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REVIEW PAPER

Looking back, looking forward: a review of the new literature on diatom teratological forms (2010–2020)

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Abstract Over the last years, issues concerning diatom teratological forms and environmental stress have received growing interest within the scientific community. Publications on this topic dated back to 1890 and were summarized in a review published in 2009 by the journal *Hydrobiologia*, accounting for high citation rates (i.e. 117 citations Scopus and 232 citations Google Scholar, October 2020). This wide interest stimulates the authors to further unravel teratological forms significance in the light of the most recent publications (2010–2020). Diatom teratological forms are one of the best individual-level biomarkers since they provide a rapid response to several environmental stressors, including new emerging pollutants. The mechanisms involved in teratological valve likely involve both cytoskeleton and silicon metabolic pathway impairments. However, teratologies do not seem to weaken the reproduction capacity and viability of the affected individuals. We recognized eight types of teratologies as involving different parts of the valve, depending on genus. In order to summarize the information obtained by several years of research, we suggest a four-step procedure aimed at providing a theoretical pathway that researchers should follow to better explain results obtained in next-future studies and representing a starting point for the development of an environmental index based on teratological forms.

Keywords Bacillariophyceae · Biomarkers · Environmental index · Freshwater diatoms · Trace metal contamination · Teratology

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Introduction

In recent years, diatomists have been more and more involved in the research of reliable and easily applicable tools for the environmental contamination assessment in freshwater ecosystems (Morin et al., 2012a). Indeed, due to their short generation times and fast growth, diatoms allow the detection of complex phenomena on a small-scale time, if compared to higher organization levels (Morin et al., 2015).

Among biomarkers, the responses at the individual level are known to be the most effective early warning systems. In this context, diatom teratologies reflect the sub-lethal responses to the environmental stresses and represent an important compromise between response sensitivity and ecosystem relevance, since alterations at the individual level of organization still represent an early end-point. The rapid response to the contamination (generally 1 week) allows recovery in the ecosystem health status, before the following organization levels (such as population, community and food chain) will be affected. Moreover, the record of the teratologies can be easily included in the routine diatom sample analysis with no further efforts, fulfilling the requests of limiting time and resources during the biomonitoring procedure (Lavoie et al., 2017).

Starting from these considerations and strongly believing in diatom teratological form potential in 2009, we published a literature review on this topic, with the aim to shed light on the enormous amount of literature concerning teratological form production and environmental stresses (Falasco et al., 2009a). In that work, 222 papers were cited and, in turn, our paper stimulated the scientific community to improve its knowledge on this topic and received great attention, as underlined by the high number of citations, i.e. 117 (source Scopus, October 2020) and 232 (Google Scholar, October 2020).

Why it is still important to study teratological forms for monitoring purposes?

Presently, there is still a wide debate about the most appropriate indicators of response to environmental stress in aquatic environments. Recent studies have highlighted the limitations of some metrics commonly used for detecting the effects of pollutants.

In the framework of the river ecosystem assessment, biomass metrics such as chlorophyll *a* or diatom density often display confusing patterns and their responses frequently result unrelated to the contamination levels. In some cases, chlorophyll *a* decreased after trace metal exposure (Pandey & Bergey, 2018; Pandey, 2020), in other cases no variation was recorded (Licursi & Gómez, 2013), in others fluctuations were observed (Mu et al., 2018), sometimes chlorophyll *a* even increased after a contamination event (Mu et al., 2017). Diatom density and chlorophyll *a* are strictly dependent on many biotic and abiotic interactions and, for this reason, they have been often criticized when used for contamination assessments (Pandey et al., 2017). Indeed, as these two metrics are easily influenced by the presence of tolerant species [such as *Eolimna minima* (Grunow) Lange-Bertalot], a disproportional growth of small adnate taxa with high reproductive rates after a contamination is often observed, with a consequent cell density increase and community biovolume decrease (Arini et al., 2012a, c). For this reason, in many cases biovolume would be a more reliable metric to consider than cell density; however, its estimation is time consuming (Pandey et al., 2017). Moreover, Kim Tiam et al. (2018) also observed that chlorophyll fluorescence could be affected by the presence of certain contaminants (such as herbicides or zinc), leading to misrepresented results.

In the same way, diversity-related metrics do not always show consistent responses to the contamination, in part due to the Intermediate Disturbance Hypothesis (Wilkinson, 1999), in part because different diversity indices provide different types of information (Pandey et al., 2017). Notwithstanding, some authors detected a decrease in species richness and Shannon diversity after trace metal exposure with stronger effects of copper (Cu) than zinc (Zn; Pandey & Bergey, 2018).

At cellular level, antioxidant enzyme activity measured in the biofilm, and in particular ascorbate peroxidase, demonstrated to be an early toxicity biomarker for Zn, responding even few hours after the contamination event (Bonet et al., 2012). However, changes in the antioxidant enzyme activity have been recently observed also in non-contaminated sites, and associated to the community succession process, calling into question the reliability of this metric in the framework of the pollution assessment (Bonet et al., 2012). Also, the production of lipid bodies in live frustules can be considered as a good marker of trace metal toxicity and recovery. In this context, Pandey & Bergey (2018) found significantly higher percentages of lipid droplets in diatoms exposed to trace metal contamination, with Cu resulting more toxic than Zn. The same results were recently obtained by Park et al. (2020) who observed a significant increase in lipid bodies volume in the genera *Amphora* Ehrenberg ex Kützing and *Nitzschia* Hassall, as response to Cu contamination. Another study statistically confirmed a positive correlation between trace metal contamination (especially Pb and Se) and lipid bodies production in *Gomphonema pseudoaugur* Lange-Bertalot, which also resulted as one of the most resistant species in communities exposed to such impairment (Gautam et al., 2017). Again, Antoni et al. (2020) observed bigger lipid bodies in cells treated with Zn than control ones. Pham (2019) found that silver nanoparticles (AgNPs) increased the total lipid production in *Thalassiosira* sp. However, the results in literature are not always consistent, as highlighted for instance by Pandey (2020), who recently observed no lipid bodies increase in diatom communities after Pb exposure.

The present review aims at analysing the progress made on diatom teratological forms during the last 10 years, offering new insights and confirming or denying previously advanced hypotheses. Based on the most recent research literature, we will analyse all those environmental impacts, which lead to the formation of abnormal diatom forms, with a focus on new emerging pollutants. We propose new insights on the mechanisms involved in the normal and abnormal valve cell formation and we will examine new results obtained on the reproduction capacity and viability of the teratological individuals. We will explore the functional responses at community level, taking in consideration diatom class sizes, life forms and ecological guilds. Finally, we propose a four-step procedure that could be used in future research to better interpret the ecological meaning of diatom teratological form's presence in the biofilm.

Methods

The present paper and the elaborations herein contained focus on research dealing with diatom teratological forms, published from 1890 up to date.

All the information concerning literature published from 1890 to 2009 were mostly contained in our previous research published in *Hydrobiologia* (Falasco et al., 2009a). From Table 1 of that paper, we extracted data on diatom species, type of deformations and possible causes inducing the production of teratological forms.

In a similar way, we treated data extracted from the most recent literature (i.e. part of 2009 up to present). To do this, we performed a bibliographic research using search engines such as Scopus®, Web of Science™ and Google Scholar. We used the software *Publish or Perish*© (version 7.0, Tarma Software Research Ltd.). All papers containing "diatom*", "terato*", "deform*" and "alter*" in their title/abstract/full text from 2009 and 2020 were selected and downloaded. The articles were then carefully screened and included if judged relevant. In particular, we excluded (i) papers with no relation whatsoever with diatoms; (ii) papers including the aforementioned words only in the introduction and discussion, but not providing new results. We excluded from the present paper all the information derived from grey literature, as required in the author's guideline of the journal. In particular, during the literature review, we found, but were not included in the analysis: technical reports ($n = 39$); articles on very local journal/in original languages ($n = 19$); bachelor/master theses ($n = 17$); PhD theses ($n = 15$); posters ($n = 3$); power point presentations ($n = 3$); abstracts in book of conferences ($n = 1$).

All the data obtained from this second research were summarized in a table containing a list of the diatom species subject to deformation, the type of teratology and the possible causes inducing it.

These two tables, the first contained in Falasco et al. (2009a) and the second produced in the present paper, were merged. After that, for each species, we added information concerning class size, life form and ecological guilds following Rimet & Bouchez (2012).

Results and discussion

In total, we analysed 409 papers, 222 already contained in Falasco et al. (2009a), 187 in the present paper. Of these 409 articles: 185 cited in their text at least one diatom species showing teratologies (about 45% of the total analysed literature); 154 hypothesized one or more causes leading to the deformations (about 38%). In total, from this literature review we were able to obtain a list of 298 taxa, which showed some kind of deformation and the corresponding hypothesized cause. Table 1 summarizes all these information.

Table 1 List of diatom species showing teratologies, types of deformation and relative description (if available), hypothesized causes and relative classification, bibliographic references

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Achnanthes brevipes C. Agardh 1824	TYPE 1; TYPE 4; TYPE 7	Lack of V-shape; fragmented raphe system; branched pseudoraphe, eccentric or unnoticeable	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Estes & Dute (1994)
	TYPE 1; TYPE 2; TYPE7	Deformed outline, abnormal striation patterns, mixed	Metals (Cd, Co, Cr, Cu, Fe, Pb and Zn) and nutrients (total phosphorus and total nitrogen)	MULTIPLE	Pandey et al. (2018b)
Achnanthes coarctata (Brébisson ex W. Smith) Grunow in Cleve & Grunow 1880	TYPE 1	Deformed outline	Low discharge, high temperatures and salinity	MULTIPLE	Lai et al. (2019)
Achnanthes lemmermannii Hustedt 1933	–	Not described	High organic matter levels	ORGANIC LOADING AND EUTROPHICATION	Dziengo-Czaja & Matuszak (2008)
Achnanthidium deflexum (Reimer) J.C. Kingston 2000	TYPE 2	Striae deformities	Mixture of metals and low pH	AMD	Leguay et al. (2016)
Achnanthidium macrocephalum (Hustedt) Round & Bukhtiyarova 1996	TYPE 1	Mainly deformed outline	Mainly Zn and Cu	TRACE METALS	Olenici et al. (2017)
Achnanthidium microcephalum Kützing 1844	–	Not described	Mixture of metals (Pb, Cu, Zn)	TRACE METALS	Simić et al. (2018)
Achnanthidium minutissimum (Kützing) Czarnecki 1994	TYPE 1	Deformed outline	Cd and Zn	TRACE METALS	Morin et al. (2007)
			Mixture of metals in the sediments	TRACE METALS	Tapia (2008)
			Mixture of metals	TRACE METALS	Falasco et al. (2009b)
			Mixture of metals (mainly Pb, Cd, Zn)	TRACE METALS	Ferreira da Silva et al. (2009)
			Thiram or hydrocarbon emulsion	PESTICIDES	Bayona et al. (2014)
			Mainly Cd and Zn (but also Pb); separately	TRACE METALS	Pandey et al. (2014)
			Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Windler et al. (2014)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
			Trace metal contamination: Cd, Cu, Fe and Zn	TRACE METALS	Cichoń (2016)
			Mainly Zn and Cu	TRACE METALS	Olenici et al. (2017)
	TYPE 1a	Invagination at one or apices (cymbelliclinum-like teratology)	Toxic effluents	MULTIPLE	Cantonati et al. (2014)
			Mixture of metals (Cu, Zn, Sb)	TRACE METALS	Cerisier et al. (2019)
			Mixture of metals (mainly Cu and Zn)	TRACE METALS	Tolotti et al. (2019)
	TYPE 2	Abnormal striation pattern	Cd contamination (100 µg Cd·l^{-1})	TRACE METALS	Morin et al. (2008a)
	TYPE7	Abnormal outline and ornamentation	Mixture of metals and low pH	AMD	Luís et al. (2011)
	TYPE 1; TYPE 2; TYPE7	Deformed outline, abnormal striation patterns, mixed	Metals (Cd, Co, Cr, Cu, Fe, Pb and Zn) and nutrients (total phosphorus and total nitrogen)	MULTIPLE	Pandey et al. (2018b)
			Ammonium, phosphorous, pharmaceutical compounds and hydrological pressure	MULTIPLE	Tornés et al. (2018)
	–	Not described	AMD	AMD	Fernández et al. (2018)
			Mixture of metals (mainly Cd and Zn)	TRACE METALS	De Jonge et al. (2008)
			Trace metals (Cd)	TRACE METALS	Duong et al. (2008)
			Mixture of metals (Zn, Fe, Al, Ni)	TRACE METALS	Morin et al. (2014)
			Multiple (mainly olive mills waterwaters and hydrological stress)	MULTIPLE	Smeti et al. (2019)
Achnanthidium pyrenaicum (Hustedt) H. Kobayasi 1997	TYPE 1	Deformed outline	Fluoranthene (200 µg l^{-1})	PESTICIDES	Rimet et al. (2004) [as *Achnanthidium biasolettianum* (Grunow) Round & Bukhtiyarova]

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
			Pesticides	PESTICIDES	Debenest et al. (2006)
			Thiram or hydrocarbon emulsion	PESTICIDES	Bayona et al. (2014)
	TYPE 1; TYPE 2	Deformed outline, abnormal striation	Mixture of metals	TRACE METALS	Falasco et al. (2009b) [as *Achnanthidium biasolettianum* (Grunow) Lange-Bertalot]
	–	Not described	Multiple (mainly olive mills waterwaters and hydrological stress)	MULTIPLE	Smeti et al. (2019)
Achnanthidium saprophilum (H. Kobayasi & Mayama) Round & Bukhtiyarova 1996	TYPE 2	Slight deformities of the valve ornamentation	Trace pollution at the sampling site	MULTIPLE	Hlúbiková et al. (2011)
	–	Not described	Trace metals (Cd)	TRACE METALS	Duong et al. (2008) [as *Achnanthidium saprophila*]
			Cd and Zn	TRACE METALS	Morin et al. (2007)
			AMD	AMD	Fernández et al. (2018)
Achnanthidium sp. (*A. minutissimum* complex)	TYPE 8	Deformed valvocopula	Mainly Zn and Cu	TRACE METALS	Olenici et al. (2019)
Achnanthidium spp.	–	Not described	Intensive agriculture and urban area	ORGANIC LOADING AND EUTROPHICATION	Straub et al. (2014)
Amphora ovalis (Kützing) Kützing 1844	TYPE 1	Deformed outline	Mainly Cd and Zn (but also Pb); separately	TRACE METALS	Pandey et al. (2014)
Amphora pediculus (Kützing) Grunow in Schmidt et al. 1875	TYPE 1	Deformed outline	Cd contamination (100 µg Cd·l^{-1})	TRACE METALS	Morin et al. (2008a)
			Mixture of metals	TRACE METALS	Falasco et al. (2009b)
	TYPE 4	Abnormal orientation of the raphe system	Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as APED (*Amphora pediculus*)]

