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Microbial gradients in a turbid estuary: Application of a new method for protozoan community analysis

Abstract—A method was developed to assess the planktonic flagellate, ciliate, and amoeboid populations across the transition from fresh to salt water in the upper St. Lawrence estuary. As in many estuarine environments the water is too turbid for examination by standard concentration and microscopy techniques. A combined system of fluorescence, Nomarski interference, and Utermöhl sedimentation (FNU) allowed us to resolve a community of 57 protozoan species across the freshwater–salt-water gradient. Colorless nanoflagellate concentrations decreased from 4.1 × 10^6 cells liter^{-1} (247 × 10^6 μm^3 liter^{-1}) in the freshwater zone to 1.7 × 10^6 cells liter^{-1} (139 × 10^6 μm^3 liter^{-1}) in the estuarine frontal region; on average this group contributed at least 45% of the total protozoan cell numbers. Nonpigmented ochromonads (*Spumella* spp.) were the consistent dominants. The heterotrophic picoplankton increased from 1.7 to 2.8 × 10^9 cells liter^{-1} across the salt-water gradient, whereas the autotrophic picoplankton decreased from 8.4 to 2.8 × 10^6 cells liter^{-1}. The frontal region of maximum fish larval biomass contained a diverse protozoan assemblage and was a transitional zone of changing microbial food-web structure.

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Planktonic flagellates and ciliates have long been identified as potentially important intermediates in aquatic food webs. Experiments last century showed that cultures of infusoria—mixed assemblages of protozoa—supported the growth of crustacean zooplankton including species of Cladocera, Anostraca, and Conchostraca (Ryder 1881). Attention has more recently focused on the role of protozoa as

grazers of bacteria and autotrophic picoplankton, as agents of nutrient regeneration, as well as food sources for higher trophic levels (Reid et al. 1991).

Estuaries represent a major, often highly productive class of aquatic ecosystems, but, although such environments have proved to be a rich source of protozoa for enrichment cultures and grazing experiments, there have been few attempts to analyze their overall microbial food-web structure. In part this relative lack of information reflects the difficulty in working with estuarine samples. These waters frequently contain high concentrations of suspended sediment that restrict use of conventional filtration and microscopy techniques.

Many other marine and freshwater environments also pose difficulties for protozoan and phytoplankton analysis by conventional microscopy. For example, Pick and Caron (1987) found that varying amounts of particulate material in their samples from Lake Ontario obscured the nanoplankton, especially colorless forms, and resulted in large (up to a factor of 3) underestimates of these populations by the traditional Utermöhl technique. Similarly, Rassoulzadegan (1991) has drawn attention to the inadequacies of the Lugol-Utermöhl method for nanoflagellate counts, and also noted the problems of identification if the preferred epifluorescence-filter method is used. This inability to identify and census the protozoa is of concern not only in estimating their biomass contribution to the microbial food web, but also because the taxonomic structure of the protozoan community is likely to have important functional implications such as feeding mechanisms, trophic relationships, and potential growth kinetics (*see* Reid et al. 1991).

In the lower reaches of the St. Lawrence River, the freshwater environment (discharge, 10^4 m^3 s^{-1}) grades into a turbid, estuarine zone of increasing salinity. This transitional region, sometimes referred to as the maximum turbidity zone, has recently been identified as a key nursery site for larval fish (Laprise and Dodson 1989). Other studies have drawn attention to the large standing stocks of bacteria (Painchaud and Therriault 1989) and the strong light limitation that might be imposed on phytoplankton photosynthesis in this turbid environment (Therriault et al. 1990). These observations implied that the riverine phytoplankton-based food chain may be largely supplanted in the transition zone by a trophic sequence leading from bacteria to fish. Nanoflagellates and ciliates would likely play a role as trophic links in such a food chain.

