

Epilithic diatom assemblages in rivers draining into Golfo Dulce (Costa Rica) and their relationship to water chemistry, habitat characteristics and land use

Astrid Michels^{1,2*}, Gerardo Umaña² and Uta Raeder¹

With 5 figures and 4 tables

Abstract: Epilithic diatom assemblages from neotropical streams draining into Golfo Dulce (Costa Rica) were studied to determine how diatoms were related to measured environmental conditions. Twenty-three sites, affected by different land use practices, were selected and monitored for 21 months. Water chemistry was characterized by moderate specific conductivity (100–300 $\mu\text{S}/\text{cm}$), neutral to alkaline pH and moderate to high values of soluble reactive phosphorus (10–70 $\mu\text{g}/\text{L}$). Anthropogenic impact was reflected in lower oxygen saturation, elevated nitrogen compounds and measured sediment load. A diverse diatom flora of 212 taxa was found. Patterns in the diatom distribution in relation to environmental variables, as revealed by canonical correspondence analysis, showed that riparian shading, pH, conductivity, current velocity and turbidity were the most important measured factors in determining species composition. The relationship between conductivity and pH was sufficiently strong to develop weighted-averaging regression and calibration models. Optima and tolerances of the most common diatom taxa are presented.

Key words: diatoms, tropical streams, water quality, monitoring, Costa Rica, weighted-averaging regression.

¹ **Authors' addresses:** Techn. Univ. Munich, Limnol. Stn, Hofmark 1–3, D-82393 Iffeldorf, Germany.

² Centro de Investigación en Ciencias del Mar y Limnología (CIMAR), University of Costa Rica, San José, Costa Rica.

* Corresponding author; current address: Paleoecological Environmental Assessment and Research Laboratory (PEARL), Department of Biology, Queen's University, Kingston, ON, Canada, K7L 3N6; E-mail: michelsa@biology.queensu.ca

Introduction

Diatoms (Bacillariophyceae) are one of the most abundant and diverse components of stream and river algal communities (STEVENSON & PAN 1999). They are very suitable biological indicators of environmental conditions in streams and rivers because they respond directly and sensitively to many physical and chemical variables such as temperature (DESCY & MOUVET 1984), pH (PAN et al. 1996) and nutrient concentrations (PRINGLE & BOWERS 1984). Studies around the world stress the importance of investigating the relationship between environmental conditions and diatom species in different geographical regions in order to enhance the use of diatoms in regional monitoring programs (VAN DE VIJVER & BEYENS 1999). A considerable number of studies using diatoms have been conducted in aquatic systems in temperate regions (e. g. POTAPOVA & CHARLES 2003, BENNION et al. 2004, SOININEN et al. 2004). However, despite the serious aquatic pollution problems in tropical surface waters, comparable studies are less common in these regions (JÜTTNER et al. 2003). In Costa Rica, only a small number of studies concerning diatom assemblages have been carried out (PAABY 1988, PRINGLE et al. 1993, SILVA-BENAVIDES 1996 a, b, MICHELS 1998 a, b, NUNN 1999, WYDRZYCKA & LANGE-BERTALOT 2001).

Golfo Dulce (Fig. 1) is a unique and relatively pristine neotropical fjord located on the southern Pacific coast of Costa Rica (SPONGBERG & DAVIS 1998). A large part of the Golfo Dulce basin is surrounded by tropical wet rainforest; the Osa Peninsula, located on the western edge of the gulf, comprises the largest remaining coastal area of tropical rainforest in the Central American Pacific (SPONGBERG & DAVIS 1998). The Golfo Dulce basin contains a variety of habitats, providing a home for many marine migratory and resident mammals with restricted distributions (HARTMANN & ACEVEDO-GUTÉRREZ 1996). Environmental conditions favored the growth of coral reefs up to the recent past (CORTÉS 1992). However, at the beginning of the 1970's, the natural environment of the Golfo Dulce area began to change due to human impacts. For example, large parts of the catchments' slopes were cleared of forest for banana and oil palm plantations, cattle farming and gold mining activities (UMAÑA 1998). As a result, the physical structure of rivers and streams in the Golfo Dulce catchment area were changed and considerably higher amounts of sediments were transported into the Pacific. The deterioration of the coral reefs was documented by CORTÉS (1990) as one of the most severe effects on the gulf. For example, the coral reef of Punta Islotes, located on the inner part of Golfo Dulce, has been massively degraded by sedimentation, so that coral coverage was down to 2% of its original expanse in 1998 (CORTÉS & HATZIOLOS 1998). For better conservation and management plans, the Golfo Dulce basin and its freshwater systems require an effective chemical and biological

monitoring program. Benthic diatom assemblages can provide valuable information about this. However, no data was yet available regarding the diatom flora of the southern part of Costa Rica in the Golfo Dulce area and this study represents the first report on diatom assemblages from rivers in the Golfo Dulce catchment.

The present paper focuses on the benthic diatom assemblages from streams and rivers draining into Golfo Dulce, which have undergone varying anthropogenic impacts. The objectives of this study were threefold: The first was to characterize the physical-chemical environment and the epilithic diatom assemblages of the main rivers that drain into Golfo Dulce. The second aim was to explore the relationships between diatom assemblages and environmental variables using canonical correspondence analysis (CCA), and the third to develop inference models for selected environmental variables on the basis of the abundance and distribution of diatom species.

Materials and methods

Study site

Over a 21-month period, data were collected in the Golfo Dulce catchment area from 23 sites on 15 streams and rivers with different surrounding land use. The 23 sites (Fig. 1) were situated along the three main rivers that drain into the Golfo Dulce basin: the Esquinas (E), Rincon (R) and the Coto Colorado (C), along their tributaries and some smaller rivers (A, B, N, P). Golfo Dulce is a fjord-like embayment located on the southwest coast of Costa Rica, between $8^{\circ} 30' N$ and $83^{\circ} 16' W$. The geology of the region is composed of marine deposits over intrusive igneous rocks of different age (JANZEN 1991). The Osa Peninsula, on the western side of the gulf, is mainly covered by Late Cretaceous sediments. The lower parts of the Osa river basins (A1, B1, R1), the Esquinas River (E4) and most of its tributaries (E5–E7) are composed of quaternary alluvial deposits (TOURNON & ALVARADO 1997). Northwest of Golfito (E1–E3) a volcanoclastic series from the Paleocene occurs, while in Golfito and its eastern region (N1–N3, P1–P2) a volcano-sedimentary series from the late Cretaceous dominates (TOURNON & ALVARADO 1997). The Coto Colorado basin (C1–C8) contains quaternary alluvial deposits (TOURNON & ALVARADO 1997). The headwaters of the Coto Colorado River drain the upper parts of the Talamanca mountains, where marine deposits from the Oligo-Miocene dominate, while in the lower parts a calcareous platform from the Eocene occurs (TOURNON & ALVARADO 1997).

The climate of the region is classified as humid to very humid (HERRERA 1985). The region has a short dry season lasting from January to March, and a wet season from April to December. Annual average rainfall ranges from 4000 to 5000 mm; however in 1997, it was reduced considerably to only 3000 mm (Instituto Meteorológico Nacional 1998) due to the El Niño Southern Oscillation.

