

Dense Mat-forming Bacterium *Thioploca ingrica* (Beggiatoaceae) in Eastern Lake Ontario: Implications to the Benthic Food Web

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ABSTRACT. Dense mats of *Thioploca ingrica*, a filamentous sulphur-oxidizing bacterium, were discovered for the first time in the upper profundal sediments of eastern Lake Ontario. This is the first report of extensive mats of the bacterium in North America. Filaments were encountered at depths between 28 and 146 m, but were absent from 228 m, and at sites that had a population of the burrowing amphipod *Diporeia*. The bacterial mats were not present at two of the sites before 1995 but their biomass increased rapidly after 1995 following the disappearance of *Diporeia*. In 2000, biomass of *Thioploca* was greatest at 32 m, averaging 206 g/m² wet, or 17.4 g/m² dry. This was up to six times the biomass of the macroinvertebrates present in the sediment, and three times the historic biomass of the burrowing amphipods. Microbial anaerobic degradation may dominate the energy pathway of the benthic community over a large area of eastern Lake Ontario, replacing the amphipod community that supported fish production. The coupling of sulphide oxidation and nitrate reduction by the vertically migrating *Thioploca* filaments may become significant in the nutrient cycling where the mats develop.

INDEX WORDS: Sulphur-oxidizing bacteria, sediments, macroinvertebrates, *Diporeia*.

INTRODUCTION

Benthic communities of the Great Lakes underwent dynamic changes over the second half of the twentieth century. Water quality deteriorated during eutrophication, resulting in many changes to the fauna (Carr and Hiltunen 1965, Cook and Johnson 1974). Following the implementation of phosphorus controls (Canada and USA 1987), there was a recovery as pollution sensitive species returned (Johnson and McNeil 1986, Krieger *et al.* 1996). Invasion by exotic species further challenged the Great Lakes ecosystem, the most dramatic change occurring after the arrival of *Dreissena* spp. The mussels altered the energy flow between the pelagic and benthos, often with unpredictable outcomes (Stewart and Haynes 1994, Howell *et al.* 1996, Nalepa *et al.* 1996, Dermott and Kerec 1997).

Surveys of the benthic fauna in eastern Lake Ontario and connecting Bay of Quinte have been conducted for two decades exploring changes resulting from phosphate reductions and shifting fish populations (Johannsson *et al.* 1985, Johnson and McNeil 1986, Johannsson *et al.* 1998). Macroinvertebrate populations and benthic biomass have been monitored following the colonization of eastern Lake Ontario by *Dreissena* spp. (Mills *et al.* 1993). Recently, the burrowing amphipod *Diporeia* spp. (Pontoporeiidae) disappeared from large areas of the upper profundal zone (30 to 60 m) in the Great Lakes, from densities over 8,000 ind/m² to below detection (< 1 ind/m²; Nalepa *et al.* 1998, Dermott 2001). The cause for the decline is unknown but occurred following the colonization of nearshore areas by the mussels *Dreissena polymorpha* or *D. bugensis* (Dermott and Munawar 1993).

The present paper reports the first occurrence of the giant filamentous sulphur bacterium *Thioploca*

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ingrica (Beggiatoaceae) in Lake Ontario, its recent increase in biomass, and formation of dense mats on the sediment surface in the upper profundal of eastern Lake Ontario. The only previous report in North America was from western Lake Erie (Maier and Murray 1965), but that population had declined until no longer detectable (Maier 1980). Little is known about the metabolism and remarkable migration behavior of the freshwater species. However, marine *Thioploca* species form massive mats on the sea floor along the west coast of South America, where they play a significant role in global denitrification (Jannasch 1995). Also briefly reviewed is the nature and metabolism of this motile filamentous organism, needed to understand the implications of the bacterial mats to the Lake Ontario food web.

