Modeling the response time of diatom assemblages to simulated water quality improvement and degradation in running waters

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Abstract: The objective of this study was to measure and model the response time of the Eastern Canadian Diatom Index (IDEC: Indice Diatomées de l'Est du Canada), a diatom-based index of biological integrity, following substrate translocation from altered sites (nutrient-enriched) to pristine sites and vice-versa. The frequency of sampling, duration (time after substrate translocation), and variety of site conditions in the present study provide strong evidence for an accelerated response of diatoms to a degradation reflecting eutrophication (within a week in certain cases) and a slower path to recovery (up to 4 weeks). Diatom response varied as a function of trophic status; oligotrophic rivers responded rapidly to a degradation, and mesotrophic or eutrophic rivers responded more slowly to an amelioration of the conditions. Variation in response time as a function of trophic status seemed to be partly linked to the diversity and complexity of the assemblages. The less diverse assemblages observed in oligotrophic waters were highly sensitive to nutrient enrichment, whereas the more diverse assemblages sampled in mesotrophic–eutrophic rivers were less sensitive to nutrient fluctuations, and major variations in nutrient concentrations took a longer time to induce a change in index values.

Résumé : L'objectif de notre recherche est de mesurer et de modéliser le temps de réaction de l'Indice Diatomées de l'Est du Canada (IDEC), un indice d'intégrité biologique basé sur les diatomées, à la suite d'un déplacement de substrats de sites altérés (enrichis en nutriments) vers des sites vierges et vice-versa. La fréquence de l'échantillonnage, la durée (temps écoulé depuis le déplacement des substrats) et la variété des conditions dans les sites de notre étude permettent d'obtenir des données probantes qui montrent une réaction accélérée des diatomées à une dégradation qui représente une eutrophisation (en moins d'une semaine, dans certains cas) et une voie de récupération plus lente (jusqu'à 4 semaines). La réaction des diatomées varie en fonction du statut trophique : les rivières oligotrophes réagissent rapidement à une dégradation, alors que les rivières mésotrophes ou eutrophes réagissent plus lentement à une amélioration des conditions. La variation du temps de réaction en fonction du statut trophique semble être reliée en partie à la diversité et la complexité des peuplements. Les peuplements moins diversifiés observés dans les eaux oligotrophes sont très sensibles à l'enrichissement par les nutriments, alors que les peuplements plus diversifiés échantillonnés dans les rivières mésotrophes–eutrophes sont moins sensibles aux fluctuations des nutriments; les variations majeurs dans les concentrations de nutriments mettent donc plus de temps à provoquer un changement dans les valeurs de l'indice.

[Traduit par la Rédaction]

Introduction

Diatoms are used in an increasing number of countries as an effective tool for monitoring the biological integrity and the water quality of water bodies. These microscopic algae are present in all aquatic ecosystems and are sensitive to variations in their environment (e.g., changes in nutrient concentrations, conductivity, pH, temperature), which makes them good indicators of anthropogenic stresses such as eutrophication (Kelly and Whitton 1995; Hall and Smol 1999). Diatom assemblages, characterized by a high diversity of taxa, yield ecological information that allows for the development of biological indices based on robust statistical analyses. Numerous diatom-based indices have been developed in various countries and are integrated into water quality monitoring programs as an additional tool for assessing ecosystem health (Coste 1982; Kelly and Whitton 1995; Prygiel and Coste 2000). In Canada, the Eastern Canadian Diatom Index (IDEC: Indice Diatomées de l'Est du Canada) was created for monitoring river eutrophication (Grenier et al. 2006; Lavoie et al. 2006*a*, 2008*a*) and has been used to

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assess the biological integrity of more than 100 streams and rivers to date (more than 1000 sites).

Diatoms integrate variations in nutrient concentrations over short periods (Lavoie et al. 2008*a*). Diatom indices are therefore complementary to invertebrate and fish indices, which integrate water and habitat quality over longer time periods (Karr and Chu 1999). However, only a few studies show evidence of the integrating potential of diatom assemblages. These studies are based on two approaches: the first consists of the evaluation of the correlation between diatom index values and environmental variables, whereas the second approach is based on the translocation of artificial substrates.

In the first approach, diatom index values (calculated from species relative abundances) are commonly correlated with water chemistry values averaged over various time periods (e.g., weekly, monthly). A study conducted by Taylor et al. (2007) suggested that diatom-based indices in general (numerous European indices were tested) have the best correlation with chemical data averaged over 1 month, starting 6 weeks before diatom sampling. Based on a similar approach using the IDEC, Lavoie et al. (2008*a*) suggested that the integration period varies with trophic status and nutrient concentration variability in the rivers. In an oligotrophic river, where nutrient concentrations were low and generally stable, they found that a natural increase of phosphorus induced a rapid change in diatom assemblage structure and IDEC value within 1 week. In a mesotrophic river, the observed integration period was approximately 2 weeks. Diatom assemblages in a eutrophic river appeared to be adapted to frequent and substantial fluctuations in nutrient concentrations, with a 5-week integration indicating a slower response to short-term fluctuations. These two studies allowed for the evaluation of the ability of diatom indices to integrate temporal variations in environmental parameters, but did not provide direct information on the response time following a degradation or an amelioration in environmental conditions.

In the second approach, artificial substrates are translocated, following a colonization period, from a polluted site to a reference site and vice-versa to measure the response time of diatom assemblages and indices. This approach has been used in a wide range of environments in several studies (e.g., Gold et al. 2002; Tolcach and Gómez 2002; Rimet et al. 2005). These studies show that diatom assemblages have a shorter response time following a degradation than following an amelioration of environmental conditions. In addition, substrate translocation simulating a sudden degradation in water quality is generally accompanied by a decrease in the number of pollution-sensitive taxa and an increase in the number of pollution-tolerant taxa. These studies provide information related to the structural modifications in diatom assemblages and the response time of indices following a change in water quality. However, there are still aspects that need further investigation: (*i*) Few studies have measured the changes in assemblages shortly after the translocation of the substrates. The short life cycle of diatoms may allow for a rapid (within a week) response of assemblages and indices. (*ii*) The time frame of the translocation studies is often inadequate to evaluate the period of time needed for a complete recovery (or degradation) of the diatom assemblages. (*iii*) The sampling frequency following substrate translocation is often too low to observe gradual changes in diatom assemblages or to determine the actual response time. (*iv*) Past studies suggest that the response time of diatom assemblages and indices may vary as a function of the pH and the trophic status of the ecosystem (Lavoie et al. 2008*a*), but these relationships have not been explored systematically. (*v*) No experimental studies have been conducted to determine the response time of the IDEC.