The major rivers draining the Osa Peninsula were sampled at sites A1, B1 and R1. Their catchments were affected by gold mining activities and deforestation, causing an

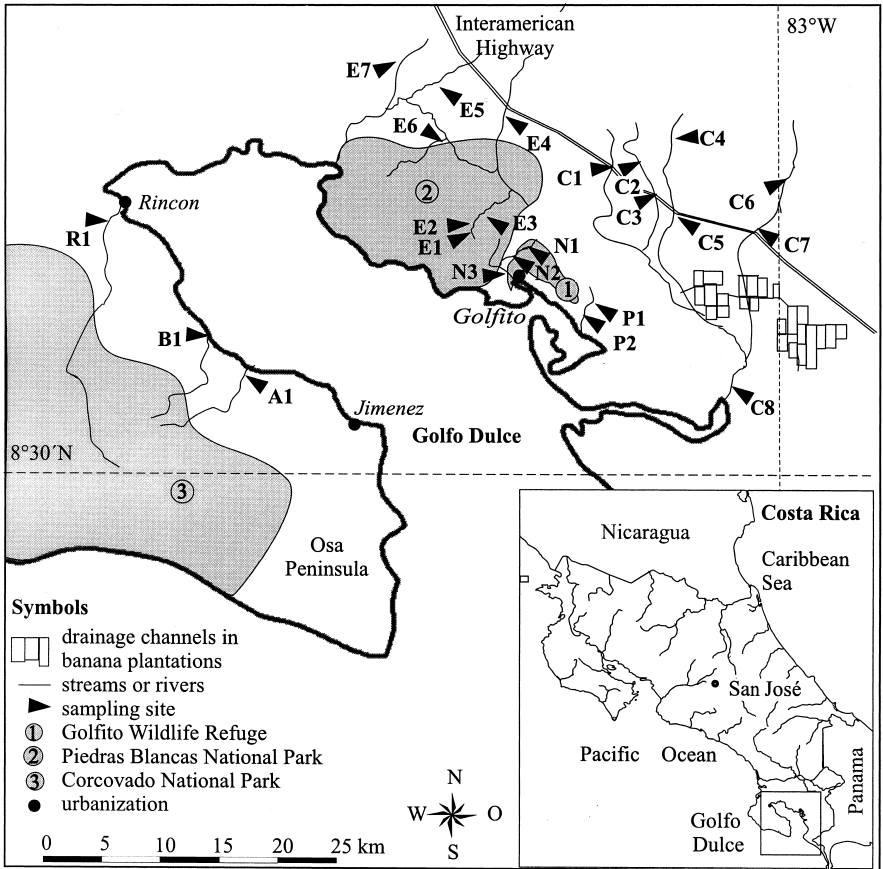


Fig. 1. Map of Golfo Dulce showing the location of the 23 sampling sites. Osa Peninsula: A1, B1, R1, Esquinas River and tributaries: E1–E7; pristine rainforest streams: E1–E3, N1–N2; streams draining the town Golfito: N3, P1–P2; Coto Colorado River tributaries: C1–C8.

increase in suspended sediments in recent years (GONZALEZ 1992). Seven sites (E1–E7) were selected along the Esquinas River and some of its tributaries. The upstream sites E1–E3 were located along a pristine rainforest stream and were unaffected by human impact; the downstream sites E4–E7 were affected by agricultural runoff from banana and oil palm plantations (UMAÑA 1998). A second rainforest stream, draining the Golfito National Wildlife Refuge was sampled at two sites (N1 and N2). Close to the town Golfito, two urban streams affected by domestic and industrial (leather tannery) sewage effluents were sampled at three sites (N3, P1, P2).

On the east side of Golfito, eight sites (C1–C8) were selected along the Coto Colorado River and some of its tributaries. With a discharge of $177 \text{ m}^3/\text{s}$, the Coto Colorado is the largest and most important river draining into the gulf (HARTMANN & ACEVEDO-GUITÉRREZ 1996). During the last thirty years, its catchment has experienced in-

Table 1. Stream-watershed physical characteristics for the investigated stream sections Abbreviations: n: number of samples; substrata: GRA = gravel, PEB = pebbles, SAN = sand, BOU = boulders; canopy: 1 = water surface exposed to full sun all day long, 2 = shade occurs < 3 h/day, 3 = shade occurs < 6 hours/day, 4 = vegetation of various heights provides shade all day; Riparian vegetation: sec. forest = secondary forest; Impact: AGR = agricultural, DOM = domestic, MIN = mining activities, IND = industrial.

Site	n	Stream name	Latitude (N)	Longitude (W)	Elevation	Catchment area (km ²)	Length (km)	Stream order	Width (m)	Depth (m)	v (cm/s)	Substrata	Canopy	Riparian vegetation	Impact
A1	1	Agujas	8° 33' 97"	83° 23' 85"	15	21.6	21.8	2	11	0.2–0.4	29	GRA + PEB	1	pasture	AGR
B1	1	Barrigones	8° 26' 92"	83° 24' 93"	15	22	29.4	3	11	0.2–0.6	47	GRA + PEB	1	pasture	AGR, DOM, MIN
R1	1	Rincon	8° 41' 69"	83° 28' 92"	2	232	104	4	17	0.2–0.5	35	PEB + SAN	1	pasture	AGR, MIN
E1	1	5 Ollas	8° 44' 27"	83° 11' 74"	40	9.2	4.7	1	7	0.3–0.5	31	GRA + PEB	1	pasture	AGR
E2	1	Piedras Blancas	9° 01' 62"	83° 14' 90"	35	18.7	8.5	2	19	0.3–0.7	28	BOU + GRA	1	field	AGR, DOM
E3	1	Bonito	8° 46' 80"	83° 12' 46"	40	7.3	7.9	2	9	0.3–0.5	31	BOU + GRA	1	pasture	AGR
E4	2	Esquinas	8° 45'	83° 11' 92"	80	34.8	31.9	3	28	0.4–1.0	38	BOU + GRA	1	field	AGR, DOM, MIN
E5	14	Gamba	8° 41' 38"	83° 11' 92"	90	4.5	2.3	1	2	0.2–0.4	26	BOU + GRA	4	rainforest	
E6	15	Gamba	8° 41' 38"	83° 11' 92"	90	4.8	2.5	1	2	0.2–0.3	26	BOU + GRA	4	rainforest	
E7	4	Gamba	8° 41' 37"	83° 11' 91"	80	4.6	2	1	2	0.3–0.4	25	BOU + GRA	2	rainforest	
N1	13	Naranjal	8° 38' 31"	83° 12' 46"	160	0.9	1	1	1.5	0.2–0.4	53	BOU + GRA	4	rainforest	
N2	11	Naranjal	8° 39' 39"	83° 10' 66"	140	2.8	1.5	1	2	0.2–0.4	45	BOU + GRA	3	rainforest	
N3	11	Canaza	8° 39' 39"	83° 10' 66"	28	0.8	0.7	1	3.5	0.2–0.4	50	GRA + PEB	1	pasture	DOM
P1	9	Purrujas	8° 37' 04"	83° 08' 13"	40	3.3	1.9	1	2	0.2–0.4	33	GRA + PEB	2	pasture	DOM
P2	6	Purrujas	8° 37' 04"	83° 08' 13"	32	2.9	2.3	1	7	0.2–0.4	39	GRA + PEB	2	field	DOM, IND
C1	17	Coto	8° 41' 92"	83° 06' 50"	70	24.8	8.8	2	22	0.3–0.8	49	BOU + GRA	2	pasture	DOM
Colorado															
C2	13	Lagarto	8° 42' 65"	83° 04' 51"	75	39.8	5	2	33	0.3–0.7	45	BOU + GRA	1	sec. forest	AGR, DOM
C3	13	Lagarto	8° 40' 84"	83° 04' 51"	35	52.8	12.5	2	28	0.4–1.0	47	BOU + GRA	1	pasture	AGR, MIN
C4	14	Claro	8° 42' 28"	83° 01' 44"	180	73.5	25.6	3	12	0.2–0.6	32	BOU + GRA	1	sec. forest	
C5	15	Claro	8° 40' 12"	83° 03' 25"	20	81.4	29.5	3	35	0.2–0.4	44	BOU + GRA	1	field	AGR, MIN
C6	15	Caracol	8° 40' 66"	83°	90	14.7	6.8	2	12	0.3–0.5	45	BOU + GRA	1	sec. forest	DOM
C7	15	Caracol	8° 39' 93"	83° 03' 25"	35	22.5	10.3	2	25	0.3–0.8	43	BOU + GRA	1	pasture	AGR, DOM
C8	11	Coto	8° 32' 53"	83° 02' 71"	20	878	969	5	60	0.5–1.8	20	PEB + SAN	1	banana and palmoil pl.	AGR, DOM, MIN