Prior to 1990, *Diporeia* spp. formed 38 to 90% of the total benthic biomass in the profundal of the Great Lakes, with standing stocks between 0.6 and 3.4 g/m² dry biomass (Johannsson *et al.* 1985, Nalepa 1989, Dermott and Kerec 1997). *Diporeia* production is supported by settling diatoms (Gardner *et al.* 1990, Johnson and Wiederholm 1992) and sediment bacteria (Marzolf 1965, Sly and Christie 1992, Goedkoop and Johnson 1994). Fitzgerald and Gardner (1993) found *Diporeia* assimilation accounted for 61% of the settling algal carbon in Lake Michigan. This amphipod is a major diet item of cold-water forage fish (sculpins, alewives, smelt) as well as whitefish and juvenile salmonids in the Great Lakes (Flint 1986, McDonald *et al.* 1990). Loss of this amphipod has eliminated a major energy pathway, causing a serious decline in the fish community (Hoyle *et al.* 1999, Owens *et al.* 2003), and leaves an open niche in the benthic community of large areas of the Great Lakes. The community in the upper profundal zone has been reduced to a few species of subsurface-feeding oligochaetes (Lumbriculidae and Tubificidae), *Pisidium* spp., the meiofauna, and sediment bacteria.

METHODS

An Ekman dredge (0.05 m²) was used to collect four to five replicate benthic samples in eastern Lake Ontario during August each year between 1991 and 2000. Samples were from the entrance to the Bay of Quinte near Conway at a depth of 32 m (44°06.5'N: 076°53.9'W), and further offshore in Lake Ontario at 29 m depth, (44°03.6'N: 076°46.6'W). These samples were screened on a 0.58 mm (#30 mesh) sieve, and the retained

residues preserved in 10% formalin. In 1999, additional samples were collected with 6.5 cm cores (0.003 m²), capped and packed on ice until returned to the lab. The benthic cores were used to examine orientation in the sediment, depth of penetration, and length of the *Thioploca* filaments. During October 1999, additional samples were collected at nine locations in eastern Lake Ontario at depths between 18 and 228 m, to determine depth and spatial distribution of the bacterial mats. At these sites, two replicate samples were collected with a PONAR grab (0.053 m²) from CSS Limnos.

Thioploca filaments retained on the 0.58 mm sieve were separated from benthic animals, detritus, and coarse sediment under a dissecting microscope at 6×, in the manner of Schulz *et al.* (1996). Biomass of the filaments was estimated by blotting on filter paper to remove excess water and weighing to the nearest 0.1 mg. Subsamples were dried at 60°C for 24 hours, cooled in a desiccator, and reweighed to calculate dry mass of the bacterial filaments. Sediment in the cores was gently washed with tap water onto a 0.18 mm meshed screen. Length of the exposed sheathed bundles (filaments) was measured under a dissecting microscope. Diameter of the sheathed bundles, and diameter of individual trichomes in the filaments were measured with a micrometer at 400× and 1,000× under a compound microscope.

RESULTS

Morphological Characteristics of *Thioploca*

Due to tangling of individual filaments (Fig. 1 a, b), the bulk of the bacterial mass was retained on the sieve. The bacterium was identified as *Thioploca* by the multiple and often braided trichomes enclosed within a common gelatinous sheath (Fig. 1 c). Diameter of the sheathed bundles (filaments) ranged from 30 to 126 µm. Filament length in the screened and preserved Ekman samples ranged between 2.2 to 5.6 cm, but up to 7.2 cm in the more gently screened cores. Mean diameter of the individual trichomes was 3.8 µm ± 0.3 µm, with the trichomes having slightly tapered terminal cells. Trichomes had numerous inclusions of sulphur averaging 1 µm in diameter (Fig. 1 d). Independent gliding mobility of the trichomes within the common sheath was estimated as up to 1.8 µm/sec or 2.6 mm/hour. Dr. Siegfried Maier (Ohio University) identified the species as *T. ingrica* (Wislouch 1912) based on mean diameter of the individual tri-