As a first step in evaluating this hypothesis we undertook a sampling cruise to quantify the microbial food-web components (bacteria, phototrophic picoplankton, phototrophic and heterotrophic protozoa) along the St. Lawrence transition zone. The cruise spanned the region from the lower freshwater section of the river into and beyond the estuarine frontal zone of greatly increased turbidity and highest fish larval biomass. We were unable to examine our protozoan samples from the transition zone with traditional Utermöhl or membrane filter techniques because of the very large concentrations of suspended sediment. In evaluating alternative techniques we found that the most successful approach for species identification as well as enumeration was an optical configuration that combined three systems: fluorescence, Nomarski differential interference contrast (DIC) optics, and inverted (Utermöhl) microscopy. This combined FNU optics system captured the advantages of three methods: Utermöhl sedimentation to minimize cellular damage, auto- and fluorochrome fluorescence to locate and characterize cells, and Nomarski contrast to highlight taxonomic features. It allowed us to differentiate very rapidly the nanoplanktonic cells from abiotic particles and to assess the population size of individual nanoflagellate, ciliate, and other protozoan species at all stations irrespective of turbidity.

Sampling was conducted at 12 stations distributed along a 60-km stretch of the upper St. Lawrence estuary (Fig. 1): four stations in the lower freshwater (but tidal) section ~30 km downstream of Quebec City (zone 1); four stations in the frontal region of increased turbidity with surface-water salinities in the range 0.7–2 psu (zone 2); and four stations 30 km farther downstream with surface-water salinities in the range 4–8 psu (zone 3). Each zone was sampled twice at low tide and twice at high tide. The cruise was undertaken during spring (10–14 May 1991) to coincide with the period of larval fish development (Laprise and Dodson 1989).

The water column at each site was initially profiled with a Sea-Bird conductivity-temper-

ature-depth system and then discrete samples were obtained near the surface (0.5 m) and near the bottom (17 m, which was at least 3 m above the sediments). Samples for bacteria were immediately fixed with 1% glutaraldehyde (final concn) and stored at 4°C. They were later stained with the fluorochrome 4′-6-diamidino-2-phenylindole (DAPI) and filtered through 25-mm-diameter, 0.22-μm pore-size, black Anapore membranes (Jones et al. 1989). The samples were then examined by epifluorescence microscopy with a UV excitation filter block and 1,000× oil immersion. To convert cell counts to total bacterial cell volume we used a value of 0.048 μm^3 per cell, which was the average of 1,550 measurements of bacterial cell size across the three zones (N. Bertrand and W. Vincent unpubl. data). Our values may underestimate the true in situ bacterial biomass because of losses and changes in cell size during storage (e.g. Turley and Hughes 1992) as well as the uncertainties of measuring cell size by epifluorescence.

Samples for autotrophic picoplankton counts were processed as by Hall and Vincent (1990). The samples were immediately preserved with 0.2% paraformaldehyde (electron microscopy grade) and stored at 4°C for up to 2 weeks. The samples were then filtered onto 0.22-μm black Nuclepore filters, stored at −20°C, and 1–6 weeks later examined by fluorescence microscopy with green and blue exchangeable filter blocks and 1,000× oil immersion. Cell counts were converted to total picoplankton cell volume using a value of 1.3 μm^3 per cell, the average of 840 measurements of picoplankton cell size from across the three zones (N. Bertrand and W. Vincent unpubl. data).

Samples for Chl *a* were passed through 25-mm Whatman GF/F glass-fiber filters which were stored frozen at −20°C. These were subsequently ground in 90% acetone, the extracts cleared by centrifugation and then assayed by spectrofluorometry. Samples for turbidity analysis were measured within 5 min of collection with a shipboard Hach turbidity meter (model 2100A).

The fish larvae samples were collected with a 1-m^2 Tucker trawl fitted with an opening-closing device and a 0.5-m standard plankton net (0.5-mm mesh). A General Oceanic flowmeter fitted at the mouth of the net measured filtration rate. At each station a 10-min tow was performed at 0.5 m and a second at 17 m, at a towing speed of ~5 km h^{-1}. The catch was preserved immediately with buffered formaldehyde (1.5% final concn) and later split and enumerated under a binocular microscope linked to a video camera and digitizing system.