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Amphora sp.	TYPE 1	Deformed outline	Multiple (probably trace metals and COD: chemical oxygen demand)	MULTIPLE	Walsh & Wepener (2009) [misidentified as *Amphora pediculus*]
			Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Park et al. (2020)
			Cu (1 mg Cu l $^{-1}$)	TRACE METALS	
Anomoeoneis costata (Kützing) Hustedt 1959	TYPE 2; TYPE 4; TYPE 7	Displaced central nodules; fragmented raphes; altered striae pattern; mixed	Osmotic stress	OTHERS	Schmid (1980) [as *Anomoeoneis sphaerophora* (Kutz.) Pfitz. f. *costata*]
Anorthoneis pulex Sterrenburg 1987	TYPE 2	Abnormal striation pattern	Unknown	UNKNOWN	Pennesi et al. (2018)
Asterionella Hassall 1850	TYPE 1	Abnormal cells	Parasitism by fungi	OTHERS	Canter & Lund (1948)
Asterionella formosa Hassall 1850	TYPE 1	90° Rotation of the valves	Cu and Fe	TRACE METALS	Cattaneo et al. (2004)
		Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
	TYPE 6	Abnormal colony formation	Hg	TRACE METALS	Tompkins & Blinn (1976)
Asterionella japonica Cleve in Cleve & Möller 1882	TYPE 1	Increased cell size	Cu (5–25 $\mu g{\cdot}l^{-1}$), Zn and Cd	TRACE METALS	Fisher & Frood (1980)a and Fisher et al. (1981)
Aulacoseira granulata (Ehrenberg) Simonsen 1979	TYPE 1	Deformed outline	Mainly Cd and Zn (but also Pb); separately	TRACE METALS	Pandey et al. (2014) [as *Melosira granulata* (Ehrenberg) Ralfs]
Aulacoseira italica (Ehrenberg) Simonsen 1979	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
Aulacoseira sp.	TYPE 2	Striae deformities (missing areolae, misaligned or shorter or deformed striae)	No trace metal enrichment, but silica conditions	MULTIPLE	Laird et al. (2015)
Bacillaria paxillifera (O.F. Müller) T. Marsson 1901	TYPE 1; TYPE 2; TYPE 5; TYPE 7	Deformed outline, abnormal striation patterns, abnormal raphe channel, mixed	Metals (Cd, Co, Cr, Cu, Fe, Pb and Zn) and nutrients (total phosphorus and total nitrogen)	MULTIPLE	Pandey et al. (2018b) [as *Bacillaria paradoxa* (Gmelin)]
Berkeleya rutilans (Trentepohl ex Roth) Grunow 1880	TYPE 1	Deformed valves, asymmetrical or even twisted	Extreme life conditions (tides)	PHYSICAL STRESS	Aleem (1950) [as *Amphipleura rutilans*]

