Vol. 37: 27–34, 1987 | MARINE ECOLOGY – PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published April 6

Mass aggregations of the free-living marine nematode *Pontonema vulgare* (Oncholaimidae) in organically polluted fjords

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ABSTRACT: Mass aggregations of the marine free-living nematode *Pontonema vulgare* containing thousands to millions of individuals were observed in the summer half-year (May to Oct) above the surface of sublittoral (mainly 6 to 9 m depth) soft bottoms of the inner Flensburg and Kiel fjords. Sediments were rich in organic matter, reduced, and black nearly to the surface. Oxygen content of the overlying water was very low (1 to 2 ml $O_2\,l^{-1}$). The aggregations occurred on dead and moribund macrofaunal animals, on beds of rotting *Ulva* sp. and *Zostera marina*, and near organic wastes from a trout farm. They marked sharply the transition zone between oxic sites ($\geq$4 ml $O_2\,l^{-1}$ in summer) inhabited by an intact macrofauna, and anoxic sites (0 to 0.5 ml $O_2\,l^{-1}$ in summer) lacking any macrofauna (including *P. vulgare*). It is concluded that these aggregations above (not within) the surface of the sediment indicate dramatic mortality of the macrofauna living there due to decreasing oxygen content and increasing H_2S content. These processes are known to occur especially in organically polluted areas. Previous taxonomic descriptions of *P. vulgare* are supplemented, and *P. balticum* (Schultz 1932) is suggested to be synonymous with *P. vulgare*.

INTRODUCTION

In the past years, SCUBA divers of Kiel University have repeatedly reported of mass aggregations of larger nematodes above the surface of sublittoral substrates of the Kiel and Flensburg inner fjords (Baltic coast, Federal Republic of Germany). Larger aggregations contained many thousand nematodes which covered the substrate completely and resembled patches of fine spaghetti. Closer analysis of several samples revealed that the nematodes belonged to the common species *Pontonema vulgare* (Bastian 1865). This species attains a length of 12 to 16 mm and a width of 170 to 220 µm; it is easily discernible with the naked eye, especially under water, where objects appear larger and closer than on land. The present paper aims to elucidate factors which might cause *P. vulgare* to form mass aggregations above the surface of the substrate.

MATERIAL AND METHODS

Aggregations of *Pontonema vulgare* were observed, photographed and collected in the course of numerous SCUBA dives in the Flensburg fjord (C. Valentin) and the Kiel fjord (M. Prein). Additional observations were made in the laboratory (S. Lorenzen).

Studies of the Flensburg fjord were mainly performed in 1980 and 1981, those in the Kiel fjord mainly in 1984 and 1985. The design of the experiments will be described together with the results obtained from them.

RESULTS

Aggregations of *Pontonema vulgare* above the substrate were exclusively found during the summer half-year (May to Oct) in clear-cut zones in the inner parts of the Flensburg and Kiel fjords (Fig. 1). In the Flensburg fjord this zone ran at 6 to 9 m depth parallel to the coastline at Stns 1 and 2 and included soft bottom as well as mussel beds *(Mytilus edulis)*, the latter being covered by much flocculent organic matter. In the Kiel fjord, aggregations occurred in the vicinity of a trout farm situated in the cooling water discharge area of a power plant (Stn 2) as well as around the quay of the Institute for Marine Science (Stn 1). The substrates in these zones are rich in organic matter: 15 to 18 % ignition loss was found at 15 m depth at Stn 2 of the

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Table 1. Portion of organic substance (= % ignition loss of the dry samples) at Stns 1 to 6 of the Flensburg fjord (± + SD, n = 12; after Valentin unpubl.

	Station; water depth					
	Stn 1; 15 m	Stn 2; 15 m	Stn 3; 15 m	Stn 4; 16 m	Stn 5; 18 m	Stn 6; 24 m
Oct 1982	16.7 ± 1.0	16.0 ± 1.1	12.9 ± 1.4	9.1 ± 2.1	10.9 ± 0.5	11.6 ± 0.8
Oct 1983	18.6 ± 2.9	14.1 ± 1.1	13.7 ± 0.7	9.2 ± 0.7	12.0 ± 0.4	13.5 ± 0.2
Oct 1984	16.3 ± 2.3	14.8 ± 2.5	13.4 ± 0.6	9.6 ± 1.1	11.3 ± 1.1	11.2 ± 0.8