tensive banana and oil palm production and is highly affected by the pesticides and fertilizers used by those industries (UMAÑA 1998). The upper sites of the Coto Colorado tributaries (C2, C4, C6) were slightly affected by cattle farming. The sampling sites on the tributaries across the Interamerican Highway (C1, C3, C5, C7), showed severe mining impact due to channel rectification, dike construction and rock excavation. The most impacted site was C8, where banana and oil palm plantations affected the river over a distance of 278 km of artificial drainage channels (UMAÑA 1998). A list of our sampling sites including morphological and habitat description data is shown in Table 1.

Field and laboratory procedures

Samples from Osa Peninsula (A1, B1, R1), Esquinas River and some of its tributaries (E4–E7) were collected in 1996. Samples along Coto Colorado River (C1–C8) and the rainforest streams (E1–E3, N1–N2) were sampled monthly between January 1997 and March 1998, while sample sites from the urban streams in Golfito (N3, P1–P2) were sampled monthly from June 1997 to April 1998. For the analyses in this paper we included only samples where the complete physico-chemical data were available, in total 204 samples. The number of samples from each site is specified in Table 1. At each site, a 1-L water sample was taken for chemical analysis and a 500 mL water sample was taken for the determination of biological oxygen demand over five days (BOD₅). Conductivity, temperature, oxygen and pH were measured in the field using portable instruments. BOD₅ was determined using the Winkler-method (SCHWOERBEL 1994). Shading was assessed using a qualitative ranking of the canopy condition at a site based on BARBOUR & STRIBLING (1991) in HAUER & LAMBERTI (1996). Sites with a closed canopy were given a ranking of 4, whereas sites with a completely open canopy were given a ranking of 1. Turbidity was estimated using a spectrophotometer, the percent transmittance was compared to that of distilled water at a wavelength of 450 nm (BROWER et al. 1990). Mean current velocity was estimated using a floating object by taking the average of five measurements (SCHWOERBEL 1994). Water samples were filtered in the field through 0.45 µm filters and transported on ice within a twenty-four hour period to the laboratory, where they were kept frozen at –20 °C until chemical analysis. They were analyzed for: nitrate-nitrogen, nitrite-nitrogen, ammonium-nitrogen, soluble reactive phosphorus (SRP), dissolved silica (according to standard methods described in DEV 1997).

One composite sample of diatoms was taken at each site. Four to five rocks of approximately 15 cm in diameter were collected in a water depth of 10–20 cm at each stream reach, the water-exposed upper surfaces of the rocks were scraped off with a toothbrush and the scraping was fixed with formalin (4%). Diatom slides were prepared following standard procedures (H₂O₂ for oxidation). For each diatom sample, one drop of suspension was placed on an alcohol-cleaned coverslip, and after air-drying, embedded with Naphrax[®] on a slide. 400 to 450 diatom valves were counted and identified for each sample using a Leitz Laborlux microscope, 1250 × magnification, Fluotar objective (N. A. 1.32).

Identification of species followed mainly KRAMMER & LANGE-BERTALOT (1986–1991), METZELTIN & LANGE-BERTALOT (1998), RUMRICH et al. (2000) and several

other papers including BOURELLY & MANGUIN (1952), COSTE & RICARD (1990), HUSTEDT (1937–1939) and REICHARDT (1988 a, b). Light micrographs of all taxa were taken and are presented in MICHELS-ESTRADA (2003).

Data analysis

Diatom data were converted to relative abundance data for statistical analyses. Species diversity was calculated using the Shannon-Weaver Index H' (SHANNON & WEAVER 1949). Relationships between species richness, diversity and water chemistry were investigated by regression analysis (SPSS version 11.0). Prior to statistical analysis, the relative abundances of the diatoms were log-transformed, in order to prevent high abundance values from unduly influencing the ordination. All environmental variables, except temperature, current velocity and pH, were either log- or square root-transformed, because of their skewed distributions (JONGMAN et al. 1996). All ordinations were performed on diatom species with relative abundances greater than 1.5% at 3 sites or more. Ordinations were performed using Canoco version 4.0 (TER BRAAK & SMILAUER 1998). Detrended correspondence analysis (DCA) was run to estimate the gradient length (i.e. maximum amount of variation in species data, HILL & GAUCH 1980). The gradient length of the first DCA axis was 3.4 SD (standard deviations), suggesting that a unimodal response model would be appropriate for analysis (JONGMAN et al. 1996). Therefore, correspondence analysis (CA) was used to determine the major structure of diatom species distribution and to show important trends of species distribution between sites by arranging the sites in order of their scores on the first CA axis (JONGMAN et al. 1996). The diatom assemblage structure was then related to the measured environmental variables using canonical correspondence analysis (CCA) (TER BRAAK 1986). Forward selection with unrestricted Monte Carlo permutation tests (999 permutations) was used to select the minimal number of environmental variables that could explain the largest amount of the variation in the species data (TER BRAAK & SMILAUER 1998). Variables with high variance inflation factors ($VIF > 10$) were eliminated. Unrestricted Monte Carlo permutation tests were used to test the significance of the ordination axes. We included all samples in the ordinations following the method of ROTT et al. (1998), WINTER & DUTHIE (2000), and POTAPOVA & CHARLES (2002), because a larger number of samples better characterize species-environment relations for individual sites in streams. We determined the spatial dependence of the diatom species data by variance partitioning according to BORCARD et al. (1992). Most of the variance explained in the species data was attributed to the environmental variables and their spatial components; therefore, we did not include spatial variables (as geographical coordinates) in the ordination analyses. We removed the effects of seasonality from the ordination results and estimated the variation explained by seasonal effects by entering seasonality (dry season = 1 December–30 April vs. wet season = 1 May–30 November) as a covariable. Regression and calibration models based on weighted averaging (WA), with classical deshrinking, were developed to quantify relations between algal abundances, pH and conductivity. Detrended canonical correspondence analysis (DCCA) was used to estimate the gradient lengths for pH and conductivity. The strengths of the relationships between pH, conductivity and diatoms were assessed using CCAs with a single environmental variable (TER BRAAK & VER-

DONSCHOT 1995). In this way, species composition was constrained to one external variable. Reliable models can be developed if the ratio of the first constrained eigenvalue (λ_1) to the second unconstrained eigenvalue (λ_2) is high (HALL & SMOL 1996). The performance of the regression models was measured by the coefficient r between the diatom-inferred and the observed values for the environmental variables and the root-mean-squared error of prediction (RMSE). Tolerance down-weighting (BIRKS et al. 1990) gave lower errors of estimation and prediction than did simple weighted averaging and results of the former analysis are presented. We used bootstrapping, in order to get more reliable and realistic estimates of the relationship between measured versus WA-inferred values and the prediction error. Regression and calibration modelling was conducted using WACALIB version 3.3 (LINE et al. 1994).