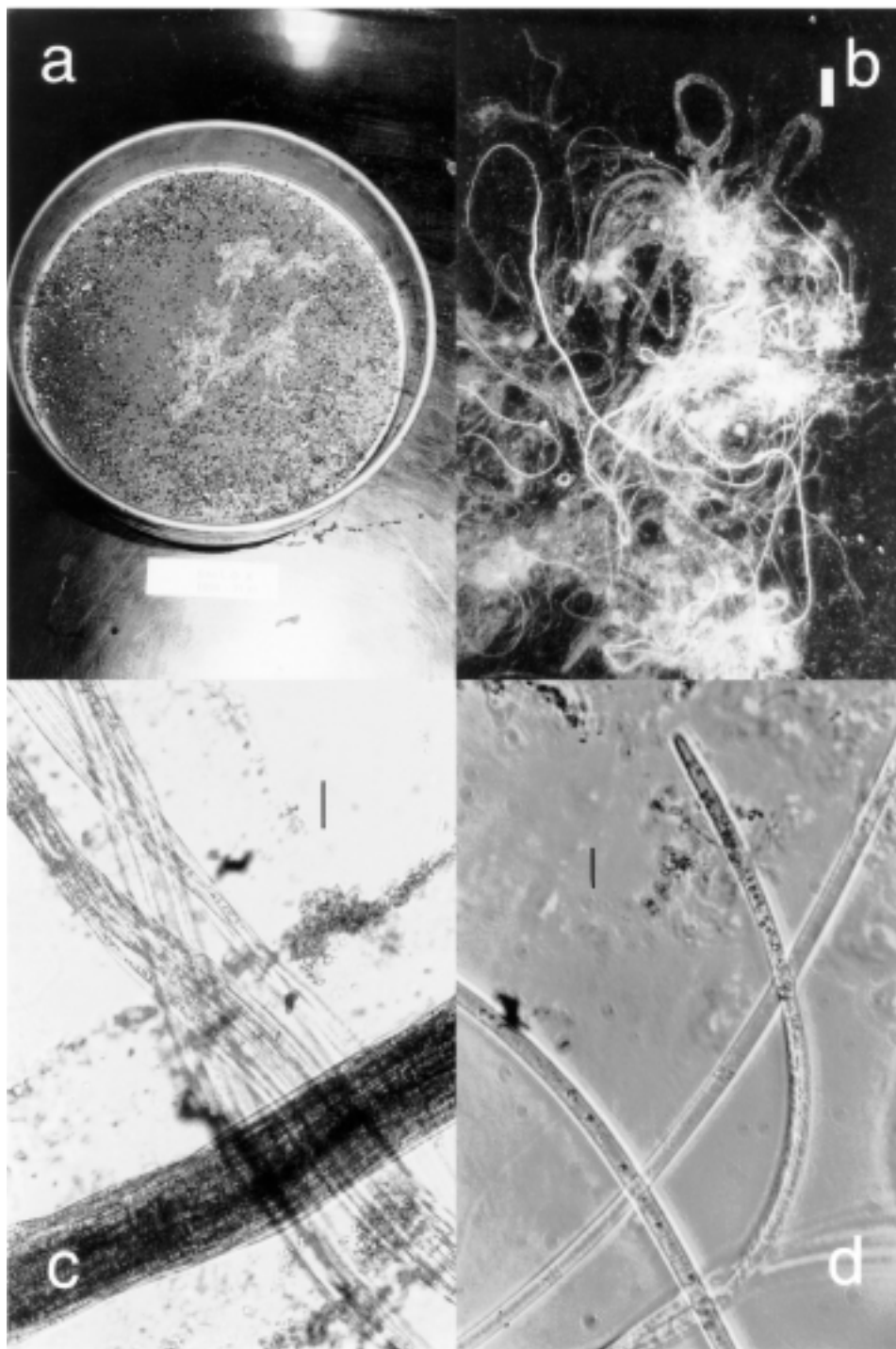


FIG. 1. (a) Filaments of *Thioploca* retained on a 22 cm diameter sieve of 0.58 mm mesh, after washing an Ekman sample (0.05 m²) collected from eastern Lake Ontario. (b) Sheathed bundles of *Thioploca* washed from the sediment. Width of largest sheathed bundles is 120 μ m. Scale bar is 1 mm. (c) *Thioploca* bundles containing between 4 and approximately 30 filaments enclosed in a common sheath. Scale bar is 20 μ m. (d) Individual trichromes of *Thioploca ingrica*, showing sulphur globules within the cells, and tapered terminal segment. Scale bar is 10 μ m.