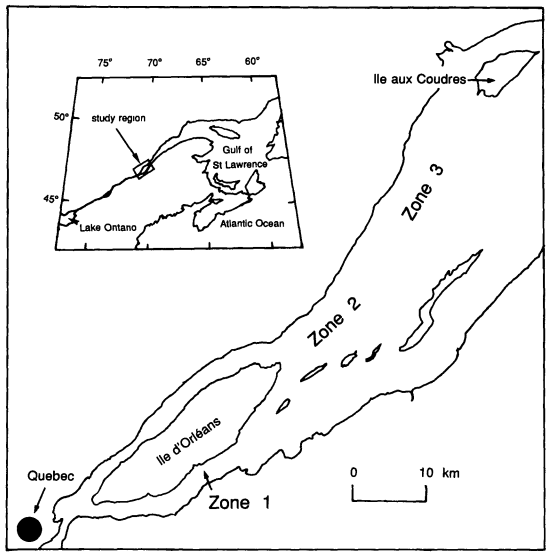

Fig. 1. Location of the three sampling zones across the St. Lawrence River freshwater–salt-water transition.

The protozoan samples were collected with Go-Flo bottles, fixed immediately with 1% glutaraldehyde and 0.1% paraformaldehyde (final concns) prepared according to Tsuji and Yanagita (1981), and stored in the dark at 4°C. This fixative and storage procedure gave excellent preservation of cell structure and autofluorescence for up to several months. However, we have not assessed the loss rate in liquid storage which may vary between protozoan groups.

For enumeration, the samples were gently mixed by inversion and 3-ml quantities were dispensed into 26-mm-diameter Utermöhl settling chambers (Utermöhl 1958). The samples were injected with the fluorochrome DAPI and left to stain and sediment for 12–24 h in the dark at 4°C. DAPI is well suited for use in settling chambers because, as pointed out by Coleman et al. (1981), it shows a >20-fold increase in fluorescence when bound to DNA. The stained cells can thus be observed while still immersed in the unbound stain. We tested concentrations from 0.01 to 1.0 $\mu g\ ml^{-1}$; at

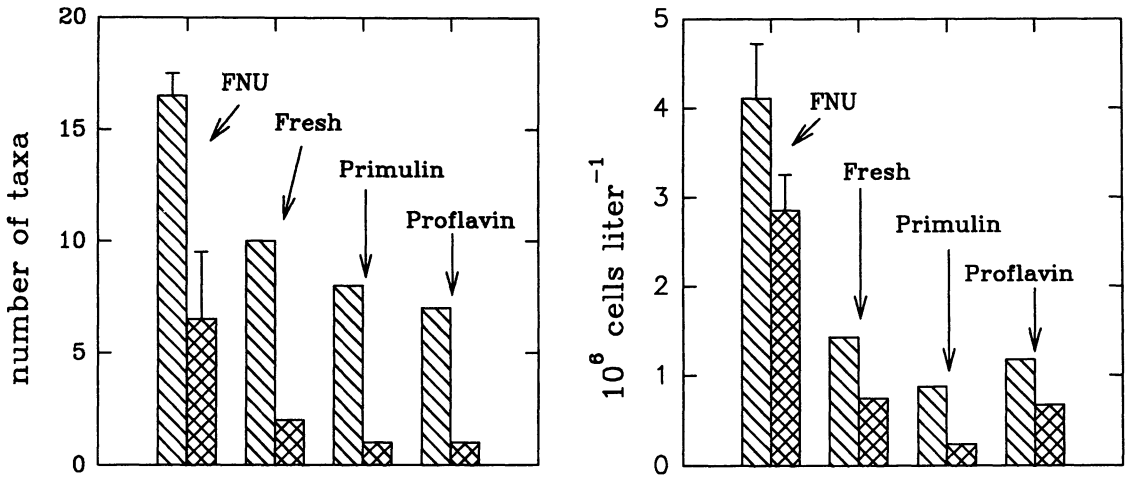

Fig. 2. Comparison of FNU with three other methods to identify taxa (left) and to enumerate (right) the protozoa in a turbid St. Lawrence River sample. The hatched bar of each pair is for the total protozoan community, and the cross-hatched bar is for the colorless (aplastidic) protozoa only. The error bars for the FNU protocol represent the standard deviation for duplicates.

the lower end of this range cells were insufficiently stained and difficult to distinguish, whereas at the higher end the stronger DAPI blue fluorescence masked the red autofluorescence of small phytoflagellates. We adopted a final DAPI concentration of 0.1 μg ml^{-1} which gave a consistently acceptable intensity of staining in our samples irrespective of turbidity.

