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Predicting river diatom removal after shear stress induced by ice melting

Francesca Bona*, Valentina La Morgia, Elisa Falasco

DBAU, Università degli Studi di Torino. Via Accademia Albertina 13, 10123 Torino, Italy

*corresponding author e-mail francesca.bona@unito.it tel +390116704520 fax +390116704508

Running title: Diatoms and shear stress in mountain rivers

Summary

The augmentation of fine particles and water velocity may have important effects on river biota which have not been fully clarified. The aim of this study is to relate the removal of diatoms to changes in environmental variables during high-stage flow in alpine streams.

To achieve this goal, we adopted a path analysis approach. We hypothesized a causal model relating diatom presence to environmental predictors and we tested it against data collected in two alpine rivers in NW (Aosta Valley): Dora di Veny, directly fed by glaciers of the M. Bianco massif, and Savara, fed by springs. TSS and velocity values were much higher in Dora di Veny, with a maximum velocity of 2.9 ms^{-1} and a maximum TSS of 2180 mgL^{-1}. Absence of epilithic diatoms was recorded only three times in Savara, while it occurred in roughly half the samples in Dora di Veny. Diatom recolonization after natural removal generally occurred in early autumn, with a dominance of tightly attached forms. According to our path model, the explanatory variables causally related to the presence/absence of diatoms were water velocity, TSS and river feeding. The model estimated both direct and indirect effect weights of water velocity, thus discriminating the respective roles of shear stress (velocity) and abrasion of the substrates/increased turbidity (TSS, partly mediated by velocity).

Our model allowed estimation of TSS and velocity threshold values, and therefore inferences on the impact of physical alterations induced by natural or human causes. From a practical point of view, this may represent an applied outcome in the environmental impact assessment of engineering works and other human activities that could increase the TSS in rivers.

key words: benthic diatoms, current velocity, ecological models, physical disturbance, path analysis

Introduction

The augmentation of fine suspended particles in rivers may be induced by natural causes, such as storm events and ice melting, or by human activities, such as flow regulation. The effects on diatoms, which are the main primary producers in the headwaters and usually account for the highest number of species among the primary producers in aquatic systems (Leira & Sabater, 2005), have been considered only recently. Past studies showed that velocity increases alone, are not sufficient to explain the algal removal during flood events (Horner *et al.*, 1990; Uehlinger, 1991; Biggs, 1996; Francoeur & Biggs, 2006) or at least that there is no clear correlation between velocity increase and algal removal. Biggs & Thomsen (1995) found that very high velocity values (up to 1.5 ms^{-1}) did not remove a tightly adherent layer of algae under laboratory conditions. High water velocity can lead to the removal of benthic algae directly by shear stress or indirectly through substrate abrasion by mobilized sediments. Already Blinn & Cole (1991) evaluated the importance of suspended solids in terms of scouring. After that, Francoeur & Biggs (2006) investigated the role and importance of suspended sediment action as a mechanism of substrate abrasion and benthic algae removal in an experiment conducted in an indoor flow tank. They found that scour by suspended sediment concentrations up to 7000 mgL^{-1} contributed to the removal of benthic algae over and above that resulting from water velocity alone. Nevertheless, there is no agreement in the literature on the threshold values of water velocity and suspended solids that can lead to significant qualitative (species composition) and quantitative (biomass) alterations.

The aim of our study was to predict the disappearance of diatoms after ice melting in kryal systems analysing the effects of shear stress induced by peaks of water velocity and suspended solidson diatom communities. The underlying hypothesis was that the presence/absence of diatoms, at a given sampling site, might be related to a set of environmental variables (reported in Fig. 1). To accomplish our aim, we hypothesized a causal model and tested it against data collected in two alpine rivers in NW Italy with two different feeding types: one is directly fed by glaciers and the other by springs. To achieve this goal, we adopted the path analysis approach suggested by Shipley (1999; 2009), which allowed us to test a multivariate causal hypothesis involving a finite set of key observed variables and incorporating the multilevel structure of our data. Thus far, the path analysis approach has been applied mainly to the analysis of cause-effect relationships in wildlife ecology (e.g. Decristophoris *et al*., 2007; Mysterud *et al.*, 2008), while there is a lack of literature data on its application to water ecology issues.

