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Turbellaria (Archoophora: Acoela) from Antarctic sea ice endofauna – examination of their micromorphology

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Abstract Acoel Turbellaria constitute a regular component of the metazoa populating Antarctic sea ice (sea-ice endofauna). Two species were collected, which differ in colour, size, shape and egg spawning season. They do not resemble any known pelagic species. Their small body diameter of less than 300 µm allows them to penetrate deeply into the network of brine channels. Their vertical distribution within one ice floe was positively correlated with the accumulation of algal biomass; maxima for both parameters were found in the bottom 5 cm of the floe. The method by which the Turbellaria invade the sea ice is not clear. At present we have no indication that they pass through a pelagic or benthic stage in their life-cycle. As the Turbellaria were found to populate sea ice in areas with water depths ranging from 370 to 4450 m, the presence of benthic phases in their life-cycle, either free-living or epizooic, is not very probable. We suggest that the Turbellaria either use migrating invertebrates as a vector for their propagation or pass through a pelagic stage in their life-cycle.

Introduction

Ice floes from polar regions have a complex three dimensional network of brine channels (Weissenberger 1992; Weissenberger et al. 1992). The channels form the habitat for a diverse assemblage of protists and small invertebrate organisms of different taxa. This assemblage of sea-ice fauna has roused the interest of marine biologists particularly during the last decade (e.g., Carey 1985; Eicken 1992; Garrison 1991; Gulliksen 1984; Hempel 1990; Horner 1985, 1990; Lønne and Gulliksen 1991; Spindler 1990, 1991, 1994, 1995; Spindler and Dieckmann 1991, 1994; Spindler et al. 1990). Diatoms and flagellates are the main primary producers in the brine channels and provide a copious food source for many sympagic protozoan and metazoan species. Furthermore, various pelagic crustaceans use the ice algal biomass developing in the lowermost decimetres of the ice floes as a food source during part of their life-cycle (Marschall 1988; O'Brien 1988; Runge et al. 1991; Stretch et al. 1988). The role of the fauna inside the brine channels for the ice-based food web is relatively unknown. Nematodes, crustaceans, turbellarians and larvae of benthic organisms were found to dominate the endofauna of Arctic sea ice from shallow sites such as the Canadian Archipelago (Carey and Montagna 1982; Cross 1982; Friedrich 1997; Gradinger et al. 1991, 1992; Grainger and Hsiao 1982; Grainger et al. 1985) while studies on the endofauna of Antarctic ice floes focused on protozoans and crustaceans like the ice-endemic harpacticoid copepod *Drescherellia glacialis* (Bermans et al. 1991; Dahms et al. 1990). Acoel Turbellaria were declared to be unknown from Antarctic waters (Sieg and Wägele 1990). During a summer expedition to the Weddell Sea we investigated the composition of the metazoan endofauna of Antarctic ice floes in detail. Turbellarians were found to constitute a major component of the endofauna, similar to the observations made in the Arctic (Gradinger et al. 1992). We present our findings on the micromorphology of sea-ice turbellarians in order to shed some light on their ecology.

Materials and methods

During the Antarctic summer expedition ANT IX/3 (15 January to 8 March 1991) of RV *Polarstern* to the Weddell Sea, ice samples

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were taken at different stations either by collecting drifting lumps of ice by hand from aboard ship or by coring floes with a 7.5-cm ice auger. Core samples were cut into segments of 10 cm in length with a saw. These segments were processed individually to analyse the vertical distribution of organisms in the core. For algal pigment analysis, ice-core samples were melted in the dark at +4°C and chlorophyll was measured fluorometrically according to Evans et al. (1987). A second set of ice samples for collection of ice endofauna was thawed as described by Spindler and Dieckmann (1986). With the aid of a dissecting microscope, turbellarians were collected alive from the water with a pipette. The collected individuals were fixed onboard immediately after picking them from the melted ice samples. Without being anaesthetized (relaxed) they were submerged in chilled 2% glutaraldehyde buffered with sodium cacodylate (0.2 M, pH 7.4), to which sucrose was added to adjust osmolality (96.5 g l^{-1}), and gently agitated. After 2 h the liquid was exchanged and the samples were stored in a refrigerator at +4°C until the end of the cruise.