After sedimentation the chambers were examined under a Zeiss Axiovert inverted microscope at 1,000× magnification with a Zeiss Plan-Neofluor 100×/1.30 objective under oil. Each field was first examined under DIC optics to identify the larger organisms. The DIC light source was turned off and the field was illuminated with violet light through the objective with Zeiss fluorescence filter set 18; this set consists of a 390–440-nm exciter filter, a 460-nm beam splitter, and a 470-nm barrier filter. We selected this filter system after comparing it against Zeiss filter sets 02 (ultraviolet), 05 (blue), and 15 (green). With filter set 18 it was possible to simultaneously view the DAPI-stained nuclei (blue) and Chl *a* autofluorescence (red) and thereby locate and differentiate colorless protozoa from photosynthetic species. Ciliates were easily located by their characteristic macro- and micronuclei, even when the cells were sequestered inside heavily agglomerated tests. The same field was then reilluminated under DIC to view the cellular structure (including flagella and cilia) of the fluorescing cells and to identify the taxa. Filter set 02 (mounted on the same block as set 18) gave a higher DAPI fluorescence and was sometimes used to verify the flagellate counts in the most turbid samples. We counted 50–150 cells in each sample.

Taxa were identified to genus with the light microscopy descriptions of Bourrelly (1966, 1968, 1970) and Chrétiennot-Dinet (1990) for flagellates, Marshall (1969) for tintinnids, and Maeda and Carey (1985) and Maeda (1986) for Oligotrichida, where possible. Broader taxonomic categories followed those adopted by Cox (1980) and Kristiansen and Andersen (1986) for phytoflagellates and Lee et al. (1985) for other protozoan groups. Community indices of diversity, evenness, and similarity were calculated as by Legendre and Legendre (1984). The Steinhaus index (S) of similarity between pairs of samples was calculated by the formula $S = 2W/(A + B)$ where A and B are the sums of the abundances of all species in each of the two samples, and W is the sum of the minimum abundance of each species that occurred in one or both samples (Legendre and Legendre 1984).

We evaluated two other enumeration methods with St. Lawrence samples from 0.5 m deep in the lower freshwater zone. Two 3-ml

Table 1. Environmental data for the St. Lawrence system in zone 1 (sampled 10–11 May 1991), zone 2 (11–12 May), and zone 3 (12–13 May). Each value is the mean (±SE) for eight samples derived from the top and bottom of the water column at four stations.

	Zone 1	Zone 2	Zone 3
Salinity (psu)	0.1(0.0)	1.7(0.6)	7.5(1.0)
Temp. (°C)	10.3(0.0	9.8(0.3)	8.2(0.4)
Turbidity (NTU units)	7.2(0.7)	47.6(11.1)	48.6(14.4)
Chl *a* (mg m^{-3})	6.7(0.3)	4.9(0.3)	2.3(0.6)
Fish larvae (No. m^{-3})	1.7(0.4)	4.5(1.1)	1.5(0.6)

samples were preserved as above and then filtered onto black membranes (0.2-μm Nuclepore) and stained with either Primulin (as by Caron 1983) or Proflavin (Haas 1982). Duplicates of a third sample from the same water bottle were preserved, stained with DAPI, and observed under fluorescence-Nomarski-Utermöhl (FNU) with the protocol outlined above. As a measure of counting error with the FNU technique, the C.V. for the duplicates was 6% for the total number of flagellate taxa and 15% for total flagellate cell counts (Fig. 2).