The findings of this research may have important applications, such as in the environmental assessment of human works producing such physical effects. Indeed, human activities have come to be a serious threat to mountainous and alpine lotic systems (Bona *et al.,* 2008). Despite the importance of hydraulic conditions to phytobenthos in rivers, velocity suitability criteria have yet to be defined for this community. Moreover, the shear stress associated with ice melting has increased in the last century, as rapid alpine glacier retreat has made large quantities of moraine detritus available for fluvial transport.

Material and methods

To assess the effects of the environmental variables on the presence/absence of diatoms at each site at each sampling time, we hypothesized a causal model and tested it against the collected data. In particular, the experimental design of this research foresaw 6 different steps focused on path analysis (Shipley, 1999): 1) specification of the hypothesized causal structure for the relationships among variables; 2) study sites selection; 3) data collection and laboratory analysis; 4) translation of the causal structure into a set of d-separation statements; 5) test of the overall fit of the model; 6) estimation of the path coefficients; 7) identification of the thresholds of environmental variables which determine diatom absence.

Study sites

On account of its hydromorphology, the Dora Baltea River drainage basin (Aosta Valley, NW Italy) is an excellent natural laboratory to investigate the ecological effects of sediment transport. Our experimental data were taken from two of its sub-basins, Dora di Veny and Savara. The headwaters of both rivers are at an altitude of 2500-2650 m a.s.l. The Dora di Veny sub-basin is directly fed by the Miage Glacier, which is heavily covered by debris and has an ablation area at quite low elevation (~1850 m a.s.l.). The bed load of the Dora di Veny catchment is the highest in the entire Aosta Valley (1926 t y^{-1} km^{-2}), while the estimated value for Savara is 93 t y^{-1} km^{-2} (Vezzoli, 2004). In both catchments, the dominant rock type is granitoid and there is a very low intensity of land use. Indeed, the main human activities are hiking and high-altitude pasturage. Soil covers just 9% of the Dora di Veny basin area and 12% of Savara because of the dominance of massive rocks and the presence of moraines and glaciers. The dominant vegetation types are coniferous forests (mainly larch) and broad alpine pastures. In both study areas, the river bed is composed of boulders and cobbles, with some gravel in a few depositional habitats.

Data collection and laboratory analysis

The main hydrological and geographical features of the two rivers and the sampling sites are summarized in Table 1. At these sites, we carried out a sampling campaign from November 2005 to October 2006. In total, 10 samplings were performed at each site; sampling was intensified up to biweekly intervals in summer.

Field activities included: 1) collection of water samples for total suspended solids (TSS) and nutrient analysis; 2) collection of epilithic phytobenthos growing on boulders which were the dominant substrates in both rivers. Highly stable boulders were chosen to avoid the effect of bedload movement. A total surface of at least 500 cm^2 provided by 5 different boulders was carefully scraped (all surfaces exposed to light, including the upstream and downstream faces) following the standard methods (EN13946, 2003). Diatom samples were preserved in ethanol 50%. We also collected material for chlorophyll *a* determination by scraping 20 cm^2 of substrate. The samples for chlorophyll *a* determination were immediately filtered (Whatman GFC) and stored frozen in the dark until analysis; 4) bed velocity (0.05 m from the bottom) was measured with a current meter (Mod RHCM Idromar). We took three velocity measurements for each site following the diatom sampling transect; 5) temperature, pH, dissolved oxygen and conductivity were measured in the field with a multiparametric probe. In the laboratory, TSS values were determined by gravimetry following the Italian standard methods (IRSA, 1994). Phosphate and nitrate concentrations were determined with a LASA 100 spectrophotometer according to IRSA (1994). Epilithic chlorophyll *a* was estimated according to the procedure described by Steinman & Lamberti (1999). Diatom samples were preserved in ethanol 50% and treated in the laboratory following the standard protocol for diatoms (EN13946, 2003). Frustules were cleaned with hydrogen peroxyde and HCl 1 N was added to remove all traces of oxidising agents from the cleaned material. Permanent slides were obtained by drying a drop of the suspension on a hot plate and slides mounted with Naphrax. Diatoms were analysed with an optical microscope and identified at the species or variety level following the Krammer & Lange-Bertalot (1986–2001) classification.