Prior to further processing, the specimens were rinsed three times with sodium cacodylate buffer (0.2 M, pH 7.4) to which 1.6 g NaCl per100 ml was added. For scanning electron microscopy (SEM) fixed specimens were transferred to graded acetone for dehydration, critical point dried, and sputter-coated with gold. Specimens were mounted with double adhesive tape on stubs and examined under a Phillips SEM 515 stereoscan.

Correlation matrix and Fisher's *r to z* probability values (Sachs 1984) were computed for the chlorophyll *a* and endofauna concentrations at station 153 (n = 7) with Statview 4.1.

The Turbellaria described in this paper were sampled at two different stations (for further details see Bathmann et al. 1992):

1. Station 127; 76°36.00 S/31°18.80 W; 30 January 1991; water depth 370 m; sample number AN93041-69/91: "whitish turbellarians" isolated from a drifting piece of brown ice, which was collected by hand.
2. Station 153; 71°05.60 S/20°45.30 W; 11 February 1991; water depths 4450 m; sample number AN93043-120/91: "whitish and orange-red turbellarians" isolated from the segments of an ice core.

Results

Distribution in the sea ice

Tidal currents and wind had broken the ice floes to pieces over vast areas in Antarctic summer 1991 and compacted the resulting slurry of smashed ice to a solid mass, several decimetres thick (so-called "porridge ice"), e.g., at station 127. This conglomerate was interspersed with drifting lumps of coloured sea ice pigmented brownish or greenish by ice algae. At station 127 we observed Crustacea, Protozoa and Turbellaria in the metazoan endofauna of the brine channels. Whitish acoel Turbellaria dominated by number.

Other areas, such as at station 153, were covered by intact ice floes. The strata of the sectioned ice core contained representatives of different microscopical metazoa: crustaceans (harpacticoid, cyclopoid and calanoid copepods and nauplii) and turbellarians which again dominated numerically (Fig. 1a). Whereas the former were restricted to the lower 25 cm of the floe, turbellarians occurred in all strata. However, highest abundances (up to 57 turbellarians l^{-1}) were found in the lowermost 5 cm of the ice core. The distribution of metazoa, and of turbellarians in particular, clearly followed that of the algal biomass, as can be seen in Fig. 1. Consequently, significant correlations of turbellarian abundances existed with concentrations of chlorophyll *a*, cyclopoid and calanoid copepods and nauplii (Table 1).

General morphological observations

Two morphs of Turbellaria were distinguished. The common one was whitish in colour and had an elongated body, 700 μm by 300 μm in size, or less. The rarer specimens were coloured bright orange-red, were somewhat smaller and globular or lemon-shaped, and 300 μm by 200 μm in size. The light microscope revealed both types to belong to the Turbellaria-Acoela.

The orange-red species

An assemblage of six coloured individuals is shown in Fig. 2. The nose-like protrusion, which was observed in many specimens, appeared to mark the anterior pole. The entire body surface was covered by cilia (Fig. 3). Occasionally we observed carpets or strands of mucus

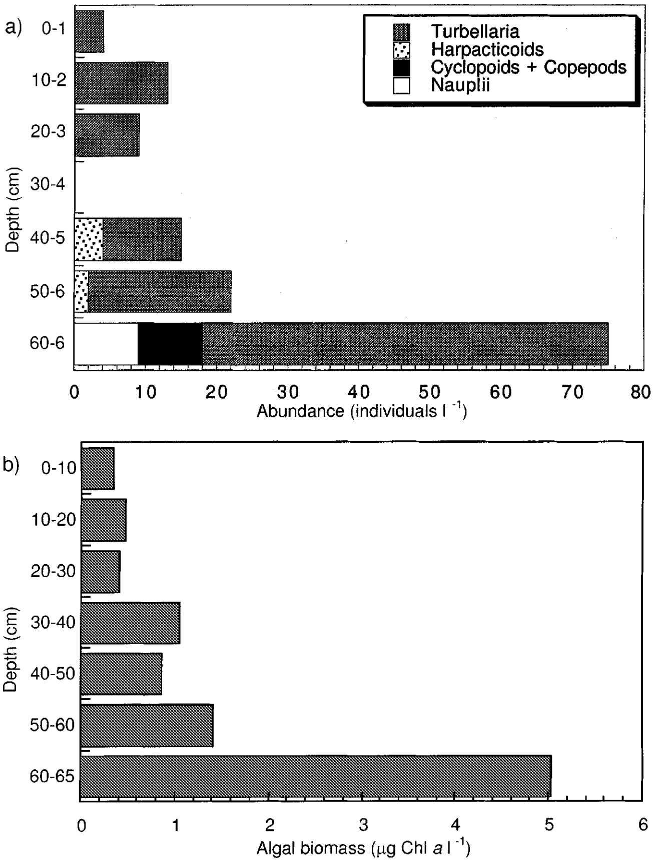

Fig. 1 Distribution of sea-ice meiofauna (**a**) and algal biomass (**b**) in a 65-cm-thick ice floe at station 153