Both Proflavin and Primulin increased the background fluorescence of the sediment particles and both gave substantially reduced total counts (Fig. 2). These differences were primarily due to the colorless flagellates which were extremely difficult to distinguish among the detrital particles. Their counts were reduced by 78% (Proflavin) or by 92% (Primulin) while the phytoflagellate yields in the Proflavin and Primulin treatments were within 16% of the FNU estimates. The FNU method also gave a strikingly superior yield of taxa: 16–17 in the test sample by comparison with 6–8 in the Proflavin and Primulin treatments.

We also tested the preservation of Chl *a* autofluorescence with glutaraldehyde-formaldehyde fixative against freshly collected, unpreserved samples. The intensity of autofluorescence was similar between the two, consistent with the observations of Tsuji and Yanagita (1981). However the total number of cell counts and our ability to locate certain taxa in the fresh, unpreserved, unstained sample was greatly reduced (Fig. 2), indicating that a live count technique could not be used on our water samples.

There were major changes in the biological

Table 2. Microbial food-web components across the St. Lawrence River transition zone, 10–13 May 1991. Each value is the mean (±SE) for eight samples as in Table 1. Heterotrophic flagellates refer to colorless (aplastidic) nanoflagellates; phototrophic flagellates refer to all plastidic species including mixotrophs.

	Zone 1	Zone 2	Zone 3
	10^6 cells per liter		
Picoplancton			
heterotrophs	1,748(554)	2,072(688)	2,760(753)
phototrophs	8.44(1.07)	3.70(0.62)	2.76(0.65)
Flagellates			
heterotrophs	4.10(0.32)	1.71(0.31)	0.95(0.18)
phototrophs	1.88(0.41)	0.63(0.12)	0.91(0.25)
total	5.97(0.39)	2.33(0.39)	1.86(0.29)
Ciliates	0.20(0.06)	0.08(0.04)	0.07(0.03)
	10^6 μm^3 (cell volume) per liter		
Picoplancton			
heterotrophs	83.9(26.6)	99.5(33.0)	132.5(36.1)
phototrophs	10.97(1.42)	4.92(0.82)	3.76(0.86)
Flagellates			
heterotrophs	247(30.5)	139(31.7)	61(17.4)
phototrophs	193(47.8)	78(18.0)	96(30.5)
total	440(41.3)	216(41.9)	156(31.6)
Ciliates	253(97.1)	100(43.8)	37(14.8)

as well as environmental properties of the St. Lawrence across the transition zone (Table 1). The change from fresh (zone 1) to slightly saline water (zone 2) was accompanied by an abrupt increase in turbidity which then remained at similar values farther down the estuary (zone 3). There was a slight decline in temperature across this salinity gradient, but a marked decrease in Chl *a*, particularly between zones 2 and 3. The larval fish populations were dominated by rainbow smelt (*Osmerus mordax*) and Atlantic tomcod (*Microgadus tomcod*) and achieved peak standing stocks in zone 2, consistent with previous observations on their distribution in the St. Lawrence system (Laprise and Dodson 1989).

Picoplanktonic organisms (cells <2 μm) were numerically the most abundant heterotrophs and phototrophs in all three zones; however their contribution to total planktonic biovolume was much smaller than that of the flagellates plus ciliates (Table 2). There was a decline in protozoan as well as photosynthetic picoplankton concentrations down the estuary, with the sharpest decrease between zones 1 and 2. Heterotrophic bacterial populations showed no significant change between zones

Table 3. Protozoan community structure and diversity across the transition zone. Percentage values are for the percent contribution of various groups to the overall protozoan community cell concentration or cell volume in each of the three zones. Each value is the mean (±SE) for the eight samples. Diversity indices are for all samples pooled by zone. Total protozoa include the flagellates and ciliates as in Table 2, plus naked and testate amoebae and plastidic and aplastidic dinoflagellates.