Data analysis and modelling

The hypothesized causal structure of the model was specified via an acyclic causal graph or path diagram (Fig. 1). This graph expresses the causal hypothesis that the presence/absence of diatoms at a given sampling site at time *t* (D_t) is due to the effect of water velocity (V), water conductivity (Cond), total suspended solids (TSS) and the availability of soluble reactive phosphorous (SRP). Some of these variables are affected by the type (kryal/rhithral) of river (RT). We considered "absence of diatoms" when no valves were detected in the whole glass slide and chlorophyll *a* was below the detection limit. The presence/absence of diatoms at time *t-1* (D_{t-1}) was also included in the graph to test for temporal auto-correlation in our dataset. According to this causal model, the presence/absence of diatoms at time *t-1* and SRP are exogenous variables (their causal parents are not explicitly modelled) and they both exert a direct influence on the presence/absence of diatoms at time *t*. Water velocity is also an exogenous variable, but it has both a direct and indirect effect on the presence/absence of diatoms, with the indirect effect mediated by the amount of TSS. Indeed, the latter variable and water conductivity are endogenous variables (i.e. variables caused by some other variables in the model) affected by water velocity and/or by the kryal or rhithral river type, respectively.

The causal structure expressed by the graph was translated into a set of direct separation (d-separation) statements which predict the conditional probabilistic independences that must be true if the causal model is correct. D-separation gives the necessary and sufficient conditions for two vertices in a graph to be observationally (probabilistically) independent upon conditioning on some other set of vertices. As an example, for a pair of non-adjacent variables (e.g. water velocity, V, and water conductivity, Cond), we identified the causal parents of each vertex in the pair (e.g. river type, RT, for the V-Cond pair) and we wrote the d-separation statement as (Cond,V)|{RT}. This statement means that vertex V is d-separated from vertex Cond, given the river type. By repeating this procedure (Shipley, 1999, 2000) for each pair of non-adjacent vertices in the graph, we identified the basis set of d-separation statements and we expressed each of them as a generalized mixed model (Shipley, 2009) in order to account for the non-independence of the observations collected at each sampling site (Table 3). As an example, Mixed models were fitted via the nlme and lme4 packages in R 2.8.1 (R Development Core Team, 2008).
Starting with this model, to identify a causal graph including only significant path coefficients we tested all sub-models by gradually reducing the number of paths and variables (Thomas *et al.,* 2007; Elliot *et al*., 2009). The overall fit of the final model was tested via the *C* statistic, which follows a chi-square distribution with degrees of freedom equal to *2k* (Shipley, 1999; 2009):

$$C= -2 \sum_{i=1}^{k} \ln (p_i) \qquad \text{(eqn1)}$$

where k is the number of d-separation statements in the basis set and p_i is the null probability of the independence test associated with the *i-th* independence claim.

The final model arising from the path analysis was used as a basis to estimate threshold values of environmental predictors that affect diatom presence in kryal systems. First, we fitted a mixed model relating the presence/absence of diatoms to the environmental variables kept in the final model. To calibrate the model, we used 70% of presence data and 70% of pseudo-absence data recorded in the field (calibration data set), while the remaining records were used afterwards to validate the model (validation data set). Second, we performed a linear stretch of the outcome of this regression model to scale the predicted values between 0 and 1 (Johnson *et al*., 2004) and we carried out model validation using confusion matrices, which classify model results according to the following rules: (i) the response of interest (presence of diatoms) is neither observed nor predicted (true negative rate); (ii) the model fails to predict diatom presence (false negative rate); (iii) the model prediction is positive but the observation negative (false positive rate); (iv) model predictions agree that a positive response occurs (true positive rate) (Gardner & Urban, 2003). We built a confusion matrix for different cut-off values discriminating between presence and absence of diatoms and we produced a receiver operating characteristic (ROC) curve based on the true and false positive rates as a measure of model performance. ROC curves were plotted using the ROCR (Sing *et al.*, 2005) package for R. This procedure allowed us to identify the cut-off value that maximised the classification accuracy of the model and we used it as a break value to discriminate presence and pseudo-absence of diatoms. The AUC (Area Under the ROC Curve) and the True Skill Statistic (Allouche *et al.*, 2006) corresponding to the break value were also computed as measures of model performance.