Results

Physico-chemical variables

The mean values of the physico-chemical variables (water temperature, conductivity, pH, oxygen saturation, $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, SRP and $\text{SiO}_4\text{-Si}$) are presented in Fig. 2, where sites were arranged in order of CA axis 1 scores. Water temperatures ranged from 23.7 °C to 34.1 °C, with a mean annual water temperature across all sites of 26.4 °C. Conductivity varied between 60 and 400 $\mu\text{S/cm}$. Sites B1 and R1 on Osa Peninsula had the lowest conductivity values (60–90 $\mu\text{S/cm}$), followed by the tributaries E1–E7 of the Esquinas River (E4). Conductivity values in the Coto Colorado River and its tributaries, C1–C8, were in the upper range of the measured values between 220 $\mu\text{S/cm}$ –300 $\mu\text{S/cm}$. Most of the sites generally were slightly alkaline with pH values between 7.2 and 8.3. The Coto Colorado sites, C1–C8, had the highest pH, with values above pH 8. Alkalinity showed a similar pattern to pH, with the highest values in the Coto Colorado and its tributaries (3.5 mmol/L).

Dissolved oxygen generally reached saturation levels or was above saturation. Oxygen deficits occurred at site C8 in the Coto Colorado River (74%), which drained a large agricultural watershed and at sites P1 and P2 (82%), where sewage from a leather tannery entered the stream. Lower oxygen saturations between 83 and 90% were also measured at sites A1, B1, R1 and N3, which were surrounded by cattle pasture and were affected by agricultural or domestic sewage runoff. BOD_5 was generally less than 2 mg/L. Only sites with mining impacts such as C5 or with tannery impact such as P2, had measured BOD_5 values of up to 8 mg/L. Nitrate-N concentrations varied between 100 and 200 $\mu\text{g/L}$. Ammonia-N was detected at low concentrations (less than 100 $\mu\text{g/L}$) at site C4, and at sites affected by domestic sewage effluents such as P1, P2 and N3, as well as sites with high sediment loads such as C5 and C8. SRP was lowest at sites C1–C7, which are tributaries of the Coto Colorado River, but high at site C8 where the river was heavily affected by banana and

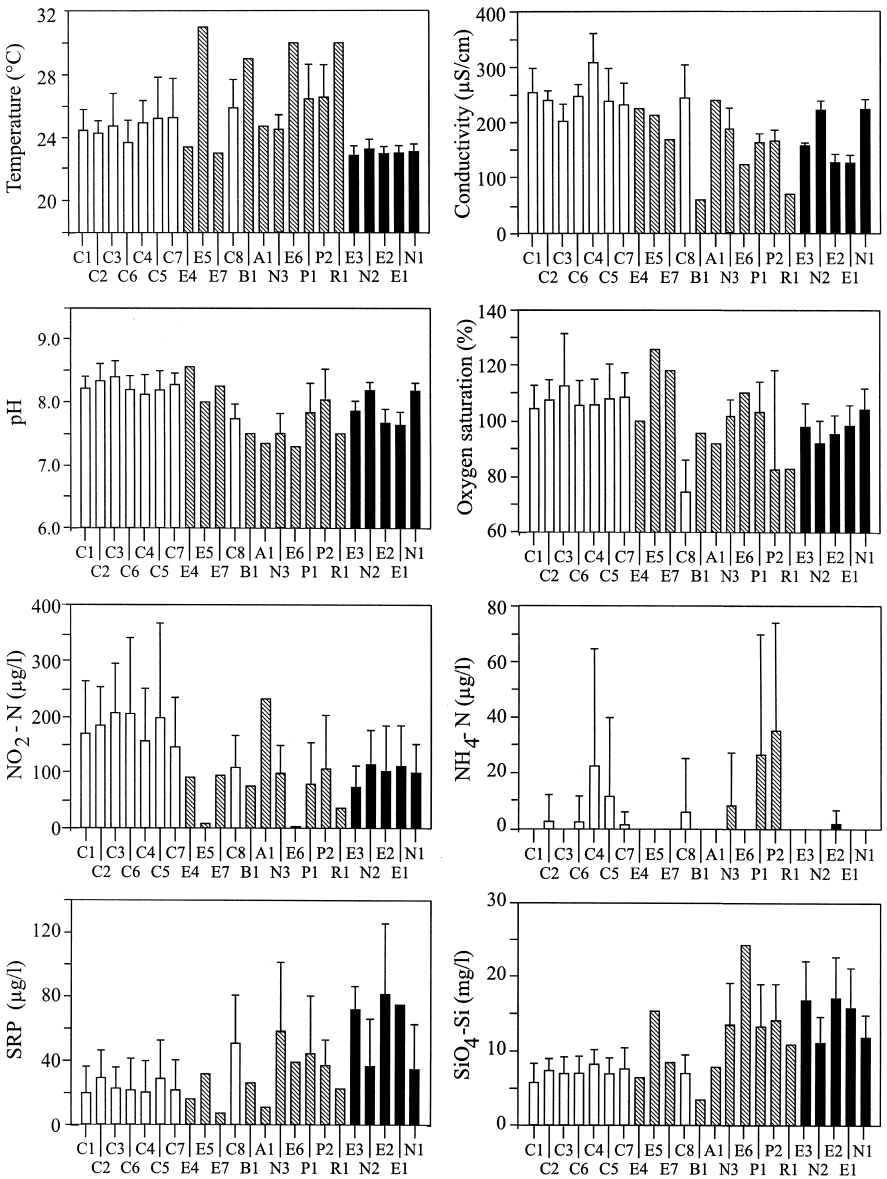


Fig. 2. Physico-chemical variables (average values, standard deviations) at the sampling sites in the period from 1997 to 1998. Sites are arranged in order of CA axis 1 scores. White bars = Coto Colorado River and tributaries (C1–C8); hatched bars = Osa Peninsula rivers (A1, B1, R1), Esquinas River (E4) and tributaries E4–E7, Golfito streams (N3, P1–P2); black bars = rainforest streams (N2–N3, E1–E3).

oil palm plantations. The highest SRP values, an average of 70 µg/L, were measured in the rainforest sites E1–E3. Dissolved silica oscillated between 3.5 and 24.8 mg/L. Highest silica concentrations were detected at Esquinas tributary E6 and at the rainforest sites E1–E3.

Correlations among the chemical variables indicate that high SRP values were paired with high dissolved silicate concentrations (Spearman's $r = 0.397$, $p < 0.01$, $n = 204$). High SRP was also negatively correlated with conductivity (Spearman's $r = -0.372$, $p < 0.01$, $n = 204$) and pH values (Spearman's $r = -0.292$, $p < 0.01$, $n = 204$). Significant positive correlations were also found between pH and conductivity (Spearman's $r = 0.421$, $p < 0.01$, $n = 204$).

Diatoms

In total 212 diatom taxa from 44 genera were identified. Richness varied between 5 and 49 taxa at individual sites. The average number of taxa per sample was 24. The Shannon-Weaver diversity H' varied between 0.2 and 2.9 with a mean value of 1.6. Diversity was highest at site C8, where the Coto Colorado River was affected by banana and oil palm plantations and lowest at the tributaries C6 and C7. Taxa richness and diversity H' increased significantly with declining pH (Spearman's $r = -0.279$, $p < 0.01$, $n = 204$, Spearman's $r = -0.286$, $p < 0.01$, $n = 204$, respectively).