	Zone 1	Zone 2	Zone 3
Total flagellate concentrations (%)			
heterotrophic	70(5)	73(5)	52(6)
phototrophic	30(3)	27(4)	47(6)
chrysomonads	54(3)	59(5)	52(7)
cryptomonads	16(2)	13(5)	24(8)
choanoflagellates	14(2)	7(2)	9(6)
Total flagellate volume (%)			
heterotrophic	57(7)	64(5)	42(9)
phototrophic	42(7)	36(5)	57(9)
chrysomonads	32(5)	40(7)	43(8)
cryptomonads	19(3)	14(4)	22(8)
choanoflagellates	21(4)	9(3)	11(9)
Total protozoa (%)			
ciliate concentrations	3(1)	3(1)	4(1)
flagellate concentrations	81(4)	85(2)	86(2)
ciliate volume	23(8)	20(7)	16(7)
flagellate volume	48(3)	46(3)	48(12)
Diversity indices			
n (No. of species)	49	43	41
H (Shannon-Weaner index)	1.19	1.35	1.40
R (evenness)	0.71	0.83	0.87

but contributed an increasing percentage of total microbial biovolume (picoplankton plus protozoa) down the estuary: 8% in zone 1, 17% in zone 2, and 30% in zone 3. Attached bacteria contributed on average 35% (SE = 6) and 38% (4) of the bacterial cell counts in zones 2 and 3 (respectively) but 17% (6) in zone 1, consistent with the pattern of increased attachment downstream previously observed by Painchaud and Therriault (1989).

There were strong similarities between zones in the overall protozoan community structure at the level of broad functional groupings (Table 3). Colorless species contributed at least 40% of the total flagellate cell numbers and biovolume, and nonpigmented chrysomonads were the consistent dominants. The ciliate contribution to total protozoan concentrations remained at 3–4% in all three zones. Pigmented (*Cryptomonas* spp.; *Chroomonas* spp.) and nonpigmented (*Chilomonas* spp.) cryptomonads were conspicuous elements of the

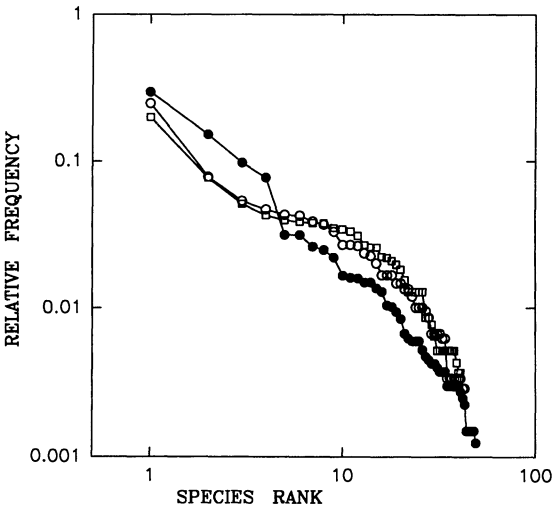

Fig. 3. Log frequency-rank diagram for the protozoan communities in the upper St. Lawrence estuary: zone 1—●; zone 2—○; zone 3—□.

protozoa in all zones, but choanoflagellates and oligotrichous ciliates were much more important in the freshwater zone 1.

A comparison of species number and evenness indicated that despite the overall functional similarity there were differences in community structure between each of the zones (Table 3). The number of flagellate plus ciliate taxa dropped slightly while diversity as measured by the Shannon-Weaner index (*H*) increased down the estuary. This apparent divergence in trends resulted from the stronger dominance upstream by a few species and thus increasing community evenness (*R*) in zones 2 and 3 (Table 3). This effect is better illustrated by the log species-rank plot in Fig. 3. Zones 2 and 3 had almost identical species curves with a sigmoidal section of dominants superimposed on an asymptotic curve. The latter is often considered to be characteristic of diverse, mature communities while a sharp initial drop in such curves implies an early successional stage (Legendre and Legendre 1984). The zone 1 plot differed in shape from the sigmoidal curves for zones 2 and 3. It had a lower final asymptotic section, but the initial part of the curve lay above the others, reflecting stronger species dominance by the first few taxa.