The objective of our study was to measure and model the response time of the diatom-based index IDEC following substrate translocation from nutrient-enriched sites (altered) to pristine sites and vice-versa. The sampling design of the present study allowed us to address the issues listed above, thus providing a more complete examination of the effects of translocation on diatom assemblages than has been achieved to date.

Materials and methods

Site selection and diatom sampling

Five pairs of rivers located in eastern Canada (Quebec) were selected to simultaneously study the response time of the IDEC following a degradation (increase in nutrient concentrations) and an amelioration of water quality (decrease in nutrient concentrations). Based on IDEC values previously calculated for these sites (Lavoie et al. 2006*a*), five rivers were representative of reference or least-impacted conditions (oligotrophic–mesotrophic) and five rivers were representative of altered conditions (mesotrophic–eutrophic). Each pair of rivers included an altered site and its specific reference site. The selected reference or least-impacted site for each pair belonged to the same ecophysiographic group as the altered site, as established in Grenier et al. (2006). Among the five pairs of rivers selected, three had naturally lower pH levels (the reference sites had a water pH naturally slightly acidic to neutral) and two were located in more alkaline environments (the reference sites had slightly alkaline water pH). The distinction between the rivers as a function of their pH at reference state (based on their geological characteristics) was necessary to determine which IDEC subindex to use (IDEC-Neutral or IDEC-Alkaline; Grenier et al. 2006).

The pairs of rivers selected for each subindex, as well as their IDEC values (data from 2003; Lavoie et al. 2006*a*) are presented (Table 1), as well as physical and chemical characteristics of each river (Table 2). Based on the nutrient criteria, the 10 study sites were grouped as a function of their trophic status using long-term data from the Ministry of the Environment of Quebec: Ste. Anne and Noire rivers are oligotrophic (total phosphorus, TP: <25 $\mu g \cdot L^{-1}$; total nitrogen, TN: <700 $\mu g \cdot L^{-1}$; Dodds et al. 1998); Shawinigan upstream, Nicolet, Des Envies, Yamaska Sud-Est, and Yamaska rivers are mesotrophic (TP: 25–75 $\mu g \cdot L^{-1}$; TN: 700–1500 $\mu g \cdot L^{-1}$; Dodds et al. 1998); and Shawinigan downstream, Nicolet Sud-Ouest and Blanche rivers are eutrophic (TP: >75 $\mu g \cdot L^{-1}$; TN: >1500 $\mu g \cdot L^{-1}$; Dodds et al. 1998).

Six concrete blocks (19 cm × 19 cm × 39 cm) were placed in each of the 10 rivers in mid-June 2006. Six nonglazed ceramic tiles (25 cm^2) were mounted on each block using plastic-coated wire. Each tile corresponded to a sam-

Table 1. Pairs of reference and altered streams with their IDEC values in circumneutral and alkaline conditions.

IDEC-Neutral						IDEC-Alkaline			
Pair 1		Pair 2		Pair 3		Pair 4		Pair 5	
IDEC	River	IDEC	River	IDEC	River	IDEC	River	IDEC	River
100	Noire	79	Shawinigan (upstream)	93	Ste. Anne	100	Yamaska Sud-Est	50	Nicolet
0	Blanche	28	Shawinigan (downstream)	19	Des Envies	23	Yamaska	19	Nicolet Sud-Ouest

Note: River status (reference or altered) and IDEC values are derived from Grenier et al. (2006) and Lavoie et al. (2006*a*).

pling period, i.e., time 0 was before translocation, the remaining five tiles corresponded to 1, 2, 4, 8, and 12 weeks following the translocation. The artificial substrates were incubated in situ for a period of 4 weeks before being translocated to allow for colonization of the tiles by the periphytic assemblages. After the 4-week incubation period, diatom assemblages were sampled from the time 0 tiles. Three blocks from each river (i.e., half of the substrates) were then translocated to the opposite environment (i.e., tiles from reference sites were moved to altered sites and vice versa). During transportation, the blocks were placed in large containers filled with 2 cm of river water (to keep moisture in the container), and the tiles were covered with a plastic film to avoid desiccation of the biofilm. No substrates were kept in the containers for more than 45 min. The blocks that were not translocated were also placed in containers and transported before returning to their initial location to ensure that these assemblages were exposed to the same stress as the translocated assemblages.

Diatom sampling was performed following the recommendations in Kelly et al. (1998) and the procedure described in Lavoie et al. (2006*a*) for the development of the IDEC. Periphyton was scraped off the tiles using a toothbrush, and the samples were preserved with Lugol's solution. The samples were digested in 30% hydrogen peroxide to remove cell content (to facilitate taxonomic identification) and were mounted on microscope slides using Naphrax. A total of 400 valves per slide were counted and identified at a 1000× magnification. The identification of the diatom taxa was performed using a diatom guide created for use with the IDEC (Lavoie et al. 2008*b*). The Shannon's diversity index was calculated for each sample collected during this study.

IDEC calculation

IDEC values are calculated based on the relative abundance of diatom taxa (Lavoie et al. 2006*b*) and reflect changes in the structure of assemblages such as a progressive increase in tolerant taxa following a degradation of the environment (mostly reflecting an alteration due to eutrophication). The IDEC was developed based on a correspondence analysis (CA) to evaluate the position of sites along the gradient of maximum variation (first ordination axis). The IDEC gradient ranges between 0 and 100, and the index value indicates the distance of an altered diatom assemblage from its specific reference assemblage. A high index value represents a non- or least-altered site, while a low index value represents a more heavily altered site. To account for ecoregion characteristics and natural pH variations, two subindices were created based on the two major groups of diatom reference assemblages observed: the IDEC-Neutral includes the sites that have reference assemblages characteristic of slightly acidic or neutral water pH, whereas the IDEC-Alkaline includes the sites that have reference assemblages characteristic of environments where pH values are naturally slightly alkaline. A detailed explanation of the methodology used to determine the reference diatom assemblages is presented in Grenier et al. (2006). Since the completion of the present study, a new version of the IDEC (IDEC 2.0; Lavoie et al. 2010) was created including samples from Ontario and the Maritimes. This new version provides a better representation of environmental conditions found in eastern Canada. However, the new version of the IDEC was not available for this study on substrate translocation.