Many of the taxa found in this study were cosmopolitan; however, 62 taxa out of 212 could not be identified to species level because they were either too rare for reliable identification or not documented in the taxonomical literature used. The most species rich genera were *Navicula* (58) Bory, *Nitzschia* (32) Hassall and *Gomphonema* (13) Ehrenberg. The 64 major species (abundances $> 3\%$) formed at least 87% of the diatom community in each sample. The average relative abundances of the most frequent and abundant (relative abundance $> 10\%$ at least at one site) taxa are presented in Fig. 3, where sites and taxa are arranged in order of CA axis 1 scores.

The Coto Colorado sites (C1–C7) and the Esquinas River (E4) are characterized by an assemblage dominated by *Achnantheidium minutissimum* and *Cymbella kolbei*, both taxa combined reaching relative abundances up to 97%. *Cymbella kolbei* also dominated the Esquinas tributaries at sites E4–E7. At sites with high sediment loads such as C5 or C8 *Nitzschia palea*, *Navicula erifuga*, *Geissleria similis*, and *Nitzschia clausii* were found in high abundances. Taxa characteristic of the Osa Pensinsula river sites (A1 and B1) were *Nitzschia palea*, *Eolimna minima*, *Navicula erifuga*, and *Geissleria similis*. Especially high abundances of *Luticola mutica* var. *intermedia* were characteristic of sites C8 and R1. Taxa characteristic of the streams draining the urban area of Golfito (N3, P1 and P2) included *Nitzschia frustulum*, *Navicula incarum*, *Sellaphora seminulum*, and *Geissleria schoenfeldii* cf. var. *tahitiensis*. In the

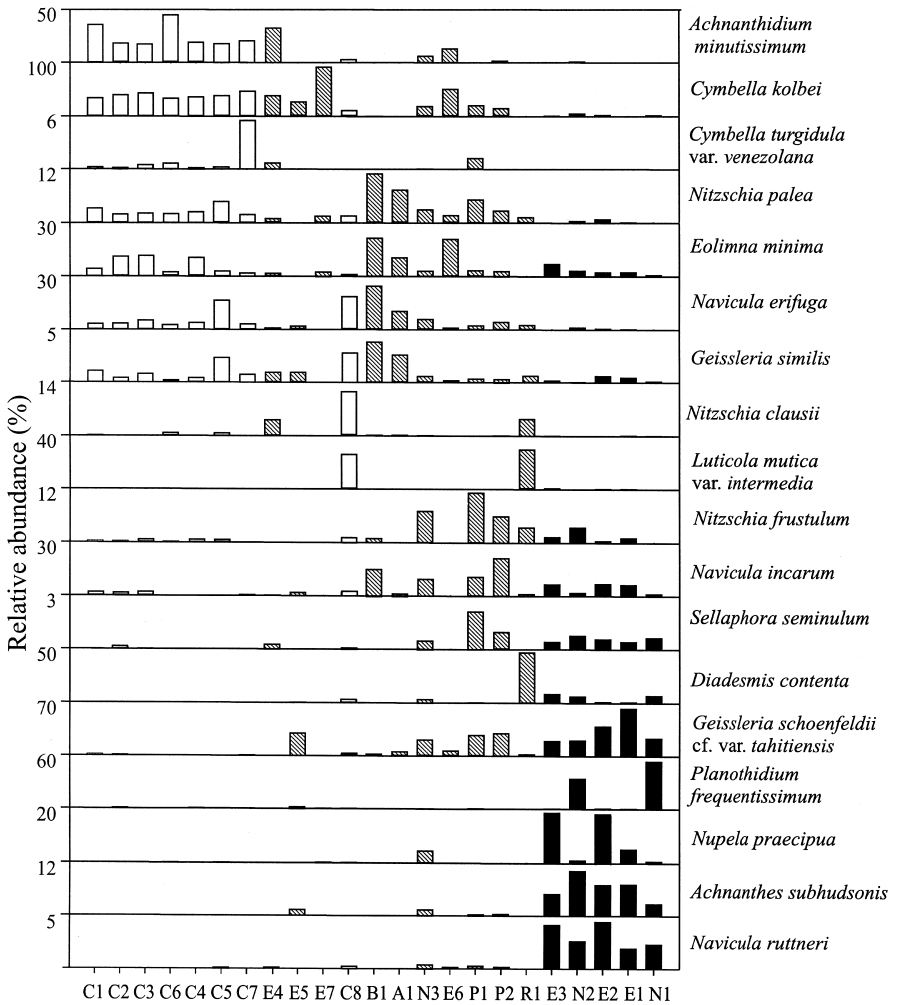


Fig. 3. Relative abundance (average values) of the dominant diatom taxa across the 23 sampling sites. Sites and taxa are arranged in order of CA axis 1 scores. Bar patterns as in Fig. 2.

pristine rainforest streams (E1–E3 and N1–N2), *Geissleria schoenfeldii* cf. var. *tahitiensis*, *Nupela praecipua*, *Achnanthes subhudsonis* and *Navicula ruttneri* occurred in higher abundances; but with the exception of *Geissleria schoenfeldii* cf. var. *tahitiensis*, these rainforest taxa were absent at most other sites. *Planothidium frequentissimum* dominated at the rainforest sites N1–N2.

CCA results

Only 130 of the total 212 taxa, which reached abundances of more than 1.5 % in two or more samples, were included in the statistical analysis. Forward selection in CCA with Monte Carlo permutations (999 iterations) identified 9 out of the 13 environmental variables, which explained a significant amount ($p < 0.05$) of the variation in the diatom data. These 9 environmental variables explained 64 % of the variance: riparian shading accounted for 44 %, pH for 14 %, conductivity for 8 %, turbidity for 8 % and current velocity for 8 %. The eigenvalue of axis 1 was $\lambda_1 = 0.399$ (Monte Carlo permutation, $p = 0.01$), and