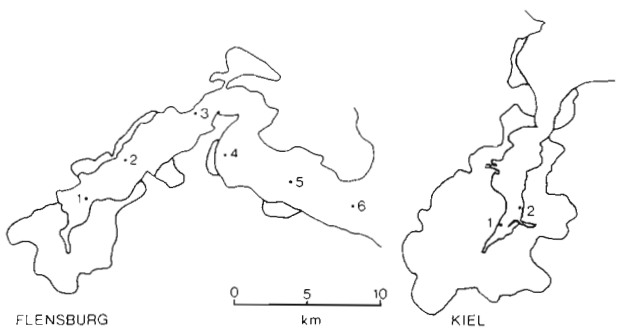

Fig. 1. (a) Flensburg and (b) Kiel fjord, Federal Republic of Germany. Patchy aggregations of *Pontonema vulgare* above the substrate were found in summer at Stns 1 and 2 of both inner fjords. In the Kiel fjord Stn 1 denotes the quay of the Institute for Marine Science, Stn 2 the discharge area of the power plant. Stippling indicates built-up areas

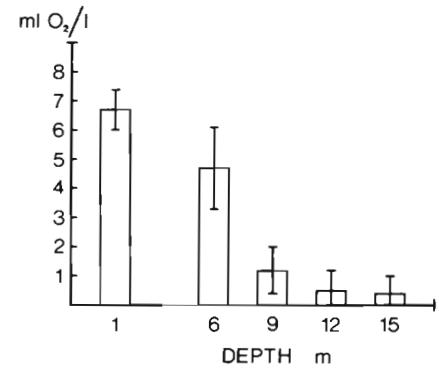

Fig. 2. Mean oxygen content at different water depths of Stn 2 of the Flensburg fjord on 8 d between 2 Jul and 21 Sep 1980. Standard deviations are shown. Between 6 and 9 m depth, where aggregations of *Pontonema vulgare* occurred above the substrate, oxygen content decreased drastically

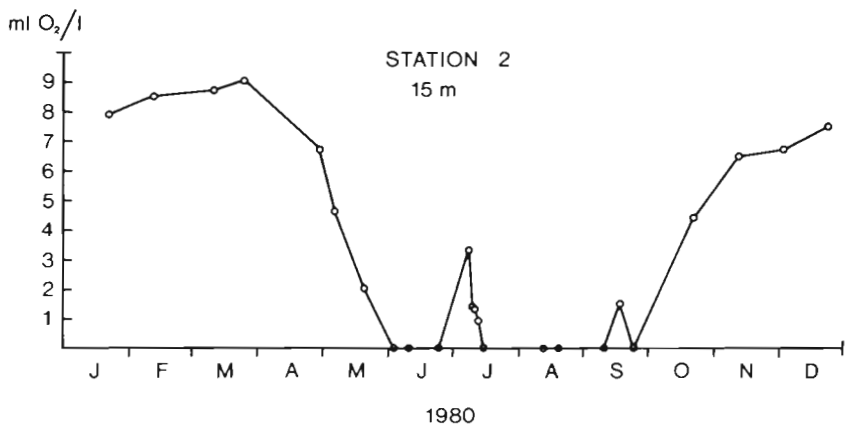

Fig. 3. Oxygen content at 15 m depth (where *Pontonema vulgare* did not occur) of Stn 2 of the Flensburg fjord from Jan to Dec 1980. The water was anoxic in summer and was only occasionally exchanged by oxygen-containing water-bodies

Flensburg fjord in October 1982, 1983 and 1984 (Table 1).

During the period of *Pontonema vulgare* aggregations, the oxygen content of near-bottom water was very low (1 to 2 ml O_2 l^{-1}; Fig. 2 & 3); the substrate was reduced and black nearly to the surface, and all representatives of the macrofauna were obviously stressed, moribund or even dead. Seastars *Asterias rubens* were lying on their aboral sides (Fig. 4b), and many endofaunal animals (e.g. sand gaper *Mya arenaria*) were lying above the substrate. In the vicinity of large aggregations of *P. vulgare*, large snow-white patches of sulphur bacteria *Beggiatoa* sp. occurred in the Kiel fjord.

