

Selectivity on epilithic diatom consumption for two tropical sympatric gobies: *Sicydium punctatum* Perugia, 1896 and *Sicydium plumieri* (Bloch, 1786)

by

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Abstract. – Rivers of the Caribbean islands harbour a freshwater fauna mainly constituted of migrant diadromous species. In these hyperturbulent ecosystems, the primary producers are mostly represented by a thin epilithic biofilm, mainly composed of diatoms. Comparison of the diatoms available from the environment with the ones consumed and located in the digestive tracts of two gobiid fish, *Sicydium punctatum* Perugia, 1896 and *Sicydium plumieri* (Bloch, 1786) were made at twelve sampling locations, located upstream or downstream of six rivers, in Guadeloupe. One hundred and ninety-one epilithic diatom species were identified. A statistical approach was used to determine diatoms that best characterize the two species digestive tracts content (*i.e.* “diagnostic species”) and to evaluate the statistical relationship between species abundances and groups of sites or conditions. Eight taxa belonging to five families were considered as significant diagnostic species of digestive tracts from fish collected upstream (*Achnanthydium subhudsonis*, *Achnanthes rupestoides*, *Diadexmis contenta*, *Diadexmis* sp., *Eolimna* sp., *Navicula (dicta) seminulum*, *Navicula difficillima* and *Nupela* sp.), and five taxa belonging to three families were considered as significant diagnostic species for fish collected downstream (*Gomphonema parvulum*, *Navicula arvensis*, *Navicula cruxmeridionalis*, *Nitzschia frustulum* and *Navicula incarum*). Results indicate selective consumption of epilithic diatoms by the two major fish observed in the mid and upper stream of Caribbean rivers

Key words
Bioindication
Caribbean Islands
Biofilm
Gobiidae
Tropical rivers

Résumé. – Consommation sélective de diatomées épilithiques chez deux espèces tropicales sympatriques : *Sicydium punctatum* Perugia, 1896 et *Sicydium plumieri* (Bloch, 1786).

Les rivières des îles des Caraïbes abritent une faune essentiellement composée d'espèces diadromes, migratrices. Dans ces écosystèmes hyperturbulents, le compartiment producteur est principalement constitué par un biofilm épilithique où les diatomées sont majoritaires. Une comparaison des assemblages diatomiques présents dans l'environnement avec ceux situés dans les tubes digestifs de deux Gobiidae, *Sicydium punctatum* Perugia, 1896 et *Sicydium plumieri* (Bloch, 1786) a été réalisée sur douze stations localisées en amont ou en aval de six rivières, en Guadeloupe. Cent quatre-vingt-onze taxons de diatomées épilithiques ont été identifiés. Une approche statistique a été utilisée pour déterminer les diatomées qui caractérisaient le mieux les contenus digestifs des deux poissons (*i.e.* “espèce indicatrice”) et évaluer la relation statistique entre les abondances diatomiques, les sites ou encore les conditions amont/aval. Huit taxons appartenant à cinq familles de diatomées se sont révélés indicateurs des contenus digestifs de poissons situés en amont des rivières (*Achnanthydium subhudsonis*, *Achnanthes rupestoides*, *Diadexmis contenta*, *Diadexmis* sp., *Eolimna* sp., *Navicula (dicta) seminulum*, *Navicula difficillima* et *Nupela* sp.), et cinq taxons appartenant à trois familles se sont révélés indicateurs chez les poissons pêchés en aval des rivières (*Gomphonema parvulum*, *Navicula arvensis*, *Navicula cruxmeridionalis*, *Nitzschia frustulum* et *Navicula incarum*). Les résultats ont montré une consommation sélective de certaines espèces de diatomées par les deux espèces de poissons majeurs des cours d'eau moyens et supérieurs aux Antilles.

The rivers of Guadeloupe and Martinique islands (French West Indies) are influenced by steep slopes and have hyperturbulent flows with a bed composed of large andesitic blocks, which only move under exceptionally

high discharge. The organization of the foodwebs is distinct compared to most European rivers, with a scarcity of phytoplanktonic, zooplanktonic, and macroalgal components (Coat *et al.*, 2009) as well as a limited aquatic insect fauna

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in the most turbulent reaches of the rivers, from mid to high elevations (Touren-Poncet, 2014). Autochthonous production consists of an epilithic biofilm growing on stones in the river bed. This biofilm, tightly affixed to the stony substrate, is one of the few perennial resources available. Considering the extreme variability of allochthonous inputs in these rivers, epilithic biofilm and diatoms therein could be regarded as pivotal for the sustainability of freshwater biodiversity in these regions (Burns and Keith 2000; Brito *et al.*, 2006; Lefrançois *et al.*, 2010).

Rivers on Guadeloupe and Martinique are inhabited by sympatric Sicydiinae gobies (genus *Sicydium*: *S. punctatum* and *S. plumieri*; Teleostei: Gobioidi). These species are prominent in the Caribbean region, the Greater Antilles and the Bahamas (Lyons, 2005; Monti *et al.*, 2010; Keith *et al.*, 2011; Tabouret *et al.*, 2011, 2015). Sicydiinae gobies are amphidromous, *i.e.* they migrate from freshwater to saltwater (seawater or mangrove) at different moments of their life cycle (Lejeune *et al.*, 2016). The adults live and reproduce in rivers and the larvae hatch in freshwaters (Bell *et al.*, 1995, 1997), then drift downstream in generally less than three days (Ellien *et al.*, 2011). After a dispersal phase, larvae return to freshwater where they undergo a true metamorphosis (Taillebois *et al.*, 2011) and immediately migrate upstream in a schooling behaviour, until they find a territory to settle and reproduce (Bell and Brown, 1995; Blob *et al.*, 2006; Maie *et al.*, 2007; Kawano *et al.*, 2013). These two species are the only fish found in the Caribbean rivers that have a trophic specialization so high, as they only scrape epilithic biofilm and diatoms off the substrate to feed (Erdmann, 1961, 1986; Coat *et al.*, 2009; Barbeyron *et al.*, 2017).

This study aims to analyse, by determining diatoms in the environment and in the gut tubes of *S. punctatum* and *S. plumieri*, whether (1) the two fish exhibit selective feeding within the available diatoms in their environment; (2) if there are any differences in available diatoms species and their consumption between upstream and downstream habitats and (3) whether these two sympatric gobies exploit the same diatom species from the biofilm.