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Biddulphia rhombus (Ehrenberg) W. Smith in Roper 1854	TYPE 1	Deformed valve outline (large and irregular indentation on one side)	External and mechanical causes	PHYSICAL STRESS	Cox (1890)
Biremis panamae Barka, Witkowski & Weisenborn in Witkowski et al. (2014)	TYPE 4	Teratological development of the raphe	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Witkowski et al. (2014)
Brachysira brebissonii R. Ross in Hartley et al. 1986	TYPE 1; TYPE 4	Deformed outline, raphe modification	Mainly Cd and Zn (but also Pb); separately	TRACE METALS	Pandey et al. (2014)
	TYPE 1; TYPE 2; TYPE 7	Deformed outline, abnormal striation patterns, mixed	Cu and Zn	TRACE METALS	Pandey & Bergey (2016)
Brachysira microcephala (Grunow) Compère 1986	TYPE 1	Deformed outline	Crowding	PHYSICAL STRESS	Barber & Carter (1981) [as *Anomoeoneis exilis* (Kütz.) Cl.]
			Mainly Cd and Zn (but also Pb); separately	TRACE METALS	Pandey et al. (2014)
	TYPE 1; TYPE 2; TYPE 7	Deformed outline, abnormal striation patterns, mixed	Cu and Zn	TRACE METALS	Pandey & Bergey (2016)
Brachysira praegeri B. Kennedy & Allott (2017)	TYPE 1	Deformed outline, at the apices	Unknown	UNKNOWN	Kennedy & Allott (2017)
Brachysira vitrea (Grunow) R. Ross in Hartley 1986	TYPE 1; TYPE 2	Abnormal outline and ornamentation	Mixture of metals and low pH	AMD	Luís et al. (2011)
	–	Not described	AMD	AMD	Fernández et al. (2018)
Caloneis bacillum (Grunow) Cleve 1894	TYPE 2	Abnormal striation	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
Ceratoneis closterium Ehrenberg 1839	TYPE 1	Abnormal outline involving apices	Low pH	pH	Rogelja et al. (2016)
Chaetoceros curvisetus Hustedt in Schmidt et al. 1920	TYPE 1	Elongated in the pervalvar axis	Cu and Hg	TRACE METALS	Thomas et al. (1980)
Chaetoceros danicus Cleve 1889	TYPE 1	Elongated in the pervalvar axis	Cu and Hg	TRACE METALS	Thomas et al. (1980)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Cocconeis euglypta Ehrenberg 1854	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
			Low discharge, high temperatures and salinity	MULTIPLE	Lai et al. (2019)
	TYPE 1; TYPE 2	Deformed outline (valves not regularly elliptic and almost parallel valve margins); abnormal striation pattern	No clear causes (probably physical parameters such as low current velocity and high light intensity which might affect silica deposition on the valve surface)	PHYSICAL STRESS	Al-Handal & Abdullah (2010)
Cocconeis pediculus Ehrenberg 1838	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
			No clear causes (probably physical parameters such as low current velocity and high light intensity which might affect silica deposition on the valve surface)	PHYSICAL STRESS	Al-Handal & Abdullah (2010)
	TYPE 1; TYPE 2	Abnormal outline and ornamentation	No clear causes (probably nutrient levels or UV exposure)	UNKNOWN	Majewska et al. (2012)
	–	Not described	Cd and Zn	TRACE METALS	Morin et al. (2007)
					Morin et al. (2008b)
			AMD	AMD	Fernández et al. (2018)
Cocconeis peltoides Hustedt 1939	–	Not described	high organic matter levels	ORGANIC LOADING AND EUTROPHICATION	Dziengo-Czaja & Matuszak (2008)
Cocconeis placentula Ehrenberg 1838	TYPE 1	Abnormal valve outline	Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as CPLA (*Cocconeis placentula*)]
			Probably low pH (but maybe also trace metals and pesticides)	MULTIPLE	Esquius et al. (2012)
			Mainly Cd and Zn (but also Pb); separately	TRACE METALS	Pandey et al. (2014)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
	TYPE 2	Abnormal striation pattern	Extreme environmental conditions (i.e. high UV radiation, high salt content, geothermal flux, large nutrient supply)	MULTIPLE	Cabrol et al. (2007)
			Thiram or hydrocarbon emulsion	PESTICIDES	Bayona et al. (2014)
	TYPE 1; TYPE 2; TYPE 7	Deformed outline, abnormal striation patterns, mixed	Low current velocity and flow, drought conditions, and consequent light intensity and high water temperature	PHYSICAL STRESS	Antoine & Benson-Evans (1984)
			Unknown	UNKNOWN	Holmes & Taylor (2015)
			High concentration of metals and total nitrogen, high conductivity and biological oxygen demand	MULTIPLE	Pandey et al. (2018a)
			Metals (Cd, Co, Cr, Cu, Fe, Pb and Zn) and nutrients (total phosphorus and total nitrogen)	MULTIPLE	Pandey et al. (2018b)
	–	Not described	High organic matter levels	ORGANIC LOADING AND EUTROPHICATION	Dziengo-Czaja & Matuszak (2008)
			Cd and Zn	TRACE METALS	Morin et al. (2008b)
			Unknown	UNKNOWN	Falasco et al. (2018a)
Cocconeis pseudolineata (Geitler) Lange-Bertalot in Werum & Lange-Bertalot 2004	TYPE 2; TYPE 3	Abnormal striation, central area	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
Cocconeis sawensis Al-Handal & Riaux-Gobin 2014	TYPE 1; TYPE 2; TYPE 4	Deflection of the raphe, abnormalities in valve outline and distortion of areola	Extreme environmental conditions (i.e. high concentration of sulphate and carbonate salts; high salinity levels)	MULTIPLE	Al-Handal et al. (2014)
Cocconeis scutellum Ehrenberg 1838	TYPE 1	Abnormal valve outline	Crowding	PHYSICAL STRESS	Barber & Carter (1981)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Cocconeis sp.	TYPE 1	Deformed outline	Multiple (probably trace metals and COD: chemical oxygen demand)	MULTIPLE	Walsh & Wepener (2009) [misidentified as *Cocconeis pediculus*]
		Shells with recesses at the poles or with concavity of the valves in the middle	Multiple	MULTIPLE	Barinova, (2017)
	TYPE 1; TYPE 2; TYPE 3	Deformed valve outline, abnormal striation pattern, displaced central area	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Falasco et al. (2009b)
Coscinodiscus sp.	TYPE 1	Morphological aberration	3 µg Hg·l^{-1}	TRACE METALS	Thomas et al. (1980)
Craticula ambigua (Ehrenberg) D.G. Mann in Round et al. 1990	TYPE 1; TYPE 2	Deformed outline and striation pattern	Textile effluent	MULTIPLE	Sierra & Gómez (2010)
Craticula cuspidata (Kützing) D.G. Mann in Round et al. 1990	TYPE 1	Abnormal valve morphology	Osmotic stress	OTHERS	Schmid (1979) [as *Navicula cuspidata* Kg.]
Craticula halophila (Grunow ex Van Heurck) D.G. Mann in Round et al. 1990	TYPE 1	Abnormal valve outline	Isoproturon (0.312 mg l^{-1})	PESTICIDES	Schmitt-Jansen & Altenburger (2005) [as *Navicula halophila*]
Craticula subminuscula (Manguin) C.E. Wetzel & Ector in Wetzel et al. 2015	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b) [as *Eolimna subminuscula* (Manguin) Moser, Lange-Bertalot et Metzeltin]
			No clear causes (probably Pb contamination)	TRACE METALS	Mora et al. (2015) [as *Eolimna subminuscula* (Manguin) Moser, Lange-Bertalot et Metzeltin]
			Mixture of metals (Cd, Ni, Zn)	TRACE METALS	Lavoie et al. (2018)
	TYPE 1; TYPE 2; TYPE 7	Deformed outline, patterns of striation, mixed	Ammonium, phosphorous, pharmaceutical compounds and hydrological pressure	MULTIPLE	Tornés et al. (2018)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
	–	Not described	AMD	AMD	Fernández et al. (2018) [as *Eolimna subminuscula* (Manguin) Moser, Lange-Bertalot & Metzeltin 1998]
Crenotia angustior (Grunow) Wojtal 2013	TYPE 1; TYPE 4	Deformed valve outline and raphe	Multiple (natural radioactivity, high salinity)	MULTIPLE	Millan et al. (2020)
Ctenophora pulchella (Ralfs ex Kützing) Schönfeldt 1907	TYPE 1	Abnormal valve outline	Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as FPUL (*Fragilaria pulchella*)]
	–	Not described	High organic matter levels	ORGANIC LOADING AND EUTROPHICATION	Dziengo-Czaja & Matuszak (2008)
Cyclotella atomus Hustedt 1937	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
			Mainly Cd and Zn (but also Pb); separately	TRACE METALS	Pandey et al. (2014)
	TYPE 2	Abnormal striation pattern	Cyanide and trace metals	MULTIPLE	Szabó et al. (2005)
	TYPE 1; TYPE 2	Deformed outline, abnormal striation	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Falasco et al. (2009b)
Cyclotella meneghiniana Kützing 1844	TYPE 2	Number of fultoportulae; shape of striation and costae; position and shape of satellite pores	Nutrient	ORGANIC LOADING AND EUTROPHICATION	Håkansson & Korhola (1998)
		Abnormal striation pattern in the edge of the valve	Cyanide and trace metals	MULTIPLE	Szabó et al. (2005)
		Abnormal striation pattern	Cd and Zn	TRACE METALS	Morin et al. (2007)
	–	Not described	Trace metals (Cd)	TRACE METALS	Duong et al. (2008)
Cylindrotheca closterium (Ehrenberg) Reimann & J.C. Lewin 1964	TYPE 1	Swollen in the central area	Cu or the metal mix solution (As, Cd, Cr, Cu, Hg, Ni, Pb, Sb, Se and Zn)	TRACE METALS	Thomas et al. (1980)
Cymatopleura elliptica (Brébisson ex Kützing) W. Smith 1851	TYPE 1	Abnormal valve outline (irregularly wavy)	External and mechanical causes	PHYSICAL STRESS	Cox, (1890)
Cymbella affiniformis Krammer 2002	TYPE 1	Deformed outline	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Windler et al. (2014)
Cymbella cymbiformis C. Agardh 1830	TYPE 1	Deformed outline	Mainly Cd and Zn (but also Pb); separately	TRACE METALS	Pandey et al. (2014)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Cymbella excisa Kützing 1844	TYPE 1; TYPE 2	Deformed outline, raphe modifications	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
Cymbella hustedtii Krasske 1923	TYPE 1	Deformed outline	Mixture of metals in the sediments	TRACE METALS	Tapia (2008)
Cymbella sp.	TYPE 1; TYPE 2; TYPE 7	Deformed outline, abnormal striation patterns, mixed	Unknown	UNKNOWN	Holmes & Taylor (2015)
Cymbella tumida (Brébisson ex Kützing) Van Heurck 1880	TYPE 1; TYPE 2; TYPE 7	Deformed outline, abnormal striation patterns, mixed	Cu and Zn	TRACE METALS	Pandey & Bergey (2016)
	TYPE 1; TYPE 2; TYPE; TYPE 4; TYPE 7	Deformed outline, abnormal striation, central area, raphe modifications, mixed	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Falasco et al. (2009b)
Cymbella turgidula Grunow in Schmidt et al. 1875	TYPE 1; TYPE 2; TYPE 7	Deformed outline, abnormal striation patterns, mixed	High concentration of metals and total nitrogen, high conductivity and biological oxygen demand	MULTIPLE	Pandey et al. (2018a)
Cymbella ventricosa Kützing 1844 [probably *Encyonema minutum* (Hilse) D.G. Mann in Round et al. 1990]	TYPE 1; TYPE 2; TYPE 7	Abnormal outline of valves; irregular striation pattern; interruption of the pseudoraphe; mixed	Low current velocity and flows, drought conditions, and consequent light intensity and high water temperature	PHYSICAL STRESS	Antoine & Benson-Evans (1984) [as *Cymbella ventricosa* Kütz. (= *C. minuta* Hisle ex Rabh.)]
Diadesmis Kützing 1844	TYPE 4	Loss of the raphe slits	Unknown	UNKNOWN	Cox (2006)
Diatoma Bory 1824	TYPE 2	Wave pattern of longitudinal ornamentations	Trace metal contamination	TRACE METALS	Dickman (1998)
Diatoma elongatum (Lyngbye) C. Agardh 1824	TYPE 1; TYPE 2; TYPE 7	Loss of transverse costae; deformities of valve outline; loss of isopolarity; mixed	Low current velocity and flows, drought conditions, and consequent light intensity and high water temperature	PHYSICAL STRESS	Antoine & Benson-Evans (1984)
Diatoma mesodon Kützing 1844	TYPE 2	Abnormal striation	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Falasco et al. (2009b)
Diatoma moniliformis (Kützing) D.M. Williams 2012	TYPE 1	Mainly deformed valve outline	Mainly Zn and Cu	TRACE METALS	Olenici et al. (2017)
	TYPE 1; TYPE 2	Abnormal outline and ornamentation	Mixture of metals	TRACE METALS	Falasco et al. (2009b)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
			No clear causes (probably nutrient levels or UV exposure)	UNKNOWN	Majewska et al. (2012)
	–	Not described	High organic matter levels	ORGANIC LOADING AND EUTROPHICATION	Dziengo-Czaja & Matuszak (2008)
Diatoma problematica Lange-Bertalot 1993	–	Not described	Intensive agriculture and urban area	ORGANIC LOADING AND EUTROPHICATION	Straub et al. (2014)
Diatoma sp.	TYPE 1; TYPE 2	Deformed outline and costae pattern	Unknown	UNKNOWN	Vasiljević et al. (2017)
Diatoma vulgaris Bory 1824	TYPE 1	Abnormal valve outline	Pesticides	PESTICIDES	Debenest et al. (2006)
		Deformed outline (pole; observed in Fig. 5)	AMD	AMD	Arena et al. (2014)
	TYPE 2	Irregular striation pattern	Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as DVUL (*Diatoma vulgaris*)]
			Mixture of metals	TRACE METALS	Falasco et al. (2009b)
			Thiram or hydrocarbon emulsion	PESTICIDES	Bayona et al. (2014)
	TYPE 1; TYPE 2; TYPE 7	Deformed outline, abnormal striation patterns, mixed	High concentration of metals and total nitrogen, high conductivity and biological oxygen demand	MULTIPLE	Pandey et al. (2018a)
	TYPE 1; TYPE 2; TYPE 7	Deformed outline, abnormal striation patterns, mixed	High metal concentrations, total nitrogen, coliforms, BOD and conductivity	MULTIPLE	Pandey et al. (2019)
	–	Not described	Trace metals (Cd)	TRACE METALS	Duong et al. (2008)
			Unknown	UNKNOWN	Falasco et al. (2012)
Didymosphenia geminata (Lyngbye) M. Schmidt in Schmidt et al. 1899	TYPE 2; TYPE 4; TYPE 7	Bifurcate or eccentric raphe; irregular striation pattern; short raphe system; mixed	Low current velocity and flows, drought conditions, and consequent light intensity and high water temperature	PHYSICAL STRESS	Antoine & Benson-Evans (1983)
	TYPE 1; TYPE 2; TYPE 4; TYPE 7	Bifurcation of the raphe (in the upper and in the lower part of the valve); sometimes valves laterally swollen; irregular striation pattern; mixed	Low current velocity and flows, drought conditions, and consequent light intensity and high water temperature	PHYSICAL STRESS	Antoine & Benson-Evans (1984)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Diploneis elliptica (Kützing) Cleve 1894	TYPE 2	Marking unsymmetrically varied (striation irregularly wavy, especially at the ends)	Unknown	UNKNOWN	Cox (1890) [as *Navicula elliptica*, Kg.]
Discostella pseudostelligera (Hustedt) Houk & Klee 2004	TYPE 2	Abnormal striation pattern in the edge of the valve	Cyanide and trace metals	MULTIPLE	Szabó et al. (2005) [as *Cyclotella pseudostelligera* Hust.]
Ditylum brightwellii (T. West) Grunow in Van Heurck 1883	TYPE 1	Increase of valvar surface	Cu	TRACE METALS	Rijstenbil et al. (1994)
Encyonema cespitosum Kützing 1849	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
	TYPE 1; TYPE 2	Abnormal outline and ornamentation	No clear causes (probably nutrient levels or UV exposure)	UNKNOWN	Majewska et al. (2012)
Encyonema lange-bertalotii Krammer 1997	TYPE 1; TYPE 2; TYPE 4	Deformed outline, abnormal striation, raphe modifications	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Falasco et al. (2009b)
Encyonema minutum (Hilse in Rabenhorst) D.G. Mann in Round et al. 1990	TYPE 1	Deformed outline	Mainly Cd and Zn (but also Pb); separately	TRACE METALS	Pandey et al. (2014)
	TYPE 2	Abnormal striation pattern	Cd and Zn	TRACE METALS	Morin et al. (2007)
	TYPE 4	Interruption of raphe, interruption of the apical raphe fissure	Cd contamination (100 µg Cd·l^{-1})	TRACE METALS	Morin et al. (2008a)
	TYPE 1; TYPE 2; TYPE 4	Deformed outline, striation pattern raphe modifications	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
Encyonema perpusillum (A. Cleve) D.G. Mann in Round et al. 1990	–	Not described	High UV radiation	PHYSICAL STRESS	Cuna et al. (2015)
Encyonema prostratum (Berkeley) Kützing 1844	TYPE 7	Abnormal outline and ornamentation	Unknown	UNKNOWN	Hustedt, (1927)
Encyonema silesiacum (Bleisch in Rabenhorst) D.G. Mann in Round et al. 1990	TYPE 1; TYPE 2	Deformed outline, abnormal striation	Mixture of metals	TRACE METALS	Falasco et al. (2009b)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
	TYPE 1; TYPE 2; TYPE 4	Deformed outline, abnormal striation, raphe modifications	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Falasco et al. (2009b)
	–	Not described	Multiple	MULTIPLE	Medvedeva et al. (2012)
Encyonema ventricosum (C. Agardh) Grunow in Schmidt et al. 1875	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
Encyonopsis minuta Krammer & E. Reichardt in Krammer 1997	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
Eolimna sp.	–	Not described	Unknown	UNKNOWN	Zimmermann et al. (2014)
Epithemia turgida (Ehrenberg) Kützing 1844	TYPE 2	Marking unsymmetrically varied (irregular costae and areolation patterns)	Unknown	UNKNOWN	Cox (1890)
Eunotia arcus Ehrenberg 1838	TYPE 1	Abnormal valve outline (irregular curves)	External and mechanical causes	PHYSICAL STRESS	Cox (1890)
Eunotia bilunaris (Ehrenberg) Schaarschmidt in Kanitz 1880	TYPE 1	Deformed outline (valves with belly-like in the middle of the valve)	Low pH	pH	Grabowska et al. (2014)
		Deformed outline	Unknown	UNKNOWN	Hustedt (1927) [as *Eunotia lunaris*]
	–	Not described	Unknown	UNKNOWN	Bertrand et al. (2014)
Eunotia exigua (Brébisson ex Kützing) Rabenhorst 1864	TYPE 1	Deformed valve outline	Mixture of metals and low pH	AMD	Luís et al. (2013)
			Mixture of metals and low pH	AMD	Luís et al. (2016)
			Cu and low pH (2.4)	AMD	Barber & Carter (1981)
	–	Not described	Mixture of metals and low pH	AMD	Leguay et al. (2016)
			AMD	AMD	Fernández et al. (2018)
Eunotia germainii J.R. Carter 1990	TYPE 1; TYPE 2	Incised ventral side or non-uniform striae distribution	pH	pH	Smith & Manoylov (2007) (as *Eunotia geitlerii* Carter 1990)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Eunotia meridionalis Lange-Bertalot & Tagliaventi in Lange-Bertalot et al. 2011	–	Not described	AMD	AMD	Fernández et al. (2018)
Eunotia minor (Kützing) Grunow in Van Heurck 1881	–	Not described	Trace metal mixture (mainly Cd and Zn)	TRACE METALS	De Jonge et al. (2008)
Eunotia monodon Ehrenberg 1843	TYPE 1	Abnormal valve outline (deep irregular indentation on concave side near one end, comma shape)	External and mechanical causes	PHYSICAL STRESS	Cox (1890)
Eunotia naegelii Migula 1907	–	Not described	Unknown	UNKNOWN	Bertrand et al. (2014)
Eunotia pectinalis (Kützing) Rabenhorst 1864	TYPE 2	Abnormal ornamentation pattern: branched striation (not described but observed in Fig. 2a)	Unknown	UNKNOWN	Adesalu (2017)
Eunotia robusta Ralfs 1861	TYPE 2	Abnormal ornamentation pattern	Unknown	UNKNOWN	Hustedt (1927)
Eunotia serra var. *diadema* (Ehrenberg) R.M. Patrick 1958	TYPE 1	Abnormal outline (concave side of the valve irregularly curved)	External and mechanical causes	PHYSICAL STRESS	Cox (1890) [as *Eunotia diadema*, Ehr.]
Eunotia sp.	TYPE 1	Abnormal outline (bent in the middle of the valve)	Cu (200 $\mu g \cdot g^{-1}$)	TRACE METALS	Cattaneo et al. (2004)
			Unknown	UNKNOWN	Jahn & Kusber (2004)
		Deformed outline	Turbulence	PHYSICAL STRESS	Clarson et al. (2009)
	TYPE 2	Abnormal fine structure arrangement	Multiple	MULTIPLE	Barinova(2017)
Eunotia spp.	TYPE 1	Deformed valve outline	Water acidification	pH	Greenaway et al. (2012)
		Deformed outline (lack of symmetry, bent or swollen)	FE, Cu, Zn, Ni	TRACE METALS	Sienkiewicz & Gąsiorowski (2016)
		Deformed valve outline	Low pH and mixture of trace metals	AMD	Sienkiewicz & Gąsiorowski (2017, 2019)
Eunotia subarcuatoides Alles, Nörpel & Lange-Bertalot 1991	TYPE 1; TYPE 4	Deformed outline and raphe	Acid precipitations (low pH and high levels of Al, Ba and Mn)	AMD	Furey et al. (2009)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Falcula hyalina Takano 1983	TYPE 1	Abnormal apices	Physical stress (shallow water, transparency and high temperature	PHYSICAL STRESS	Donadel & Torgan (2016)
Fallacia cassubiae Witkowski 1991	–	Not described	High organic matter levels	ORGANIC LOADING AND EUTROPHICATION	Dziengo-Czaja & Matuszak (2008)
Fallacia pygmaea (Kützing) Stickle & D.G. Mann in Round et al. 1990	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b) [as *Navicula pygmaea* (Ehrenberg) Pantocsek]
Fistulifera pelliculosa (Brébisson) Lange-Bertalot 1997	TYPE 1	Deformed outline	Ge (high Ge/Si ratio)	TRACE METALS	Chiappino et al. (1977)
Fragilaria capitellata (Grunow in Van Heurck) J.B. Petersen 1946	TYPE 1	Abnormal valve outline	Pesticides	PESTICIDES	Debenest et al. (2006) [as *Fragilaria capucina* Desm. var. *capitellata* (Grunow)]
	TYPE 2	Abnormal striation pattern	Cd and Zn	TRACE METALS	Morin et al. (2007) [as *Fragilaria capucina* var. *capitellata*]
	–	Not described	Cd and Zn	TRACE METALS	Morin & Coste (2006) [as *Fragilaria capucina* Desm. v. *capitellata* (Grunow) Lange-Bertalot]
			Intensive agriculture and urban area	ORGANIC LOADING AND EUTROPHICATION	Straub et al. (2014) [as *Fragilaria capucina* var. *capitellata*]
Fragilaria capucina Desmazières 1830	TYPE 1	Asymmetrically abnormal; bent valves: notched or incised	Cd, Cu, Fe and Zn	TRACE METALS	McFarland et al. (1997)
			Cd and Zn	TRACE METALS	Morin et al. (2007)
		Lack of longitudinal symmetry	Trace metal contamination	TRACE METALS	Dickman (1998)
		Deformed outline	Cd	TRACE METALS	Duong et al. (2008)
			Cd	TRACE METALS	Morin et al. (2008c)
			Trace metal contamination: Cd, Cu, Fe, and Zn	TRACE METALS	Cichoń (2016)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
	TYPE 1; TYPE 2; TYPE 7	Deformed outline, abnormal striation patterns, mixed	Mainly Cd and Zn (but also Pb); separately	TRACE METALS	Pandey et al. (2014)
			Cu and Zn	TRACE METALS	Pandey & Bergey (2016)
			High concentration of metals and total nitrogen, high conductivity and biological oxygen demand	MULTIPLE	Pandey et al. (2018a)
			Metals (Cd, Co, Cr, Cu, Fe, Pb and Zn) and nutrients (total phosphorus and total nitrogen)	MULTIPLE	Pandey et al. (2018b)
	–	Not described	Cu and Zn	TRACE METALS	Morin & Coste (2006)
			Mixture of metals (Cd, Cu, Pb, Zn)	TRACE METALS	Lavoie et al. (2012)
			AMD	AMD	Fernández et al. (2018)
Fragilaria crotonensis Kitton 1869	TYPE 1	Abnormal valve outline (abnormal and bent frustules with notched or incised valves)	Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as FCRO (*Fragilaria crotonensis*)]
		Asymmetrical, abnormal and bent frustules with notched or incised valves	Cd and Zn	TRACE METALS	Nunes et al. (2003)
		Deformed outline	Mixture of metals (mainly Pb, Cd, Zn)	TRACE METALS	Ferreira da Silva et al. (2009) [as *Fragilaria* cf. *crotonensis* Kitton]
			Low discharge, high temperatures and salinity	MULTIPLE	Lai et al. (2019)
	–	Not described	copper	TRACE METALS	Fontana et al. (2014)
Fragilaria gracilis Østrup 1910	TYPE 1	Abnormal valve outline	Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as FCGR (*Fragilaria capucina* var. *gracilis*)]
		Bent or twisted valves in their middle part	1.5 µg Cd l^{-1} and 50 µg Zn l^{-1}	TRACE METALS	Gold (2002) [as *Fragilaria capucina* Desmazieres var. *gracilis* (Oestrup) Hustedt fo. *teratogene*]
		Wiggly frustules, losing transverse symmetry	Cd and Zn	TRACE METALS	Morin & Coste (2006)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
		Sigmoid outline	Cd and Zn	TRACE METALS	Morin et al. (2008b) [as *Fragilaria capucina* var. *gracilis*]
		Sigmoid outline	Unknown	UNKNOWN	Cantonati & Lange-Bertalot (2011)
Fragilaria nanoides Lange-Bertalot in Lange-Bertalot & Metzeltin 1996	TYPE 1	Abnormal valve outline	Cu	TRACE METALS	Ruggiu et al. (1998) [misidentified as *Synedra tenera* W. Smith]
	TYPE 3	Distorted central area	Cu (2,000 $\mu g \cdot g^{-1}$)	TRACE METALS	Cattaneo et al. (2004) [misidentified as *Fragilaria* cf. *tenera*]
Fragilaria neotropica P.D. Almeida, E. Morales & C.E. Wetzel in Almeida et al. (2016)	TYPE 1	Deformed outline (zig-zag central area and deflected apices)	Probably trace metals	TRACE METALS	Almeida et al. (2016)
Fragilaria pararumpens Lange-Bertalot, G. Hofmann & Werum in Hofmann et al. 2013	–	Not described	Multiple (mainly olive mills waterwaters and hydrological stress)	MULTIPLE	Smeti et al. (2019) [as *Fragilaria* cf. *pararumpens*]
Fragilaria recapitellata Lange-Bertalot & Metzeltin in Metzeltin et al. 2009	TYPE 1	Mainly deformed valve outline	Mainly Zn and Cu	TRACE METALS	Olenici et al. (2017)
	TYPE 2; TYPE 3	Abnormal striation, central area	Mixture of metals	TRACE METALS	Falasco et al. (2009b) [as *Fragilaria capucina* var. *capitellata* (Grunow) Lange-Bertalot]
	–	Not described	AMD	AMD	Fernández et al. (2018) [as *Fragilaria capucina* var. *capitellata* (Grunow) Lange-Bertalot 1991]
			Multiple (mainly olive mills waterwaters and hydrological stress)	MULTIPLE	Smeti et al. (2019)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Fragilaria rumpens (Kützing) G.W.F. Carlson 1913 (Kützing) Lange-Bertalot]	TYPE 1	Asymmetrical, abnormal and bent frustules with notched or incised valves	Cd and Zn	TRACE METALS	Nunes et al. (2003) [as *Fragilaria capucina* Desmazières var. *rumpens*
		Deformed valve outline (mainly the loss of the double symmetry)	Mixture of metals in the sediments	TRACE METALS	Tapia (2008) [as *Synedra rumpens* Kützing]
			Mixture of metals	TRACE METALS	Falasco et al. (2009b)
			Mixture of metals (mainly Pb, Cd, Zn)	TRACE METALS	Ferreira da Silva et al. (2009)
			Mainly Zn and Cu	TRACE METALS	Olenici et al. (2017)
	TYPE 3	Distorted central area	Cu (2,000 $\mu g \cdot g^{-1}$)	TRACE METALS	Cattaneo et al. (2004) [as *Fragilaria capucina* var. *rumpens*]
	TYPE 1; TYPE 2	Abnormal outline and ornamentation	Mixture of metals and low pH	AMD	Luís et al. (2011)
	TYPE 1a; TYPE 7	Central-both margins, “cymbelloid” and “cymbelliclinum-like shape”; central-one margin; mixed	Mixture of metals (mainly As and Pb)	TRACE METALS	Tolotti et al. (2019)
	TYPE 1; TYPE 2	Deformed outline and disruptions in the arrangement of fine structure elements	Multiple	MULTIPLE	Barinova, (2017)
	TYPE 1; TYPE 2; TYPE 3	Deformed outline, abnormal striation, central area	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Falasco et al. (2009b)
	–	Not described	Multiple (mainly olive mills waterwaters and hydrological stress)	MULTIPLE	Smeti et al. (2019)
Fragilaria schulzii C. Brockmann 1950	–	Not described	High organic matter levels	ORGANIC LOADING AND EUTROPHICATION	Dziengo-Czaja & Matuszak (2008)
Fragilaria sp.	TYPE 1	Sigmoid outline	Unknown	UNKNOWN	Buczkó et al. (2009) [misidentified as *Fragilaria incisa* (C.S.Boyer) Lange-Bertalot]