Aggregations of *Pontonema vulgare* above the surface of the substrate were found to mark sharply the boundary between the oxic zone (more than 4 ml O_2 l^{-1} during summer), inhabited by an intact epi- and endofauna, and the anoxic zone (0 to 0.5 ml O_2 l^{-1} during summer) lacking any macrofauna (*P. vulgare* included). At Stns 1 and 2 of the Flensburg fjord, the depth at which the former zone occurred was 0 to 6 m

and that of the latter more than 9 m. In the latter, the sediment was black up to the surface and had – like the near-bottom water – a strong odour of H_2S.

Each of the aggregations of *Pontonema vulgare* covered an area from a few cm^2 (Fig. 4a, b) up to more than 1 m^2 (Fig. 5b, c). Within an aggregation, most nematodes lay loosely on the surface of the substrate and could be easily dislocated by gentle fanning hand-

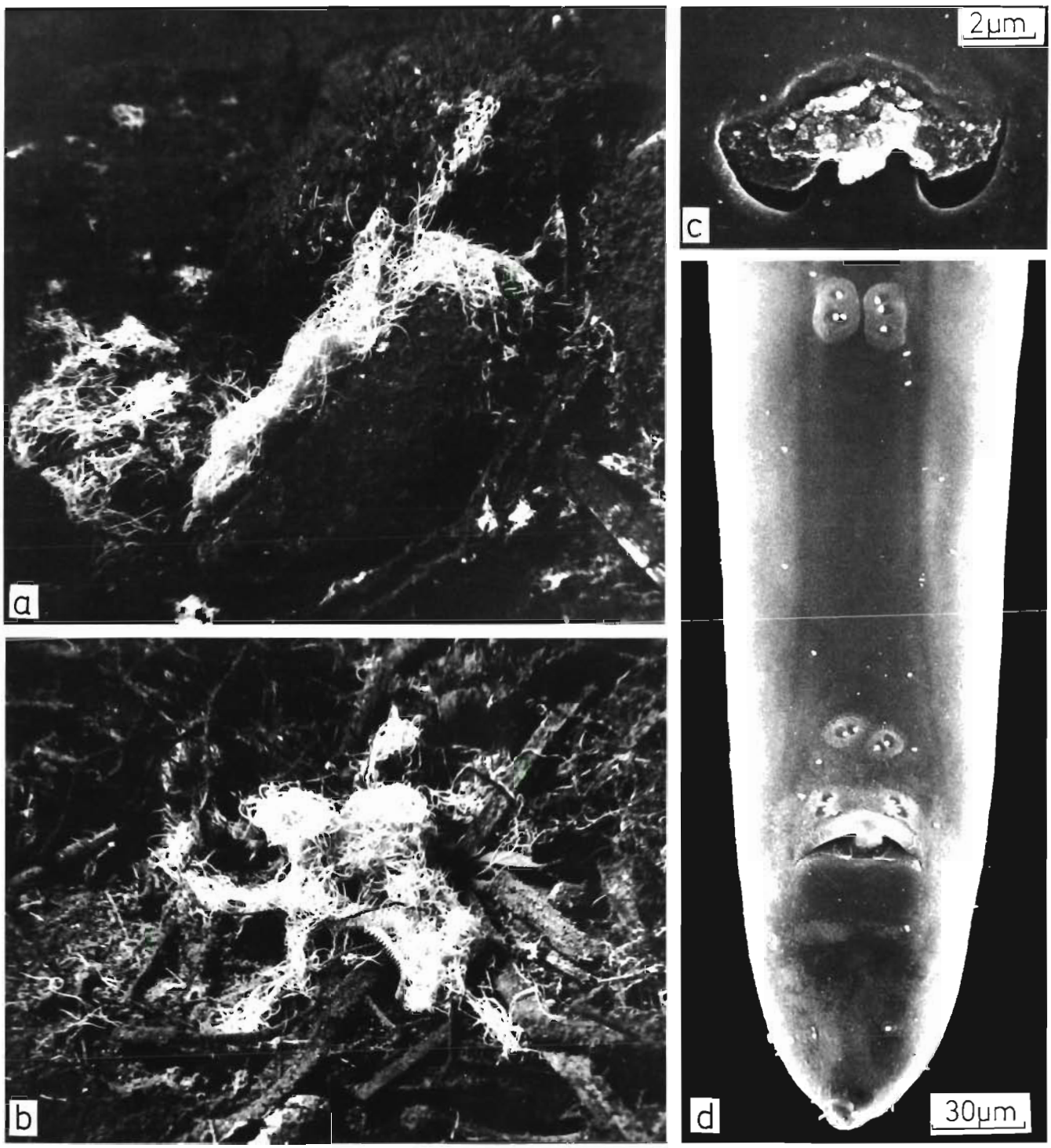

Fig. 4. *Pontonema vulgare*. (a) Hundreds of individuals of *P. vulgare* have invaded a 4.5 cm long common mussel *Mytilus edulis* that still reacted with shell closure upon contact-stimuli. (b) *P. vulgare* on a starfish *Asterias rubens* that still moved. (c) Lateral view of an amphid. (d) Ventral view of the posterior region of a male; the arrangement of the preanal papillae in pairs can be clearly recognized