After validation, we used the estimates of the fixed effects of the model to build a response surface describing the "probability" of presence (p_D) of diatoms according to the values of the environmental predictors. The response surface provides a visually appealing graphical summary, allowing rapid identification of the thresholds of environmental variables for which the response (presence/absence of diatoms) achieves the desired (presence) value (as in spatial regression models, O'Connell & Wolfinger 1997). To indicate these thresholds, we also plotted on the response surface the cut-off value maximising the classification accuracy of the model.

To obtain a robust estimate of the response surface, we repeated model validation, performing 999 replicates with different calibration and validation data sets. The results of the validation procedures were used to estimate the mean threshold values for environmental predictors involved in the model.

Results

A list of dominant taxa of the two rivers is reported in table 3. When present, the diatom communities of Dora di Veny and Savara were very similar and mainly composed by pioneer (i.e. *Achnanthidium pyrenaicum, A. minutissimum*) and reophylus species (*Fragilaria arcus*) typical of alpine headwaters. Prostrate taxa dominated the communities even though some stalked genera such as *Gomphonema* (*G. olivaceum*, G. *pumilum* var. *elegans*) and *Cymbella* (i.e. *C. excisa*) were detected. Silt tolerant taxa such as *Navicula* and *Nitzschia* were more abundant in Dora di Veny.

Table 4 summarizes the mean and standard deviation of the water quality metrics and current velocity for each river. There was a significant difference (Kruskal-Wallis test) between the two rivers in conductivity ($p<0.001$), velocity ($p<0.05$), TSS ($p<0.001$) and chlorophyll *a* ($p<0.001$). The last variable was low or below the detection limit when no or very few diatoms were found. In general, data from Dora di Veny showed greater variability due to the glacial feeding. Nutrients, measured as nitrate and SRP, were low in both rivers, particularly in Dora di Veny.

The seasonal trends of water velocity and TSS (Fig. 2) are of particular interest in view of the objective of the present study. In Dora di Veny, the peaks are much more pronounced, with a maximum velocity of 2.87 m s^{-1} and a maximum TSS of 2182 mgL^{-1}. Diatom removal was recorded three times in Savara, while it occurred in most samples from Dora di Veny.

The path analysis procedure allowed us to define a simple model explaining the observed pattern of presence/absence of diatoms (D_t). This model (Fig. 3) was based on a d-separation statement ((RT,D_t)|{V,TSS}, D_t£ RT+V+TSS+SRP+D_{t-1}+(1|Site), estimated RT coefficient = 1.37 • 0.87 s.e., null probability = 0.12) and it included three explanatory variables (water velocity, TSS and river type). Its fit was satisfactory ($C = 4.24$, $df = 2$, $p>0.05$) and all path coefficients were significant (Table 5). According to this model, water velocity has both a direct and indirect effect (mediated by TSS) on the presence/absence of diatoms. While the indirect effect weight is equal to -0.23, the direct effect weight is -0.37. The river type (rhithral/kryal) also influences the presence of diatoms via its effect on TSS, which are higher in the kryal (mean value = 306.8 mg L^{-1} • 526.6 SD) than in the rhithral river (mean value = 10.2 • 12.9 SD).

This final model relates the presence of diatoms to total suspended solids, water velocity and river type. Fitting generalized linear mixed models with these variables to the calibration data sets, we obtained 999 replicates of a response surface describing the "probability" of presence (p_D) of diatoms according to the values of water velocity and TSS in kryal systems. Each response surface was also characterized by estimates of the AUC (Area Under the ROC Curve) and of the True Skill Statistic as measures of model performance.