MATERIALS AND METHODS

Samples were collected in February and March 2013, in six rivers of Guadeloupe Island (Fig. 1; Tab. I) known for their pristine or polluted contexts (OEG databases, 2013). In each river, the biofilm and fish were sampled upstream and

downstream in riffles. At these twelve sampling locations, epilithic biofilm was scraped from the surface of submerged rocks with a knife and a brush, according to standard NF T 90-354 (20 cm under the surface and 100 cm² collected on at least five stones), and each sample was fixed in buffered formaldehyde at a final concentration of 10 percent. The preparation and mounting of diatoms were also made in accordance with standard protocol NF T 90-354. Because identification of diatoms is based on microscopic examination of their siliceous frustules, samples were treated with hot concentrated hydrogen peroxide (H₂O₂ 30%) to eliminate protoplasm and, when appropriate, with hydrochloric acid (removal of carbonates). After drying, the diatoms were mounted in refractive resin, Naphrax (Northern Biological Supplies Ltd., England – Refractive index = 1.74) and then identified. The counting protocol and identification of diatom valves is defined by the European Standard EN 14407

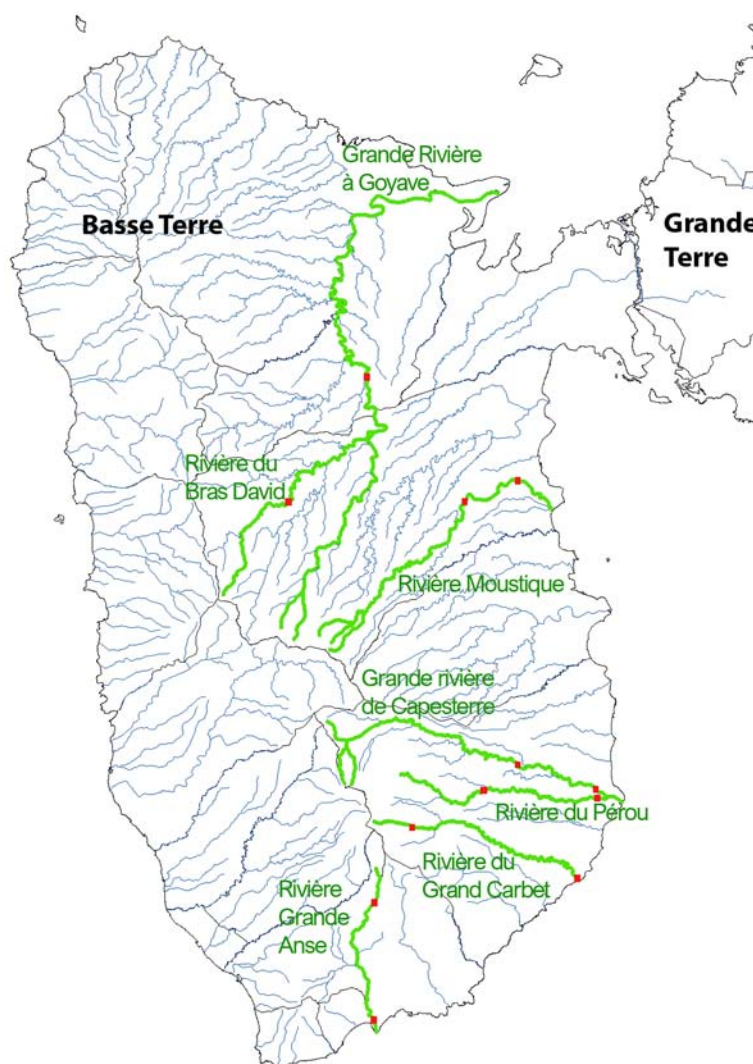
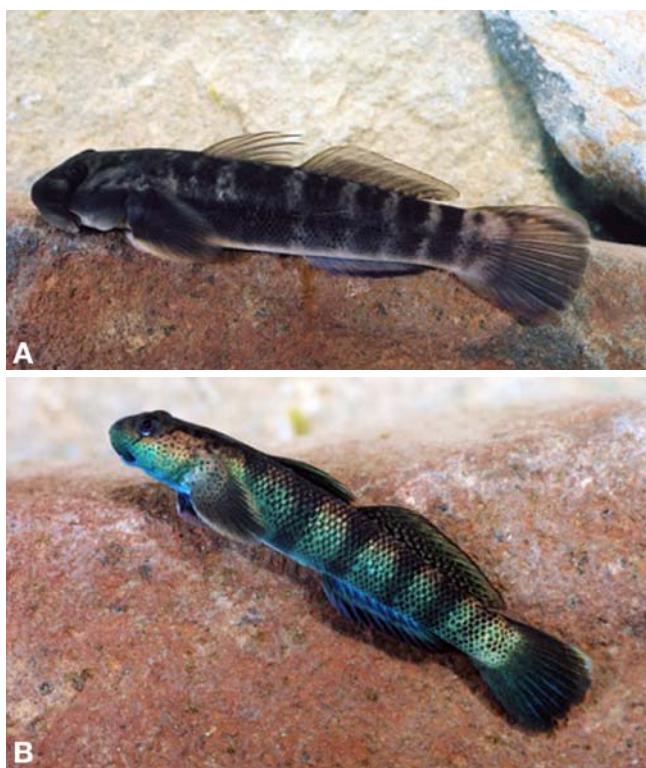


Figure 1. – Locations of the upstream and downstream sampling sites.

Table I. – Rivers, sites and number of fish sampled. Pu: *Sicydium punctatum*, Pl: *Sicydium plumieri*.

River	Site	N	Location WGS84 (UTM-UPS)
Grande Rivière à Goyave	Upstream	5 Pu	648418/1775875
	Downstream	5 Pu	653283/1775472
Rivière Moustique	Upstream	8 Pu, 3 Pl	647422/1788595
	Downstream	8 Pu, 3 Pl	649799/1789578
Grande Rivière de Capesterre	Upstream	5 Pu, 10 Pl	649550/1777258
	Downstream	15 Pu, 5 Pl	653197/1775959
Rivière du Grand Carbet	Upstream	8 Pl	645062/1774248
	Downstream	13 Pu, 3 Pl	652422/1771991
Rivière du Pérou	Upstream	5 Pu, 8 Pl	648418/1775875
	Downstream	13 Pu, 8 Pl	653283/1775472
Rivière Grande Anse	Upstream	0	643411/1770863
	Downstream	5 Pu	643210/1765781

Figure 2. – *Sicydium plumieri* (A) and *Sicydium punctatum* (B). Pictures and copyright Erick Vigneux.