movements. Many aggregations were so dense that the underlying sediment could no longer be seen. Aggregations were never found to be thicker than about 5 to 10 mm, i.e. all nematodes were near the substrate.

In the Flensburg fjord, small aggregations of *Pontonema vulgare* were repeatedly found to be associated with a dead polychaete or a moribund or dead sand gaper *Mya arenaria* situated within the substrate. Moribund sand gapers reacted upon stimulus with shell closure although the mantle cavity and presumably the whole soft body contained large quantities of *P. vulgare*. The same phenomenon was observed in live mussels *Mytilus edulis*: a later dissection of the specimen shown in Fig. 4a, which at its original location still reacted upon stimuli with shell closure, revealed that hundreds of individuals of *P. vulgare* had entered the mantle cavity and the entire soft body including the large adductor muscle; the gills were completely disorganized thus being unable to create any effective water current. Also on a starfish *Asterias rubens* lying on its aboral surface and still moving, large numbers of *P. vulgare* were observed (Fig. 4b).

In the Kiel fjord, aggregations of *Pontonema vulgare* were frequently found on dead fish or jellyfish *Aurelia aurita*. In all cases, *P. vulgare* apparently fed on the dead and moribund animals.

When *Pontonema vulgare* formed larger aggregations (about 1 dm^2 or more, Fig. 5a to c), these occurred not on dead or moribund animals but on beds of dead thalli of the green algae *Ulva* sp., on beds of rotting eelgrass *Zostera marina* and on sediments near the site receiving organic wastes produced by the net cage trout farm. In these cases, the source of food for *P. vulgare* remains unknown.

Samples taken from the aggregations of *Pontonema vulgare* contained not only many adult males and females, but also a high percentage (more than 50 %) of individuals of all 4 juvenile stages.

Aggregations of *Pontonema vulgare* above the sediment do not occur throughout the whole summer. If, through adequate weather conditions, the bottom water is exchanged with fresh oxygen-rich water, the nematodes disappear into the sediment, even when it is black beneath the surface. In the Kiel fjord, this happened on 28 September 1984. The upper 1 to 2 mm of the substrate was brown, yet underneath this layer the sediment was still deep black. *P. vulgare* occurred within the sediment together with a further nematode fauna rich in specimens and poor in species (mainly *Monhystera disjuncta* Bastian 1865).

In autumn, swarms of gobies *Pomatoschistus microps* and *Gobius niger* were observed to occur in visual range of mass aggregations of *Pontonema vulgare*. It was never observed that they or other animals preyed upon *P. vulgare*.

In order to investigate whether *Pontonema vulgare* shows a patchy distribution not only above, but also within the sediment, 2 series each of 15 parallel samples (each 10 cm^2 and 5 cm deep) were taken by SCUBA diving on 28 December 1984 at Stn 2 of the Flensburg fjord. One series was taken from 9 m depth where *P. vulgare* forms aggregations above the sediment during summer, the other was taken from 12 m depth where *P. vulgare* does not occur during summer. The latter series of samples did not contain any *P. vulgare*, but numerous other nematodes. In the former series, nematodes of different species occurred, and *P. vulgare* was distributed in the following way: 13 samples contained 0 to 2 specimens, 1 sample 3, and 1 sample 16 specimens; that is, the distribution was patchy.