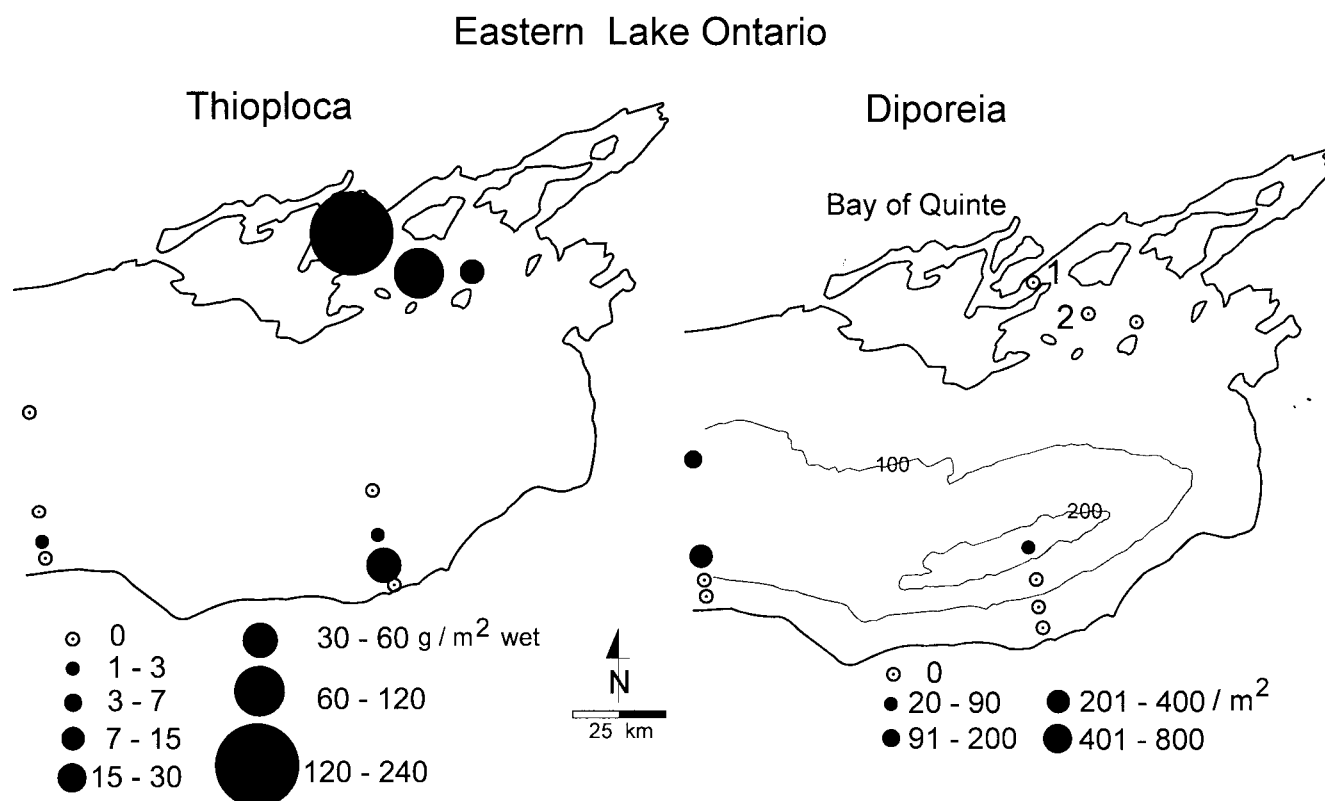


FIG. 2. Wet weight of *Thioploca* (g/m^2) and density of *Diporeia* (ind/m^2) in eastern Lake Ontario during 1999. Contour lines are 100 and 200 meters. Sites sampled annually between 1991 and 1999 at the entrance to Bay of Quinte and in Lake Ontario are marked 1 and 2 respectively.

chomes, the differential characteristic separating the species (Maier 1984, 1989).

Sediment Populations

Dense mats of *Thioploca* were first observed in benthic samples from the entrance to the Bay of Quinte and Lake Ontario in 1997. Weight of the mats at the Lake Ontario site increased rapidly after 1997 (Fig. 2, Table 1). Both sites had a thin layer < 5 mm of brown oxidized silt overlying dark anoxic mud. Minimum oxygen concentration, measured 0.5 m off the bottom using an oxygen meter, was 150 μM . Oxygen levels in the bottom water of the lower Bay of Quinte and eastern Lake Ontario are typically above 20% of saturation (> 90 μM O_2) during the summer (Hurley 1972, Sly and Christie 1992). Field observations indicated over 50% of the mud surface had exposed filaments of *Thioploca*. Filaments protruded from the sediment surface < 1 cm, appearing similar to the photos depicted in Huettel *et al.* (1996). Sediment sections revealed

white sheathed filaments vertically oriented into the sediments, with a maximum length of about 10 cm. Within the retrieved core tubes, the filaments extended between 2.0 and 8.5 cm below the mud surface.