2004 (see also Stoermer *et al.*, 1996). Four hundred diatom valves were counted and identified to the species level for each sample.

Fish were captured using a backpack electrofishing device (DEKA 3000 Gerätebau, Marsberg, Germany). Individuals were kept alive in ice, then killed and dissected the same day in the laboratory. Fish bodies were preserved in ethanol and digestive parts in formaldehyde solution to determine the diatom communities in diets. Because of a

strong morphological convergence between the two-targeted Sicydiinae species at a juvenile stage, species identifications for the smallest individuals (under 50 mm in total length) were genetically determined by amplifying and sequencing part of the mitochondrial Cytochrome Oxidase I (COI) according to the method described in Lord *et al.* (2012). The diatom assemblages of the entire digestive tract of the fish (*i.e.* oesophagus to anus) were analyzed, as described above for epilithic diatom communities. No methodological difficulties have been encountered with regard to the identification of diatoms ingested by fish. Sixty-two quantitative lists of diatoms were thus obtained, both for diatoms on stones and for diatoms located in the digestive tracts of the fish.

The statistical approach used to determine diatoms that best characterize the two species digestive tracts content (*i.e.* “diagnostic species”), and evaluate the statistical relationship between species abundances and groups of sites or conditions, is described in De Cáceres *et al.* (2012). The method uses two data elements: (1) a community data matrix (here, the abundances of diatoms); and (2) a vector that describes the classification of samples into groups. This latter vector was made by their distribution in six predetermined groups obtained independently of species data: upstream stones, downstream stones, and digestive tracts of *Sicydium punctatum* located upstream, of *S. punctatum* located downstream, of *Sicydium plumieri* located upstream, and of *S. plumieri* located downstream. The package *indicpecies* (De Cáceres and Jansen, 2014) and its function *multi-patt* developed for the R environment (R Development Core Team, 2008) were used to measure the association between each diatom species and each group. This function calculates an *IndVal* index, which is the product of two components: ‘A’, the probability that the sample belongs to the target group, given the fact that the species has been found, and named *positive predictive value*; and ‘B’, the probability of finding the species in elements belonging to the group, and named *sensitivity*. Finally, the statistical significance of this relationship was tested using a permutation test (De Cáceres, 2013).

RESULTS

The results of these analyses are presented in Table II and coupled with indications on, first, diatom species biovolumes (μm^3 , Lecoine *et al.*, 1993; Rimet and Bouchez, 2012). For undetermined species, biovolumes have been calculated according to their shape and mathematical equations (Hillebrand *et al.*, 1999). The second information is on the diatom status (abundance of species in Diatom Index of water quality database for French West Indies (Gueguen *et al.*, 2013) with $\geq 10\%$: dominant taxon, $[5\%-10\%]$: main taxon, $[2.5\%-5\%]$: secondary taxon, $< 2.5\%$: rare taxon. The

Table II. – A: Diatom species found in *Sicydium* species guts in the upstream locations. a) biovolumes (μm^3), b) diatom status (abundance of species in Diatom Index of water quality database for French West Indies (Gueguen et al., 2013) with $\geq 10\%$: dominant taxon, [5%-10%]: main taxon, [2.5%-5%]: secondary, < 2.5%: rare, c) type of association, and d) shape. B: Diatom species found in *Sicydium* species guts, in the downstream locations. a) biovolumes (μm^3), b) diatom status (abundance of species in Diatom Index of water quality database for French West Indies (Gueguen et al., 2013) with $\geq 10\%$: dominant taxon, [5%-10%]: main taxon, [2.5%-5%]: secondary, < 2.5%: rare, c) type of association, and d) shape.

Code	Fish species	Biovolume	Diatom species	Upstream					p-value	
				Family	Status	Association	Shape	A		B
ADSH	<i>S. punctatum</i>	66	<i>Achnanthyidium subhudsonis</i>	Achnanthydiaceae	dominant	solitary	pedunculate	0.358909	1.0000	0.0332
ARPU	<i>S. punctatum</i>	191	<i>Achnanthes rupestoides</i>	Achnantheaceae	dominant	solitary	pedunculate	0.480083	0.7273	0.0295
DCOT	<i>S. plumieri</i>	129	<i>Diademsis contenta</i>	Diademsidaceae	dominant	colonial	ribbon-shaped	0.452786	0.8889	0.0307
DI05	<i>S. plumieri</i>	30	<i>Diademsis</i> sp. 5	Diademsidaceae	main	colonial	ribbon-shaped	0.794521	0.3333	0.0228
EO06	<i>S. plumieri</i>	88	<i>Eolimna</i> sp. 6	Sellaphoraceae	dominant	solitary	motile	0.337014	1.0000	0.0489
ND02	<i>S. plumieri</i>	69	<i>Navicula (dicta) seminulum</i>	Sellaphoraceae	dominant	solitary	motile	0.390477	0.8889	0.0194
NDIF	<i>S. plumieri</i>	55	<i>Navicula difficillima</i>	Naviculaceae	secondary	solitary	motile	0.954344	0.4445	0.0166
NUPI	<i>S. plumieri</i>	89	<i>Nupela sp1</i>	Diademsidaceae	dominant	solitary	motile	0.433017	1.0000	0.0125
Downstream										
GPAR	<i>S. punctatum</i>	331	<i>Gomphonema parvulum</i>	Gomphonemataceae	dominant	solitary	pedunculate	0.479289	0.7895	0.0461
NARI	<i>S. plumieri</i>	51	<i>Navicula arvensis</i>	Naviculaceae	secondary	solitary	motile	0.743709	0.3636	0.024
NCXM	<i>S. plumieri</i>	113	<i>Navicula cruxmeridionalis</i>	Naviculaceae	dominant	solitary	motile	0.455251	0.7273	0.0234
NIFR	<i>S. plumieri</i>	258	<i>Nitzschia frustulum</i>	Bacillariaceae	dominant	solitary	motile	0.39144	0.9091	0.0173
NINK	<i>S. plumieri</i>	325	<i>Navicula incarum</i>	Naviculaceae	dominant	solitary	motile	0.533299	0.6364	0.0313

third information is the type of association, and the fourth the shape of the diatoms. The two latest criteria are presented in Table III.