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
			Trace metal contamination: Cd, Cu, Fe, and Zn	TRACE METALS	Cichoń (2016)
	TYPE 1; TYPE 3	Not described	Trace metals mixture	TRACE METALS	León et al. (2018)
	–	Not described	Unknown	UNKNOWN	Soylu (2015)
Fragilaria spp.	–	Not described	Cd and Zn	TRACE METALS	Morin et al. (2008b)
Fragilaria striatula Lyngbye 1819	TYPE 1	Deformed valves, asymmetrical or even twisted	Extreme life conditions (tides)	PHYSICAL STRESS	Aleem (1950)
Fragilaria vaucheriae (Kützing) J.B. Petersen 1939	TYPE 1	Asymmetrically abnormal; bent valves	Cd, Cu, Fe and Zn	TRACE METALS	McFarland et al. (1997) [as *Fragilaria capucina* var. *vaucheriae* (Kütz.) Lange-Bertalot]
		Abnormal valve outline	Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as FCVA (*Fragilaria capucina* var. *vaucheriae*)]
			Pesticides	PESTICIDES	Debenest et al. (2006) [as *Fragilaria capucina* var. *vaucheriae* (Kutz.)]
			Mixture of metals in the sediments	TRACE METALS	Tapia (2008) [as *Synedra vaucheriae* (Kützing) Kützing]
			Mainly Zn and Cu	TRACE METALS	Olenici et al. (2017)
	TYPE 1; TYPE 2	Abnormal outline and ornamentation	No clear causes (probably nutrient levels or uv exposure)	UNKNOWN	Majewska et al. (2012) [as *Fragilaria capucina* var. *vaucheriae* (Kützing) Lange-Bertalot]
	TYPE 1; TYPE 2; TYPE 3	Deformed outline, abnormal striation, central area	Mixture of metals	TRACE METALS	Falasco et al. (2009b) [as *Synedra vaucheriae* (Kützing) Kützing]
	TYPE 1; TYPE 2; TYPE 7	Abnormal outline of valves; irregular striation patterns; interruption of pseudoraphe; mixed	Low current velocity and flows, drought conditions, and consequent light intensity and high water temperature	PHYSICAL STRESS	Antoine & Benson-Evans (1984)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
	–	Not described	Cd and Zn	TRACE METALS	Morin & Coste (2006) [as *Fragilaria capucina* var. *vaucheriae* (Kützing) Lange-Bertalot]
			Intensive agriculture and urban area	ORGANIC LOADING AND EUTROPHICATION	Straub et al. (2014) [as *Fragilaria capucina* var. *vaucheriae*]
			AMD	AMD	Fernández et al. (2018) [as *Fragilaria capucina* var. *vaucheriae* (Kützing) Lange-Bertalot 1980]
Fragilariforma virescens (Ralfs) D.M.Williams & Round 1988	TYPE 1	Abnormal valve outline	Low pH (3)	pH	Barber & Carter (1981) [as *Fragilaria virescens* Ralfs]
Fragilariforma virescens var. *subsalina* (Grunow in Van Heurck) Bukhtiyarova 1995	–	Not described	High organic matter levels	ORGANIC LOADING AND EUTROPHICATION	Dziengo-Czaja & Matuszak (2008) [as *Fragilaria virescens* var. *subsalina* (Ralfs) Grunow]
Frustulia curvata Kulichová & Urbánková in Urbánková et al. (2015)	TYPE 1	Deformed outline (asymmetry)	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Urbánková et al. (2015)
Gomphonella olivacea (Hornemann) Rabenhorst 1853	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b) [as *Gomphonema olivaceum* (Hornemann) Kützing]
	TYPE 2	Abnormal striation patterns	Fluoranthene (200 µg l^{-1})	PESTICIDES	Rimet et al. (2004) [as *Gomphonema olivaceum* (Hornemann) Brébisson]
	–	Not described	AMD	AMD	Fernández et al. (2018) [as *Gomphonema olivaceum* (Hornemann) Brébisson 1838]