Average biomass (wet-blotted) of *Thioploca* filaments retained on the sieve at the Lake Ontario site ranged from 2.9 g/m^2 (S.E. = 0.01, $n = 5$) to 83.0 g/m^2 (S.E. = 21.9, $n = 4$) in 1997 and 2000 respectively. At the Bay of Quinte entrance site, the wet biomass of *Thioploca* was 21.3 g/m^2 (S.E. = 3.9, $n = 5$); 123.9 g/m^2 (S.E. = 25.2, $n = 5$); and 206.2 g/m^2 (S.E. = 25.1, $n = 4$) in Aug 1998, 1999, and 2000 respectively. Average percent dry weight of the filaments was 8.45%, hence dry biomass at these two sites was between 1.8 and 17.4 g/m^2 . Dry biomass of *Thioploca* in 1999 and 2000 was greater than the average dry biomass of 3.6 g/m^2 of the amphipod *Diporeia* at the Lake Ontario site in 1991 (Table 1). Oligochaete worms (mostly Tubificidae) were the next most abundant benthic macroinvertebrate at the site, but averaged only 1.6 g/m^2 in 2000

TABLE 1. Number of replicates, mean density and standard error (S.E.) of amphipod *Diporeia* (ind/m²), and dry biomass (mg/m²) of amphipods, *Oligochaeta*, *Pisidium* (shell-free), and *Thioploca* at the Lake Ontario site.

| | n | Amphipod | | Oligochaeta | Pisidium | Thioploca |
|--------------|---|-------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|
| | | Density ind/m ² | Biomass mg/m ² | Biomass mg/m ² | Biomass mg/m ² | Biomass mg/m ² |
| 23 July 1991 | 4 | 6,473 | 3,596 | 146 | 251 | 0 |
| S.E. | | (1,270) | (162) | (15) | (38) | — |
| 4 Aug 1993 | 4 | 1,087 | 443 | 182 | 167 | 0 |
| S.E. | | (395) | (175) | (25) | (54) | — |
| 2 Aug 1995 | 5 | 0 | 0 | 343 | 132 | 5 |
| S.E. | | — | — | (85) | (17) | — |
| 6 Aug 1997 | 5 | 0 | 0 | 905 | 22 | 244 |
| S.E. | | — | — | (229) | (7) | (8) |
| 4 Aug 1998 | 5 | 0 | 0 | 869 | 15 | 2,362 |
| S.E. | | — | — | (196) | (3) | (408) |
| 5 Aug 1999 | 5 | 0 | 0 | 999 | 17 | 6,541 |
| S.E. | | — | — | (113) | (3) | (259) |
| 2 Aug 2000 | 4 | 0 | 0 | 1,651 | 3 | 7,011 |
| S.E. | | — | — | (345) | (1) | (1,852) |

(Table 1). The oligochaetes have also increased since 1995, taking advantage of the increased sediment bacterial biomass and deposited organic matter (Table 1).

Mats were not noticed in samples collected at the sites between 1985 and 1995 (Dermott, unpubl. data). *Thioploca* filaments were not detected in samples from 1991 and 1993 when the amphipod was common, but occurred sparsely in 1995, after the amphipod had disappeared (Table 1). In 1997, dry biomass of *Thioploca* was 0.2 g/m² at the Lake Ontario site, and increased to 6.5 g/m² by 1999. At the same time, oligochaete biomass increased, and biomass of the pea clams *Pisidium* spp. decreased. Other macroinvertebrates were insignificant components of the benthos (< 6% of benthic biomass) at these two sites between 1995 and 1999. No *Dreissena* spp. were collected on the soft sediments at either site prior to 1999, but dry shell-free biomass of the mussels had increased to 0.6 g/m² at the Lake Ontario site by August 2000.