In total, one hundred and ninety-one epilithic diatom

species were identified (App. I) and numbered according to the classification and criteria used in the Caribbean area (Asconit consultants, 2014). Within these 191 species, only eight belonging to five families were considered as significant diagnostic species of digestive tracts from fish collected upstream (*Achnanthyidium subhudsonis*, *Achnanthes rupestoides*, *Diademsis contenta*, *Diademsis* sp5, *Eolimna* sp6, *Navicula (dicta) seminulum*, *Navicula difficillima* and *Nupela* sp1). Five species belonging to three families were considered as significant diagnostic species of digestive tracts from fish collected downstream (*Gomphonema parvulum*, *Navicula arvensis*, *Navicula cruxmeridionalis*, *Nitzschia frustulum* and *Navicula incarum*). The significant results ($p < 0.05$) mean that these diatom species can be interpreted as taxonomic signatures of the fish digestive tract contents.

Additional information is given by the examination of the A and B components of the diatom species indicative value. Some of these species indicate a feeding choice general to a group because they appear in all digestive tracts of a defined group of fish (i.e. B = 1). This is the case, upstream, of *Achnanthyidium subhudsonis* for *S. punctatum* and also *Eolimna* sp. 6 and *Nupela* sp1 for *S. plumieri*, but are not restricted to it (A = 0.358909, 0.337014 and 0.433017, respectively). These species could be defined as a common (A ≠ 1) and very appreciated (B = 1) food source upstream.

DISCUSSION

When looking at the biovolumes, the results show smaller species consumed upstream, which is consistent with the results obtained by Passy (2007), who showed that species of short stature are highly correlated to high current velocity. From our analyses we found that whether upstream or downstream, *S. punctatum* appear more specialized than *S. plumieri*, which feed significantly on more taxonomically variable and less dominant species.

The diatom morphotypes show neat differences between the two fish species, with an apparent preference (either upstream or downstream) for pedunculate species by *S. punctatum*. *Sicydium plumieri*, on the contrary, fed significantly on ribbon-shaped diatoms upstream. These results can be compared with previous research done on the teeth of these tropical gobies, which have been qualified as having “the most remarkable dentitions in the animal kingdom” (Berkovitz, 2013) because of the huge replacement processes occurring on teeth worn on the rocks during scraping. *Sicydium plumieri* was defined as a “stone biting goby”, scraping algae from rock surfaces with his strong unicuspid teeth and *S. punctatum* as an “algae eating goby”, feeding on filamentous algae and other soft vegeta-

Table III. – Type of association and shape of diatom taxa.

Life form		Commentary
Type of association	Shape	
Solitary	Free	Planktonic Moving cell
	Fixed	Prostrated Adnate Tuft forming Stalk forming
		Patched on the substratum by the whole cell Mucilage pad and patched on the substratum Mucilage pad Mucilage stalk
Colonial	Chain colony Ribbon colony Zig-zag colony Rosette colony Star colony Arbuscular colony Mucous tubule colony	

tion because of its more fragile tricuspid teeth extremities (Watson, 2000). Our results partially corroborate this latter hypothesis, with *S. punctatum* selecting pedunculate cells, less firmly attached to the substrate.

The ecological profiles of common ($A \neq 1$) and very appreciated ($B = 1$) diatom species in upstream locations (*Achnanthydium subhudsonis* for *S. punctatum* and *Eolimna* sp6 and *Nupela* sp1 for *S. plumieri*), when compared with the analysis of 458 pairs of diatom inventory/physico-chemical data (Gueguen *et al.*, 2013), reveal that they are more commonly found in high quality sites. On the contrary, no diatom was consumed exclusively by a group (*i.e.* occurs in sites or species belonging to this group only, with $A = 1$), which means that trophic niche of these two fish is, at least partially, overlapping. These elements are consistent with the general ecological conclusion that grazers are typically generalist feeders (Cummins, 1973). When looking at the proportion of samples of a given group where one or another indicative species is found (*coverage*), the values indicate full coverage for *S. punctatum* upstream and downstream (with values of 1 and 1) and partial fulfilment of the mission for the indicative species regarding *S. plumieri* (with 0.789473 and 0.909091, respectively). These elements could be linked with the greater number of indicative species in the digestive tract of this latter species, suggesting more extensive feeding territories or more efficient scraping strategy.

The notion of relative availability of food resources actively searched by species in the upper parts of the rivers has been evoked to play a key role in the migration of amphidromous species (Gross *et al.*, 1988). Amphidromy represents a successful adaptation to the colonisation of tropical island systems (McDowall, 2007; Keith and Lord, 2011). Sicydiinae gobies, as well as other taxonomic groups (molluscs, crustaceans) living in swiftwater, show the ability to adapt to varying environments by selecting their food

based on the abundance and composition of stream algae (Kido, 1996; this study). Moreover, the climbing aptitude of these Sicydiinae is closely linked to the oral movements made when grazing biofilm. This hypothesis of possible coopting of similar movements, named *exaptation*, has been evidenced on a relative, *Sicyopterus stimpsoni* in Hawai'i, and generalized to Sicydiinae (Cullen *et al.*, 2013). The relative order in the emergence of the evolutionary forces that led to the actual mechanisms of climbing and grazing is currently unknown, but may relate to the origin of these abilities in species found at high altitudes in the French Caribbean. Our results

identify several species of diatoms particularly consumed by these fish upstream, and their spatial repartition and nutritive characteristics would be interesting to assess, specially the species-specific capacity of diatoms to survive fish ingestion (Grubach, 2010). Diet gaps or shifts have been demonstrated to have ecological and evolutionary consequences for gobies because a failure of food availability and changes in diets could cause a decrease in reproductive fitness (Jackson *et al.*, 2002; review in Jackson and Rundle, 2008).

Bioindication based on epilithic diatomic counts is the most powerful tool used for ecological management in this region where the complexity of freshwater ecosystem function leads to a scarcity of other bioindication candidates. Taking into account its good integration capabilities and a pivotal role in the input of energy in aquatic ecosystems, the biofilm (and its diatomic component) is found to be highly consumed and therefore *biologically redesigned* (redesigned by the selective trophic exploitation of some of its components). Our work shows selective consumption of diatom taxa by the two major fish observed in the mid and upper stream of Caribbean rivers. In addition, some research done on tropical crustaceans showed that these species could be also selective in their diatom consumption (Abreu *et al.*, 2007) with an unknown impact on biofilm structure and components. These are crucial elements that need to be further studied in order to refine bioindicative conclusions based on diatom assemblages in these regions.