By averaging the results of the validation procedures, we obtained the response surface shown in Fig. 4. The corresponding receiver operating characteristic (ROC) curve based on the true and false positive rates is shown in Fig. 5. The average AUC (Area Under the ROC Curve) was 0.86 (0.07 SD), while the mean value of the True Skill Statistic was 0.69 (0.13 SD). These results were considered satisfactory, since AUC values fell in the 0.7-0.9 range, indicating a reasonable discrimination ability appropriate for many uses (Swets,1988; Pearce & Ferrier, 2000). The mean break value (cut-off) maximising the classification accuracy of the model was 0.64 (0.18 SD).

Via the response surface, we identified threshold values of V and TSS. As shown in Fig. 4, these threshold values can be described by a straight line connecting all surface points maximising the classification accuracy of the model. According to our results, even in the absence of TSS, a water velocity > 2.00 m s^{-1} (0.89) is able to cause the removal of diatoms, while from a theoretical point of view a large amount of TSS would be required to cause diatom removal if water velocity is low.

Discussion

*Ecological characterization of the sites*The overall water characteristics resulting from this study confirm that both rivers are oligotrophic, as expected from the limited human activities in the water basin and the low river orders. Diatom communities perfectly reflected the ecological status of the rivers, mainly consisting of oligo and β-mesosaprobic taxa typical of alpine lotic systems. When present, the diatom community was composed of a low number of taxa, probably due to the extreme environmental growth conditions in terms of physical disturbance and scarcity of nutrients. In general, the communities in Savara were richer than those in Dora di Veny, especially during summer when the nutrient content showed a slight increase. In 24 of 41 samples taken in Dora di Veny, we observed complete, albeit temporary, removal of diatoms from the sampled substrates. This effect can be considered an extreme endpoint in comparison to previous experimental studies. For example, Francoeur & Biggs (2006) detected diatom removal as high as 60% in terms of chlorophyll *a* when they induced TSS values of almost 7000 mgL^{-1}. TSS concentrations measured in our natural system did not reach such a high value, with maximum concentrations lower than 2200 mgL^{-1}, and chl *a* was below 0.001 $\mu g\ cm^{-2}$ at all sites with the absence of diatoms, thus confirming the severity of the impact and the importance of this algal component to the periphytic community. The range of water velocity values measured in our study is comparable to those set up in laboratory experiments conducted in previous studies. Other minor effects induced by substrate abrasion and reported by several authors included a shift in the periphytic community composition and physiognomy (Biggs & Thomsen, 1995; Francoeur & Biggs, 2006; Peterson *et al*., 1990; Peterson & Stevenson, 1992).

Application of path analysis

Our path analysis approach allowed us to consider the main variables known to influence diatom presence, thus clarifying the relative effect of each of them, without artificial reproduction of the complex and extremely variable natural conditions characteristic of kryal systems. According to our findings, the presence of diatoms was affected by water velocity and TSS concentration. The latter was in turn affected by the river type (kryal/rhithral). In contrast, nutrients and water conductivity were excluded from the final causal model because of a lack of significance of their direct effect on diatoms. Moreover, data on the presence of diatoms did not appear to be significantly auto-correlated, suggesting that the temporal interval between subsequent samplings was long enough to ensure data independence. Thus, the final causal model included only three environmental variables (TSS, V, RT) and it allowed estimation of their effect weights on diatom presence. TSS had the major effect in terms of direct action, followed by water velocity, but the latter had the highest total effect (direct and indirect). These results agree with the general findings of Biggs & Thomsen (1995) suggesting that periphyton removal results from the combined effect of water velocity and TSS, while according to Heinlein (2000) water velocity can play a major role in diatom removal. However, thus far the respective weights of these two factors have not been quantitatively assessed.

While traditional statistical approaches such as single equation regression analysis can only capture the direct effects of included independent variables, path analysis allows estimation of direct and indirect weights. This distinction is particularly important for the understanding of ecological phenomena and for the identification of key variables in ecological processes. This is especially true if we consider that the path analysis models allow testing of a hypothesized causal structure against observed association patterns (Shipley 2000). In this framework, we can clarify causation relationships rather than just describing the strength of correlations between variables.