During October 1999, *Thioploca* was also found at several locations along the south shore of eastern Lake Ontario. Wet biomass ranged between 0.007 g/m² at 146 m to 29.6 g/m² at a depth of 31 m near

the south shore (Fig. 2). No *Thioploca* was found at 228 m near the deepest part of Lake Ontario. *Thioploca* was not found at sites where *Diporeia* was present (Fig. 2). No *Thioploca* filaments were seen in the sandy sediments at shallow sites (< 20 m depth) along the south shore (Fig. 2), which may be unfavorable habitat for this microaerobic bacterium.

DISCUSSION

Remarkable Behavior

Thioploca belongs to the colorless filamentous bacteria involved in the oxidative side of the sulphur cycle that are often linked to the anoxic boundary layer and may span heterotrophy to obligate chemolithoautotrophy (Gray and Head 1999). Generally, they depend on hydrogen sulphide as an energy source (electrons) and use nitrate as the electron acceptor. Both *Thioploca* and the closely related *Beggiatoa* are capable of gliding, however only *Thioploca* migrates vertically and possesses multiple filaments within a common gelatinous polysaccharide sheath (Huettel *et al.* 1996). *Beggiatoa* are restricted to a narrow zone where oxygen

and hydrogen sulphide overlap at the interface between the oxidized upper and reduced lower sediment horizons (Jørgensen and Revsbech 1983).

Thioploca spp. are microaerobic, having a lower tolerance to oxygen and sulphide concentrations than *Beggiatoa* (Jørgensen and Gallardo 1999). Almost all knowledge on migration behavior, *Thioploca* physiology, and its role in the environment is from the marine species. *Thioploca* filaments undergo vertical migrations (up to 10 cm/day), in response to nitrate and oxygen concentrations in the overlying water, and to take advantage of varying nutrients levels in the sediments (Huettel *et al.* 1996). The migration of marine *Thioploca* is explained by chemotactic responses, a positive response to nitrate overrides the phobic response to oxygen above 50 μM (Huettel *et al.* 1996). They respond positively to low sulphide ($< 100 \mu\text{M}$), but negatively to high sulphide. *Thioploca* spp. are capable of chemoautotrophy using H_2S from the lower sediments as a source of energy and NO_3^- from the upper layers of sediment and overlying water as the electron acceptor. As a result of vertical migration, *Thioploca* is active in coupling the nitrogen, sulphur and carbon cycles (Jørgensen and Gallardo 1999).

Distribution

Vast mats of *Thioploca* spp. occur on sediments in the low oxygen region along 3,000 km of the Peruvian and Chilean coast, forming a biomass up to 1 kg/m² (wet weight) compared to 115 g/m² of benthic infauna in the same area (Gallardo 1977). On the continental shelf off Chile, *Thioploca* spp. occur in water depths from 34 m to 122 m, with total wet biomass ranging from 100 to 800 g/m². The thickest mats were found at depths between 50 and 100 m (Schulz *et al.* 1996). In Lake Ontario, *Thioploca ingrica* was densest at 32 m depth, present between 28 and 146 m, but absent from the deepest part of the lake at 228 m.

The first two species described (*T. schmidlei* and *T. ingrica*) were from European freshwater sediments (Lauterborn 1907, Wislouch 1911, 1912). As *Thioploca* has not been kept in axenic culture, the most reliable discriminatory trait is the range of single filament (trichome) diameter, 2.0 to 4.5 μm for *T. ingrica* and 5.0 to 9.0 μm for *T. schmidlei*. Both species were confirmed in Lake Constance (Koppe 1924) and mats resembling *T. schmidlei* were found on sediments at 430 m in Lake Baikal (Namsaraev *et al.* 1994). *T. ingrica* has also been reported in

freshwater springs in Saxony, Germany (Maier and Preissner 1979, Maier 1984), and in Randersfjord, Denmark (Teske *et al.* 1995).

Maier and Murray (1965) reported *T. ingrica* in western Lake Erie, but that population had declined until no longer detectable near the Bass Islands (Maier 1980). Maier did not mention the presence of mats, nor report density or depth distribution in Lake Erie. *Thioploca* spp. have not been previously reported in the other Great Lakes, and there are no published records of *Thioploca* spp. in other sediments from North America. The only previous report of dense mats of *T. ingrica* is in the profundal of Lake Biwa, Japan (Nishino *et al.* 1998), where they related the recent increase of the mats to lake eutrophication. The deepest sampling station (90 m) in Lake Biwa contained the greatest abundance of bacterial filaments measured as 2.7 meters of filaments per cm³ of sediment.