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REFERENCES

- ABREU P.C., BALLESTER E.L.C., ODEBRECHT C., WASIELESKY W., CAVALLI R.O., GRANALI W. & ANESIO A.M., 2007. – Importance of biofilm as food source for shrimp (*Farfantepenaeus paulensis*) evaluated by stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). *J. Exp. Mar. Biol. Ecol.*, 347: 88-96.
- ASCONIT CONSULTANTS, 2014. – Mise au point d'un indice de bioindication de la qualité de l'eau des cours d'eau antillais à partir des diatomées: l'IDA – Programme d'étude et de recherche 2009-2012. In: Guide méthodologique pour la Mise en Œuvre de l'IDA, volumes 1 & 2 (Asconit, ed.), Vol. 1: 536 p.; Vol. 2: 474 p.
- BARBEYRON C., LEFRANÇOIS E., MONTI D., KEITH P. & LORD C., 2017. – Gardening behaviour of *Sicydium punctatum* (Gobioidei: Sicydiinae): *in vitro* experiments in the context of chlordecone pollution in Guadeloupe Island rivers. *Cybium*, 41(2): 85-92.
- BELL K.N.I. & BROWN J.A., 1995. – Active salinity choice and enhanced swimming endurance in 0-d-old to 8-d-old larvae of diadromous gobies, including *Sicydium punctatum* (Pisces), in Dominica, West-Indies. *Mar. Biol.*, 121: 409-417.
- BELL K.N.I., PEPIN P. & BROWN J.A., 1995. – Seasonal, inverse cycling of length and age-at-recruitment in the diadromous gobies *Sicydium punctatum* and *Sicydium antillarum* in Dominica, West Indies. *Can. J. Fish. Aquat. Sci.*, 52: 1535-1545.
- BELL K.N.I., PEPIN P. & BROWN J.A., 1997. – Variation in age-at-recruitment can drive recruitment dynamics: the example of *Sicydium* spp. (Pisces: Gobiidae) in Dominica, West Indies. *Micronesica*, 30: 25.
- BERKOVITZ B.K.B., 2013. – Teeth of rock-climbing gobies: the most remarkable dentitions in the animal kingdom? *Nothing but the Tooth*, 2013: 113-118.
- BLOB R.W., RAI R., JULIUS M.L. & SCHOENFUSS H.L., 2006. – Functional diversity in extreme environments: effects of locomotor style and substrate texture on the waterfall climbing performance of Hawaiian gobiid fishes. *J. Zool.*, 268: 315-324.
- BRITO E.F., MOULTON T.P., SOUZA M.L. & BUNN S.E., 2006. – Stable isotope analysis indicates microalgae as the predominant food source of fauna in a coastal forest stream, south-east Brazil. *Austral Ecol.*, 31: 623-633.
- BURNS A. & KEITH F.W., 2000. – Biofilms as food for decapods (Atyidae, Palaemonidae) in the River Murray, South Australia. *Hydrobiologia*, 437(1-3): 83-90.
- COAT S., MONTI D., BOUCHON C. & LEPOINT G., 2009. – Trophic relationships in a tropical stream food web assessed by stable isotope analysis *Freshw. Biol.*, 54(5): 1028-1041.
- CULLEN J.A., MAIE T., SCHOENFUSS H.L. & BLOB R.W., 2013. – Evolutionary novelty versus exaptation: Oral kinematics in feeding versus climbing in the waterfall-climbing Hawaiian goby *Sicyopterus stimpsoni*. *PLOS ONE*, 8(1): e53274.
- CUMMINS K.W., 1973. – A Worldwide Directory of Stream Ecologists. 67 p. Michigan State University Institute of Water Research Ed. Technical Report No. 28.
- DE CÁCERES M., 2013. – How to use the indicpecies package (ver. 1.7.1). – Centre Tecnologic Forestal de Catalunya, Ctra. St. Llorenç de Morunys, 25280, Solsona, Catalonia, Spain. 29 p. <https://cran.r-project.org/web/packages/indicpecies/vignettes/indicpeciesTutorial.pdf>
- DE CÁCERES M. & JANSEN F., 2014. – The indicpecies package. R CRAN library, <http://www.r-project.org>.
- DE CÁCERES M., LEGENDRE P., WISER S.K. & BROTONS L., 2012. – Using species combinations in indicator value analyses. *Methods Ecol. Evol.*, 3(6): 973-982.
- ELLIEN C., VALADE P., BOSMAN J. & KEITH P., 2011. – Influence of salinity on larval development of *Sicyopterus lagocephalus* (Pallas, 1770) (Gobioidei). *Cybium*, 35(4): 381-390.
- ERDMAN D.S., 1961. – Notes on the biology of the gobiid fish *Sicydium plumieri* in Puerto Rico. *Bull. Mar. Sci. Gulf Caribb.*, 11: 448-456.
- ERDMAN D.S., 1986. – The green stream goby, *Sicydium plumieri*, in Puerto Rico. *Trop. Fish Hobbyist*, 2: 70-74.
- GROSS M.R., COLEMAN R.M. & McDOWALL R.M., 1988. Aquatic productivity and the evolution of diadromous fish migration. *Science*, 239: 1291-1293.
- GRUBACH P.G., 2010. – The capacity of diatom species to survive ingestion by the algivorous minnow, *Pimephales notatus*. Masters Thesis, 70 p. John Carroll University.
- GUEGUEN J., EULIN A., LEFRANÇOIS E., BOUTRY S., ROSEBERY J., COSTE M. & DELMAS F., 2013. – Mise au point d'un indice de bioindication de la qualité de l'eau des cours d'eau antillais à partir des diatomées: l'IDA. Rapport final du programme d'étude et de recherche 2009-2012. Asconit Ed., 249 p.
- HILLEBRAND H., DÜRSELEN C.D., KIRSCHTEL D., POLLINGER U. & ZOHARY T., 1999. – Biovolume calculation for pelagic and benthic microalgae. *J. Phycol.*, 35: 403-424.
- JACKSON A.C. & RUNDLE S.D., 2008. – Diet-shifts by an estuarine goby (*Pomatoschistus microps*) in the face of variable prey availability. *J. Exp. Mar. Biol. and Ecol.*, 361(1): 1-7.
- JACKSON A.C., RUNDLE S.D. & ATTRILL M.J., 2002. – Fitness consequences of prey depletion for the common goby *Pomatoschistus microps*. *Mar. Ecol. Prog. Ser.*, 242: 229-235.
- KAWANO S.M., BRIDGES W.C., SCHOENFUSS H.L., MAIE T. & BLOB R.W., 2013. – Differences in locomotor behavior correspond to different patterns of linear and nonlinear morphological selection in two species of waterfall-climbing gobiid fishes. *Evol. Ecol.*, 27: 949-969.
- KIDO H.M., 1996. – Diet and food selection in the endemic Hawaiian amphidromous goby, *Sicyopterus stimpsoni* (Pisces: Gobiidae). *Environ. Biol. Fish.*, 45: 199-209.
- KEITH P. & LORD C., 2011. – Tropical freshwater gobies: amphidromy as a life cycle. In: The Biology of Gobies (Patzner R.A., Van Tassell J.L., Kovacic M. & Kapoor B.G., eds), pp. 243-268. Science Publishers Inc.
- KEITH P., LORD C., LORION J., WATANABE S., TSUKAMOTO K., COULOUX A. & DETTAI A., 2011. – Phylogeny and biogeography of Sicydiinae (Teleostei: Gobiidae) inferred from mitochondrial and nuclear genes. *Mar. Biol.*, 158: 311-326.
- LECOINTE C., COSTE M. & PRYGIEL J., 1993. – Omnidia software for taxonomy, calculation of diatom indices and inventories management. *Hydrobiologia*, 269-270: 509-513.
- LEJEUNE L., TABOURET H., TAILLEBOIS L., MONTI D. & KEITH P., 2016. – Larval traits of the Caribbean amphidromous goby *Sicydium punctatum* (Gobioidei: Sicydiinae) in Guadeloupe. *Ecol. Freshw. Fish*, 25: 272-280.
- LEFRANÇOIS E., COAT S., VACHIÉRY N., LEPOINT G., GROS O. & MONTI D., 2010. – Epilithic biofilm as key factor for small-scale fisheries in river mouths of Caribbean Islands. *Fish. Manage. Ecol.*, 18: 211-220.
- LORD C., LORION J., DETTAI A., WATANABE S., TSUKAMOTO K., CRUAUD C. & KEITH P., 2012. – From endemism to widespread distribution: phylogeography of three amphidromous *Sicyopterus* species (Teleostei: Gobioidei: Sicydiinae). *Mar. Ecol. Prog. Ser.*, 455: 269-285.
- LYONS J., 2005. – Distribution of *Sicydium valenciennes* 1837 (Pisces: Gobiidae) in Mexico and Central America. *Hydrobiologia*, 15: 239-243.