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
			Cd and Zn	TRACE METALS	Morin & Coste (2006) [as *Gomphonema olivaceum* (Hornemann) Brébisson]
Gomphonema coronatum Ehrenberg 1840	TYPE 1; TYPE 2	Deformed outline, abnormal striation	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Falasco et al. (2009b)
Gomphonema exilissimum (Grunow) Lange-Bertalot & E. Reichardt in Lange-Bertalot & Metzeltin 1996	–	Not described	AMD	AMD	Fernández et al. (2018)
Gomphonema gracile Ehrenberg 1838	TYPE 1	Abnormal outline of valves	Cd and Zn	TRACE METALS	Morin & Coste (2006)
		Deformed outline (marked invagination on the side opposite to the stigma; boomerang shape)	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Cerisier et al. (2019)
		Deformed outline (boomerang shape). In all cases, the invagination of the frustule was located opposite to the stigma present in the central area	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Coquillé & Morin (2019)
Gomphonema graciledictum E. Reichardt (2015)	TYPE 1	Inflation in the middle of the valve	Unknown	UNKNOWN	Reichardt (2015)
Gomphonema micropus Kützing 1844	TYPE 1	Abnormal valve outline	Pesticides	PESTICIDES	Debenest et al. (2006)
	TYPE 2; TYPE 4; TYPE 7	Abnormal striation, raphe modifications, mixed	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Falasco et al. (2009b)
Gomphonema parvulum Kützing 1849	TYPE 1	Deformed outline	Pesticides	PESTICIDES	Debenest et al. (2006)
			Mixture of metals	TRACE METALS	Falasco et al. (2009b)
			Textile effluent	MULTIPLE	Sierra & Gómez (2010)
			Unknown	UNKNOWN	Bes et al. (2012)
				TRACE METALS	Pandey et al. (2014)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
			Mainly Cd and Zn (but also Pb); separately		
	TYPE 2	Interrupted striation pattern; irregularly directed striae; insert of short striae; abnormal stigma	Nutrient loading, especially of nitrogen	ORGANIC LOADING AND EUTROPHICATION	Murakami & Kasuya (1993)
		Abnormal striation pattern	Cu and Zn pollution	TRACE METALS	Morin & Coste (2006)
		Abnormal striation pattern	Cu and Zn pollution	TRACE METALS	Morin et al. (2007)
	TYPE 1; TYPE 2	Abnormal poroids shape or pattern in correspondence of apical pore field or deformed apices	Cd contamination (100 μg Cd·l^{-1})	TRACE METALS	Morin et al. (2008a)
		Abnormal outline and ornamentation	No clear causes (probably nutrient levels or UV exposure)	UNKNOWN	Majewska et al. (2012)
	TYPE 2; TYPE 4	Abnormal ornamentation pattern and raphe structure	Cd	TRACE METALS	Duong et al. (2008)
				TRACE METALS	Morin et al. (2008c)
	TYPE 1; TYPE 2; TYPE 4	Abnormal pattern of striation, deformed or interrupted raphe and deformities in valve outline	Ni (155.5 μg g^{-1}), Cu (35 μg g^{-1}), and Pb (20.45 μg g^{-1})	TRACE METALS	Gómez et al. (2008)
	TYPE 1; TYPE 2; TYPE 7	Multiple (outline, ornamentation and mixed)	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Falasco et al. (2009b)
		Multiple (outline, ornamentation and mixed)	Cu and Zn	TRACE METALS	Pandey & Bergey (2016)
		Multiple (outline, ornamentation and mixed)	High concentration of metals and total nitrogen, high conductivity and biological oxygen demand	MULTIPLE	Pandey et al. (2018a)
		Multiple (outline, ornamentation and mixed)	High metal concentrations, total nitrogen, coliforms, BOD and conductivity	MULTIPLE	Pandey et al. (2019)
	-	Not described	AMD	AMD	Fernández et al. (2018)
Gomphonema pseudoaugur Lange-Bertalot 1979	TYPE 1	Deformed outline (mainly swollen in the middle of the valve)	Trace metals mixture (especially Pb and Se)	TRACE METALS	Gautam et al. (2017)
Gomphonema pumilum (Grunow) E. Reichardt & Lange-Bertalot 1991	TYPE 1; TYPE 2; TYPE 7	Multiple (outline, ornamentation and mixed)	Cu and Zn	TRACE METALS	Pandey & Bergey (2016)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Gomphonema rosenstockianum Lange-Bertalot & E. Reichardt in Lange-Bertalot 1993	TYPE 1; TYPE 3; TYPE 4	Deformed outline, central area, raphe modifications	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Falasco et al. (2009b)
	–	Not described	AMD	AMD	Fernández et al. (2018)
Gomphonema tergestinum (Grunow in Van Heurck) Fricke in Schmidt et al. 1902	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
Gomphonema truncatum Ehrenberg 1832	TYPE 2	Irregular striation pattern	Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as GTRU (*Gomphonema truncatum*)]
	TYPE 1; TYPE 2; TYPE 4; TYPE 7	Abnormal outline, abnormal striation, raphe alterations, mixed	Cd	TRACE METALS	Kim Tiam et al. (2019)
	–	Not described	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Kim Tiam et al. (2019)
Gomphosphenia lingulatiformis (Lange-Bertalot & E. Reichardt) Lange-Bertalot 1995	TYPE 1	Deformed valve outline	NO CLEAR CAUSES (PROBABLY PB CONTAMINATION)	TRACE METALS	Mora et al. (2015)
Grammatophora marina (Lyngbye) Kützing 1844	TYPE 1	Abnormal valve outline (one side wavy, unsymmetrical)	EXTERNAL AND MECHANICAL CAUSES	PHYSICAL STRESS	Cox (1890)
Guinardia delicatula (Cleve) Hasle in Hasle & Syvertsen 1997	–	Not described	OIL SPILL	OTHERS	Tabassum et al. (2015)
Guinardia flaccida (Castracane) H. Peragallo, 1892	–	Not described	Oil spill	OTHERS	Tabassum et al. (2015)
Gyrosigma fasciola J.W. Griffith & Henfrey 1856	TYPE 1	Abnormal outline involving apices	Low pH	pH	Rogelja et al. (2016)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Halamphora normanii (Rabenhorst) Levkov 2009	TYPE 1	Deformed valve outline	Trace metal mixture (mainly Zn)	TRACE METALS	Podda et al. (2014)
Halamphora veneta (Kützing) Levkov 2009	TYPE 1	Deformed outline (dorsal margin bulging and ventral margin concave)	Hg	TRACE METALS	Mu et al. (2017)
		Deformed valve outline	Mixture of metals (Cd, Ni, Zn)	TRACE METALS	Lavoie et al. (2018) [as *Amphora veneta*]
		Deformed outline (dorsal margin bulging and ventral margin concave)	Pb	TRACE METALS	Mu et al. (2018)
	TYPE 1; TYPE 2; TYPE 7	Abnormal outline, abnormal striation, mixed	Unknown	UNKNOWN	Holmes & Taylor (2015) [as *Amphora veneta* Kützing]
Hannaea arcus (Ehrenberg) R.M. Patrick in Patrick & Reimer 1961	TYPE 1	Notched or incised valves	Cd, Cu, Fe and Zn	TRACE METALS	McFarland et al. (1997)
		Notched in the central part of the valve	Multiple	MULTIPLE	Barinova (2017)
Hannaea arcus var. *amphioxys* (Rabenhorst) R.M. Patrick in Patrick & Reimer 1966	TYPE 1; TYPE 2; TYPE 7	Abnormal outline of valves; irregular striation pattern; interruption of pseudoraphe; mixed	Low current velocity and flows, drought conditions, and consequent light intensity and high water temperature	PHYSICAL STRESS	Antoine & Benson-Evans (1984) [as *Ceratoneis arcus* var. *amphioxys* (Rabh.) Brun]
Hantzschia amphioxys (Ehrenberg) Grunow in Cleve & Grunow 1880	-	Not described	AMD	AMD	Fernández et al. (2018)
Hantzschia yili Q.M. You & Kociolek in You et al. (2015)	TYPE 7	Mixed teratology involving fibulae and areolar arrangement	Unknown	UNKNOWN	You et al. (2015)
Humidophila gallica (W. Smith) R.L. Lowe, Kociolek, Q. You, Q. Wang & J. Stepanek 2017	TYPE 1; TYPE 2; TYPE 7	Deformed contour of the valves; pores and spines irregularly distributed or absent; mixed	Unstable environmental conditions: wide oscillations of temperature, moisture conditions and light	PHYSICAL STRESS	Granetti (1978) [as *Navicula gallica* (W. Smith) Van Heurck]
	–	Not described	Harsh conditions; subterranean environment	PHYSICAL STRESS	Borrego-Ramos et al. (2018)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Humidophila perpusilla (Grunow) R.L. Lowe, Kociolek, J.R. Johansen, Van de Vijver, Lange-Bertalot & Kopalová in 2014	TYPE 1; TYPE 4	Deformed valve outline and raphe	Multiple (natural radioactivity, high salinity)	MULTIPLE	Millan et al. (2020)
Lemnicola exigua (Grunow) Kulikovskiy, Witkowski & Pliński in Pliński & Witkowski 2011	TYPE 1; TYPE 2; TYPE7	Abnormal outline, abnormal striation, mixed	Cu and Zn	TRACE METALS	Pandey & Bergey (2016)
			High concentration of metals and total nitrogen, high conductivity and biological oxygen demand	MULTIPLE	Pandey et al. (2018a) [as *Achnanthes exigua*]
Lemnicola hungarica (Grunow) Round & Basson 1997	TYPE 2	Irregular striation pattern	Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as AHUN (*Achnanthes hungarica*)]
Licmophora C. Agardh 1827	TYPE 2	Abnormal branching costae	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Gordon & Drum (1994)
Licmophora ovata (W. Smith) Grunow 1867	TYPE 1	Abnormal valve outline (a large, shallow indentation on one side, giving a gracefully varied outline)	External and mechanical causes	PHYSICAL STRESS	Cox (1890) [as *Licmophora ovata*, Ehr.]
Licmophora gracilis (Ehrenberg) Grunow 1867	TYPE 1	Deformed valves, asymmetrical or even twisted	Extreme life conditions (tides)	PHYSICAL STRESS	Aleem (1950)
Luticola muticopsis (Van Heurck) D.G. Mann in Round et al. 1990	TYPE 1; TYPE 2; TYPE 7	Multiple (outline, ornamentation and mixed)	Metals (Cd, Co, Cr, Cu, Fe, Pb and Zn) and nutrients (total phosphorus and total nitrogen)	MULTIPLE	Pandey et al. (2018b)
Lyrella lyra (Ehrenberg) Karajeva 1978	TYPE 1	Abnormal valve outline (one side indented in a large, easy curve)	External and mechanical causes	PHYSICAL STRESS	Cox (1890) [as *Navicula lyra*, Ehr.]
Mastogloia abnormis Al-Handal & Pennesi in Al-Handal et al. 2016	TYPE 4	Fragmented raphe slit	No clear causes (probably physical parameters such as low current velocity and high light intensity which might affect silica deposition on the valve surface)	PHYSICAL STRESS	Al-Handal et al. (2016)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Mastogloia smithii Thwaites ex W. Smith 1856	TYPE 1; TYPE 2; TYPE 7	Multiple (outline, ornamentation and mixed)	Metals (Cd, Co, Cr, Cu, Fe, Pb and Zn) and nutrients (total phosphorus and total nitrogen)	MULTIPLE	Pandey et al. (2018b)
Mastogonia actinoptychus (Ehrenberg) Ehrenberg 1844	TYPE 3	Double centre (two distinct central spaces from which the costae radiate)	Unknown	UNKNOWN	Cox (1890)
Mayamaea atomus (Kützing) Lange-Bertalot 1997	TYPE 1; TYPE 2; TYPE 4; TYPE 7	Abnormal outline, abnormal striation, raphe alterations, mixed	Cd	TRACE METALS	Kim Tiam et al. (2019)
	–	Not described	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Kim Tiam et al. (2019)
Mayamaea permitis (Hustedt) Bruder & Medlin 2008	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
	TYPE 1; TYPE 2; TYPE 3; TYPE 4; TYPE 7	Raphe aberrations; altered shape and location of central nodule; striae alterations	Anti-microtubule drugs	OTHERS	Blank & Sullivan (1983) [misidentified as *Navicula saprophila* Lange-Bertalot & Bonik]
	–	Not described	Cd and Zn	TRACE METALS	Morin & Coste (2006) [as *Mayamaea atomus* var. *permitis* (Hustedt) Lange-Bertalot]
Melosira nummuloides (Dillwyn) C. Agardh	–	Not described	High organic matter levels	ORGANIC LOADING AND EUTROPHICATION	Dziengo-Czaja & Matuszak (2008)
Melosira varians C. Agardh 1827	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
Meridion circulare (Greville) C. Agardh 1831	TYPE 1	Deformed outline	Pesticides	PESTICIDES	Debenest et al. (2006)
			Cd and Zn	TRACE METALS	Morin & Coste (2006)
Navicula antonii Lange-Bertalot & Rumrich in Rumrich et al. 2000	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
Navicula Bory 1822	TYPE 2	Abnormal branching costae	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Gordon & Drum (1994)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Navicula capitatoradiata H. Germain 1981	TYPE 1; TYPE 2	Deformed outline, abnormal striation	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
Navicula cryptocephala Kützing 1844	TYPE 1	Deformed valves, asymmetrical or even twisted	Changes in pH and salt concentration	MULTIPLE	Aleem (1950)
		Deformed outline	Culture conditions, but also in the original field material (high nutrient levels)	ARTIFICIAL GROWTH CONDITIONS + ORGANIC LOADING AND EUTROPHICATION	Novis et al. (2012)
Navicula cryptotenella Lange-Bertalot in Krammer & Lange-Bertalot 1985	TYPE 1; TYPE 4	Deformed outline, raphe modifications	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
	–	Not described	Intensive agriculture and urban area	ORGANIC LOADING AND EUTROPHICATION	Straub et al. (2014)
Navicula cryptotenelloides Lange-Bertalot 1993	–	Not described	Cu and Zn	TRACE METALS	Morin & Coste (2006)
Navicula detenta Hustedt 1943	–	Not described	High organic matter levels	ORGANIC LOADING AND EUTROPHICATION	Dziengo-Czaja & Matuszak (2008)
Navicula gregaria Donkin 1861	TYPE 1	Deformed outline	Crowding	PHYSICAL STRESS	Barber & Carter (1981)
			Mixture of metals	TRACE METALS	Falasco et al. (2009b)
			Cu and Zn separately	TRACE METALS	Pandey et al. (2015)
	TYPE 3	Abnormal valve outline; unusual striation; unusual length:width ratio	Salinity	PHYSICAL STRESS	Cox, (1995)
	–	Not described	High organic matter levels	ORGANIC LOADING AND EUTROPHICATION	Dziengo-Czaja & Matuszak (2008)
Navicula lanceolata (C. Agardh) Kützing 1844	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
	TYPE 1; TYPE 2; TYPE 7	Multiple (outline, ornamentation and mixed)	Cu and Zn	TRACE METALS	Pandey & Bergey (2016)
	–	Not described	Cu and Zn	TRACE METALS	Morin & Coste (2006)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Navicula muscatinei Reimer & J.J. Lee 1988	TYPE 1; TYPE 2; TYPE 4; TYPE 7	Displacement of the central nodule; abnormal striation pattern; recurvature of one or both ends of the raphe; double or bifurcated raphe; sometimes spherical outline of the valves; mixed	Exceeded the lower limit for sexual reproduction	OTHERS	Lee & Xenophontes (1989)
Navicula recens (Lange-Bertalot) Lange-Bertalot in Krammer & Lange-Bertalot 1985	TYPE 1	Deformed outline	Cu and Zn separately	TRACE METALS	Pandey et al. (2015)
	TYPE 1; TYPE 4	Deformed outline, raphe modification	Mainly Cd and Zn (but also Pb); separately	TRACE METALS	Pandey et al. (2014)
	TYPE 1; TYPE 2; TYPE 7	Multiple (outline, ornamentation and mixed)	Metals (Cd, Co, Cr, Cu, Fe, Pb and Zn) and nutrients (total phosphorus and total nitrogen)	MULTIPLE	Pandey et al. (2018b)
Navicula reichardtiana Lange-Bertalot in Lange-Bertalot & Krammer 1989	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
	–	Not described	Intensive agriculture and urban area	ORGANIC LOADING AND EUTROPHICATION	Straub et al. (2014)
Navicula rostellata Kützing 1844	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
Navicula samoensis Grunow in Schmidt et al. 1877	TYPE 2; TYPE 3; TYPE 7	Double centre (a second median nodule appears, with the striae radiating from it in all directions)	Unknown	UNKNOWN	Cox (1890)
Navicula sp.	TYPE 1	Deformed outline	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Park et al. (2020)
			Cu (1 mg Cu l^{-1})	TRACE METALS	
	TIPE 2	Abnormal striation pattern	Cu (1 mg Cu l^{-1})	TRACE METALS	
Navicula tripunctata (O.F. Müller) Bory 1822	TYPE 1	Deformed outline	Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as NTPT (*Navicula tripunctata*)]
			Mixture of metals	TRACE METALS	Falasco et al. (2009b)
			Multiple (probably trace metals and COD: chemical oxygen demand)	MULTIPLE	Walsh & Wepener (2009)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
			low discharge, high temperatures and salinity	MULTIPLE	Lai et al. (2019)
Navicula trivialis Lange-Bertalot 1980	TYPE 2	Irregular striation pattern	Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as NTRV (*Navicula trivialis*)]
Navicula veneta Kützing 1844	TYPE 1	Deformed outline	mixture of metals	TRACE METALS	Falasco et al. (2009b)
Navigiolum ricula (M.H. Hohn & Hellerman) C.E. Wetzel & Ector 2018	–	Not described	AMD	AMD	Fernández et al. (2018) [as *Achnanthes ricula* Hohn & Hellerman 1963]
Neidiomorpha binodis (Ehrenberg) Cantonati, Lange-Bertalot & N.Angeli 2010	TYPE 1	Deformed outline	Low discharge, high temperatures and salinity	MULTIPLE	Lai et al. (2019)
Nitzschia acicularis (Kützing) W. Smith 1853	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
Nitzschia alba J.C. Lewin & R.A. Lewin 1967	TYPE 1	Deformed outline	Ge (high Ge/Si ratio)	TRACE METALS	Chiappino et al. (1977)
Nitzschia amphibia Grunow 1862	TYPE 1	Deformed outline	Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as NAMP (*Nitzschia amphibia*)]
			Cu and Zn separately	TRACE METALS	Pandey et al. (2015)
	TYPE 1; TYPE 2; TYPE 5	Deformed valve outline, displaced raphe canal and abnormal striation pattern	No clear causes (probably Pb contamination)	TRACE METALS	Mora et al. (2015)
Nitzschia archibaldii Lange-Bertalot 1980	TYPE 1	Abnormal valve outline	Fluoranthene (200 μg l^{-1})	PESTICIDES	Rimet et al. (2004)
	–	Not described	Cd and Zn	TRACE METALS	Morin & Coste (2006)
Nitzschia brevissima Grunow in Van Heurck 1881	TYPE 1	Deformed outline	Probably the use of algicide or algistatic compounds	PESTICIDES	Ács & Lakatos (1989)
Nitzschia capitellata Hustedt in Schmidt et al. 1922	TYPE 1; TYPE 5	Deformed valve outline, displaced raphe	No clear causes (probably Pb contamination)	TRACE METALS	Mora et al. (2015)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Nitzschia dissipata (Kützing) Rabenhorst 1860	TYPE 5	Deformed raphe channel	Cd	TRACE METALS	Morin et al. (2008c)
			Thiram or hydrocarbon emulsion	PESTICIDES	Bayona et al. (2014)
	TYPE 1; TYPE 5; TYPE 7	Deformed outline, raphe channel modification, mixed	mixture of metals	TRACE METALS	Falasco et al. (2009b)
	–	Not described	Cd and Zn	TRACE METALS	Morin & Coste (2006)
			Unknown	UNKNOWN	Falasco et al. (2012)
			Intensive agriculture and urban area	ORGANIC LOADING AND EUTROPHICATION	Straub et al. (2014)
Nitzschia dubiformis Hustedt 1939	TYPE 1	Deformed outline (bent in the middle of the valve)	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Stachura-Suchoples et al. (2016) [as *Nitzschia* sp. aff. *dubiiformis* Hustedt]
Nitzschia exilis Sovereign 1958	TYPE 1; TYPE 2; TYPE 5; TYPE 7	Multiple (outline, ornamentation, raphe channel and mixed)	metals (Cd, Co, Cr, Cu, Fe, Pb and Zn) and nutrients (total phosphorus and total nitrogen)	MULTIPLE	Pandey et al. (2018b)
Nitzschia fonticola (Grunow) Grunow in Van Heurck 1881	TYPE 5	Distorted raphe channel	Cd and Zn	TRACE METALS	Morin & Coste (2006)
		Deformed raphe channel	Thiram or hydrocarbon emulsion	PESTICIDES	Bayona et al. (2014)
	TYPE 1; TYPE 2; TYPE 5	Deformed outline, abnormal striation, raphe channel modification	mixture of metals	TRACE METALS	Falasco et al. (2009b)
Nitzschia frustulum (Kützing) Grunow in Cleve & Grunow 1880	TYPE 1	Deformed outline	TiO_2 nanoparticles	TRACE METALS	Jia et al. (2019)
	TYPE 1; TYPE 2; TYPE 5; TYPE 7	Multiple (outline, ornamentation, raphe channel and mixed)	Cu and Zn	TRACE METALS	Pandey & Bergey (2016)
		Deformed outline, patterns of striation, mixed, deformed or dislocated raphe channel	Ammonium, phosphorous, pharmaceutical compounds and hydrological pressure	MULTIPLE	Tornés et al. (2018)
	–	Not described	AMD	AMD	Fernández et al. (2018)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Nitzschia hantzschiana Rabenhorst 1860	TYPE 1; TYPE 2	Abnormal outline and ornamentation	Mixture of metals and low pH	AMD	Luís et al. (2011)
Nitzschia homburgiensis Lange-Bertalot 1978	–	Not described	AMD	AMD	Fernández et al. (2018)
Nitzschia inconspicua Grunow 1862	TYPE 1	Abnormal valve outline	Cd	TRACE METALS	Morin et al. (2008c)
	TYPE 5	Raphe channel modification	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
	–	Not described	AMD	AMD	Fernández et al. (2018)
Nitzschia intermedia Hantzsch ex Cleve & Grunow 1880	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
Nitzschia laevis Hustedt 1939	TYPE 1	Deformed outline	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Stachura-Suchoples et al. (2016) [as *Nitzschia* sp. aff. *laevis* Hustedt]
Nitzschia liebethruthii Rabenhorst 1864	TYPE 1	Deformed outline	Hg and Sn	TRACE METALS	Saboski (1977)
			Extreme environmental conditions (i.e. high UV radiation, high salt content, geothermal flux, large nutrient supply)	MULTIPLE	Cabrol et al. (2007)
Nitzschia linearis (C. Agardh) W. Smith 1853	TYPE 1	Deformed outline	Mainly Zn and Cu	TRACE METALS	Olenici et al. (2017)
	TYPE 7	Mixed	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
	TYPE 1; TYPE 5	Deformed outline, raphe channel modification	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Falasco et al. (2009b)
	TYPE 1; TYPE 2; TYPE 5; TYPE 7	Multiple (outline, ornamentation, raphe channel and mixed)	Cu and Zn	TRACE METALS	Pandey & Bergey (2016)
	–	Not described	Cd and Zn	TRACE METALS	Morin & Coste (2006)
Nitzschia longissima (Brébisson in Kützing) Ralfs in Pritchard 1861	TYPE 1	Abnormal outline involving apices	Low pH	pH	Rogelja et al. (2016)
Nitzschia palea (Kützing) W. Smith 1856	TYPE 1	Deformed outline	Artificial growth conditions: nutrient deficiency	ARTIFICIAL GROWTH CONDITIONS	Cholnoky-Pfannkuche (1971)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
			Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as NPAL (*Nitzschia palea*)]
		Deformed apices	Cd contamination (100 µg $Cd{\cdot}l^{-1}$)	TRACE METALS	Morin et al. (2008a)
		Deformed outline	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Falasco et al. (2009b)
			Mixture of metals	TRACE METALS	Falasco et al. (2009b)
			Cu and Zn separately	TRACE METALS	Pandey et al. (2015)
	TYPE 1; TYPE 2	Abnormal outline and ornamentation	No clear causes (probably nutrient levels or UV exposure)	UNKNOWN	Majewska et al. (2012)
		Valve expanded or constricted on one side; abnormal ornamentation	acephate (50 mg l^{-1})	PESTICIDES	Wang et al. (2020)
	TYPE 5	Central location of the raphe system; curved raphe channel occasionally doubled back; abnormal arrangements of fibulae	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Estes & Dute (1994)
		Abnormal raphe canal, interruption in the fibulae	Cd	TRACE METALS	Morin et al. (2008c)
	TYPE 1; TYPE 5	Deformed outline, raphe modification	Mainly Cd and Zn (but also Pb); separately	TRACE METALS	Pandey et al. (2014)
		Deformed shape (bump on one site of the valve), abnormal raphe canal, interruption in the fibulae	Different concentrations of cadmium	TRACE METALS	Cerisier et al. (2019)
	TYPE 1; TYPE 2; TYPE 5	Abnormal pattern of striation, deformed or interrupted raphe and deformities in valve outline	Ni (155.5 µg g^{-1}), Cu (35 µg g^{-1}),and Pb (20.45 µg g^{-1}),	TRACE METALS	Gómez et al. (2008)
		Irregular striae, irregular and interrupted fibulae, raphe channel deviation, abnormal outline	Cd (ca. 40 µg Cd l^{-1})	TRACE METALS	Kim Tiam et al. (2018)
		Irregular striation pattern, double fibulae row, mixed	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Bagmet et al. (2020)
	TYPE 1; TYPE 2; TYPE 5; TYPE 7	Multiple (outline, ornamentation, raphe channel and mixed)	Cu and Zn	TRACE METALS	Pandey & Bergey (2016)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
		Abnormal shape, irregular striae, raphe canal deviations, fibulae/canal interruption, irregular fibulae, mixed	Cd	TRACE METALS	Kim Tiam et al. (2019)
	–	Not described	Cd and Zn	TRACE METALS	Morin & Coste (2006)
			Cd and Zn	TRACE METALS	Morin et al. (2007)
			Trace metals (Cd)	TRACE METALS	Duong et al. (2008)
			Unknown	UNKNOWN	Falasco et al. (2012)
			Multiple	MULTIPLE	Medvedeva et al. (2012)
			Mixture of metals (Pb, Cu, Zn)	TRACE METALS	Simić et al. (2018)
			AMD	AMD	Fernández et al. (2018)
			Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Kim Tiam et al. (2019)
Nitzschia palea var. *debilis* (Kützing) Grunow in Cleve & Grunow 1880	TYPE 1	deformed valve outline	Mixture of metals (Cd, Ni, Zn)	TRACE METALS	Lavoie et al. (2018)
Nitzschia paleacea (Grunow) Grunow in Van Heurck 1881	TYPE 5	Deformed raphe channel	Thiram or hydrocarbon emulsion	PESTICIDES	Bayona et al. (2014)
	–	Not described	AMD	AMD	Fernández et al. (2018)
Nitzschia pusilla Grunow 1862	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b) [as *Nitzschia pusilla* (Kützing) Lange-Bertalot]
Nitzschia recta Hantzsch ex Rabenhorst 1862	–	Not described	Intensive agriculture and urban area	ORGANIC LOADING AND EUTROPHICATION	Straub et al. (2014)
Nitzschia scalaris (Ehrenberg) W. Smith 1853	TYPE 2; TYPE 5; TYPE 7	One part of the cell keel is distorted and instead of it appear two nodules on the face of the shell with irregularly radiating striae; mixed	Unknown	UNKNOWN	Cox (1890)
Nitzschia sinuata (Thwaites in W. Smith) Grunow in Cleve & Grunow 1880	TYPE 1	Abnormal valve outline	High pH (8.5)	pH	Barber & Carter (1981)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Nitzschia sp.	TYPE 1	Deformed outline	Low discharge, high temperatures and salinity	MULTIPLE	Lai et al. (2019)
			Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Park et al. (2020)
	TYPE 5	Deformed raphe channel	Cu (1 mg Cu l^{-1})	TRACE METALS	Park et al. (2020)
	TYPE 7	Mixed	Cu (1 mg Cu l^{-1})	TRACE METALS	Park et al. (2020)
	TYPE 1; TYPE 2; TYPE 7	Multiple (outline, ornamentation and mixed)	Unknown	UNKNOWN	Holmes & Taylor (2015)
	TYPE 1; TYPE 2; TYPE 5; TYPE 7	Multiple (outline, ornamentation, raphe channel and mixed)	Metals (Cd, Co, Cr, Cu, Fe, Pb and Zn) and nutrients (total phosphorus and total nitrogen)	MULTIPLE	Pandey et al. (2018b)
Nitzschia umbonata (Ehrenberg) Lange-Bertalot 1978	TYPE 1; TYPE 2	Deformed outline and striation pattern	Textile effluent	MULTIPLE	Sierra & Gómez (2010)
	TYPE 2; TYPE 5	Displaced raphe and abnormal striation pattern	No clear causes (probably Pb contamination)	TRACE METALS	Mora et al. (2015)
	TYPE 1; TYPE 2; TYPE 5	Abnormal pattern of striation, deformed or interrupted raphe and deformities in valve outline	Ni (155.5 $\mu g\ g^{-1}$), Cu (35 $\mu g\ g^{-1}$),and Pb (20.45 $\mu g\ g^{-1}$),	TRACE METALS	Gómez et al. (2008)
Nitzschia vasta Hustedt 1939	–	Not described	AMD	AMD	Fernández et al. (2018)
Nupela gracillima (Hustedt) Lange-Bertalot 1993	–	Not described	AMD	AMD	Fernández et al. (2018)
Nupela troglophila Falasco, C.E. Wetzel & Ector in Falasco et al. (2015)	TYPE1; TYPE 2; TYPE 4; TYPE 7	Abnormal outline, abnormal striation pattern and raphe; mixed	Extreme environmental conditions subterranean environment, extreme life conditions	PHYSICAL STRESS	Falasco et al. (2015)
Odontella antediluviana (Ehrenberg) Peragallo 1903	TYPE 2; TYPE 3; TYPE 7	Central part of the cell irregularly areolate with a tendency to two centres; mixed	Unknown	UNKNOWN	Cox (1890) [as *Amphitetras antediluviana*, Ehr.]
Olifantiella muscatinei (Reimer & J.J. Lee) Van de Vijver, Ector & C.E. Wetzel 2018	TYPE 1; TYPE 2; TYPE 4	Apical valve asymmetry; irregular arrangement of striae; atypical raphe systems	Not sure, probably anti-biofouling paint	OTHERS	Jung & Park (2019)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Olifantiella onnuria S.W. Jung & J.S. Park 2019	TYPE 1; TYPE 2; TYPE 4	Apical valve asymmetry; irregular arrangement of striae; atypical raphe systems	Not sure, probably anti-biofouling paint	OTHERS	Jung & Park (2019)
Opephora olsenii M.Møller 1950	-	Not described	High organic matter levels	ORGANIC LOADING AND EUTROPHICATION	Dziengo-Czaja & Matuszak (2008)
Oricymba tianmuensis W. Zhang & Y.-L. Li in Zhang et al. (2015)	TYPE 2	Abnormal areolae pattern	Unknown	UNKNOWN	Zhang et al. (2015)
Pantocsekiella ocellata (Pantocsek) K.T. Kiss & Ács in Ács et al. 2016	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b) [as *Cyclotella ocellata* Pantocsek]
Paralia sp.	TYPE 1	Oval shape	Unknown	UNKNOWN	Oreshkina et al. (2013)
Parlibellus protractus (Grunow) Witkowski, Lange-Bertalot & Metzeltin 2000	–	Not described	High organic matter levels	ORGANIC LOADING AND EUTROPHICATION	Dziengo-Czaja & Matuszak (2008) [as *Navicula protracta* (Grun.) Cleve]
Phaeodactylum tricornutum Bohlin 1897	TYPE 1	Abnormal outline (irregular boundaries or shrivelled shape)	Zn, Cu	TRACE METALS	Renzi et al. (2014)
Pinnularia acidophila G. Hofmann & Krammer in Krammer 2000	–	Not described	AMD	AMD	Fernández et al. (2018)
Pinnularia aljustrelica Luís, S.F.P. Almeida & Ector in Luís et al. 2012	–	Not described	AMD	AMD	Fernández et al. (2018)
Pinnularia biceps W. Gregory 1856	TYPE 1; TYPE 2; TYPE 7	Multiple (outline, ornamentation and mixed)	High metal concentrations, total nitrogen, coliforms, BOD and conductivity	MULTIPLE	Pandey et al. (2019)
Pinnularia borealis Ehrenberg 1843	TYPE 1; TYPE 2; TYPE 7	Multiple (outline, ornamentation and mixed)	metals (Cd, Co, Cr, Cu, Fe, Pb and Zn) and nutrients (total phosphorus and total nitrogen)	MULTIPLE	Pandey et al. (2018b)
Pinnularia brebissonii (Kützing) Rabenhorst 1864	TYPE 2; TYPE 3; TYPE 4; TYPE 7	Raphe system (absent, distorted, angular); displaced central area; abnormal striation pattern; mixed	Artificial conditions	ARTIFICIAL GROWTH CONDITIONS	Hostetter & Rutherford (1976)
Pinnularia conica H.P. Gandhi 1957	TYPE 1; TYPE 4	Deformed outline, raphe modification	Mainly Cd and Zn (but also Pb); separately	TRACE METALS	Pandey et al. (2014)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
	TYPE 1; TYPE 2; TYPE 7	Multiple (outline, ornamentation and mixed)	Cu and Zn	TRACE METALS	Pandey & Bergey (2016)
Pinnularia gibba (Ehrenberg) Ehrenberg 1843	TYPE 1; TYPE 2	Deformed outline and striation pattern	Textile effluent	MULTIPLE	Sierra & Gómez (2010)
	TYPE 1; TYPE 4	Deformed outline and/or unusual raphe system (fragmented, displaced)	FE, Cu, Zn, Ni	TRACE METALS	Sienkiewicz & Gąsiorowski (2016)
	TYPE 1; TYPE 2; TYPE 4	Abnormal pattern of striation, deformed or interrupted raphe and deformities in valve outline	Ni (155.5 μg g^{-1}), Cu (35 μg g^{-1}),and Pb (20.45 μg g^{-1}),	TRACE METALS	Gómez et al. (2008)
	TYPE 1; TYPE 2; TYPE 4; TYPE 7	Abnormal striation pattern; deformed or interrupted raphe; deformities of the outline of the valves; anomalies in the striation or in the raphe line; mixed	Water quality: high level of nutrients, BOD_5, COD (chemical oxygen demand), pH, Cu (up to 59 μg l^{-1}) and Zn (from 23 μg l^{-1})	MULTIPLE	Gómez & Licurs, (2003)
	–	Not described	Low pH and mixture of trace metals	AMD	Sienkiewicz & Gąsiorowski (2017, 2019)
Pinnularia mesolepta (Ehrenberg) W. Smith 1853	TYPE 1; TYPE 2; TYPE3; TYPE 4; TYPE 7	Abnormal outline, abnormal striation, wide central area or lack of central area, raphe alterations, mixed	Cd	TRACE METALS	Kim Tiam et al. (2019)
	–	Not described	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Kim Tiam et al. (2019)
Pinnularia obaesa Van de Vijver (2008)	TYPE 2	Alterations in striae structure	Unknown (maybe drought impact)	UNKNOWN	Van de Vijver (2008)
Pinnularia subcapitata var. *elongata* Krammer 1992	–	Not described	AMD	AMD	Fernández et al. (2018)
Planothidium delicatulum (Kützing) Round & Bukhtiyarova 1996	–	Not described	High organic matter levels	ORGANIC LOADING AND EUTROPHICATION	Dziengo-Czaja & Matuszak (2008)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Planothidium dispar (Cleve) Witkowski, Lange-Bertalot & Metzeltin, 2000	-	Not described	High organic matter levels	ORGANIC LOADING AND EUTROPHICATION	Dziengo-Czaja & Matuszak (2008) [as *Achnanthes dispar* Cleve]
Planothidium dubium (Grunow) Round & Bukhtiyarova 1996	TYPE 2	Abnormal striation pattern	Fluoranthene (200 µg l^{-1})	PESTICIDES	Rimet et al. (2004)
Planothidium frequentissimum (Lange-Bertalot in Krammer & Lange-Bertalot) Lange-Bertalot 1999	TYPE 2	Abnormal striation pattern	Fluoranthene (200 µg l^{-1})	PESTICIDES	Rimet et al. (2004)
	TYPE 3	Double central area	Cd and Zn	TRACE METALS	Morin et al. (2007)
	TYPE 2; TYPE 7	Striation and mixed teratology	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Arini et al. (2013)
	TYPE 1; TYPE 2; TYPE 7	Deformed outline, patterns of striation, mixed	High concentration of metals and total nitrogen, high conductivity and biological oxygen demand	MULTIPLE	Pandey et al. (2018a)
			Ammonium, phosphorous, pharmaceutical compounds and hydrological pressure	MULTIPLE	Tornés et al. (2018)
	TYPE 1; TYPE 3; TYPE 7	Deformed outline, central area, mixed	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
	TYPE 1; TYPE 3; TYPE 4	Deformations on valve outline, cavum bearing and raphe	Multiple (natural radioactivity, high salinity)	MULTIPLE	Millan et al. (2020)
	TYPE 1; TYPE 2; TYPE 3; TYPE 4; TYPE 7	Striation pattern (mainly); raphe system; outline and central area (less frequent); mixed (most rare)	Cd (20 and 100 µg l^{-1})	TRACE METALS	Arini et al. (2013)
	–	Not described	Cd and Zn	TRACE METALS	Morin et al. (2008b)
			AMD	AMD	Fernández et al. (2018)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Planothidium hauckianum (Grunow) Bukhtiyarova 1999	TYPE 1	Lack of bilateral symmetry	Trace metal contamination (Cd, Cr, Cu, Fe, Ni, Pb, Zn)	TRACE METALS	Dickman (1998) [as *Achnanthes hauckiana* Grun.]
Planothidium lanceolatum (Brébisson ex Kützing) Lange-Bertalot 1999	TYPE 2	Abnormal striation pattern	Fluoranthene (200 μg l^{-1})	PESTICIDES	Rimet et al. (2004)
	TYPE 3	Doubled hood in the central area	Unknown	UNKNOWN	Hustedt (1950) [as *Achnanthes lanceolata* var. *bimaculata*]
			Unknown	UNKNOWN	Geitler (1977)
			Unknown	UNKNOWN	Bukhtiyarova (2017) [as *Planothidium bilensis* Bukhtiyarova]
		Longitudinal area curving near the pole	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Jahn et al. (2017)
	–	Not described	Cd and Zn	TRACE METALS	Morin & Coste (2006)
					Morin et al. (2007)
			Trace metal mixture (mainly Cd and Zn)	De Jonge et al. (2008)	
			AMD	AMD	Fernández et al. (2018)
Planothidium victori Novis, Braidwood & Kilroy (2012)	TYPE 1	Abnormal valve outline (especially involving the apices)	Artificial growth conditions, but also in the original field material (high nutrient levels)	ARTIFICIAL GROWTH CONDITIONS	Novis et al. (2012)
Pseudonitzschia pungens (Grunow in Cleve & Möller) Hasle 1993	TYPE 1; TYPE 2; TYPE 7	1–3 Swellings on the margin; undulations of the margin and sometimes a slight disorder of interstriae; mixed	Organic compound	OTHERS	Takano & Kikuchi (1985) [as *Nitzschia pungens* Grunow]
Pseudonitzschia pungens f. *multiseries* (Hasle) Hasle 1993	TYPE 1	Sickle-shaped, beaked and lobed cells with ondulations of the margins	Nutrient depletion	OTHERS	Subba Rao & Wohlgeschaffen (1990) [as *Nitzschia pungens* Grunow f. *multiseries* Hasle]
Pseudonitzschia subfraudulenta (Hasle) Hasle 1993	TYPE 2	Only one row of poroids per stria	Unknown	UNKNOWN	Teng et al. (2013)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Pseudostaurosira binodis (Ehrenberg) Edlund in Edlund et al. 2001	TYPE 1	Abnormal valve outline	Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as FCBI (*Fragilaria construens* f. *binodis*)]
Pseudostaurosira brevistriata (Grunow in Van Heurck) D.M.Williams & Round 1987	TYPE 1	Abnormal valve outline	Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as FBRE (*Fragilaria brevistriata*)]
Reimeria sinuata (W. Gregory) Kociolek & Stoermer 1987	TYPE 1; TYPE 2	Deformed outline, abnormal striation	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
	TYPE 1; TYPE 2; TYPE 3	Deformed outline, abnormal striation, central area	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Falasco et al. (2009b)
Reimeria uniseriata S.E. Sala, J.M. Guerrero & Ferrario 1993	TYPE 1	Abnormal valve outline	Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as RUNI (*Reimeria uniseriata*)]
Rexlowea navicularis (Ehrenberg) Kociolek & E.W. Thomas 2010	TYPE 7	Abnormal striation pattern and lack of raphe slit	Unknown	UNKNOWN	Kociolek & Thomas (2010)
Rhaphoneis amphiceros (Ehrenberg) Ehrenberg 1844	TYPE 1	Abnormal valve outline (irregular side of the shell)	External and mechanical causes	PHYSICAL STRESS	Cox (1890)
Rhizosolenia hyalina Ostenfeld in Ostenfeld & Schmidt 1901	–	Not described	Oil spill	OTHERS	Tabassum et al. (2015)
Rhizosolenia imbricata Brightwell 1858	–	Not described	Oil spill	OTHERS	Tabassum et al. (2015)
Rhoicosphenia abbreviata (C. Agardh) Lange-Bertalot 1980	TYPE 2	Irregular striation pattern	Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as RABB (*Rhoicosphenia abbreviata*)]
Rhopalodia gibba (Ehrenberg) O. Müller 1895	TYPE 1; TYPE 2; TYPE 7	Multiple (outline, ornamentation and mixed)	Unknown	UNKNOWN	Holmes & Taylor (2015)
Rhopalodia sp.	TYPE 1; TYPE 2; TYPE 7	Multiple (outline, ornamentation and mixed)	Unknown	UNKNOWN	Holmes & Taylor (2015)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Sellaphora labernardierei Beauger, C.E. Wetzel & Ector in Beauger et al. (2016)	TYPE 1; TYPE 2	Abnormal valve outline (loss of symmetry relative to both axes; abnormal outline as bent) and changes in striation patterns	High nutrient	ORGANIC LOADING AND EUTROPHICATION	Beauger et al. (2016)
Sellaphora nigri (De Notaris) C.E. Wetzel & Ector in Wetzel et al. 2015	TYPE 1	Deformed outline	Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as NMIN (*Navicula minima*)]
			Cd and Zn	TRACE METALS	Morin & Coste (2006) [as *Eolimna minima* (Grunow) Lange-Bertalot]
			Mixture of metals	TRACE METALS	Falasco et al. (2009b)
			Thiram or hydrocarbon emulsion	PESTICIDES	Bayona et al. (2014) [as *Eolimna minima*]
	TYPE 1; TYPE 2; TYPE 7	Slight asymmetrical outline of the valve and normal striation pattern; valvar shape almost regular with abnormal striae orientation; irregular valvar shape with abnormal striae orientation; irregular valve outline: abnormal shape; mixed	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Granetti (1968a, b) [as *Navicula minima* Grun.]
		Multiple (outline, ornamentation and mixed)	High concentration of metals and total nitrogen, high conductivity and biological oxygen demand	MULTIPLE	Pandey et al. (2018a) [as *Eolimna minima*]
		Multiple (outline, ornamentation and mixed)	Ammonium, phosphorous, pharmaceutical compounds and hydrological pressure	MULTIPLE	Tornés et al. (2018)
	TYPE 1; TYPE 2; TYPE 4; TYPE 7	Interruption of raphe, abnormal poroids shape or pattern in correspondence of apical pore field, abnormal striation pattern, atypical valve outline and distal raphe fissures; mixed	Cd contamination (100 µg $Cd \cdot l^{-1}$)	TRACE METALS	Morin et al. (2008a) [as *Eolimna minima* (Grunow) Lange-Bert.]
	–	Not described	Trace metals (Cd)	TRACE METALS	Duong et al. (2008) [as *Eolimna minima*]