Metabolism

Maier and Gallardo (1984), using ¹⁴C-labelled substrates combined with autoradiography, revealed *Thioploca* strongly incorporates acetate, amino acids, glucose, glycine, and bicarbonate but does not take up methanol or methane. It is regarded as a mixotrophic sulphide oxidizer. In Lake Baikal, chemosynthesis by *Thioploca* was considered low, having low CO₂ fixation rates (Namsaraev *et al.* 1994), however high methane production was reported in Lake Baikal at the expense of organic matter. Fossing *et al.* (1995) measured carbon oxidation rates of up to 50 mM C/m²/day in the upper 10 cm of the *Thioploca* covered sediment off Chile.

Nitrate serves as a respiratory (dissimilatory) electron acceptor for *Thioploca*. The marine species are highly efficient nitrate scavengers. *Thioploca*'s filaments possess enormous vacuoles (80% of cell volume) that serve as reservoirs of the electron acceptor ("anaerobic lung") in which nitrate concentration can be 0.5 M, or 20,000 times greater than in the ambient water (Fossing *et al.* 1995). By squeezing sediment mats of *Thioploca*, Thamdrup and Canfield (1996) increased pore-water nitrate concentration 100 times to 3 mM as bursting vacuoles released large amounts of nitrate. Freshwater *Thioploca* may not accumulate nitrate to the same degree, since Maier (1989) found differences in the ultrastructure of the vacuoles between *T. ingrica* and the larger marine *Thioploca*. It is not clear if the bacterium performs dissimilatory nitrate reduction to ammonia or denitrification (reduction of ni-

trate to nitrogen or nitrogen oxides). Preliminary evidence points to the former pathway (Jørgensen and Gallardo 1999).

Thioploca have sulphur inclusions in their cytoplasm originating from sulphide oxidation. According to Schulz *et al.* (1996), *Thioploca* mats were found in brownish sediments containing low levels of sulphide (below 7 μM). Although no direct proof was provided, high rates of sulphate reduction (up to 56 mM SO_4^- /m²/day) indicate that *Thioploca* may cause the low sulphide concentrations (Fossing *et al.* 1995). It is not known how *Thioploca* utilize hydrogen sulphide at concentrations below 1 μM , as diffusion into the sheaths is very low at this concentration. However, Fukui *et al.* (1999) found the sheaths were covered by thin filaments of *Desulfonema*, a sulphate-reducing bacterium, which could be responsible for hydrogen sulphide recycling in organically-rich sediments. By active migration between the sulphide rich deeper sediment and nitrate rich surface layers, *Thioploca* couples oxidation of sulphide with the reduction of nitrate.

Implications to Lake Ontario Food Web

Marine *Thioploca* species are believed to depend indirectly on high levels of phytoplankton production in zones of intense upwelling (Jørgensen and Gallardo 1999). Their biomass is low in winter, but high during summer and early fall when organic deposition is highest and bottom water oxygen concentration is low (Gallardo *et al.* 1995). The *Thioploca* population in Lake Ontario may well depend on the same carbon source, i.e., settling phytoplankton. Settling organic material not consumed by the benthic fauna is processed by bacterial hydrolysis, fermentation, release of reduced substances (ethanol, hydrogen), and respiration. Oxidation of carbon is balanced by reduction of oxygen, nitrates, sulphates and oxides of Mn and Fe (Thamdrup and Canfield 1996). In this complex web, *Thioploca* is coupled to sulphides as a source of energy and nitrates as electron acceptor, and may also assimilate low molecular weight organics or carbonate.