- McDOWALL R.M., 2007. – On amphidromy, a distinct form of diadromy in aquatic organisms. *Fish Fish.*, 8(1): 1-13.
- MAIE T., SCHOENFUSS H.L. & BLOB R.W., 2007. – Ontogenetic scaling of body proportions in waterfall-climbing gobiid. *Copeia*, 3: 755-764.
- MONTI D., KEITH P. & VIGNEUX E., 2010. – Atlas des Poissons et des Crustacés d'eau douce de la Guadeloupe. Collection Patrimoines naturels 69, 128 p. Muséum national d'Histoire naturelle, Paris.
- OEG DATABASE, 2013. – Analyses des polluants dans les rivières de Guadeloupe, 2010-2012, available at http://www.eauguadeloupe.com/jupgrade/telechargements/cat_view/17-donnees/7-donnees-milieux-micropolluants.html.
- PASSY S.I., 2007. – Diatom ecological guilds display distinct and predictable behaviour along nutrient and disturbance gradients in running waters. *Aquat. Bot.*, 86: 171-178.
- R DEVELOPMENT CORE TEAM, 2008. – R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at <http://www.r-project.org>.
- RIMET F. & BOUCHEZ A., 2012. – Life-forms, cell-sizes and ecological guilds of diatoms in European rivers + appendix 1 (Excel file). *Knowl. Manage. Aquat. Ecosyst.*, 406(1): 1-14.
- STOERMER E.F., EMMERT G., JULIUS M.L. & SCHELSKE C.L., 1996. – Paleolimnological evidence of rapid recent change in Lake Erie's trophic status. *Can. J. Fish. Aquat. Sci.*, 53: 1451-1448.
- TABOURET H., LORD C., BAREILLE G., PECHEYRAN C., MONTI D. & KEITH P., 2011. – Otolith microchemistry in *Sicydium punctatum*: indices of environmental condition changes after recruitment. *Aquat. Living Resour.*, 24: 369-378.
- TABOURET H., MONTI D., MARTIN J., BERAIL S., PECHEYRAN C., KEITH P. & BAREILLE G., 2015. – Do *Sicydium punctatum* adults move in the Caribbean estuaries? New insight from strontium isotopes. *Vie Milieu*, 65: 85-89.
- TAILLEBOIS L., KEITH P., VALADE P., TORRES P., BALOCHE S., DUFOUR S. & ROUSSEAU K., 2011. – Involvement of thyroid hormones in the control of larval metamorphosis in *Sicyopterus lagocephalus* (Teleostei: Gobioidi) at the time of river recruitment. *Gen. Comp. Endocrinol.*, 173(2): 281-288.
- TOURON-PONCET H., 2014. – Biodiversité des communautés d'invertébrés benthiques des rivières de la Guadeloupe et réponses aux perturbations anthropiques. Thèse de Doctorat, 236 p. Université Toulouse III, France.
- WATSON R.E., 2000. – *Sicydium* from the Dominican Republic with description of a new species Teleostei Gobiidae. *Stuttg. Beitr. Naturk.*, Ser. A Biol., 608: 1-31.

Appendix I. – List of diatoms species found.