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
			AMD	AMD	Fernández et al. (2018) [as *Eolimna minima* (Grunow) Lange-Bertalot & Schiller 1997]
			Cd and Zn	TRACE METALS	Morin et al. (2007) [as *Eolimna minima* (Grunow) Lange-
Bertalot]					
Sellaphora pupula (Kützing) Mereschkovsky 1902	TYPE 1	Deformed valve outline	No clear causes (probably Pb contamination)	TRACE METALS	Mora et al. (2015)
Sellaphora rhombelliptica (Gerd Moser, Lange-Bertalot & Metzeltin) C.E. Wetzel & Ector in Wetzel et al. 2015	–	Not described	AMD	AMD	Fernández et al. (2018) [as *Eolimna rhombelliptica* Gerd Moser 1998]
Sellaphora saugerresii (Desmazières) C.E. Wetzel & D.G. Mann in Wetzel et al. 2015	TYPE 1	Deformed outline	Low discharge, high temperatures and salinity	MULTIPLE	Lai et al. (2019) [as *Sellaphora seminulum* (Grunow) D.G. Mann 1989]
	TYPE 4	Interruption of raphe	Cd contamination (100 µg Cd·l^{-1})	TRACE METALS	Morin et al. (2008a) [as *Naviculadicta seminulum* [Grunow] Lange-Bert.]
	TYPE 1; TYPE 2; TYPE 7	Slightly asymmetrical valve outline and normal striation pattern; valvar shape almost regular with abnormal striae orientation; irregular valvar shape with abnormal striae orientation; irregular valve outline; mixed	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Granetti (1968a, b) [as *Navicula seminulum* Grun.]
	–	Not described	Mixture of metals (mainly Cd and Zn)	TRACE METALS	De Jonge et al. (2008)
Skeletonema costatum (Greville) Cleve 1873	TYPE 1	Swollen frustule	Cu	TRACE METALS	Morel et al. (1978)
		Elongated in the pervalvar axis	Cu and Hg	TRACE METALS	Thomas et al. (1980)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Stauroneis kriegeri R.M. Patrick 1945	–	not described	AMD	AMD	Fernández et al. (2018)
Staurosira construens Ehrenberg 1843	TYPE 1	Abnormal valve outline	Crowding	PHYSICAL STRESS	Barber & Carter (1981) [as *Fragilaria construens* (Ehr.) Grun.]
		Abnormal valve outline (outgrowth in the central part)	Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as FCON (*Fragilaria construens*)]
	TYPE 1; TYPE 2; TYPE 7	Multiple (outline, ornamentation and mixed)	Metals (Cd, Co, Cr, Cu, Fe, Pb and Zn) and nutrients (total phosphorus and total nitrogen)	MULTIPLE	Pandey et al. (2018b)
	TYPE 1; TYPE 2; TYPE 7	Multiple (outline, ornamentation and mixed)	High concentration of metals and total nitrogen, high conductivity and biological oxygen demand	MULTIPLE	Pandey et al. (2018a)
Staurosira venter (Ehrenberg) Cleve & J.D. Möller 1879	TYPE 1	Abnormal valve outline	Cd, As, Pb and Hg in the water column; Cd, Cu, Hg, Pb and Zn in the sediments	TRACE METALS	Peres-Weerts (2000) [as FCVE (*Fragilaria construens* f. *venter*)]
	TYPE 1; TYPE 2	Deformed outline, abnormal striation	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
	–	Not described	High organic matter levels	ORGANIC LOADING AND EUTROPHICATION	Dziengo-Czaja & Matuszak (2008) [as *Fragilaria construens* var. *venter* (Ehr.) Grunow]
			AMD	AMD	Fernández et al. (2018)
Staurosirella pinnata (Ehrenberg) D.M. Williams & Round 1988	TYPE 1	Small size and almost “centric” or distorted morphology	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Round (1992) [as *Fragilaria pinnata* Ehr.]
		Deformed outline	Fluoranthene (200 µg l^{-1})	PESTICIDES	Rimet et al. (2004) [as *Staurosira pinnata* (Ehrenberg) Lange-Bertalot]
			Mixture of metals	TRACE METALS	Falasco et al. (2009b) [as *Fragilaria pinnata* Ehrenberg]