Experiments

A 3 wk *in situ* experiment to demonstrate the expulsion of endofaunal species from the substrate by oxygen deficiency and related factors was started on 18 February 1981 at Stn 2 of the Flensburg fjord in 6 m depth. At this site, *Pontonema vulgare* formed many aggregations in summer. A plexiglass cylinder (20 cm diameter, 50 cm long) was placed vertically (20 cm deep) into the sediment and closed on its top with a screw-cap (Fig. 6a, b). Near-bottom water for the measurement of oxygen content was taken from time to time through a sealable tube in the lower part of the cylinder. The removed water was replaced by surrounding water through a second sealable opening in the upper part of the cylinder. Water temperature was 1 °C. The O_2 content was 8.1 ml $O_2\,l^{-1}$ at the beginning and decreased during the course of the experiment to 2.9, 1.4 and 0.5 ml $O_2\,l^{-1}$ on the 9th, 16th and 22nd days, respectively. During the experiment, *P. vulgare* and the polychaete *Scoloplos armiger* moved from the substrate and then up the cylinder wall. On the 14th day (Fig. 6b), the uppermost individuals of *P. vulgare* and *S. armiger* were 10 to 12 cm above the substrate surface which was brown as in the control area. *S. armiger* died by the 22nd day (no data are available for *P. vulgare*).

In early October 1984, several thousand specimens of *Pontonema vulgare* together with black sediment and water from the collecting site were vigorously mixed and put into an unaerated glass aquarium at 13 °C. Within 1 d, aggregations of *P. vulgare* occurred above the surface of the sediment, indicating that aggregations may be formed rather quickly.

DISCUSSION

A patchy distribution of *Pontonema vulgare* was reported by earlier authors. For example, Stewart