ACHD	ACHNANTHIDIUM F.T. Kützing	BR01	<i>Brachysira</i> sp1
AD05	<i>Achnantheidium</i> sp5	CA01	<i>Caloneis</i> sp1
AD07	<i>Achnantheidium</i> sp7	CAGR	<i>Cyclotella atomus</i> var. <i>gracilis</i> Genkal & Kiss
AD11	<i>Achnantheidium</i> sp11	CEUG	<i>Cocconeis euglypta</i> Ehrenberg
AD13	<i>Achnantheidium</i> sp13	CLCT	<i>Caloneis lancettula</i> (Schulz) Lange-Bertalot & Witkowski
AD14	<i>Achnantheidium</i> sp14	CMLF	<i>Craticula molestiformis</i> (Hustedt) Lange-Bertalot
AD15	<i>Achnantheidium</i> sp15	CPL1	<i>Cocconeis placentula</i> var. <i>placentula sensu</i> Jahn et al. (2009)
AD18	<i>Achnantheidium</i> sp18	CPLA	<i>Cocconeis placentula</i> Ehrenberg var. <i>placentula</i>
AD19	<i>Achnantheidium</i> sp19	CPLI	<i>Cocconeis placentula</i> Ehrenberg var. <i>lineata</i> (Ehr.) Van Heurck
ADCT	<i>Achnantheidium catenatum</i> (Bily & Marvan) Lange-Bertalot	CRA4	<i>Craticula</i> sp4
ADEG	<i>Achnantheidium exiguum</i> (Grunow) Czarnecki	CTRO	<i>Cymbella tropica</i> Krammer var. <i>tropica</i> Krammer
ADMI	<i>Achnantheidium minutissimum</i> (Kützing) Czarnecki	CYC1	<i>Cyclostephanos</i> sp1
ADSH	<i>Achnantheidium subhudsonis</i> (Hustedt) H. Kobayasi	CYM1	<i>Cymbella</i> sp1
AFON	<i>Amphora fontinalis</i> Hustedt	DCOF	<i>Diadsmis confervacea</i> Kützing var. <i>confervacea</i>
AM10	<i>Amphora</i> sp10	DCOT	<i>Diadsmis contenta</i> (Grunow ex V. Heurck) Mann
AMMO	<i>Amphora montana</i>	DCRS	<i>Diadsmis confervacea</i> Kützing f. <i>rostrata</i> (Krasske) Metzeltin & Lange-Bertalot
AMUS	<i>Adlafia muscora</i> (Kocielek & Reviere) Moser Lange-Bertalot & Metzeltin	DEN1	<i>Denticula</i> sp1
APED	<i>Amphora pediculus</i> (Kützing) Grunow	DI05	<i>Diadsmis</i> sp5
ARPU	<i>Achnanthes rupestoides</i> Hohn var. <i>uniseriata</i> Lange-Bertalot & Monnier	EADN	<i>Epithemia adnata</i> (Kützing) Brebisson
ASTG	<i>Amphora subturgida</i> Hustedt	EEX1	<i>Eunotia exigua</i> forme 1
BNE1	<i>Brachysira neoexilis</i> forme 1		
BNE2	<i>Brachysira neoexilis</i> forme 2		

ELEP	<i>Eolimna lepidula</i> (Manguin) Metzeltin & Lange-Bertalot	GO68	<i>Gomphonema</i> sp68
ENMI	<i>Encyonema minutum</i> (Hilse in Rabh.) D.G. Mann	GO71	<i>Gomphonema</i> sp71
EO01	<i>Eolimna</i> sp1	GO76	<i>Gomphonema</i> sp76
EO02	<i>Eolimna</i> sp2	GO77	<i>Gomphonema</i> sp77
EO03	<i>Eolimna</i> sp3	GO79	<i>Gomphonema</i> sp79
EO05	<i>Eolimna</i> sp5	GO80	<i>Gomphonema</i> sp80
EO06	<i>Eolimna</i> sp6	GO81	<i>Gomphonema</i> sp81
EOMI	<i>Eolimna minima</i> (Grunow) Lange-Bertalot	GO82	<i>Gomphonema</i> sp82
EORH	<i>Eolimna rhombelliptica</i> Moser Lange-Bertalot & Metzeltin	GO85	<i>Gomphonema</i> sp85
EORU	<i>Eolimna ruttneri</i> (Hustedt) Lange-Bertalot & Monnier	GO89	<i>Gomphonema</i> sp89
ESBM	<i>Eolimna subminuscula</i> (Manguin) Moser Lange-Bertalot & Metzeltin	GO91	<i>Gomphonema</i> sp91
ESLE	<i>Encyonema silesiacum</i> (Bleisch in Rabh.) D.G. Mann	GO92	<i>Gomphonema</i> sp92
ESUB	<i>Eunotia subarcuatoides</i> Alles Nörpel & Lange-Bertalot	GO96	<i>Gomphonema</i> sp96
EUNO	EUNOTIA C.G. Ehrenberg	GOMP	GOMPHONEMA C.G. Ehrenberg
FCRS	<i>Frustulia crassinervia</i> (Breb.) Lange-Bertalot & Krammer	GPAR	<i>Gomphonema parvulum</i> (Kützing) Kützing var. <i>parvulum f. parvulum</i>
FFON	<i>Fragilaria fonticola</i> Hustedt	GPP1	<i>Gomphosphenia</i> sp1
FGOU	<i>Fragilaria goulardii</i> (Brébisson) Lange-Bertalot	GPUM	<i>Gomphonema pumilum</i> (Grunow) Reichardt & Lange-Bertalot
FGRA	<i>Fragilaria gracilis</i> Østrup	GYRE	<i>Gyrosigma reimeri</i> Sterrenburg
FMUD	<i>Fallacia muraloides</i> (Hustedt) D. Mann	LAEQ	<i>Luticola aequatorialis</i> (Heiden) Lange-Bertalot & Ohtsuka
FR01	<i>Fragilaria</i> sp1	LU01	<i>Luticola</i> sp1
FSAP	<i>Fistulifera saprophila</i> (Lange-Bertalot & Bonik) Lange-Bertalot	LUTI	LUTICOLA D.G. Mann
FSBH	<i>Fallacia subhamulata</i> (Grunow in V. Heurck) D.G. Mann	MAPE	<i>Mayamaea atomus</i> var. <i>permitis</i> (Hustedt) Lange-Bertalot
FTNR	<i>Fallacia tenera</i> (Hustedt) Mann in Round	MRCO	<i>Mayamaea recondita</i> (Hustedt) Lange-Bertalot
GAFF	<i>Gomphonema affine</i> Kützing	NA46	<i>Navicula</i> sp46
GBOB	<i>Gomphonema bourbonense</i> E. Reichardt & Lange-Bertalot	NA58	<i>Navicula</i> sp58
GBPA	<i>Gomphonema brasiliense</i> ssp. <i>pacificum</i> Moser Lange-Bertalot & Metzeltin	NA62	<i>Navicula</i> sp62
GDEC	<i>Geissleria decussis</i> (Ostrup) Lange-Bertalot & Metzeltin	NACD	<i>Nitzschia acidoclinata</i> Lange-Bertalot
GDES	<i>Gomphonema designatum</i> E. Reichardt	NACI	<i>Nitzschia acicularis</i> (Kützing) W.M. Smith
GE01	<i>Geissleria</i> sp1	NAMP	<i>Nitzschia amphibia</i> Grunow f. <i>amphibia</i>
GEXL	<i>Gomphonema exilissimum</i> (Grun.) Lange-Bertalot & Reichardt	NANT	<i>Navicula antonii</i> Lange-Bertalot
GLGN	<i>Gomphonema lagenula</i> Kützing	NAR1	<i>Navicula arvensis</i> forme 1
GO48	<i>Gomphonema</i> sp48	NARV	<i>Navicula arvensis</i> Hustedt
GO49	<i>Gomphonema</i> sp49	NCLA	<i>Nitzschia clausii</i> Hantzsch
GO51	<i>Gomphonema</i> sp51	NCTE	<i>Navicula cryptotenella</i> Lange-Bertalot
GO53	<i>Gomphonema</i> sp53	NCXM	<i>Navicula cruxmeridionalis</i> Metzeltin, Lange-Bertalot & Garcia-Rodriguez
GO54	<i>Gomphonema</i> sp54	ND02	<i>Navicula (dicta) seminulum</i> forme 2
GO58	<i>Gomphonema</i> sp58	ND03	<i>Navicula (dicta) seminulum</i> forme 3
GO59	<i>Gomphonema</i> sp59	NDEN	<i>Nitzschia denticula</i> Grunow
GO61	<i>Gomphonema</i> sp61	NDIF	<i>Navicula difficillima</i> Hustedt
GO62	<i>Gomphonema</i> sp62	NDMA	<i>Nitzschia dissipata</i> (Kützing) Grunow fo. <i>maewensis</i> Foged
GO64	<i>Gomphonema</i> sp64	NER2	<i>Navicula erifuga</i> forme 2
GO67	<i>Gomphonema</i> sp67	NER3	<i>Navicula erifuga</i> forme 3
		NERI	<i>Navicula erifuga</i> Lange-Bertalot
		NESC	<i>Navicula escambia</i> (Patrick) Metzeltin & Lange-Bertalot