Piecewise regression models

Differences in the IDEC value between the translocated substrates and the in situ substrates that remained at the hosting site (ΔIDEC) were calculated for each of the six sampling periods (time 0 (immediately before transfer) and weeks 1, 2, 4, 8, and 12 after translocation) and plotted. The response of the ΔIDEC in the period following substrate translocation clearly suggested a two-phase pattern in the diatom assemblage turnover. The initial phase was characterized by a rapid change in the structure of the assemblages, whereas the second phase showed a stabilization in the rate of assemblage change, as revealed by the ΔIDEC. Piecewise regressions were therefore chosen to model the response of the ΔIDEC. When the ΔIDEC stabilizes at a value near zero, the breakpoint time (c), at which the regression line for the first phase intersects the regression line for the second phase, indicates the time at which the translocated and in situ assemblages have converged in structure. Two different piecewise regression models were used to represent the time course of the ΔIDEC: the first (and simpler) of the two models, M1, represents the two phases with separate regression lines that intersect at breakpoint time c, with the slope of the regression set to zero for time > c. This constraint on the second slope reflects an assumption of no further change in the ΔIDEC after time c. The second model, M2, also represents the two phases with separate regressions that intersect at time c, but has no restriction on the slope for time > c. This model assumes that the rate of change in ΔIDEC undergoes a transition at time c, but does not assume that the ΔIDEC stabilizes completely after time c. For both models, the slope prior to convergence measures the initial rate of convergence (negative slope coefficient) or, potentially, divergence (positive slope coefficient) between

Table 2. Mean values for water chemistry variables from January to December 2006.

	Noire	Blanche	Shawinigan upstream	Shawinigan downstream	Ste. Anne	Des Envies	Yamaska Sud-Est	Yamaska	Nicolet	Nicolet Sud-Ouest
Total phosphorus ($\mu g \cdot L^{-1}$)	9	96	23	100	16	37	22	38	34	91
Total nitrogen ($\mu g \cdot L^{-1}$)	236	860	260	778	235	731	438	585	1308	1099
Ammonia ($\mu g \cdot L^{-1}$)	22	33	30	330	20	70	18	76	35	55
Dissolved organic carbon ($mg \cdot L^{-1}$)	5.8	5.5	4.6	7.7	3.9	6.7	4.2	6.1	7.8	10.4
Chlorophyll *a* ($mg \cdot m^{-3}$)	2.98	6.75	NA	3.39	1.77	4.65	2.01	8.34	6.70	9.05
Coliforms (CFU, $100 \cdot mL^{-1}$)	9	246	NA	3638	14	233	126	403	914	203
Conductivity ($\mu S \cdot cm^{-1}$)	16.1	82.7	22	141.4	21.6	81.5	86.0	165.8	218.7	216.4
pH	5.8	7.2	6.8	7.0	6.0	7.0	7.2	7.4	7.6	7.7
Suspended solids ($mg \cdot L^{-1}$)	2	60	NA	7	5	11	10	12	13	95
Turbidity (NTU)	1.0	30.9	NA	6.5	2.2	14.3	4.0	5.7	5.0	29.4
Water temperature (°C)	9.5	9.7	NA	10.5	10.0	10.5	10.5	9.2	10.9	12.0
Subindex	IDEC-Neutral	IDEC-Neutral	IDEC-Neutral	IDEC-Neutral	IDEC-Neutral	IDEC-Neutral	IDEC-Alkaline	IDEC-Alkaline	IDEC-Alkaline	IDEC-Alkaline
Trophic category	Oligotroph	Eutroph	Oligotroph	Eutroph	Oligotroph	Mesotroph	Oligotroph	Mesotroph	Mesotroph	Eutroph

Note: CFU, colony-forming unit; NTU, nephelometric turbidity unit; NA, not available. The trophic categories are based on Dodds et al. (1998) using long-term data from the Ministry of the Environment of Quebec; data from the Ministry of the Environment, Quebec.

two assemblages. An *F* test was used to determine whether the additional complexity of M2 provided an improvement in fit over M1, i.e., whether the slope for the second phase was statistically indistinguishable from zero as assumed by M1. The *F* statistic was calculated as

$$F_{p-q,\,n-p} = \frac{(\mathrm{RSS}_1 - \mathrm{RSS}_2)/(p-q)}{\mathrm{RSS}_2/(n-p)}$$

where RSS_i is the residual sum of squares for model i (1 or 2), q is the number of parameters for M1 (3), p is the number of parameters for M2 (4), and n is the sample size. A major advantage of piecewise regression over many previous approaches to ecological degradation and recovery is that it yields not only point estimates of response times, but also measures of uncertainty about these estimates in the form of confidence intervals. Piecewise regression has been used previously to identify transition points in the response of species or ecological processes (Toms and Lesperance 2003) and between phases characterizing particle movement in a lotic ecosystem (Ryan et al. 2002). Piecewise regressions were performed using SYSTAT version 11 (Systat Software Inc., 2004).