Table 1 Correlation matrix for turbellarian abundance with other parameters determined at station 153 ($n = 7$)

Parameter	Mean depth in ice floe	Harpacticoids	Calanoids + Cyclopoids	Nauplii	Chlorophyll *a*
Turbellaria	n.s.	n.s.	0.942	0.942	0.946
P values	–	–	0.0004	0.0004	0.0003

(Fig. 4). These strands appeared to originate from a frontal organ in the anterior pole (not shown). In some cases detritus or diatoms were glued to the body surface by the mucus. In areas with scattered ciliation, probably an artefact due to cilia lost during sample treatment, the surface of the epidermal cells became visible. It showed a fine granular structure typical for the tips of close microvilli in a brushborder (Fig. 4). Once, several keeled capsules were found attached to a specimen (Fig. 5); the nature of these capsules has not yet been identified.

The whitish species

The morphology of the whitish specimens was different in many aspects from that of the orange-red specimens and it is most probably a different species. The shape of the body resembled a slender drop or a stout spindle with some variation. The body surface was evenly ciliated (cf. Figs. 6–8). A frontal organ opened at the anterior pole (Fig. 9). The inconspicuous mouth area was situated in the centre of the ventral side, often just before a ventrocaudal swelling (Figs. 11–13). Pennate diatoms and detritus particles, which could not be identified, were glued by mucus to the surface of some individuals, especially to their anterior parts (Fig. 10). Mucus coverage was not as heavy as in the orange-red species.

The posterior fifth of the body often formed a globular tail, which was separated by a waist from the an-

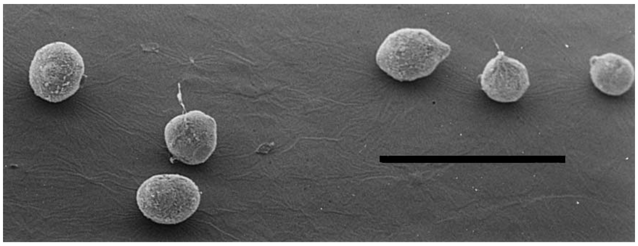

Fig. 2–14 Scanning electron micrographs of acoel Turbellaria from Antarctic sea ice

Fig. 2 Orange-red species. Low power micrograph of six specimens. *Scale bar* 1 mm

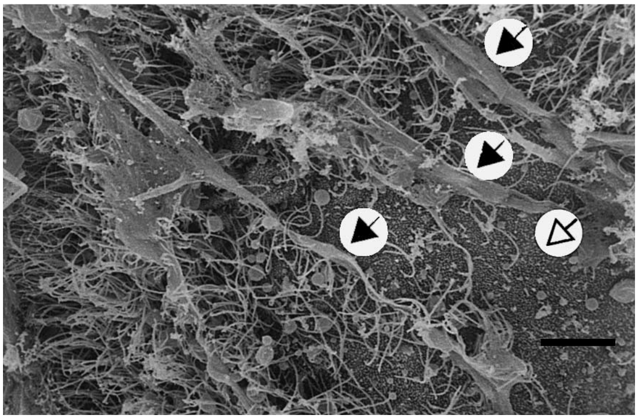

Fig. 4 Orange-red species. Ciliated surface covered by strands of mucus (*filled arrow heads*). In places of reduced ciliation the epidermal surface showed the fine granular pattern of the tips of microvilli from a dense brushborder (*unfilled arrow head*). *Scale bar* 10 μm