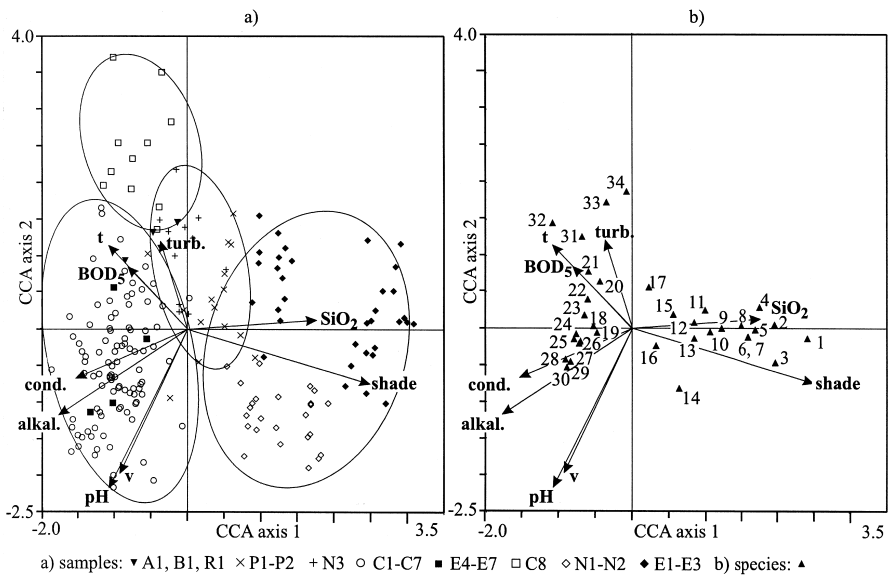


Fig. 4. CCA ordination of samples (a) and species (b) from the 23 sites in relation to the 9 forward-selected environmental variables ($\lambda_1 = 0.399$, $\lambda_2 = 0.15$). Abbreviations: Temp. = temperature; turb.0 = 0 turbidity; cond. = conductivity; alkal. = alkalinity; BOD₅ = biological oxygen demand in 5 days, v = current velocity. b) Species abbreviations: 1: *Gomphosphenia lingulatiforme*; 2: *Nupela praecipua*; 3: *Planothidium salvadorianum*; 4: *Luticola goeppertiana*; 5: *Navicula ruttneri*; 6: *Navicula ruttneri* var. *chilensis*; 7: *Achnanthes subhudsonis*; 8: *Gyrosigma scalproides*; 9: *Navicula arvensis* var. *maior*; 10: *Sellaphora seminulum*; 11: *Nitzschia levidensis*; 12: *Geissleria schoenfeldii* cf. var. *tahitiensis*; 13: *Diademesmia contenta*; 14: *Planothidium frequentissimum*; 15: *Navicula incarum*; 16: *Achnantheidium exiguum*; 17: *Amphora acutiuscula*; 18: *Gomphonema parvulum* var. *lagenula*; 19: *Nitzschia amphibia*; 20: *Navicula subrynchocephala*; 21: *Navicula symmetrica*; 22: *Navicula erifuga*; 23: *Nitzschia palea*; 24: *Amphora montana*; 25: *Navicula reichardtiana*; 26: *Cymbella kolbei*; 27: *Eolimna subminuscule*; 28: *Cymbella turgidula* var. *venezolana*; 29: *Achnantheidium minutissimum*; 30: *Gomphonema pumilum*; 31: *Nitzschia clausii*; 32: *Fallacia pygmaea*; 33: *Luticola mutica* var. *intermedia*; 34: *Navicula viridula*.

of axis 2 was $\lambda_2 = 0.150$, and accounted for 11.7% of the variance in the diatom data.

CCA axis 1 was highly related to a gradient of shade, conductivity, alkalinity and silica, separating the rainforest samples (E1–E3) on the right-hand side from the Coto Colorado River (C1–C8) samples on the left-hand side in the ordination diagram (Fig. 4 a, b). Sites from the Esquinas River (E4) and the tributaries (E5–E7) were located within the Coto Colorado River sample group. Species such as *Nupela praecipua* (2), *Planothidium salvadorianum* (3), *Navicula ruttneri* (5, 6) and *Achnanthes subhudsonis* (7), located on the right-hand side of the first axis, reflected the environmental conditions of the rainforest streams and prefer low-light conditions with low conductivity, elevated silica concentrations and circum-neutral streamwater. Species common in the Coto Colorado River sample-group, such as *Cymbella kolbei* (27) and *Achnanthydium minutissimum* (30), were placed on the opposite environmental gradient and prefer open-canopy situations with higher conductivity and alkalinity levels. Samples from streams draining the semiurban area of Golfito (N3, P1–P2) and from the Osa Peninsula (A1, B1, R1) were located in the center of the diagram between the rainforest sites and Coto Colorado sites. This sample group was characterized by circum-neutral waters, moderate conductivity but elevated turbidity. Diatoms most indicative of such environmental conditions were *Navicula incarum* (16), *Geissleria schoenfeldii* cf. var. *tahitiensis* (13), *Achnanthydium exiguum* (17), *Nitzschia palea* (24) and *Amphora acutiuscula* (18).

CCA axis 2 was mainly related to current velocity, pH, BOD₅ and turbidity. Sites from the Coto Colorado River (C8), affected by agricultural practices from banana and oil palm plantations, were separated in ordination space on the second CCA axis in the upper left-hand side of Fig. 4. Several species such as *Luticola mutica* var. *intermedia* (34), *Nitzschia clausii* (32) and *Navicula erifuga* (23) were positively related to turbidity and the BOD₅ gradient. The eigenvalues of axis 3 ($\lambda_3 = 0.082$) and 4 ($\lambda_4 = 0.044$) were much smaller and not significant at the 0.05 level. Seasonality was included as a covariable to remove seasonal effects from the analysis. The eigenvalue extracted indicated that less than 1% of the species data could be attributed to seasonal variation in the environmental data.

Diatom-based regression and calibration models

Weighted-averaging regression and calibration with tolerance down-weighting were used to quantify relationships between relative algal-abundances and pH and conductivity (square root transformed). DCCA gradient lengths longer than 2 SD, indicating that unimodal-based methods of regression can be applied (BIRKS 1995), were calculated for conductivity and pH. Conductivity

Table 2. CCA results indicating the strength of conductivity and pH.

Variable	CCA		
	λ_1	λ_1/λ_2	p
Conductivity	0.17	0.43	0.001
pH	0.14	0.31	0.001

Table 3. Comparison of the predictive power of diatom-based models for conductivity and pH with and without bootstrapping. r is the correlation coefficient between diatom-inferred and measured conductivity or pH. RMSE is the root mean square error.

	r	RSME	
		simple	bootstrapped
Conductivity	0.72	0.66	2.10
pH	0.69	0.65	0.39

Table 4. Apparent optima and tolerances and effective number of occurrences (Hill's N2) of the most common diatom taxa for conductivity ($\mu\text{S}/\text{cm}$) and pH in Golfo Dulce basin. Taxa are in order of increasing conductivity optima. Tolerance limits of conductivity (min and max) are presented as back transformed from the square root values that were used in developing the models. N is the number of samples in which the taxon occurred.

Taxon	Conductivity				pH	
	N2	Optimum	min	max	Optimum	Tolerance
<i>Nupela praecipua</i>	16.89	148.44	113.81	187.67	7.65	0.26
<i>Geissleria schoenfeldii</i> cf. var. <i>tahitiensis</i>	58.12	157.83	115.73	206.46	7.77	0.35
<i>Navicula ruttneri</i>	31.09	162.85	115.95	217.69	7.85	0.33
<i>Diadesmis contenta</i>	11.44	163.13	97.44	245.65	7.67	0.27
<i>Navicula seminulum</i>	15.37	165.18	118.32	219.83	7.89	0.41
<i>Achanthes subudsonis</i>	16.16	168.38	120.22	224.64	7.87	0.34
<i>Navicula similis</i>	18.66	168.46	97.12	259.33	7.96	0.37
<i>Navicula incarum</i>	37.87	169.91	121.60	226.29	7.84	0.43
<i>Nitzschia frustulum</i>	10.63	189.97	143.55	242.87	7.82	0.31
<i>Nitzschia palea</i>	43.69	206.72	143.79	281.03	7.98	0.43
<i>Nitzschia clausii</i>	8.16	216.14	127.46	328.09	7.82	0.31
<i>Eolimna minima</i>	43.23	217.71	150.14	297.81	8.11	0.38
<i>Navicula erifuga</i>	40.62	222.22	157.69	297.79	7.99	0.38
<i>Luticola mutica</i>	9.46	223.53	152.36	308.29	7.75	0.24
<i>Planothidium frequentissimum</i>	22.93	225.70	200.19	252.75	8.18	0.17
<i>Cymbella turgidula</i> var. <i>venezolana</i>	3.08	234.45	186.02	288.48	8.25	0.21
<i>Cymbella kolbei</i>	92.35	244.67	197.52	296.85	8.22	0.33
<i>Achnantheidium minutissimum</i>	57.12	244.89	203.04	290.65	8.22	0.28