An analysis of community structure at the level of individual protozoan taxa revealed dif-

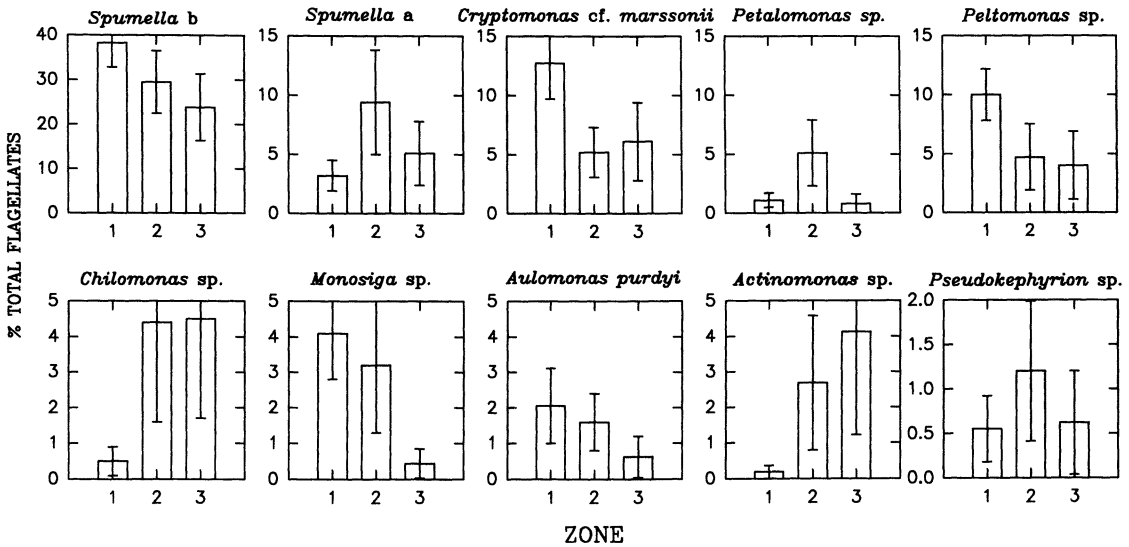

Fig. 4. Changes in flagellate community structure in the upper St. Lawrence estuary. Each value is the mean percent (±SE) contribution of a species to the total nanoflagellate population.

ferences in the species associations which characterized each zone. Similarity index (the Steinhaus index, S) calculations showed that there was a close relationship between the communities in zones 2 and 3 (S = 62.4%) by comparison with zones 2 and 1 (S = 41.6%). There was a striking difference between zones 1 and 3 (S = 35.1%) that was not apparent from the general groupings in Table 3.

Several protozoan species occurred among the dominants throughout the sampling region (Fig. 4). There was large within-zone variability, but different species showed contrasting distributional patterns across the three zones. Some species, such as the overall dominant *Spumella* sp. b, a colorless chrysomonad, and the choanoflagellates *Monosiga* sp. and *Aulomonas purdyi,* were more commonly encountered in zone 1 and declined in relative abundance from zone 1 to 2 to 3. Species such as *Cryptomonas* cf. *marssonii* and the colorless prymnesiomonad *Peltomonas* sp. showed a marked decline in proportional abundance between zones 1 and 2, then maintained the same contribution in zone 3. Other species peaked in importance in zone 2, for example a colorless euglenoid *Petalomonas* sp. and the loricated chrysophyte, *Pseudokephyrion* sp. The colorless cryptomonad *Chilomonas* was common in zones 2 and 3, while a actinomonad heliozoan *Actinomonas* sp., as well as the colonial choanoflagellate *Desmarella* sp., increased in relative abundance from zone 1 to 3. Even related species seemed to show different zonal preferences; for example, the larger celled *Spumella* (sp. a, 5-μm diameter) peaked in proportional abundance inside zone 2, whereas *Spumella* sp. b (3.5-μm diameter) peaked in zone 1.