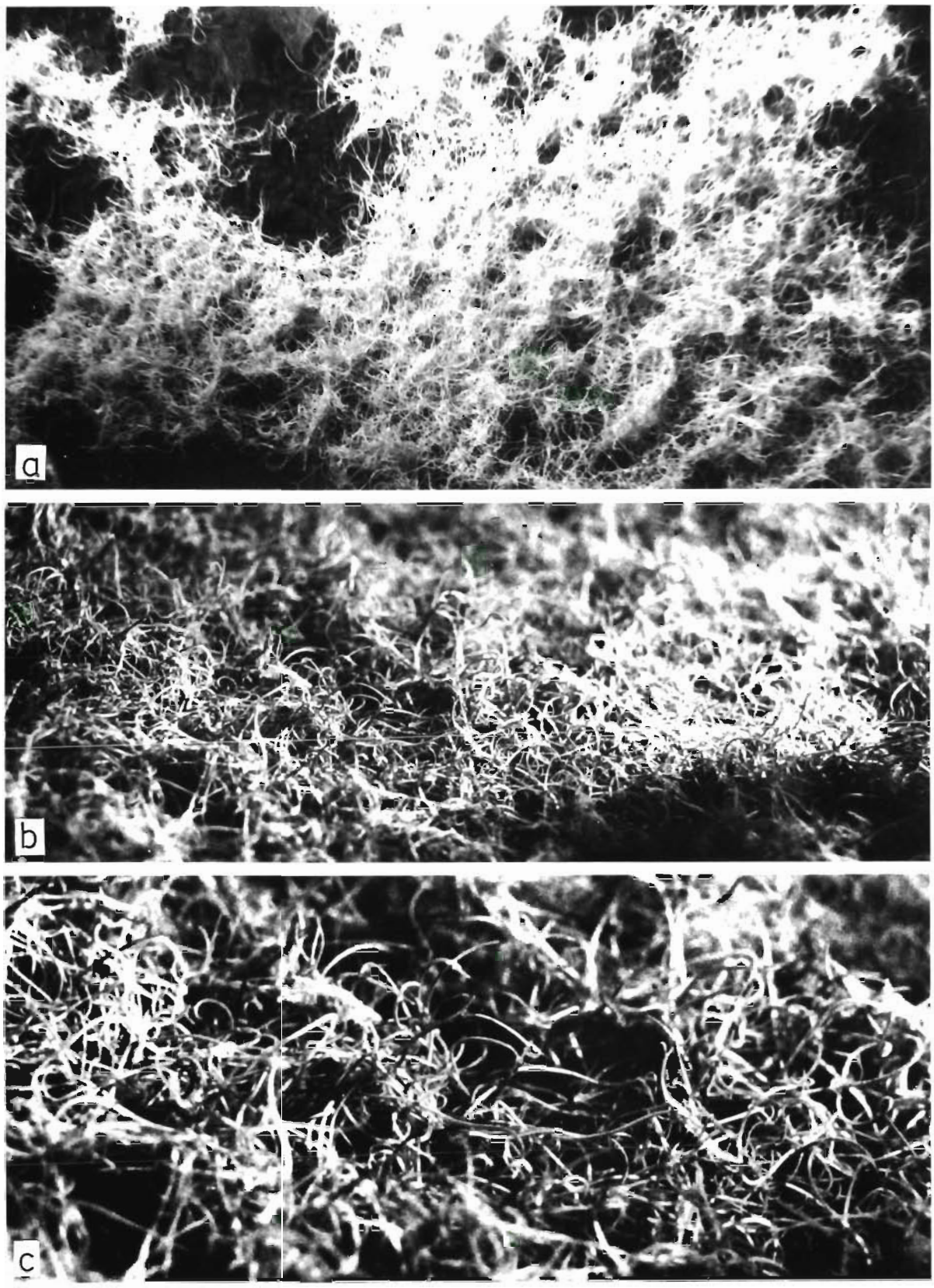

Fig. 5. *Pontonema vulgare*. (a) Large-area aggregations on dead thalli of *Ulva* sp. in the Flensburg fjord. (b, c) Large-area aggregations on soft bottoms at Stn 2 in the Kiel fjord

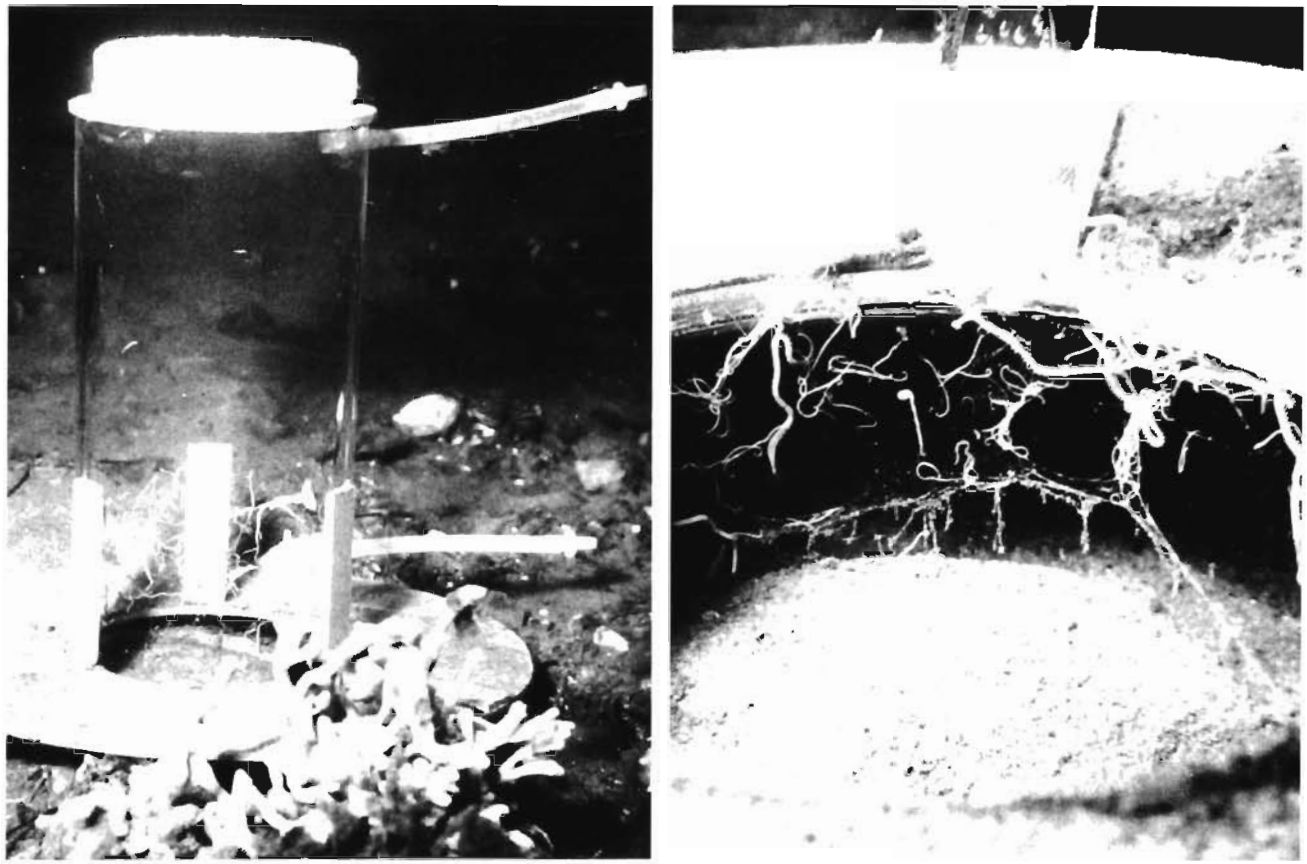

Fig. 6. *Pontonema vulgare*. (a, b) 14 d after starting the cylinder experiment (description see text), *P. vulgare* and the polychaete *Scoloplos armiger* had crawled up to 12 cm up the wall of the closed cylinder, due to low oxygen content