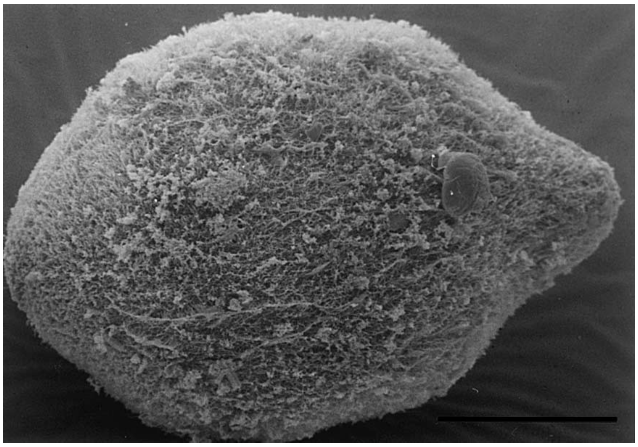

Fig. 3 Orange-red species. Enlarged specimen from Fig. 2 showing the nose-like anterior pole and the dense ciliation of the surface. *Scale bar* 0.1 mm

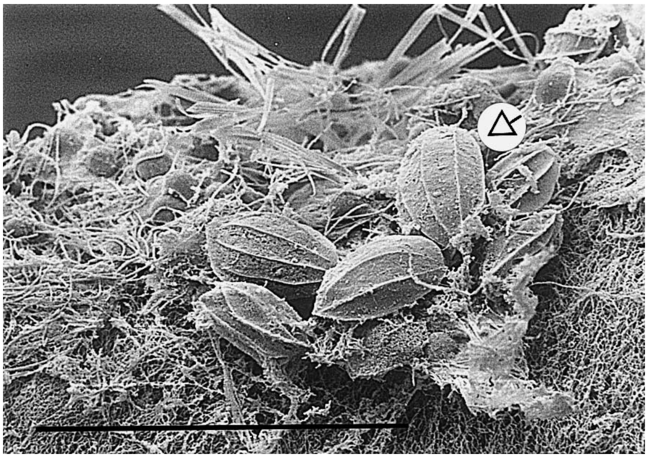

Fig. 5 Orange-red species. Keeled capsules (*arrow*) of unknown nature attached to the surface, observed only once. *Scale bar* 0.1 mm

terior body. The trunk next to the tail appeared ventrally swollen in many specimens. The size of this swelling varied from barely perceivable to half of the height of the body. Voluminous swellings distorted the animal's shape to that of a banana, the convex side being dorsal (Figs. 6–8).

In many specimens, the body wall of the ventral swelling was ruptured. The observed stages allowed us to reconstruct the process of rupturing. The rupturing of the body wall started with a small inconspicuous break of the surface in the middle of the posterior region of the swelling, i.e., next to the tail area (Fig. 11). The break enlarged, and globular structures became visible (Fig. 12). In the final stage the hernia-like swelling was split and shed more than three dozen globules (Fig. 13). They could be identified as eggs in histological sections. The diameters of the largest eggs differed among individuals and ranged from 30 μm to about 90 μm (Fig. 14).

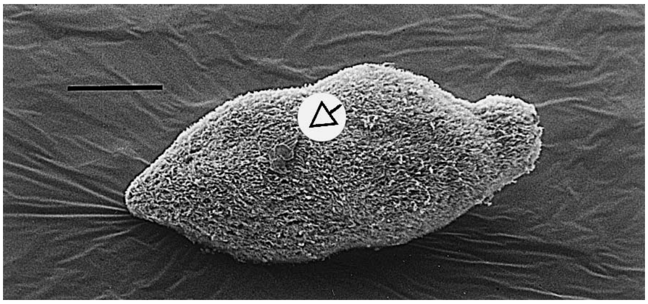

Fig. 6 Whitish species. Its shape is more elongate compared with the orange-red species (cf. Fig. 3). Abdominal swelling and tail are not very prominent in this specimen. The mouth area is marked by an *arrow*. *Scale bar* 0.1 mm

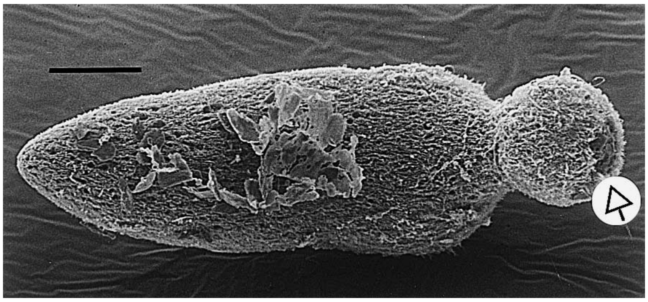

Fig. 7 Whitish species. This slender specimen shows a distinct globular tail. The tail is separated from the body by a waist and has a shallow terminal cavity (*arrow*) (sucker?). The mouth area is concealed by adhering detritus. *Scale bar* 0.1 mm