The ciliate community dominants included *Strombidium* sp., *Strobilidium* sp., and various tintinnids with clear and agglomerated loricas. The samples also contained at least five amoeboid taxa including naked and testate species such as *Paulinella ovalis* (cf. Johnson et al. 1988), as well as several pigmented and nonpigmented dinoflagellate species. The ciliates and amoebae occurred at lower concentration (by a factor of at least 10) than the nanoflagellates and were undersampled in our study. Future methods development should pay special attention to these taxa which because of their large size may constitute a major fraction of the total protozoan community biovolume. In our study the ciliate concentrations ranged from 70 to 200 cells ml^{-1}—values about an order of magnitude higher than for the oligotrophic Great Lakes (e.g. Carrick and Fahnenstiel 1990) at the head of the St. Lawrence system. However, the nanoflagellate

concentrations recorded in our study are closely comparable with the range for the Great Lakes at the same time of year (e.g. ~2–6 × 10^6 cells liter^{-1} in Lake Ontario, Pick and Caron 1987). These comparisons should be viewed with caution, however, given the differences in methodology.

Application of the FNU method revealed a species abundance and diversity in the Upper St. Lawrence estuary that was impossible to discern by traditional Utermöhl or membrane filter techniques. The FNU protocol can resolve nanoflagellates as small as 2–3 μm and their flagella (e.g. *Spumella* sp. b) as well as the cilia, collars, fine pseudopodia, pseudopodial veils, chloroplasts, macro- and micronuclei, and other cellular features of taxonomic importance. It is not, however, a substitute for the standard filtration and epifluorescence methods for picoplanktonic cells <2 μm such as bacteria and *Synechococcus*; these smallest cells would require very long sedimentation times, are especially subject to convective motions in the chamber, often exhibit Brownian movement during observation, and may be better observed in immersion oil mounts.

The St. Lawrence samples were dominated by 47 flagellate taxa, with an additional 10 ciliate and amoeboid taxa. Concentration techniques such as reverse filtration would improve our assessment of rare species, but the present level of community resolution allows us to conclude that the region of maximum fish larval abundance was associated with a high-diversity microzooplankton community. This downstream section of the St. Lawrence system is a transitional region of changing microbial food-web composition. Bacterial populations were proportionately more important than upstream, but less so than farther downstream. Chl *a* concentrations declined slightly, but there was an abrupt fall in autotrophic picoplankton. Heterotrophic flagellates and ciliates were conspicuous elements of the food web in all three zones, but the transitional zone 2 had a distinctive protozoan assemblage with greater affinities to the community of downstream, more saline zone 3, than to the upstream freshwater community.

Nonpigmented protozoa including colorless cryptomonads, colorless chrysomonads, choanoflagellates, actinomonads, ciliates, and amoebae were a diverse and abundant component of the plankton in all zones. These organisms would be among the least represented with methods such as standard Utermöhl or membrane filter techniques. Colorless flagellates dominated the protozoan cell counts even in the freshwater zone. These organisms are likely to feed on the picoplankton community which throughout the system was strongly dominated both in terms of cell concentration and biomass by heterotrophic bacteria, consistent with the view that microheterotrophic production is a highly significant component of carbon and energy flux through large river systems (Findlay et al. 1991).

Our analyses suggest that protozoan community size may be severely underestimated in some environments by conventional filtration and microscopy techniques. Our estimates of total protozoan biovolume in zone 2 translate to an approximate mean value of 42 μg C liter^{-1} (conversion equation as used by Joint 1991). If we assume a C : Chl *a* value of 17 (Paerl et al. 1976), the phytoplankton community in this zone, including the pigmented flagellates, amounts to ~83 μg C liter^{-1}. These calculations imply that protozoa were a substantial component of the food resources available to higher trophic levels such as crustacean zooplankton and fish larvae. Heterotrophic picoplankton make a large contribution to the total planktonic biomass in this system (Table 2) and their productivity is supported by a broad range of allochthonous (Painchaud and Therriault 1989) as well as autochthonous inputs. The protozoan community described here is likely to play a critical role in making some of this bacterial carbon and energy available to larger animals in the highly turbid St. Lawrence transition zone.

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