Results

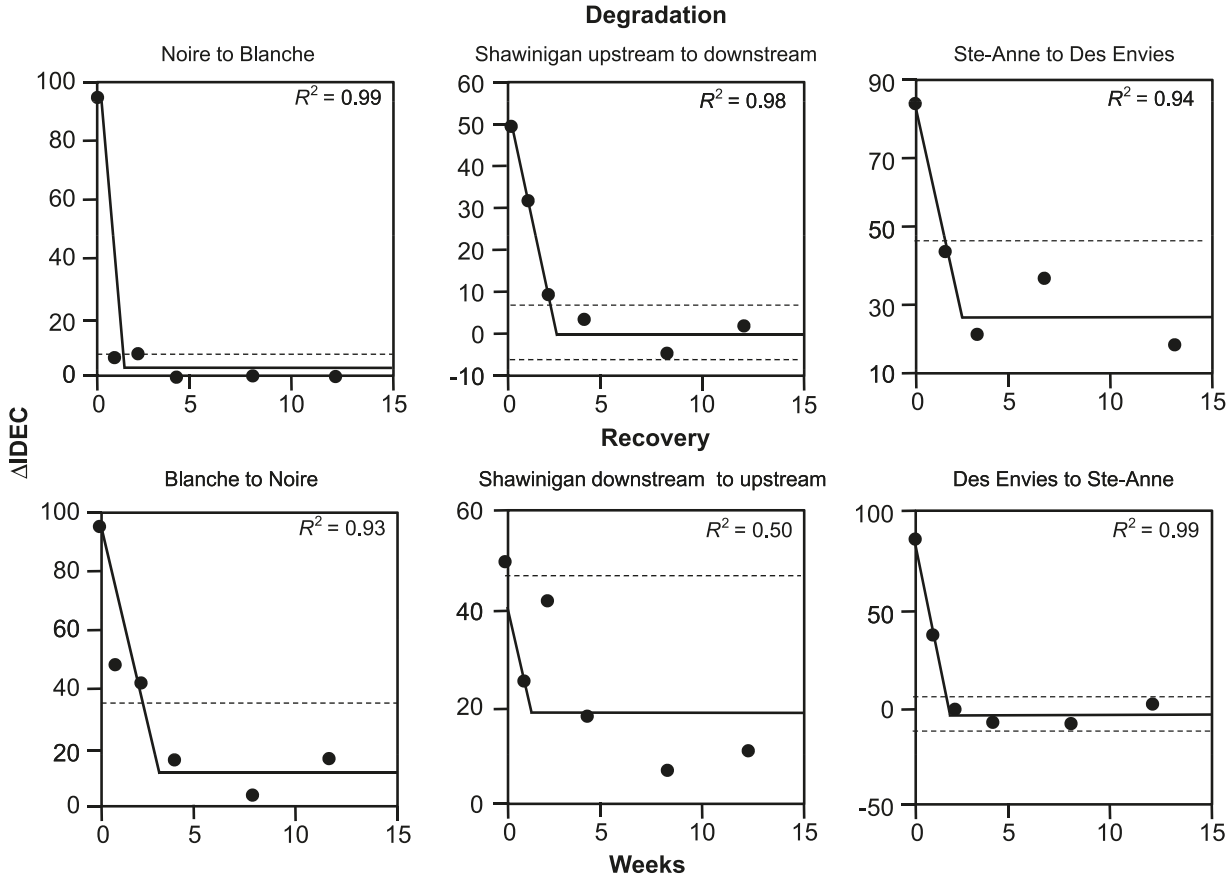
Diatom community structure and diversity

The diatom communities observed in the selected altered sites were different than what was observed in the pristine or least-impacted sites. In summary, nutrient-rich sites were colonized by species such as *Melosira varians*, *Nitzschia palea*, *Navicula capitatoradiata*, *Cocconeis placentula* var. *euglypta*, *Nitzschia amphibia*, *Navicula gregaria*, *Navicula germainii*, *Navicula tripunctata*, *Achnanthidium minutissimum*, *Nitzschia inconspicua*, and *Reimeria sinuata*. The species found in less-impacted sites included *A. minutissimum*, *Tabellaria flocculosa*, *Fragilaria capucina*, *Brachysira microcephela*, *Brachysira brebissonii*, *Staurosirella pinnata*, *Achnanthidium rivulare*, and various species of *Eunotia*.

The translocation of the substrates into their specific hosting site resulted in a drastic change in community structure. For example, the translocation of the assemblage from Noire River to Blanche River (degradation in naturally slightly acidic – neutral pH waters) resulted in a large drop in the relative abundance of *T. flocculosa* (43% to 1.5%), while *M. varians* (a species typical of polluted waters; Leland et al. 2001) increased from 0% to 28%. For the opposite translocation, the recovery simulated from Blanche River to Noire River resulted in a slower reorganization of the assemblage; *T. flocculosa* increased from 0% to 18.5% within 1 week. In naturally alkaline environments, the translocation from Yamaska Sud-Est River to Yamaska River (degradation) induced a large drop in *A. rivulare* (52% to 16% in 1 week) and an increase in *C. placentula* var. *euglypta* and *R. sinuata* (species typical of polluted waters; Rott et al. 1998; Krstic et al. 1999) from 0% to 32% within 2 weeks and 3% to 35.5% within 1 week, respectively. The change in diatom community structure after the 12 weeks of incubation in the hosting site is summarized in Appendix A, Table A1.

Average diversity values (Shannon's diversity index) for the different environmental conditions were calculated. Diversity

Fig. 1. IDEC-Neutral: piecewise regression showing the relationship between the differences in IDEC values (ΔIDEC) between the translocated blocks and the blocks that remained in situ and the number of weeks following substrate translocation in naturally circumneutral environments. Translocation from altered sites to reference sites (recovery) and vice-versa (degradation) is indicated. The dotted lines indicate the confidence interval for ΔIDEC after convergence.



was lower in environments with naturally slightly acidic to neutral water pH and oligotrophic conditions, in which assemblages were often dominated by *T. flocculosa* and *A. minutissimum*.