(1906, p. 102, 104) found the species in the intertidal zone of St. Andrews (North Sea coast of Scotland) 'very common under stones between the tide-marks. It is essentially a sociable animal, 20 or 30 often found together under one stone; it is not usual to find individuals isolated'. Later Jennings & Colam (1970, p. 212) confirmed Stewart's finding when collecting *P. vulgare* 'from sand and mud beneath the stones in the mid-tide zone at Filey Brigg on the Yorkshire (England) coast. Aggregations of several hundred individuals tightly entwined were commonly found'. Menzel (1920, p. 158) found 'mass aggregations of *Oncholaimus vulgaris (= P. vulgare)* on posts with *Mytilus*'* in Trieste harbour (Adriatic Sea). Our results confirm the aggregation behaviour of *P. vulgare*. Unknown up to now was firstly the large size which the aggregations may reach and secondly their occurrence above the surface of the substrate under suboxic and H_2S-rich conditions.

Buerkel (1900) was able to demonstrate a reason for the aggregation behaviour of *Pontonema vulgare*. In the inner Kiel fjord, he lured marine organisms into traps provided with fresh and rotting mussel meat. If the traps were placed in the vicinity of mussel beds, he found *P. vulgare* daily 'in such extraordinary large numbers, that an exact count, and thereby an exact statement about the mean daily catch, was generally impossible. The bait . . . was covered over and over with the 2 to 2.5 cm long worms.' (p. 22)*. *P. vulgare* has been known since 1874 to be 'extraordinarily abundant on mud bottoms in several fathoms depth' in the Kiel fjord, especially 'most numerous between the lumps of *Mytilus edulis* (Bütschli 1874, p. 39)*. Rasmussen (1973, p. 54) observed *P. vulgare* in aquaria and concluded that 'Its importance as a scavenger in the soft bottom communities seems to be very great. Even larger dead bottom invertebrates (*Mytilus*, decapods, etc.) are devoured. Thus one 33 mm long, dead *Crangon crangon* was eaten up (only skin left) by several hundred adult *P. vulgare* specimens (15 to 20 mm long) in less than 12 h'. Jensen (pers. comm.) has made observations in the Mariager fjord and Isefjord (Denmark) which argue for a role for *P. vulgare* as 'scavenger including patchy distribution patterns in oxygen-deficient bottoms where specimens of *P. vulgare* accumulate around/in dead or suffering animals'.

* Quotation translated from German

Our results confirm the above cited observations that *Pontonema vulgare* feeds on dead and moribund animals. Additionally, mats of rotting *Ulva* sp. and *Zostera marina* as well as soft bottoms of high organic content apparently provide food for *P. vulgare*, since on these substrates the nematode was found to form the largest aggregations ever observed.

The luring experiments by Buerkel (1900) as well as the aggregation behaviour observed in the aquarium clearly indicate that aggregations of *P. vulgare* are formed by migratory activities of that species. Gerlach (1977, p. 162) observed the same phenomenon in the free-living marine nematode *Sabatieria migrans* (Comesomatidae) which was attracted by decaying fish in experiments performed on a Bermuda beach.

While patchy distribution of food and migratory activities turn out to be important causes for aggregations of *Pontonema vulgare*, these factors do not explain why aggregations are formed above the surface of the substrate. The cylinder experiment of February/March 1981 yields an answer: low oxygen content and related factors (especially increasing H_2S content) force *P. vulgare* to move out of the sediment.

From our observations we conclude that mass aggregations of *Pontonema vulgare* above the sediment indicate dramatic mortality within an ecosystem rich in organic matter. When oxygen decreases dramatically and H_2S increases, many macrofaunal animals are killed. *P. vulgare* turns out to be the only important scavenger in such a situation. One step further in this process would signify the complete death of all benthic macrofauna (including *P. vulgare*) of the respective sites, as may be seen in the inner Flensburg fjord, where *P. vulgare* experiences its mass occurrence exactly in the transition zone between oxic and anoxic sites, the latter being free of any benthic macrofauna (including *P. vulgare*).