It is hypothesized that an essential part of *Thioploca*'s activity, the chemotactic movement into the nitrate rich surface sediments, was severely restricted by the burrowing amphipods in eastern Lake Ontario, thus preventing formation of dense mats. Before 1991, dense *Diporeia* populations (up to 16,000 ind/m², Dermott 2001) would have

greatly tilled the sediment surface, increasing the depth of the oxygenated layer. As a detritivore feeding on settled algae and sediment bacteria, the amphipods may have also fed on the exposed filaments of *Thioploca*. Morita *et al.* (1981) reported ingestion of *Thioploca* by the marine burrowing amphipod *Ampelisca araucana*, which fills a niche similar to that of *Diporeia*. In the presence of *Diporeia* in aquaria (1,500/m²), *Thioploca* biomass decreased by 36% after 30 days, compared to a decrease of 7% in sediment without amphipods (Dermott, unpublished). In addition to *Diporeia*, the isopod *Caecidotea racovitza* had also been abundant at the same sites in Lake Ontario (Johnson and McNeil 1986). Both amphipods and isopods graze on bacterial and fungal filaments (Graca *et al.* 1993), hence formation of the *Thioploca* mats may have been prevented by these crustacea.

It is uncertain if *Thioploca* uses the same organic matter that supported the amphipod population, as the bacterial energy pathway is quite different. In the absence of *Diporeia*, settling detritus may contribute more to sediment anoxia through bacterial biodegradation and production of hydrogen sulphide, which becomes an energy source for this potentially mixotrophic bacterium. In addition, a steady rise in nitrate has occurred in the bottom water of the lower Bay of Quinte since 1972, from 2.5 μM to over 5.6 μM in 1997 (150 to 350 $\mu\text{g/L}$; K.H. Nicholls, Ontario Ministry of Energy and Environment, unpubl. data). A similar doubling of nitrate has occurred in Lake Ontario (L'Italien *et al.* 2000). Increasing nitrate concentrations favor the metabolic pathways of *Thioploca* and could be another cause for the recent success of the mats.

With the demise of the amphipod population in eastern Lake Ontario, *Thioploca* has become the predominant benthic organism in the upper profundal sediments. The reduced benthic macroinvertebrate community now consists of Oligochaeta, the ostracod *Candona* spp., and a few Sphaeriidae. Mean dry biomass of the bacterial mats (7.0 g/m²) is now much greater than that of the macrobenthos at the same site, and also greater than the maximum amphipod biomass of 5.9 g/m² at the site during 1988 (Dermott 2001). Undoubtedly, *Thioploca* biomass has become considerably greater than that of all other organisms. We can also expect a dramatic increase in benthic metabolic activity as a result of *Thioploca*'s presence. At the Lake Ontario site, Johnson and Brinkhurst (1971) calculated microbial respiration as 363 cal/m² /day, while *Diporeia* respiration was 226 cal/m² /day or 31% of the total

benthic community respiration (Johnson 1970). In contrast, carbon oxidation rates in marine *Thioploca* mats (774 g/m²) were up to 50 mM C/m²/day in the upper 10 cm of sediments (Fossing *et al.* 1995), and more than 30 mM C/m²/day in the upper 1 cm of sediments (Thamdrup and Canfield 1996). Considering that oxidation of common organic substrates (such as glucose or palmitic acid) yields more than 100 cal/mM C (e.g., Lehninger 1975), values can be calculated in a range of 3,000 to 5,000 cal/m²/day. If this is applied as a rough estimate to the biomass of the *Thioploca* mats in eastern Lake Ontario, their metabolic activity would range between 536 to 1,330 cal/m²/day, up to double that of all other benthic organisms combined, including microbes.

The benthic food web in a large area of eastern Lake Ontario has shifted from amphipod consumption of settling detritus to microbial degradation. Favorable sediments exist in other North American lakes, especially sediments with low oxygen levels such as in central Lake Erie (Charlton *et al.* 1993). *Thioploca* mats have been recently observed in samples from central and eastern Lake Erie, Cayuga Lake, Lake Champlain, and also eastern Lake Superior (Dermott, unpubl. data), indicating that this bacterium is now widespread in the Great Lakes. With the reduction of *Diporeia* populations elsewhere in the Great Lakes (Nalepa *et al.* 1998), *Thioploca* may become a major component of the benthic community in the upper profundal zone of the lakes. The *Thioploca* mats may be a major trophic sink for nutrients and carbon, their development may reduce energy flow from the benthic community back to the pelagic and fish communities. Where present, the bacteria mats will likely play a significant role in the geochemistry and nutrient recycling of the lakes, as they do in marine upwelling regions (Jørgensen and Gallardo 1999). The details of *Thioploca*'s metabolism in the Great Lakes remain a matter for future studies.

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