Regarding the estimated threshold values of TSS and velocity, we found that velocity equal to or higher than 2 ms^{-1} can induce diatom removal even in the absence of TSS, while TSS concentrations should remain above 1900 mgL^{-1} to produce the same effect. Although our 2 ms^{-1} threshold value for water velocity seems higher than the values considered by Biggs & Thomsen (1995) and Heinlein (2000), only a few data on threshold values for these variables are available, and these authors referred to partial rather than complete removal; hence, the comparison with literature data is not straightforward.

Our values were estimated via regression analysis and their accuracy in predicting diatom presence was tested on subsets of data (validation datasets) not involved in the model calibration. The outcome of the validation procedure suggested that the predictive ability of the model was satisfactory, since the area under the Receiver Operating Characteristic curve was larger than 0.7 (Pearce & Ferrier 2000). This criterion is commonly accepted to compare models and to choose the most appropriate one in decision-making processes related to ecological issues (e.g. La Morgia *et al*., 2008).

Once the factors affecting diatom presence were identified and weighted, the modelling approach also allowed the setting of thresholds for the matching pairs of TSS and water velocity (Fig. 4). It should be emphasized that these thresholds do not have universal application but can be considered for alpine streams and rivers with environmental characteristics comparable to those of the two rivers considered here: oligotrophic waters, low saline content, most of the primary production borne by diatoms.

Diatom response and pattern of recolonization

An important issue is the permanent or temporary nature of the impact on the river ecosystem. Our data show that the diatom communities recovered in nearly two months at the sites particularly affected by physical disturbance, while the recolonization process seemed to be more efficient at the less disturbed Savara sites, where we observed well developed and relatively rich communities in October, even consisting of late colonizer species (such as *Gomphonema calcifugum* and *G. olivaceum*). The situation was different in the glacier fed

Dora di Veny. The upper site (V1) was least affected by the shear stress and abrasion of the substrate, probably due to the constraining effect of an upstream lake. Indeed, the pioneer community observed in the first phase of recovery was mainly composed of early colonizer species, such as *Achnanthidium pyrenaicum*, *A. minutissimum* s.l. and *Fragilaria arcus*. The downstream sampling sites (V2, V3 and V4) always showed higher flow velocity and TSS, and the removal of the diatom communities was a permanent phenomenon throughout summer at all the sites. The partial recovery of the communities started in late autumn, but they never reached high richness values and a mature stage even in winter.
We can thus hypothesize that a permanent physical disturbance, even if natural, slows diatom community recovery, which never reaches the mature stage, with cascade effects on the grazer communities. Complete removal of the primary producers for such a long period may have consequences on the entire food web of the fluvial reach. Within the framework of environmental impact assessment, our research may help to improve the traditional evaluation metrics such as biotic indices. Indeed, the consequences of physical disturbance on diatom communities, whether natural or anthropogenic, are not revealed by the application of diatom indices. To obtain a more detailed overview of the potential impacts affecting high mountain stream communities, it is important to consider their composition (in terms of growth forms) and their possible adaptation to physical disturbance. On the other hand, the increase of fine particles in the river could have different repercussions on the diatom communities when caused by human activity. Diatom communities colonizing naturally disturbed environments could be more adapted to face adverse conditions than those living in undisturbed ones.

In conclusion the modelling procedure based on path analysis led to discrimination of the respective effects of shear stress (velocity) and abrasion of the substrate (TSS, partly mediated by velocity) on the diatom presence in these ecosystems. This approach seems to be a promising tool in the field of water ecology, particularly when a set of multiple variables must be considered to explain the response of all biological components to an environmental disturbance. The same statistical approach could be used in order to evaluate the contribution of environmental variables on colonization and spread of invasive taxa (for instance *Didymosphenia geminata*) and for conservation purposes (e.g. habitat restoration for aquatic endangered species).
From a practical point of view, this may represent an applied outcome in the environmental impact assessment of engineering works and other human activities that could increase the

TSS in rivers, such as those encountered in river management (channel widening, deepening, regrading, realignment), water exploitation (construction of dams), forestry operations, and gravel extraction. In spite of differences in the conceptual models underlying the functioning of river systems, our approach could be used in future to estimate the weights and threshold values of the environmental predictors involved in different river types.

