lorenzen, S. (1973). Die Familie Epsilonematidae (Nematodes). Mikrofauna Meeresboden 25: 1–86

McLaren, D. J. (1976). Sense organs and their secretions. In: Croll, N. A. (ed.) The organization of nematodes. Academic Press, London, pp. 139–161

Meyers, S. P., Hopper, B. E. (1966). Attraction of the marine nematode, *Metoncholaimus* sp., to fungal substrates. Bull. mar. Sci. Gulf Caribb. 16: 143–150

- Nicholas, W L. (1975). The biology of free-living nematodes, Clarendon Press, Oxford
- Warwick, R. M. (1977). The structure and seasonal fluctuations of phytal nematode associations on the Isles of Scilly. In: Keegan, B. F., Céidigh, P. Ó., Boaden, P. J. S. (eds) Biology of benthic organisms. Pergamon Press, Oxford, pp. 577–585
- Wieser, W (1954). Untersuchungen über die algenbewohnende Mikrofauna mariner Hartböden. Hydrobiologia 6: 144–217
- Wieser, W. (1959). Zur Ökologie der Fauna mariner Algen mit besonderer Berücksichtigung des Mittelmeeres. Int. Revue Ges. Hydrobiol. 44: 137–180

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