IDEC response time following translocation

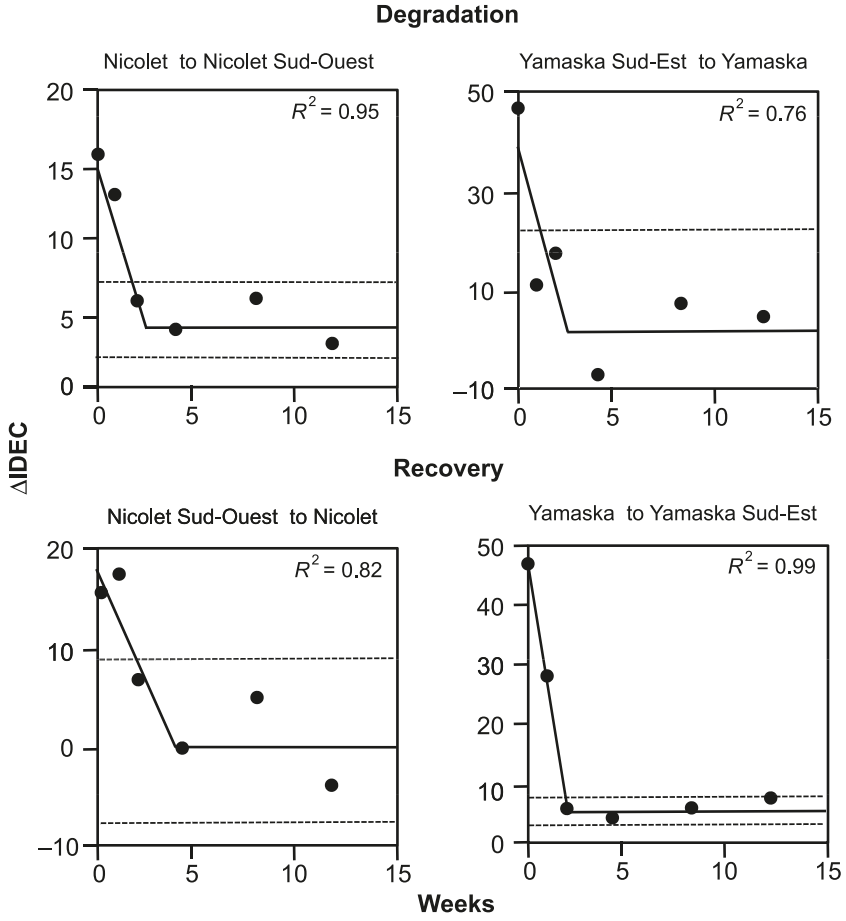
For the rivers with a naturally acidic to neutral water pH, translocation of the blocks from the Noire River (reference site) to the Blanche River (altered site) was followed by a rapid decrease in IDEC values (Fig. 1). At time 0, before the transfer, the IDEC values of these two sites were at opposite extremes of the pollution gradient (ΔIDEC = 97), near to the maximum gradient length of 100 units. Only 1 week after the translocation, the ΔIDEC had fallen to 6 units and the IDEC value of the translocated assemblage had nearly reached that at the hosting site. Four weeks after the translocation, the IDEC values had reached convergence. The changes observed for the translocation in the opposite direction were more gradual. One week after the transfer to the Noire River, the assemblage originating from the Blanche River started to converge, with a 49-unit difference from the host assemblage. After 12 weeks of incubation at the hosting site, the assemblage from the Blanche River was still different from the assemblage in the Noire River (ΔIDEC = 12). A similar pattern was observed in the Shawinigan River, where a rapid degradation (decrease in IDEC value) was observed within a 3-week period, while the recovery (increase in IDEC value) was more gradual. However, this trend was inverted in the case of the Ste. Anne and Des Envies rivers; the degradation of the assemblage in the Ste. Anne River was not completed after 12 weeks, while the assemblage in the Des Envies River had completely recovered after 2 weeks.

Rivers with a naturally alkaline pH showed less pronounced differences in IDEC values than rivers with a naturally slightly acidic to neutral pH (Fig. 2). This result was due to the reference conditions in naturally alkaline environments that are not true pristine conditions. Instead, the reference rivers represented the sites that were the least impacted (mesotrophic) and were selected for this study because of the difficulty of finding pristine conditions in the St. Lawrence Lowlands. Although the gradient in IDEC value (difference between reference or least-impacted sites and altered sites) was shorter in rivers with naturally alkaline pH, a similar pattern of change after translocation was observed in alkaline and acidic–neutral rivers. For example, the degradation and recovery of the assemblages from Nicolet River (mesotrophic) and Nicolet Sud-Ouest (eutrophic) were mostly completed within 4 weeks.

Modeling the response time

The comparisons of fit between M1 and M2 by means of

Fig. 2. IDEC-Alkaline: piecewise regression showing the relationship between the differences in IDEC values (ΔIDEC) between the translocated blocks and the blocks that remained in situ and the number of weeks following substrate translocation in naturally alkaline environments. Translocation from altered sites to reference sites (recovery) and vice-versa (degradation) is indicated. The dotted lines indicate the confidence interval for ΔIDEC after convergence.



F tests ($p > 0.08$ for all 10 comparisons of M1 and M2) indicated that it was reasonable to assume that the ΔIDEC stabilized after an initial phase of rapid change that preceded the breakpoint time *c*. Therefore, the emphasis hereafter is on the results of the piecewise regressions for M1 (Table 3; Figs. 1 and 2). Estimates of the slope of the postrecovery period (time > *c*) are based on few points, suggesting that statistical power was low in comparisons of M1 and M2. However, the consistency of results across trials ($p > 0.08$ for all 10 *F* tests comparing M1 and M2), as well as the apparent absence of a common postrecovery trend in ΔIDEC across trials (Figs. 1 and 2) provide little support for the more complex model M2.

The M1 model showed that the diatom communities and the IDEC values responded quickly to a translocation simulating a degradation of the environment (eutrophication). For example, the translocation of the diatom assemblages from Noire River to Blanche River (degradation) resulted in a response of the IDEC with an R^2 of 0.99. During the initial phase of the response, the IDEC value decreased at a rate of 91 units per week, which was the fastest rate observed during this study. Convergence occurred 1 week following the translocation, when the IDEC value of the translocated assemblage and the assemblage from the hosting site converged (at time *c*). The confidence intervals for *c* and for ΔIDEC after convergence are also presented (Table 3).

In the case of a recovery, IDEC values varied at a slower rate during the first phase of the response. For example, the tanslocation from Nicolet Sud-Ouest River to Nicolet River resulted in an average increase in IDEC value of 4.5 units per week during the course of the first phase. The convergence between the assemblages from the two rivers took 4 weeks and was therefore slower than the convergence associated with degradation.

The R^2 values presented (Table 3) are generally high, with the lowest value (0.50) observed for the recovery of the diatom assemblage in the Shawinigan River. The rate of change of IDEC values during the first phase of the response varied from 4.5 to 91 units per week. The rates of change during the first phase were faster in the environments with a naturally slightly acidic to neutral water pH (ranging from 20.5 to 91 units per week) than in the naturally alkaline environments (ranging from 4.5 to 21.5 units per week). Changes in IDEC values were also more rapid when the translocation simulated a degradation (ranging from 5 to 91 units per week) than when simulating an amelioration of the conditions (ranging from 4.5 to 49 units per week).

Table 3. Post-translocation rates of degradation and recovery for the 10 streams grouped according to their IDEC subindex.