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Stephanodiscus niagarae Ehrenberg 1845	TYPE 1	Morphological variation	Trophic status and other environmental variables	MULTIPLE	Theriot & Stoermer (1981, 1984a, b, c), Theriot et al. (1988a, b), Håkansson & Kling (1990) and Edlund & Stoermer (1991)
	TYPE 2	Central area like a fish net; irregularly shaped and sized valve areolae variously orientated; different structures and placement of the central fultoportulae	Eutrophication and industrial pollution or contamination by trace metals and other toxic chemicals	MULTIPLE	Yang & Duthie (1993)
Stephanodiscus parvus Stoermer & Håkansson 1984	TYPE 2	Abnormal orientation of the slits of the areolae, sometimes irregularly shaped	Eutrophication and industrial pollution or contamination by trace metals and other toxic chemicals	MULTIPLE	Yang & Duthie (1993)
Stephanopyxis palmeriana (Greville) Grunow 1884	TYPE 1	Bulbous protrusions; bent outline	Cu and Hg	TRACE METALS	Thomas et al. (1980)
Stictodiscus californicus Greville 1861	TYPE 3	Doubled centre	Unknown	UNKNOWN	Cox (1890)
Surirella angusta Kützing 1844	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
	–	Not described	Mixture of metals (Cd, Cu, Pb, Zn)	TRACE METALS	Lavoie et al. (2012)
Surirella brebissonii var. *kuetzingii* Krammer & Lange-Bertalot 1987	TYPE 1	Deformed outline	Mixture of metals	TRACE METALS	Falasco et al. (2009b)
Surirella chilensis C. Janisch in Schmidt et al. 1875	TYPE 1	Deformed outline	Extreme environmental conditions (i.e. high UV radiation, high salt content, geothermal flux, large nutrient supply)	MULTIPLE	Cabrol et al. (2007)
Surirella elegans Ehrenberg 1843	TYPE 1; TYPE 2; TYPE 4; TYPE 7	Multiple (outline, ornamentation, raphe channel and mixed)	Cu and Zn	TRACE METALS	Pandey & Bergey (2016)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Surirella minuta Brébisson ex Kützing 1849	TYPE 1	Deformed outline	Mixture of metals in the sediments	TRACE METALS	Tapia (2008)
Surirella ovalis Brébisson 1838	TYPE 5	Aberrant or surplus raphes	Strong light	PHYSICAL STRESS	Schmid (1979)
	–	Not described	Unknown	UNKNOWN	Hustedt (1927)
Surirella peisonis Pantocsek 1902	TYPE 5	Aberrant or surplus raphes	Strong light	PHYSICAL STRESS	Schmid (1979)
		Disorientated and lengthened fibulae	Colchicine	OTHERS	Schmid (1980, 1984)
Synedra Ehrenberg 1830	TYPE 1	Kidney shape with two unequal lobes	Artificial conditions	ARTIFICIAL GROWTH CONDITIONS	Round (1993)
Synedra goulardii Brébisson ex Cleve & Grunow 1880	TYPE 1	Abnormal valve outline	Trace metals mixture	TRACE METALS	León et al. (2018)
	TYPE 2	Altered striation pattern	Mixture of metals in the sediments	TRACE METALS	Tapia (2008)
Synedra goulardii var. *telezkoensis* Poretzky ex Proschkina-Lavrenko 1950	TYPE 1; TYPE 2	Deformed outline and disruptions in the arrangement of fine structure elements	Multiple	MULTIPLE	Barinova (2017)
Synedra sp.	TYPE 1	Irregular outline and/or symmetry loss	Multiple (copper and ammonia)	MULTIPLE	Corbella et al. (1958)
Synedra tabulata (C. Agardh) Kützing 1844	TYPE 1	Deformed valves, asymmetrical or even twisted	Changes in pH and salt concentration	MULTIPLE	Aleem (1950)
Synedropsis hyperborea (Grunow) Hasle, Medlin & Syvertsen 1994	TYPE 1	Deformed valves, asymmetrical or even twisted	Changes in pH and salt concentration	MULTIPLE	Aleem (1950) [as *Synedra hyperborea*]
Tabellaria flocculosa (Roth) Kützing 1844	TYPE 1	Deformed valve outline (mainly the loss of the double symmetry)	Cu (0.3; 6; 10 μg l^{-1})	TRACE METALS	Gonçalves et al. (2019)
			Zn (500; 1000 μg l^{-1})	TRACE METALS	Gonçalves et al. (2019)
	TYPE 6	Abnormal colony formation	Cd (from 0.001 mg·l^{-1})	TRACE METALS	Adshead-Simonsen et al. (1981)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Tabellaria sp.	TYPE 1	Deformed outline	Turbulence	PHYSICAL STRESS	Clarson et al. (2009)
Tabularia (Kützing) D.M. Williams & Round 1986	TYPE 1; TYPE 2	Bent frustules; asymmetrical valves; abnormal striation pattern, irregular margins	Saline discharge and industrial contamination	MULTIPLE	Sterrenburg (1973)
Tabularia fasciculata (C. Agardh) D.M. Williams & Round 1986	TYPE 1; TYPE 2	Abnormal outline and ornamentation	No clear causes (probably nutrient levels or UV exposure)	UNKNOWN	Majewska et al. (2012) [as *Fragilaria fasciculata* (Agardh) Lange-Bertalot]
	TYPE 1; TYPE 2; TYPE 7	Multiple (outline, ornamentation and mixed)	High concentration of metals and total nitrogen, high conductivity and biological oxygen demand	MULTIPLE	Pandey et al. (2018a)
	–	Not described	High organic matter levels	ORGANIC LOADING AND EUTROPHICATION	Dziengo-Czaja & Matuszak (2008) [as *Fragilaria fasciculata* (Agardh) Lange-Bertalot]
Tabularia variostriata M.A. Harper in Harper et al. (2009)	TYPE 2	Abnormal striation pattern	Unknown	UNKNOWN	Harper et al. (2009)
Tabularia waernii Snoeijs in Snoeijs & Kuylenstierna 1991	TYPE 1; TYPE 2	Abnormal outline and ornamentation	No clear causes (probably nutrient levels or UV exposure)	UNKNOWN	Majewska et al. (2012)
Thalassiosira decipiens (Grunow) E.G. Jørgensen 1905	TYPE 2	Abnormal areolae pattern	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	McMillan & Johansen (1988)
Thalassiosira duostra C. Pienaar in Pienaar & Pieterse 1990	TYPE 2	Fasciculated pattern of areolae; loss of some tangential areolae	Si limitation	OTHERS	Torgan et al. (2006)
Thalassiosira eccentrica (Ehrenberg) Cleve 1904	TYPE 1	Abnormal valve morphology	Colchicine	OTHERS	Schmid (1980, 1984)
	TYPE 2	Fasciculated arrangement of areolae or valves consisting of independent scales	Osmotic stress	OTHERS	Schmid (1984)
Thalassiosira pseudonana Hasle & Heimdal 1970	TYPE 1	morphological alterations	Cu^{2+} ($10^{-8.6}$ to $10^{-8.3}$ M)	TRACE METALS	Thomas et al. (1980)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Triceratium affine Grunow in Van Heurck 1883	TYPE 2	Marking unsymmetrically varied (areolation irregular)	Unknown	UNKNOWN	Cox (1890)
Triceratium favus Ehrenberg 1840	TYPE 1	Abnormal valve outline (one angle is wanting, the process is present at the deformed angle but it is asymmetrically placed)	External and mechanical causes	PHYSICAL STRESS	Cox (1890)
Triceratium formosum var. *pentagonalis* A.W.F. Schmidt in Schmidt et al. 1882	TYPE 1	Abnormal valve outline (one of the indentations is obliterated)	External and mechanical causes	PHYSICAL STRESS	Cox (1890) [as *Triceratium formosum*, Brightwell, var. *pentagonalis*, Grun.]
Triceratium robustum Greville 1861	TYPE 1	Abnormal valve outline (one angle is replaced by two smaller ones, giving a trapezoidal form to the cell	External and mechanical causes	PHYSICAL STRESS	Cox (1890)
Trinacria regina Heiberg 1863	TYPE 1	Eccentric curvature	Unknown	UNKNOWN	Mitlehner (2019)
Tryblionella apiculata W. Gregory 1857	TYPE 1; TYPE 2; TYPE 5; TYPE 7	Multiple (outline, ornamentation, raphe channel and mixed)	Metals (Cd, Co, Cr, Cu, Fe, Pb and Zn) and nutrients (total phosphorus and total nitrogen)	MULTIPLE	Pandey et al. (2018b)
Tryblionella compressa (J.W. Bailey) Poulin in Poulin et al. 1990	TYPE 1; TYPE 2; TYPE 5; TYPE 7	Multiple (outline, ornamentation, raphe channel and mixed)	Metals (Cd, Co, Cr, Cu, Fe, Pb and Zn) and nutrients (total phosphorus and total nitrogen)	MULTIPLE	Pandey et al. (2018b) [as *Nitzschia compressa*]
Ulnaria acus (Kützing) Aboal in Aboal et al. 2003	TYPE 1	Abnormal outline of the valve	Metals (Ge; Sn)	TRACE METALS	Basharina et al. (2012) [as *Synedra acus*]
	TYPE 2	Abnormal ornamentation pattern	Metals (Ge; Ti; Zr; Sn)		
	–	Not described	Cd and Zn	TRACE METALS	Morin & Coste (2006) [as *Fragilaria ulna* var. *acus* (Kützing) Lange-Bertalot]
Ulnaria contracta (Østrup) E. Morales & M.L. Vis 2007	–	Not described	Mixture of metals (Pb, Cu, Zn)	TRACE METALS	Simić et al. (2018) [as *Fragilaria ulna* var. *contracta* Main]
Ulnaria spp.	–	Not described	Cd and Zn	TRACE METALS	Morin et al. (2008b)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
Ulnaria titicacaensis E. Morales, Ector & P.B. Hamilton in Morales et al. (2014)	TYPE 2	Abnormal striation pattern	Multiple (oil, gasoline and solid waste contaminants in the strait water)	MULTIPLE	Morales et al. (2014)
Ulnaria ulna (Nitzsch) Compère 2001	TYPE 1	Deformed outline	Pesticides	PESTICIDES	Debenest et al. (2006)
			Mixture of metals in the sediments	TRACE METALS	Tapia (2008) [as *Synedra ulna* (Nitzsch) Ehrenberg]
			Trace metal contamination: Cd, Cu, Fe, and Zn	TRACE METALS	Cichoń (2016)
			Low discharge, high temperatures and salinity	MULTIPLE	Lai et al. (2019)
	TYPE 2	Abnormal outline of valves; irregular striation pattern; interruption of the pseudoraphe	Low current velocity and flow, drought conditions, and consequent light intensity and high water temperature	PHYSICAL STRESS	Antoine & Benson-Evans (1984) [as *Synedra ulna*]
		Aberrations in the pattern of areolae; sternum can be broad; valves can present gaps; rimoportula displayed along one-quarter of length; interconnected or missing striae	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Estes & Dute (1994) [as *Synedra ulna* (Nitzsch) Ehr.]
		Abnormal striation pattern	Cd and Zn	TRACE METALS	Morin & Coste (2006)
			Cd and Zn	TRACE METALS	Morin et al. (2007) [as *Ulnaria ulna* (Nitzsch) Lange-Bertalot]
			Cd and Zn	TRACE METALS	Morin et al. (2008b)
			Cd	TRACE METALS	Morin et al. (2008c)
			Mixture of metals in the sediments	TRACE METALS	Tapia (2008) [as *Synedra ulna* (Nitzsch) Ehrenberg]
	TYPE 7	Sigmoid outline and abnormal ornamentation	Unknown	UNKNOWN	Hustedt (1927) [as *Synedra ulna*]
	TYPE 1; TYPE 2	Abnormal outline and ornamentation	Mixture of metals	TRACE METALS	Falasco et al. (2009b)