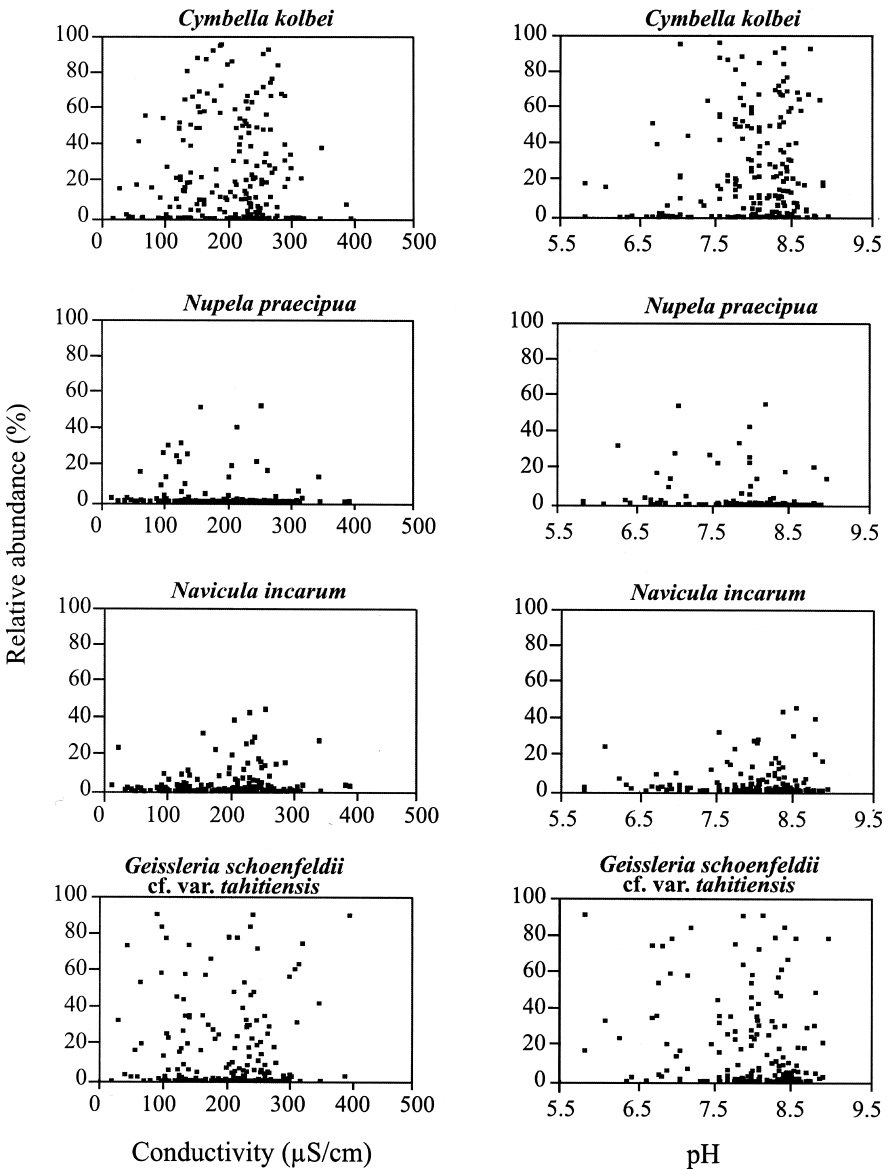


Fig. 5. Relative abundances of common diatom taxa in relation to pH and conductivity.

ranged from 60 to 396 $\mu\text{S}/\text{cm}$ and pH ranged from 7.0 to 8.8. The strengths of the relationship between conductivity, pH and diatoms were determined using constrained CCAs. Conductivity was slightly more correlated with diatom community structure than pH ($\lambda_1/\lambda_2 = 0.43$ vs. 0.31, Table 2).

The predictive power of the diatom-based calibration models for conductivity and pH, both with and without bootstrapping is summarized in Table 3. Conductivity provided a slightly higher correlation coefficient r between observed and diatom-inferred values than pH (0.72 vs. 0.69, Table 3).

Apparent optima and tolerances for conductivity and pH of the 18 most common diatom taxa together with the effective number of occurrences (Hill's N_2) are listed in Table 4. Conductivity optima ranged from 100 $\mu\text{S}/\text{cm}$ to 330 $\mu\text{S}/\text{cm}$ and pH optima ranged from 7.1 to 8.6. Taxa in Table 4 are ordered according to their conductivity optima.

Relative abundances of *Cymbella kolbei*, *Nupela praecipua*, *Navicula incarum* and *Geissleria schoenfeldii* cf. var. *tahitiensis*, taxa which had more than 10 % of their variances explained by conductivity or pH, are shown in Fig. 5. The conductivity models explain (in the same order) 16 %, 20 %, 15 % and 22 % of the variance and the pH model explained 18 %, 8 %, 14 % and 15 %.

Discussion

Stream water chemistry

Tropical streams and rivers have been generally considered poor in nutrients and ions, because most tropical land-masses are derived from the fragmentation of the ancient Paleozoic proto-continent of Gondwana, and have a legacy of long-eroded land surfaces (FURCH 1984, TALLING & LEMOALLE 1998). However, the ionic concentrations of our study sites were high, compared to values reported from major tropical rivers in South America or Africa (ALLAN 1995), but were in the same range as those reported from neotropical volcanic areas, where geological materials are recent basaltic rocks with marine intrusions, which release large amounts of ions (RAMOS-ESCOBEDO & VAZQUEZ 2001).

The Golfo Dulce area emerged from the sea first as a series of volcanic islands in the late Jurassic, as a result of the tectonic activities of the Cocos and the Caribbean plates (JANZEN 1991), which may explain the higher ionic concentrations in stream water. The Coto Colorado River sites showed higher values in conductivity, pH and alkalinity than those measured in the streams and rivers from the Osa Peninsula. This can be related to differences in the local geology: the Coto Colorado basin is dominated by the presence of lifted marine deposits from the late Cretaceous period, which are rich in calcium carbonate (TOURNON & ALVARADO 1997).

The concentrations of SRP at the undisturbed rainforest sites were higher than expected. A median of 70 $\mu\text{g}/\text{L}$ SRP was calculated, suggesting a high natural background. Phosphorus is initially derived from the weathering of

rocks, and volcanic rocks are frequently a particularly rich source (PAYNE 1986). Several rivers draining volcanic fields in the African Rift Valley have high natural levels of phosphate (TALLING & LEMOALLE 1998). PRINGLE et al. (1993) reported that the high phosphorus content of streams draining the Costa Rican Atlantic slopes is caused by geothermally-modified groundwater associated with underlying volcanic activity. These phosphorus-rich groundwaters can account for half of a stream's discharge, and thus can alter stream chemistry (PRINGLE et al. 2001). However, the Golfo Dulce drainage basin is not affected by active volcanism and is geologically one of the oldest regions of Costa Rica. Therefore, it can be concluded that the high phosphorus concentrations in the rainforest streams from Golfo Dulce reflect the dissolution of volcanic rocks, deposited in the Upper Cretaceous Period, rather than recent geothermal activity. Volcanic rocks are also a source of dissolved silica, and highest silica concentrations measured in this study correspond to the highest SRP levels.