NFIC	<i>Nitzschia filiformis</i> var. <i>conferta</i> (Richter) Lange-Bertalot	NSRH	<i>Navicula subrhynchocephala</i> Hustedt
NFIL	<i>Nitzschia filiformis</i> (W.M. Smith) Van Heurck var. <i>filiformis</i>	NSUA	<i>Nitzschia subacicularis</i> Hustedt in A. Schmidt et al.
NGRE	<i>Navicula gregaria</i> Donkin	NTEN	<i>Navicula tenelloides</i> Hustedt
NHUB	<i>Navicula humboldtiana</i> Lange-Bertalot & Rumrich	NTER	<i>Nitzschia terrestris</i> (Petersen) Hustedt
NI41	<i>Nitzschia</i> sp41	NTPT	<i>Navicula tripunctata</i> (O.F. Müller) Bory
NI43	<i>Nitzschia</i> sp43	NUP1	<i>Nupela</i> sp1
NI47	<i>Nitzschia</i> sp47	NUP2	<i>Nupela</i> sp2
NI73	<i>Nitzschia</i> sp73	NURU	<i>Nupela rumrichorum</i> Lange-Bertalot
NI76	<i>Nitzschia</i> sp76	PACR	<i>Pinnularia acrospheria</i> W. Smith var. <i>acrospheria</i>
NIFR	<i>Nitzschia frustulum</i> (Kützing) Grunow var. <i>frustulum</i>	PI40	<i>Pinnularia</i> sp50
NIGE	<i>Nitzschia ingenua</i> Hustedt	PLBI	<i>Planothidium biporum</i> (Hohn & Hellerman) Lange-Bertalot
NIGR	<i>Nitzschia gracilis</i> Hantzsch	PLEV	<i>Pleurosira laevis</i> (Ehrenberg) Compere f. <i>laevis</i> Ehrenberg
NINC	<i>Nitzschia inconspicua</i> Grunow	PLFR	<i>Planothidium frequentissimum</i> (Lange-Bertalot) Lange-Bertalot
NINK	<i>Navicula incarum</i> Lange-Bertalot & Rumrich	PRBU	<i>Planothidium robustius</i> (Hustedt) Lange-Bertalot
NINT	<i>Nitzschia intermedia</i> Hantzsch ex Cleve & Grunow	PTS1	<i>Platessa</i> sp1
NITZ	NITZSCHIA A.H. Hassall	RGIB	<i>Rhopalodia gibba</i> (Ehr.) O. Muller var. <i>gibba</i>
NLGC	<i>Navicula longicephala</i> Hustedt var. <i>longicephala</i>	RH01	<i>Rhopalodia</i> sp1
NLIN	<i>Nitzschia linearis</i> (Agardh) W.M. Smith var. <i>linearis</i>	RH04	<i>Rhopalodia</i> sp4
NLOR	<i>Nitzschia lorenziana</i> Grunow in Cleve et Möller	RHOP	RHOPALODIA O Müller
NMIC	<i>Nitzschia microcephala</i> Grunow in Cleve & Moller	ROPE	<i>Rhopalodia operculata</i> (Agardh) Hakansson
NNGO	<i>Naviculadicta nanogomphonema</i> Lange-Bertalot & Rumrich	SDRO	<i>Simonsenia delognei</i> Lange-Bertalot ssp. <i>rossii</i>
NPA2	<i>Nitzschia palea</i> forme 2	SE02	<i>Sellaphora</i> sp2
NPA3	<i>Nitzschia palea</i> forme 3	SMST	<i>Seminavis strigosa</i> (Hustedt) Danieleadis & Economou-Amilli
NPA5	<i>Nitzschia palea</i> forme 5	SPUP	<i>Sellaphora pupula</i> (Kützing) Mereschkowksy
NPA6	<i>Nitzschia palea</i> forme 6	SSEM	<i>Sellaphora seminulum</i> (Grunow) D.G. Mann
NPAE	<i>Nitzschia paleacea</i> (Grunow) Grunow in van Heurck	STAU	STAURONEIS C.G. Ehrenberg
NPAL	<i>Nitzschia palea</i> (Kützing) W. Smith	STHE	<i>Stauroneis thermicola</i> (Petersen) Lund
NQDJ	<i>Navicula quasidisjuncta</i> Lange-Bertalot & Rumrich	TDEB	<i>Tryblionella debilis</i> Arnott ex O'Meara
NROS	<i>Navicula rostellata</i> Kützing	ULAN	<i>Ulnaria lanceolata</i> (Kütz.) Compère
NRVL	<i>Navicula rivulorum</i> Lange-Bertalot & Rumrich	UPSG	<i>Ulnaria pseudogaillonii</i> (Kobayasi & Idei) Idei
NSIA	<i>Navicula simulata</i> Manguin		
NSLC	<i>Navicula salinicola</i> Hustedt		