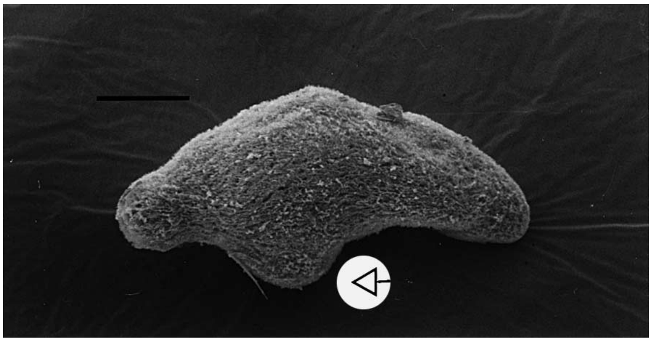

Fig. 8 Whitish species. Specimen has a prominent abdominal swelling (*arrow*) that distorts the individual to a crescent and obscures the tail. *Scale bar* 0.1 mm

Discussion

We describe micromorphological features of acoel Turbellaria which were obtained from the brine channel system of Antarctic sea ice, which have rarely been seen before (Garrison and Buck 1991). Westblad (1952) was hesitant in evaluating badly preserved material from South Georgia. But although only one species was

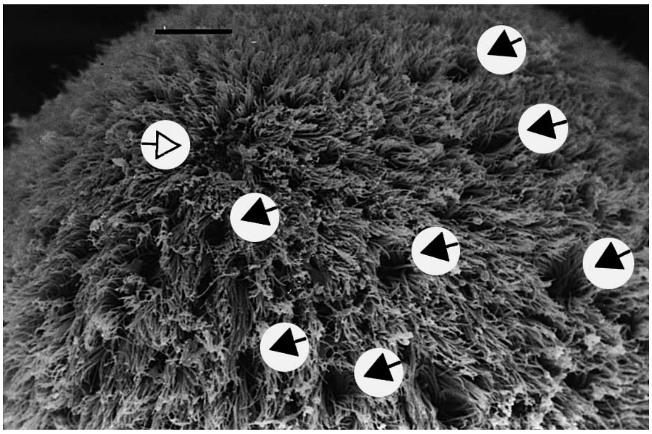

Fig. 9 Whitish species. Frontal pole. The *unfilled arrow head* points to the opening of the frontal organ. Circular areas, where cilia were reduced or missing (*filled arrow heads*), probably correspond to the openings of gland cells. *Scale bar* 10 μm

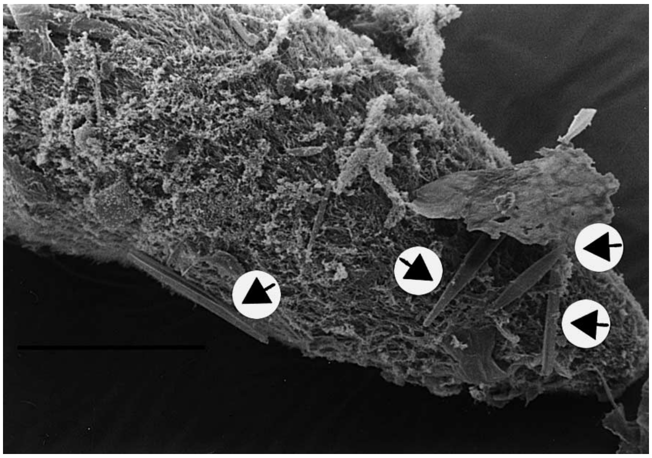

Fig. 10 Whitish species. Anterior end. Unidentified detritus and pennate diatoms (*arrow heads*) adhering to the surface. *Scale bar* 0.1 mm

known to him from Antarctic waters (*Rimicola glacialis* Böhmig), he described two further species and tentatively assigned them to the genera *Anaperus* and *Convoluta*. More data are reported from Arctic sea-ice Turbellaria (see Introduction). However, the description of the anatomy, taxonomy or ecology of Arctic, as well as of Antarctic, Turbellaria is still wanting.