Species assemblages

The diatom assemblages from the rainforest streams were very distinct from those found at open canopy sites, with small diatoms such as *Planothidium frequentissimum*, *Nupela praecipua* and *Achnanthes subhudsonis* dominating. ROBINSON & RUSHFORTH (1987) investigated the effects of canopy cover and physical disturbance on benthic diatom assemblages, and found that some species, for example *Planothidium frequentissimum*, developed more successfully at low light intensities. Species-environment analyses (CCA) of our data showed that light incidence was an important factor in determining species composition. High abundances of *Planothidium frequentissimum*, *Nupela praecipua* and *Achnanthes subhudsonis* at the closed canopy rainforest sites, suggest that these taxa might be well adapted to low light incidence. These observations are further supported by results of MICHELS (1998 a) and NUNN (1999), which showed that *Nupela praecipua* was predominant in slow-flowing streams with closed canopy in Costa Rica and by JÜTTNER et al. (2003), which reported high abundances of *Achnanthes subhudsonis* in forested streams in Kathmandu Valley, in the lower Himalayas. High abundances of *Planothidium frequentissimum* and *Achnanthes subhudsonis* at our turbulent sites with high current velocity, suggest that these taxa may also be well adapted to physical disturbance.

To our knowledge, there is no ecological information available for many of our common rainforest stream taxa, such as *Geissleria schoenfeldii* cf. var. *tahitiensis*, *Navicula incarum*, *Planothidium salvadorianum* and *Navicula ruttneri*. According to our data, these taxa are shade-adapted diatoms that prefer neutral to alkaline conditions and phosphorus-rich waters. High abundances of

Geissleria schoenfeldii cf. var. *tahitiensis* at sites charged with domestic sewage waters indicate some tolerance to organic pollution.

In contrast to the rainforest sites, the Coto Colorado sites with low anthropogenic impact were characterized by higher light intensities and high turbulence and current velocity. *Achnantheidium minutissimum* and *Cymbella kolbei* were the most common taxa in the diatom assemblages at these sites. *Achnantheidium minutissimum*, the most common species globally (KRAMMER & LANGE-BERTALOT 1986–1991), is regarded as an early colonizer after storm and scouring events and often dominates physically disturbed substrates (STEINMAN & MCINTIRE 1986). Its coexistence with *Cymbella kolbei* in high abundances at these sites suggests that the latter species might also be resistant to physical disturbance.

Taxa composition at sites with severe mining impacts and high sediment loads was very different from the sites with low anthropogenic impact. Many of the abundant taxa such as *Nitzschia clausii*, *Nitzschia palea* and *Navicula erifuga* are commonly found in turbid waters with higher ionic content and low oxygen saturation (KRAMMER & LANGE-BERTALOT 1986–1991). As conductivity did not change significantly between sites in our study, we conclude that turbidity and oxygen depletion are the major factors favouring these taxa at our sites with high sediment loads.

Environmental gradients

CCA showed that diatom species distribution was strongly associated with our measured environmental gradients. One of the major variables effecting a change of diatom assemblages was riparian shading, separating the small first-order rainforest streams from the larger higher-order rivers. Increased light at the sampling sites was due to deforestation and agricultural practices and not a consequence of stream size increasing. Hence, the shading gradient is associated to a land use gradient, covering the range from natural streams with rainforest-covered stream banks to altered streams with removed streamside vegetation. Other variables related to land use, such as turbidity and BOD₅, also explained a significant amount of variance in the diatom assemblages.

Results from CCA confirmed that diatom species distribution was also strongly associated with pH and conductivity, indicating that basin geology was a significant contributing factor. Conductivity and pH are among the most important correlates with benthic river diatoms in a variety of studies (KOLBE 1927, HUSTEDT 1953, PAN et al. 1996, STEVENSON & PAN 1999, PAN et al. 2000, WINTER & DUTHIE 2000, POTAPOVA & CHARLES 2003). Nutrients (N and P) were not important variables in our species-environment analysis (CCA), suggesting that agricultural land use practices in our study area did not cause significant organic pollution or eutrophication. Overall, our results indi-

cate that anthropogenic impact on our streams was highest at sites with increased sediment loads such as C5, C8, P1 and P2. Similar results are reported by UMAÑA (1998), who showed that suspended solids was the variable best reflecting the environmental situation in Golfo Dulce streams. Therefore, practical measures to improve water quality in rivers and streams draining Golfo Dulce should include keeping a minimum distance of 50 m from the streams and the construction of sediment traps in the streambed.

Results from ordination analyses suggest that seasonal variation of the measured environmental variables did not have any significant effect on diatom species composition. In the tropics, seasonal patterns are linked to precipitation, causing changes in discharge and sediment loads in lotic ecosystems. In the present study, precipitation was significantly less in the rainy season of 1997 due to the El Niño Southern Oscillation, which might explain, to some part, why no seasonal effects were detected. NEWBOLD et al. (1995) investigated seasonality of hydrologic characteristics and solute dynamics in Costa Rican streams and found that temporal patterns in water chemistry were primarily governed by stream flow. This suggests that measuring discharge might be an important tool to reveal seasonal affects in tropical streams.

Diatom-based regression and calibration models

Our results demonstrate that diatoms can be related to environmental variables in tropical streams and rivers. The relationships between observed and inferred environmental variables were significant ($p < 0.05$). Differences between correlation coefficients ($r = 0.72$ vs. $r = 0.66$ for conductivity and 0.69 vs. 0.65 for pH) and root means squared errors (2.1 vs. 2.3 for conductivity and 0.39 vs. 0.48 for pH) derived from weighted-averaging models constructed with and without bootstrapping were small, suggesting that our 204-sample calibration set reliably estimated the optima of the diatom taxa along the conductivity and pH gradients. However, the correlation coefficients between observed and diatom-inferred values were relatively low compared to other studies (LELAND et al. 2001, PAN et al. 1996). LELAND et al. (2001) examined the distribution of benthic diatoms in the San Joaquin River (California) in relation to salinity and other environmental variables. Their conductivity model yielded a highly significant correlation ($r = 0.97$) between observed and diatom-inferred conductivity. Compared to our study, their dataset spanned a much broader conductivity gradient up to $2000 \mu\text{S}/\text{cm}$. PAN et al. (1996) developed diatom inference models for pH in streams from the Mid Atlantic Highlands region of the United States, which produced an apparent correlation $r = 0.95$ (WA). The reason for the low predictive power of our models compared to other inference models is the relatively short gradient of our measured environmental varia-

bles. DCCA analyses revealed that the diatom flora in our dataset exhibited a small species turnover of 2.2 SD for conductivity and 2.0 SD for pH.

Nonetheless, our models were reliable in terms of their estimation of species optima. Our apparent optima for conductivity were generally within the tolerances reported by POTAPOVA & CHARLES (2003) and LELAND et al. (2001). Relative position of diatom taxa along the conductivity gradient generally corresponds to the rank on the scales reported by LELAND et al. (2001) and POTAPOVA & CHARLES (2003). However, optima for species known to be abundant in brackish waters like *Navicula erifuga* and *Nitzschia clausii* were underestimated in our study, as our data set did not include sites with high conductivity levels. For pH, our optima tended to be higher than those published by PAN et al. (1996), because the pH range in our data was skewed towards the alkaline side of the pH spectrum. Accuracy and robustness of estimated species optima relies on sample size, range of environmental conditions and evenness of sample distribution. Our inference models would improve if more sites would be added to increase the range of the environmental variables: at the high end for conductivity and at the low end of pH. We will further investigate diatom species responses to environmental variables on a larger data set from Costa Rican lowland streams in subsequent papers.

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