	R^2	Rate of convergence (ΔIDEC per week)	Time to convergence (c, weeks)	Confidence interval for c	Confidence interval for ΔIDEC after convergence
Degradation					
IDEC-Neutral					
Noire to Blanche	0.99	91.0	1.0	0.9–1.2	–3.8–7.3
Shawinigan upstream to downstream	0.98	20.5	2.5	1.8–3.5	–7.0–8.4
Sainte-Anne to Des Envies	0.94	43.0	1.4	0.5–4.3	0.2–49.2
IDEC-Alkaline					
Nicolet to Nicolet Sud-Ouest	0.95	5.0	2.5	1.4–4.2	1.5–7.2
Yamaska Sud-Est to Yamaska	0.76	15.5	2.6	0.7–9.7	–21.1–23.1
Recovery					
IDEC-Neutral					
Blanche to Noire	0.93	27.5	2.8	1.4–5.7	–8.5–33.1
Shawinigan downstream to upstream	0.50	25.0	1.2	0.1–11.7	–5.7–45.7
Des Envies to Sainte-Anne	0.99	49.0	1.8	1.3–2.5	–9.8–4.3
IDEC-Alkaline					
Nicolet Sud-Ouest to Nicolet	0.82	4.5	4.0	0.6–27.1	–8.5–9.1
Yamaska to Yamaska Sud-Est	0.99	21.5	2.0	1.8–2.3	1.7–8.3

Note: The distinction between the subindices IDEC-Neutral and IDEC-Alkaline was based on these natural pH values modeled from the geological characteristics of the sites (Grenier et al. 2006).

IDEC response time in relation to pH and trophic status

The response of the IDEC seemed to vary as a function of trophic status and translocation type (degradation or amelioration) (Table 4; Fig. 3). Regardless of the subindex used (IDEC-Neutral versus IDEC-Alkaline), the results suggested that the degradation of an assemblage was faster than its recovery. The response time of the IDEC as a function of the trophic status indicated that the time needed for a complete degradation or recovery increased with the trophic status. An additive linear model was used to test the relationships between response time (dependent variable; estimated from piecewise regressions) and trophic status ($\mu g \cdot L^{-1}$ total P, $\log_{10}$-transformed), pH (categorical variable: IDEC-Neutral or IDEC-Alkaline), and type of translocation (categorical variable: degradation or recovery). Because there are uncertainties about response time estimates, and therefore the reliability of these estimates varied broadly (Table 3), cases in the linear model were weighted proportionally to the inverse of the variance in response time yielded by the piecewise regressions. The linear model indicated that response time increased with trophic status ($P < 0.001$) and type of translocation ($P = 0.006$), with no apparent effect for pH ($P = 0.36$).

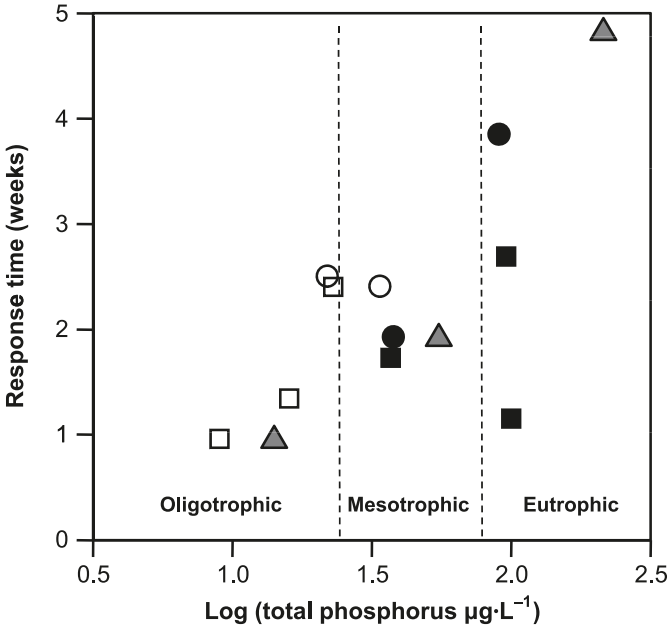
Discussion

The general objective of this study was to measure and model the response time of the IDEC following a translocation of diatom assemblages from an altered site to a reference site and vice-versa. The results indicate that the response to the simulated environmental conditions (mainly changes in nutrient concentrations) was more rapid for a degradation than for a recovery. The methods proposed here improve on previous work by providing quantitative estimates of turnover rate and their associated uncertainty in diatom assemblages. The frequency of sampling, duration (time after substrate translocation), and variety of site conditions in the present study provide strong evidence for an accelerated response of diatoms to a degradation (within a week in certain cases) and a slower path to recovery (up to 4 weeks for the Nicolet Sud-Ouest River). Based on the results from the piecewise regressions, a general model was proposed for the response of diatom assemblages as a function of environmental conditions, i.e., trophic status and type of simulated change (degradation or amelioration).

Variability in response time

de la Rey et al. (2008) showed that diatom species diversity tends to be higher at intermediate than at low levels of pollution. Lavoie et al. (2008*a*) also suggested that diatom assemblages are less diverse in oligotrophic environments than in mesotrophic and eutrophic environments and that there is a link between the trophic status of the ecosystem and the response time of diatom assemblages. Their study monitored the IDEC over time in three rivers and compared the IDEC values with phosphorus concentrations expressed as a one-time measurement and as averages over 1-week, 3-week, and longer periods. Their results and those of the present study indicate that the IDEC integrates variability over a period of time that is dependent on the trophic status of the river and the variability of nutrient concentrations. For example, in an oligotrophic river (Ste. Anne River), where nutrient concentrations were low and generally stable, an increase in phosphorus induced a rapid change in diatom assemblage structure and IDEC value within the following week. In a study conducted by Pan and Lowe (1994), algal assemblages dominated by *A. minutissimum*, *C. placentula*, and *Fragilaria ulna* were primarily phosphorus-limited and responded after only 6 days of nutrient enrichment. Their results were comparable with the 1-week interval between TP increase and IDEC value decrease found by Lavoie et al. (2008*a*) and the mean response time of 1.2 weeks in oligo-

Fig. 3. Relationship between response time of diatom assemblages and stream trophic status (µg·L^{-1} total phosphorus, $\log_{10}$-transformed). Different symbols and fill patterns are used to represent translocation types (recovery: open symbols; degradation: solid symbols) and pH status (alkaline: circles; neutral: squares). Data from Lavoie et al. (2008*a*) are also presented (gray triangles).