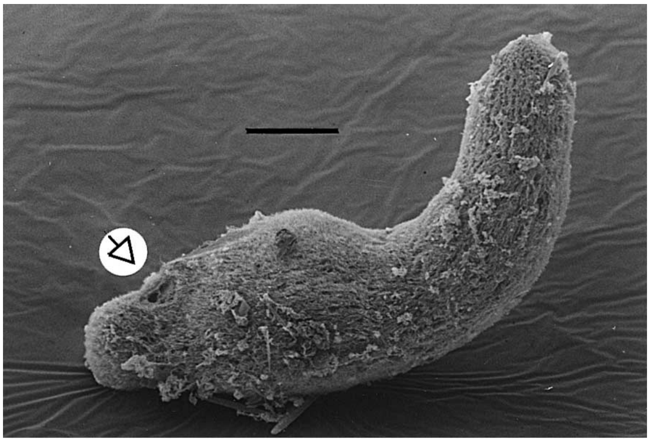

Fig. 11 Whitish species. Beginning rupture (*arrow*) of the body wall at the caudal end of the swelling. *Scale bar* 0.1 mm

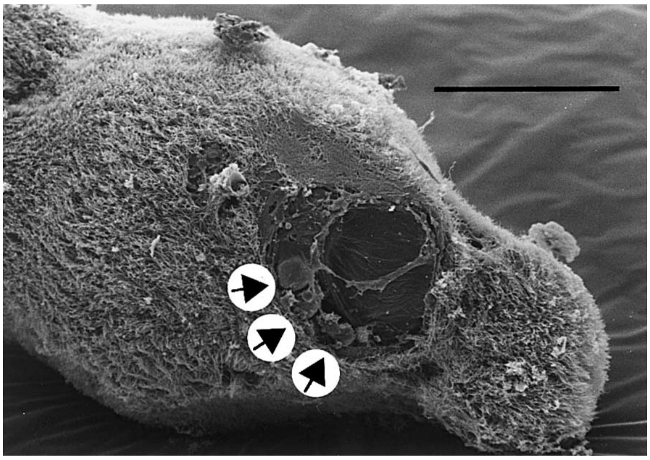

Fig. 12 Whitish species. Extended rupture of the body wall, displaying few globular eggs (*arrow heads*). *Scale bar* 0.1 mm.

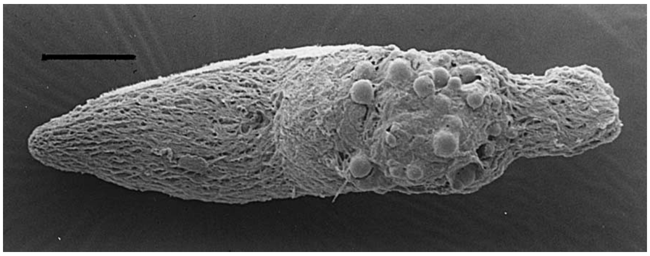

Fig. 13 Whitish species. Completed rupture of the ventral swelling with hernia-like evisceration of its contents containing globular eggs. *Scale bar* 0.1 mm

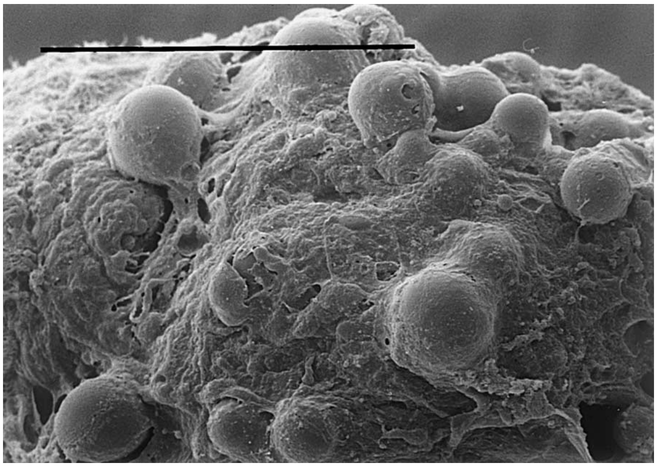

Fig. 14 Whitish species. Detail of Fig. 13. The eggs emerge successively from the eviscerated tissue and are supposed to be shed one by one to surrounding water, as soon as they are completely liberated. *Scale bar* 0.1 mm

We distinguished two morphs of Turbellaria with a morphology so different that we recognize them to be two different species. With regard to the colour, the orange-red species might be tentatively placed near the genus *Polychoerus* (Hyman 1951). The full taxonomical classification of the species will require detailed histological studies on the epidermis, which are still only beginning.