It is highly probable that mass aggregations of *Pontonema vulgare* above the surface of sublittoral sediments can only be observed by SCUBA diving and not by sampling with grabs from on board ship, because grab sampling disturbs the surface layer of the sediment.

APPENDIX

Taxonomic remarks

(1) In the Kiel Bight, 2 species of *Pontonema* are known, *P. vulgare* and *P. balticum* (Schulz 1932) (= *Paroncholaimus balticus* Schulz 1932; this species is known exclusively from the sublittoral zone of the Kiel Bight). According to Kreis (1934), the 2 species differ from each other in 7 characters. Of these differences, 6 are due to errors by Kreis and one is obviously due to the fact that Schulz's slides were squeezed. Since all characters of our specimens agree well with the descriptions of both species, we suggest *P. balticum* to be a new synonym of *P. vulgare*.

(2) Contrary to existing descriptions of *P. vulgare*, the preanal papillae of males are not unpaired, but paired (Fig. 4d & 7). In a typical case there are 3, 2 and 3 short papillae on each preanal papilla of the foremost, middle and hindmost (closest to anus) pair, respectively. Pronounced intraspecific variation exists concerning the number and distribution of the short

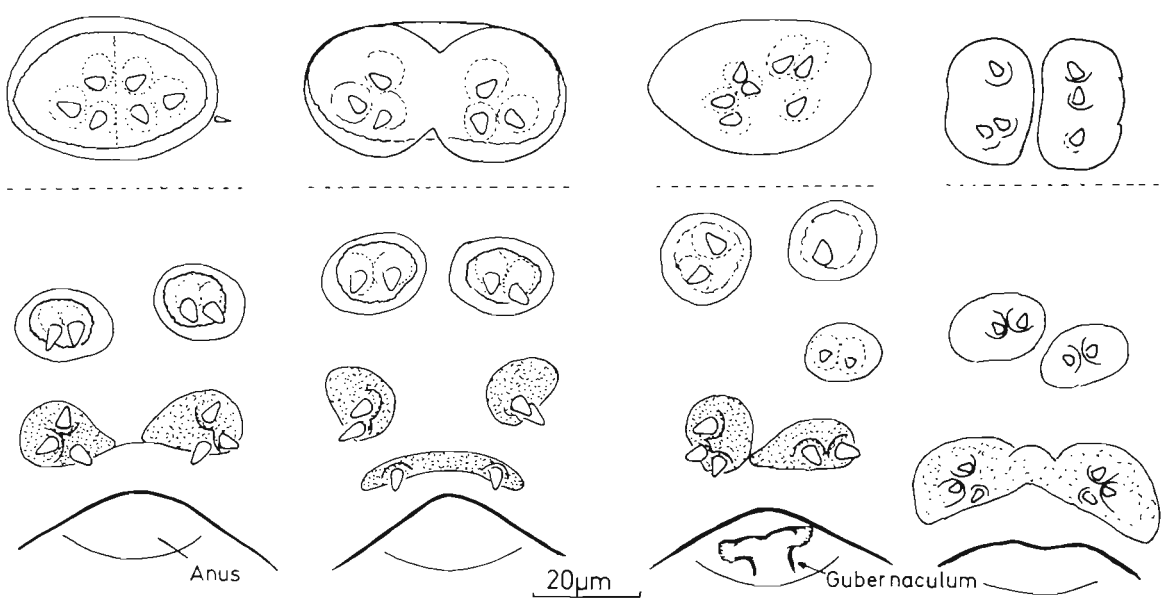

Fig. 7. *Pontonema vulgare*. Ventral view of the preanal papillae of 4 males; note the arrangement in pairs and the individual variability

papillae as well as the shape and arrangement of the preanal papillae.

(3) Only the posterior part of the amphideal fovea penetrates into the body wall (Fig. 4c).

Acknowledgements. We acknowledge the help of M. Wahl (Kiel) in performing the cylinder experiment and for supplying the respective oxygen data, and the help of the staff of the Aquakulturgesellschaft Ostseeforelle, Kiel, during the diving investigations. Furthermore we appreciate information given by Dr. F. Riemann (Bremerhaven, FRG) and Dr. P. Jensen (Helsingör, Denmark).

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This article was submitted to the editor, it was accepted for printing on February 12, 1987