trophic rivers observed in the present study. In a mesotrophic river (Nicolet River), the response time observed by Lavoie et al. (2008*a*) was approximately 2 weeks. This result is also similar to the average 2.3 weeks observed in the present study for a response in the IDEC following a degradation or a recovery in mesotrophic environments. In a eutrophic river (Boyer River), Lavoie et al. (2008*a*) showed that diatom assemblages are adapted to frequent and major fluctuations in nutrient concentrations. In their study, the IDEC showed a slower response to short-term fluctuations and integrated nutrient concentrations over a period of 5 weeks. This period is longer than found in the present study, where the response time of the IDEC to a simulated amelioration of the water quality averaged 2.7 weeks in eutrophic conditions. Although interpretation of the effects of trophic status on response times in the present study must be tempered because trophic status was confounded with the type of translocation, the findings presented in Lavoie et al. (2008*a*) and in the present study suggest that oligotrophic rivers are more sensitive to nutrient variations than eutrophic rivers and that their diatom assemblages are markedly altered by nutrient increase. In contrast, diatom assemblages are less sensitive to nutrient fluctuations in eutrophic rivers, which are integrated more slowly into index values. A marked and prolonged change in TP concentration is required to provoke a change in diatom assemblage structure and IDEC values in eutrophic rivers. Lavoie et al. (2008*a*) proposed a relationship between river trophic status and temporal integration of TP concentrations by diatom assemblages. The response time of diatom assemblages modeled in the present study agrees with the temporal integration of TP concentrations proposed in their study.

Table 4. Average response time of the IDEC, Shannon's diversity index, and total phosphorous (TP) values following a simulated degradation or amelioration of the conditions.

	Average response time (weeks)	Shannon's diversity index	TP (µg·L^{-1})
Degradation	2.0	2.1	21
Recovery	2.4	2.7	72
Oligotrophic conditions*	1.2	2.0	13
Mesotrophic conditions*	2.3	2.6	31
Eutrophic conditions*	2.7	2.4	96

*Site classification based on trophic status followed the criteria in Dodds et al. (1998).

Iserentant and Blancke (1986) transferred artificial substrates between two streams characterized by different pollution levels in naturally circumneutral waters and observed that the assemblages responded more rapidly to the simulated degradation than to the simulated amelioration. In their study, the sudden water quality degradation was accompanied by a marked reduction of pollution-sensitive taxa and a large increase in pollution-tolerant taxa within 4 weeks after the translocation. They noted drastic changes in assemblage structure 2 weeks after the translocation to the impacted site, whereas 45 days were not sufficient for a complete turnover of the assemblage in the case of recovery. Ivorra et al. (1999), Tolcach and Gómez (2002), and Gold et al. (2002) also found that diatom assemblages in naturally circumneutral environments achieved greater turnover when translocated to a polluted site (within 2 weeks) than when translocated to a reference site. Hirst et al. (2004) also observed that the response of diatom assemblages to a sudden acidification of the environment was faster than the return to normal conditions. The sensitivity of different European diatom indices was studied by Rimet et al. (2005) in a translocation experiment simulating an amelioration of the conditions in an environment with naturally alkaline water pH. Their results indicated that most of the changes in the assemblages were observed during the first phase of the sampling strategy, 20 to 30 days after the transfer.

Complexity of the diatom assemblages

It is possible that the nutrients accumulated in the biofilm might have sustained the diatoms for a period of time. This process has been observed in water courses and lakes undergoing restoration, where nutrients included in the sediments and in the biota continued to be available for a period of time and therefore slowed down the recovery process. However, in this study, the colonization of the substrate took place over a period of 4 weeks, allowing for the establishment of a mature diatom community. Although the communities were mature and similar to what was observed on natural substrates, there was no thick accumulation of biomass on the substrates, which might have limited the diffusion of nutrients after substrate translocation.

The variation in response time as a function of trophic status may in part be related to the diversity and complexity of the assemblages prior to translocation. The results from this study suggest that the assemblages sampled in the selected oligotrophic sites respond more rapidly to an alteration (reflecting mainly an increase in nutrients). This

difference in response time may be due to a sudden decrease in abundance of dominant taxa that are sensitive to eutrophication. It seems unlikely that the longer response time observed in the mesotrophic and eutrophic environments could be attributed to differences in colonization rates. Most of the dominant taxa at all sites were present at varying abundances during the whole sampling period. Colonization likely played only a minor role in modifying abundances. Instead, the longer integration period in mesotrophic and eutrophic environments may be attributed in part to the complexity of the diatom assemblage and the tolerance of the taxa. This result suggests that the complexity of the assemblages influences the time needed for assemblage restructuring. In an assemblage dominated by numerous pollution-tolerant taxa, there are no drastic changes in assemblage structure following a change in environmental conditions because responses can be highly variable among taxa. However, in an assemblage dominated by only a few taxa, a change in the abundance of a taxon will rapidly influence the structure. Diversity–stability relationships have been the subject of numerous theoretical and empirical studies in ecology (e.g., MacArthur 1955; May 1973; Steiner et al. 2006). Our results agree with previous studies on assemblage resistance and resilience, which found that population and assemblage diversity influence the temporal stability (e.g., McCann 2000; Cottingham et al. 2001). The results suggest that more diverse diatom assemblages are more stable and more resistant to nutrient variations in the environment. The response time seems, therefore, attributed to the sensitivity (resistance) of the taxa to fluctuations in nutrients and to the complexity of the assemblage (resilience). The results obtained in the present study also reflect the hysteresis process described in Beisner et al. (2003) in lake eutrophication, where the responses to reduction and increase in nutrient inputs do not simply follow the same trajectories in opposite directions. As stated by Lake et al. (2007), for a variety of causes, such as different dispersal capabilities, priority effects, and the playing out of interactions, it may take a longer time to fully restore an assemblage to the targeted state than to degrade it. Thus, the restoration pathway may show hysteresis or follow Sarr's (2002) "broken leg" model, in which the assemblage follows a lengthy and nonlinear trajectory to recovery. In the case of diatoms, more diverse assemblages often result when environmental conditions are perturbed (e.g., eutrophication). The taxa may have different sensitivity to pollution, but will generally be less sensitive to the frequent fluctuations in nutrient concentrations characterizing mesotrophic and eutrophic environments. These assemblages are more resilient and complex. The return to the original assemblage will necessitate a longer time because the tolerant taxa are capable of supporting a decrease in nutrient concentrations for a certain period of time before the pollution-sensitive taxa recolonize and become dominant again.