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Table 1. Main hydrological and geographical features of the two sampled rivers (Regione Valle d'Aosta, 1993; Vezzoli, 2004)

	Dora di Veny	Savara
Basin area (km^2)	96 (27% glaciers)	147 (10% glaciers)
Altitude of springs (m a.s.l.)	2512	2650
River length (km)	15	27
River mean slope (%)	8.17	12.50
Median basin altitude (m a.s.l.)	2633	2501
Altitude of sampling sites (m a.s.l.)	1956; 1720; 1501; 1285	2030; 1670; 1290

Table 2. The basis set of d-separation statements implied by Fig. 1. According to Shipley (1999, 2000), the basis set was obtained by considering that each set of unique pairs of non-adjacent vertices in the graph is conditioned on the set of variables that are direct causes ("causal parents") of both vertices.

D-separation statements	Mixed model	Variable whose partial regression slope should be zero
(Cond,V)|{RT}	V~Cond+RT+(1|Site)	Cond
(Cond,SRP)|{RT}	SRP~Cond+RT+(1|Site)	Cond
(Cond,D_{t-1})|{RT}	D_{t-1}~Cond+RT+(1|Site)	Cond
(TSS,Cond)|{V,RT}	Cond~TSS+V+RT+(1|Site)	TSS
(TSS,SRP)|{V,RT}	SRP~TSS+V+RT+(1|Site)	TSS
(TSS,D_{t-1})|{V,RT}	D_{t-1}~TSS+V+RT+(1|Site)	TSS
(RT,D_t)|{V,TSS,SRP,D_{t-1}}	D_t~RT+V+TSS+SRP+D_{t-1}+(1|Site)	RT

Table 3. List of dominant diatom taxa in Savara and Dora di Veny.

	DOMINANT TAXA (> 5%; in order of abundance)
Savara	*Achnanthidium pyrenaicum* (Hustedt) Kobayasi; *Fragilaria arcus* (Ehrenberg) Cleve; *Achnanthidium minutissimum* (Kützing) Czarnecki s.l.; *Cymbella excisa* Kützing; *Diatoma vulgaris* Bory; *Gomphonema pumilum* var. *elegans* Reichardt et Lange-Bertalot; *Encyonema minutum* (Hilse) Mann
Dora di Veny	*Achnanthidium minutissimum* (Kützing) Czarnecki s.l.; *Achnanthidium pyrenaicum* (Hustedt) Kobayasi; *Gomphonema olivaceum* (Hornemann) Brébisson; *Fragilaria capucina* var. *vaucheriae* (Kützing) Lange-Bertalot; *Fragilaria arcus* (Ehrenberg) Cleve; *Encyonema minutum* (Hilse) Mann; *Cymbella excisa* Kützing; *Gomphonema pumilum* var. *elegans* Reichardt et Lange-Bertalot

Table 4 . Summary of water quality, current velocity and chlorophyll *a* data for the two rivers.

	RIVER DORA DI VENY			RIVER SAVARA		
	N	Mean	SD	N	Mean	SD
Temperature (°C)	40	5.1	2.2	33	5.5	2.7
pH	40	7.87	0.28	33	7.54	0.057
Conductivity (mS cm^{-1})	40	0.274	0.106	33	0.131	0.0068
N-NO_3(mg L^{-1})	40	0.294	0.135	33	0.376	0.076
SRP (µg L^{-1})	40	10.0	18.8	33	48.8	8.72
TSS (mg L^{-1})	40	306.8	526.6	33	10.19	12.93
Water velocity (m s^{-1})	40	1.33	0.543	33	1.07	0.445
Chlorophyll *a* (µg cm^{-2})	40	0.054	0.096	33	0.113	0.093

Table 5. Unstandardized path coefficients of the causal graph in Fig. 2.

Path coefficient	Estimate	Std. Error	*p* value
b1 (V-->D_t)	-3.09	1.01	0.029
b2 (V-->TSS)	1.82	0.47	<0.001
b3 (TSS-->D_t)	-0.88	0.22	<0.001
b6 (RT-->TSS)	-2.57	0.72	16