In cross-section, both species are round with a diameter of less than 300 μm. This value refers to fixed specimens, which were probably contracted as they were not anaesthetized before fixation. Their narrow bodies make them well adapted to roaming through the network of brine channels with diameters usually below 1 mm (Weissenberger 1992; Weissenberger et al. 1992). As we repeatedly found specimens with diatoms attached to their body surface, we assume that the flatworms move through brine channels in search of diatoms which, after contact, will become entangled in the mucus secreted by the frontal glands, and ingested. This suggestion is in agreement with findings on sea-ice Turbellaria from the Arctic, which were of comparable size, and were observed with more than a dozen ingested pennate diatoms (R. Gradinger, unpublished observations). Grainger and Hsiao (1982) also identified chlorophytes and diatom frustules in the guts of ice turbellarians from Frobisher Bay, Canada. As acoel turbellarians are a dominant element of the Antarctic sea-ice endofauna, they may significantly contribute to the grazing on ice algae, as described for Arctic multiyear ice floes (Gradinger et al., in press).

Release of eggs was observed only in individuals of the whitish species, which had probably entered the spawning season. Shedding of eggs by body rupture is not uncommon among the Acoela (Apelt 1969; Ax and Apelt 1970; Hyman 1951). For the whitish species, we assume that the eggs are not deposited in gelatinous capsules, but drop one by one from the ruptured tissue. It seemed that the eggs emerge gradually from the surrounding tissue, and adhere to the maternal body for a while, until they are completely liberated and shed into the water. The true diameter of mature eggs is probably underestimated, as the drying procedure for SEM specimens usually causes some tissue shrinkage.

At present we can only speculate on the fate of the released eggs. As spawning occurs during the Antarctic summer in January/February, the eggs or the hatched juveniles will be released from the thawing ice to the water column. It would appear favourable for the turbellarian offspring to stay permanently in the surface layer in order to invade remaining ice floes, or new ice that will develop only a few months later. Unfortunately, knowledge of pelagic acoels is very scanty and refers mainly to representatives from warm or temperate waters (Brauner 1920; Bush 1984; Dörjes 1970; Hyman 1939; Löhner and Micoletzky 1911). Recent papers on pelagic Turbellaria from all oceans focus on aspects of their mutualism with bacteria or microalgae or their mixotrophy (Stoecker et al. 1989; Trench and Winsor 1987) and do not describe their reproductive strategies.

Sea-ice Turbellaria are capable of swimming. As they are small and fully ciliated, low sinking rates can be assumed. However, these turbellarians are not reported from plankton samples so far, and so it is very probable that they show neither long-distance swimming nor drifting during Antarctic summer.

As soon as they are released from the melting sea ice, eggs, juveniles or fully developed turbellarians have to meet the problem of sedimenting to the sea floor, which aggravates the recolonization of sea ice. Though sea ice may develop in the beginning over comparatively shallow depths, the release of Turbellaria will occur predominantly over greater depth. The recorded water depths of about 370 m at station 127, and 4450 m at station 153 (see Bathmann et al. 1992) would make it very difficult for the small turbellarians to reach the surface again, if they have been sedimented to the benthos. At present it is not clear how the sea-ice Turbellaria avoid sedimentation and recolonize the newly forming sea ice by the beginning of the Antarctic winter.

An interesting finding was made by Hyman (1951), who described the acoel *Ectocotyla paguri*. This species is unique in possessing a caudal adhesive disc and living commensally on hermit crabs. The globular "tail" of our whitish species could be such an adhesive organ. In the lowermost layer of the ice floes the whitish turbellarians are associated with representatives of various crustacean taxa (see Fig. 1a). Thus specimens that are about to be released from the ice could attach to free-swimming copepod crustaceans, or to euphausiids harvesting ice algae from the lower surface of the ice. Crustaceans would provide a suitable vector and allow the turbellarians to shuttle between the water column and the brine channel system, as the crustaceans will return from their pelagic phase to the newly formed sea ice to graze there during Antarctic winter.

Other acoel species that appear similar to the whitish one described here are known to be commensals with various species of sea urchins (Echinodermata: Echinoidea) (Dörjes 1972). Sea urchins are very common in the benthic coenoses of Antarctica and could serve as benthic hosts for Turbellaria. However, there is currently no evidence for such an interrelation between sea-ice Turbellaria and benthic or pelagic invertebrates.

For a further understanding of the ecology of Antarctic sea-ice Turbellaria, more detailed examinations are badly needed, and we are continuing the evaluation of our preserved specimens with detailed ultrastructural studies.

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