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Appendix A

Appendix A continues on the following page.

Table A1. Changes in the relative proportions of the dominant species after 12 weeks in the hosting sites for (*a*) subindex IDEC-Neutral and (*b*) subindex IDEC-Alkaline.

(*a*) IDEC-Neutral

Degradation

Noire to Blanche		Shawinigan upstream to downstream		Ste. Anne to Des Envies	
% of dominant species at week 0	% of dominant species at week 12	% of dominant species at week 0	% of dominant species at week 12	% of dominant species at week 0	% of dominant species at week 12
TFLO = 41.0	ASHU = 16.1	ADMI = 30.4	GOMP1 = 26.0	ADMI = 38.6	ARIV = 14.5
EUNO = 17.7	NGER = 8.8	ADMCF1 = 15.3	ESLE = 13.5	TFLO = 20.2	PTLA = 9.4
EBIL = 5.5	MVAR = 8.3	EUNO = 5.7	NGRE = 9.2	BBRE = 10.1	CPLE = 8.0
EINC = 3.6	ESLE = 6.4	SPIN = 5.4	ADMI = 8.7	EUNO = 5.5	ADMI = 7.5
BBRE = 2.9	NPAD = 5.7	TFLO = 4.5	NPAD = 7.0	FCAPF = 2.9	NAMP = 6.3

Recovery

Blanche to Noire		Shawinigan downstream to upstream		Des Envies to Ste. Anne	
% of dominant species at week 0	% of dominant species at week 12	% of dominant species at week 0	% of dominant species at week 12	% of dominant species at week 0	% of dominant species at week 12
RSIN = 26.6	EUNO = 20.8	CPLE = 35.2	ADMI = 16.0	NPAD = 9.9	ADMI = 22.7
CPLE = 10.9	BBRE = 12.6	RSIN = 28.1	CPLE = 13.6	NPAL = 7.2	TFLO = 14.4
ARIV = 10.1	TFLO = 10.7	ADMI = 10.2	ARIV = 9.7	NGRE = 5.0	BBRE = 4.9
ESLE = 8.5	EBIL = 6.8	ARIV = 5.5	EUNO = 6.1	ARIV = 4.8	FCAPF5 = 4.1
PTLA = 8.0	CPLE = 5.6	ESLE = 5.0	TFLO = 3.9	NCRY = 4.8	BMIC = 3.2

(*b*) IDEC-Alkaline

Degradation

Nicolet to Nicolet Sud-Ouest		Yamaska Sud-Est to Yamaska	
% of dominant species at week 0	% of dominant species at week 12	% of dominant species at week 0	% of dominant species at week 12
ADMI = 41.7	NCPR = 15.3	ARIV = 52.2	NCPR = 14.9
RSIN = 15.9	CPLE = 11.4	ADMI = 11.9	ADMI = 12.5
CPLE = 9.8	MVAR = 11.2	ADLA = 9.2	CPLE = 10.6
NPAD = 3.2	NPAD = 9.7	ESLE = 3.7	NGRE = 6.7
ESLE = 2.9	NTPT = 5.4	FCAPF5 = 3.7	ESLE = 6.3

Recovery

Nicolet Sud-Ouest to Nicolet		Yamaska to Yamaska Sud-Est	
% of dominant species at week 0	% of dominant species at week 12	% of dominant species at week 0	% of dominant species at week 12
CPLE = 29.9	ADMI = 32.7	MVAR = 13.3	ADLA = 22.3
RSIN = 20.4	NCPR = 7.3	ESLE = 9.5	ADMI = 17.2
ADMI = 10.6	NPAD = 7.3	NCPR = 9.3	ARIV = 16.7
NCTE = 3.5	NTPT = 6.5	ADMI = 8.1	GENT = 7.4
NINC = 3.3	CPLE = 6.3	FCAPF5 = 4.7	AMSA = 3.4

Note: ADLA = *Achnanthidium* cf. *latecephalum* Kobayasi 1997; ADMCF1 = *Achnanthidium microcephalum* (Kützing) 1844 form 1; ADMI = *Achnanthidium minutissimum* (Kützing) Czarnecki 1994; AMSA = *Achnanthes minutissima* var. *saprophila* Kobayasi & Mayama 1982; ARIV = *Achnanthidium rivulare* Potapova & Ponader 2004; ASHU = *Achnanthes subhudsonis* Hustedt 1921; BBRE = *Brachysira brebissonii* Ross 1986; BMIC = *Brachysira microcephala* (Grunow) Compère 1986; CPLE = *Cocconeis placentula* var. *euglypta* (Ehrenberg) Grunow 1884; EBIL = *Eunotia bilunaris* (Ehrenberg) Mills 1934; EINC = *Eunotia incisa* Gregory 1854; ESLE = *Encyonema silesiacum* (Bleisch) Mann 1990; EUNO = *Eunotia* spp.; FCAPF5 = *Fragilaria capucina* Desmazières 1825 form 5; GENT = *Gomphonema entolejum* Østrup 1903; GPAR = *Gomphonema parvulum* (Kützing) Kützing 1849; MVAR = *Melosira varians* Agardh 1827; NAMP = *Nitzschia amphibia* Grunow 1862; NCPR = *Navicula capitatoradiata* Germain 1981; NCRY = *Navicula cryptocephala* Kützing 1844; NCTE = *Navicula cryptotenella* Lange-Bertalot 1985; NGER = *Navicula germainii* Wallace 1960; NGRE = *Navicula gregaria* Donkin 1861; NINC = *Nitzschia inconspicua* Grunow 1862; NPAD = *Nitzschia palea* var. *debilis* (Kützing) Grunow 1880; NPAL = *Nitzschia palea* (Kützing) W. Smith 1856; NTPT = *Navicula tripunctata* (Müller) Bory 1822; PTLA = *Planothidium lanceolatum* (Brébisson) Round & Bukhtiyarova 1996; RSIN = *Reimeria sinuata* (Gregory) Kociolek & Stoermer 1987; SPIN = *Staurosirella pinnata* (Ehrenberg) Williams & Round 1987; TFLO = *Tabellaria flocculosa* (Roth) Kützing 1844.