Table 1 continued

Diatom taxa	Type of teratology	Description	Causes	Type of causes	References
			No clear causes (probably nutrient levels or UV exposure)	UNKNOWN	Majewska et al. (2012)
	TYPE 1; TYPE 3	Not described	trace metals mixture	TRACE METALS	León et al. (2018)
	TYPE 1; TYPE 2; TYPE 7	Notched or incised valves; asymmetrical bent frustules; abnormal striae; patterned axial area; mixed	Cd, Cu, Fe and Zn	TRACE METALS	McFarland et al. (1997) [as *Fragilaria ulna* (Nitz.) Lange-Bertalot]
		Deformed outline, abnormal striation, mixed	Trace metals (Cd)	TRACE METALS	Duong et al. (2008)
			Mainly Cd and Zn (but also Pb); separately	TRACE METALS	Pandey et al. (2014)
			Cu and Zn	TRACE METALS	Pandey & Bergey (2016)
			High concentration of metals and total nitrogen, high conductivity and biological oxygen demand	MULTIPLE	Pandey et al. (2018a)
			Metals (Cd, Co, Cr, Cu, Fe, Pb and Zn) and nutrients (total phosphorus and total nitrogen)	MULTIPLE	Pandey et al. (2018b) [as *Synedra ulna*]
			High metal concentrations, total nitrogen, coliforms, BOD and conductivity	MULTIPLE	Pandey et al. (2019)
	TYPE 1; TYPE 2; TYPE 3; TYPE 7	Deformed outline, abnormal striation, central area, mixed	Artificial growth conditions	ARTIFICIAL GROWTH CONDITIONS	Falasco et al. (2009b)
	–	not described	Trace metals	TRACE METALS	Salusso & Moraña (2015)
			AMD	AMD	Fernández et al. (2018)

Which kind of stress teratological forms can assess?

Most of the research focussing on diatom teratologies suggested that abnormal form (presence/absence) detection is a good and reliable signal for the identification of an environmental stress. Deformity frequency ranging from 0 to 0.5% should be considered as naturally occurring (Morin et al., 2008a, 2012a; Arini et al., 2012b), while higher percentages can be considered warning signals of contamination. But the absence of deformity can help in the interpretation of certain results. This was the case of the research carried out by Tudesque et al. (2012), who tried to untangle the impact of toxicant and suspended solid load, when studying a gold mining impact. The absence of teratological forms in the samples led authors to state that the changes recorded in the diatom flora were mainly related to suspended solids load rather than trace metals.

Teratological forms can be considered one of the best early detection systems also to track past environmental conditions, as highlighted in many recent publications in the field of the paleolimnology. With this regard, diatom teratological forms have been encountered in a sediment core sample recovered from Młynek Lake (northern of Poland) and related to the increase of anthropogenic activities and nutrient concentrations starting from 1900 AD (Zalat et al., 2018). Cuna et al. (2014, 2015) observed teratological valves of *Encyonema perpusillum* (A. Cleve) D.G. Mann in Round et al. in a core sample of Lake Luna (central Mexico). This was probably caused by the exposure to high UV radiation, typical of the high mountain lakes characterized by very transparent waters. The presence of teratological forms in core sediments can also be related to water acidification and trace metal deposition (Hodgson et al., 2000; Greenaway et al., 2012). Fontana et al. (2014) observed *Fragilaria crotonensis* Kitton abnormal forms in a core sample dated 1988–2010 in the Guarapiranga Reservoir (São Paulo State, Brazil). The presence of teratological forms was induced by copper sulphate that was used to face a cyanobacteria bloom in the reservoir. Also, high phosphorous concentrations can be responsible of teratological diatom formations, as demonstrated by Moos & Ginn (2016), who detected high percentages of abnormal *Staurosira construens* Ehrenberg in a core sample of Musselman Lake (Ontario, Canada).

One of the main issues related to the use of teratological forms in the environmental stress evaluation and to the development of a reliable index is that abnormal form production can be related to a wide range of stresses. However, in an optimistic perspective, this could also be considered an advantage. Figure 1 offers an overview of the different kinds of environmental stresses, which have been recognized as possible causes of the teratological forms production and the relative percentages of papers published in literature from 1890 up to date.

Based on our data (Falasco et al., 2009a and the present paper), we noticed that most of the teratological form detection has been observed under “TRACE METALS” contamination, accounting almost 29% of the published literature. It is noted that “MULTIPLE” stress is the second major cause (17%) of teratological form production and includes two or more environmental stressors at the same time. Many sources of impact are included in this category: beside trace metal contamination, we grouped all those contaminations related to the industrial production (some new emerging pollutants such as pharmaceutical and toxic compounds in general), high nutrient concentrations, high conductivity and/or organic load, hydrological pressure (and the consequent low discharge, high temperatures and salinity). Under the category “UNKNOWN” (about 16%), we grouped published papers in which it was not possible to hypothesize a clear cause for the teratological form development. “ARTIFICIAL GROWTH CONDITIONS” (almost 11%) includes culture growth conditions of monospecific strains or communities, but also all those studies carried out under artificial controlled conditions in which teratologies developed also in the absence of impact (control conditions). Additionally, “PHYSICAL STRESS” (about 8%) includes extreme life conditions (such as tides, subterranean environments, water turbulence), external and mechanical causes of damage, extreme or unstable life conditions, biofilm crowding, hydrological pressure and its consequences (such as increase in light intensity and water temperature), UV radiations. Acid Mine Drainage “AMD” (5%) leads to peculiar environmental conditions characterized by low pH and high trace metal concentrations (generally as a mixture). The category “OTHER” (almost 5%) deals with all those impacts

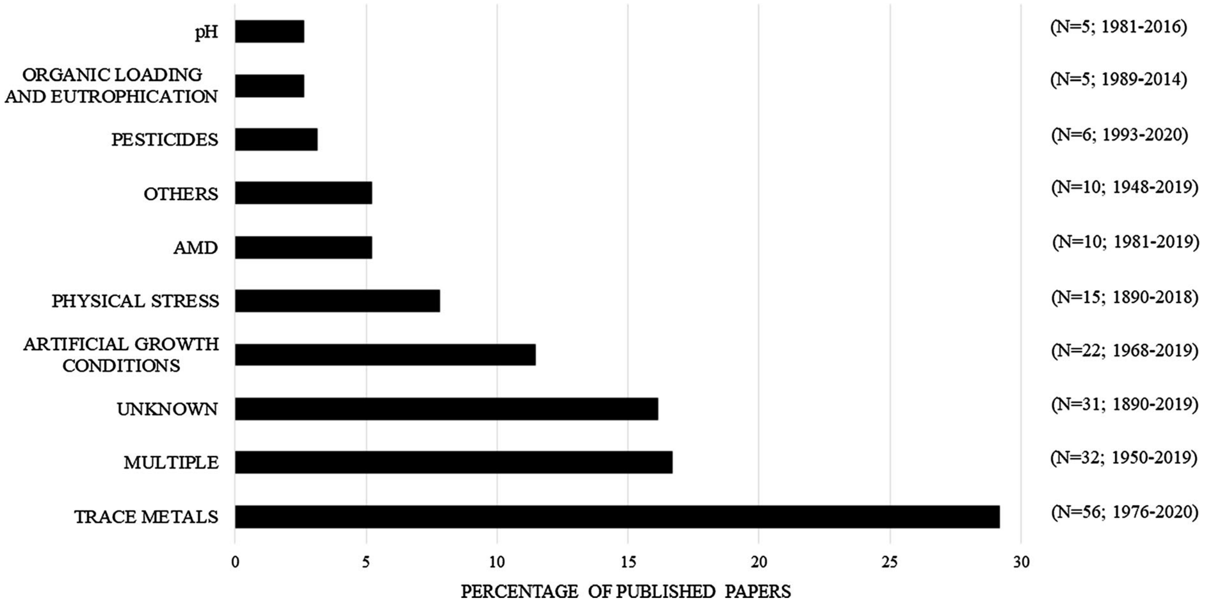


Fig. 1 Percentage of published papers relating teratological form production to a specific environmental stress

for which few observations were detected in literature and includes osmotic stress, silica limitation, experiments with microtubule inhibitors (such as colchicine), parasitism by fungi, exceeded lower limit for sexual reproduction, anti-biofouling paints, nutrient depletion and organic compounds. Other categories include "ORGANIC LOADING AND EUTROPHICATION" (almost 3%) which includes mainly high nutrient or organic matter concentrations. Under the category "PESTICIDES" (almost 3%) we included the fungicide thiram (dithiocarbamate), hydrocarbon emulsion, fluoranthene and isoproturon. In another category under "pH" (almost 3%), we grouped studies mainly conducted in acid environments, even though in one case the possible cause of impact was recognized as alkaline waters (pH 8.5).

In the following sections, we provide an overview of the most recent published literature concerning some of the above-cited stress in relation to the production of abnormal forms.

Trace metals

Trace metal contamination in the water column is not an easily detectable parameter, especially when the effective concentrations are very low and the variability of runoff inputs and flow regime over time is high (Leguay et al., 2016). Water chemical analysis does not provide information concerning the bioavailable metal species (Pandey et al., 2014) and does not take into account the mixture effects of multiple trace metals on biota (Pandey et al., 2019). Moreover, intermittent pollution is difficult to assess through chemical analyses since the measurement should be performed exactly during the pollutant release (Lainé et al., 2014). On the contrary, extra- and intracellular trace metal content in the biofilm could provide important information on the severity and time frame of trace metal contamination. Intracellular trace metal concentration represents a good proxy of free metal ion gradient (Lavoie et al., 2012; Kim Tiam et al., 2018), even though internalization show different patterns and time frames depending on metal. Moreover, it is already known that the affinity of trace metals with the dissolved organic carbon (DOC) can cause ions complexation reducing metal bioavailability (Ahmed et al., 2013). Finally, intracellular concentration analyses are not easy to be carried out considering the costs and the equipment required and could be hardly included in the routine monitoring programs carried out by the Environmental Agencies.

The presence of trace metals in the environment strongly influences diatom health, so that either deficiency or excess of certain elements can lead to the cell death (see Masmoudi et al., 2013; Jones et al., 2018 for a review). In general, trace metal excess has more negative consequences on diatom life cycle, than metal scarcity, affecting diatom communities at different organization levels, from community structure to the individual level. Different metal stress-mediated mechanisms are activated to mitigate cell damages induced by trace metals. Diatoms can internally trap trace metals through glutathione and phytochelatins (Branco et al., 2010; Figueira et al., 2014) or excrete them in the external environment, with different efficiency degrees depending on species (Kim Tiam et al., 2019). In our previous review, basing on studies up to 2009, we proposed the production of extracellular polymeric substances (EPS) as one of these defence tools. Following that hypothesis, EPS that contain carbohydrates with negatively charged groups could bind metal cations preventing trace metal adsorption. The protective role of EPS from various stressors, such as metal toxicity, has been supposed in many publications (Aguilera et al., 2008; Miao et al., 2009; Schröfel et al., 2011; Morin et al., 2012a; Naveed et al., 2019). Contrarily to this hypothesis, more recent works found opposite trends, observing a decrease of about 50% EPS in diatoms exposed to cadmium (Cd; Santos et al., 2013). In that work, the authors described a new defence mechanism associated with the frustulins, a family of glycoproteins composing the valves. The cysteine-rich domain of these proteins contains sulfhydryl groups and would act as trace metal chelating agents on the cell surface (Santos et al., 2013). The protective role of EPS has been also recently disputed under experimental conditions by Chaumet et al. (2019), who tested toxicokinetic and toxicodynamic modelling of diuron under different flow conditions. However, evidence suggests that the thick and complicated 3D structure of mature biofilms forms a protective layer which limits the exposure of the inner zones to the external stressors and decreases toxicity of contaminants (Ivorra et al., 2000; Gold et al., 2003a, b). Concerning trace metal pollution, the protective effect of a thick matrix results in a less pronounced effect on primary production and community composition (Ivorra et al., 2000; Gold et al., 2003a, b). In this context, the microdistribution of diatoms within the biofilm, their growth forms and cell size can affect community responses to environmental stressors and deserve a deeper analysis (Ivorra et al., 2002; Morin et al., 2012a; Belando et al., 2017; Kiran Marella et al., 2020).

At a community scale, trace metal contamination selects for tolerant species which are generally represented by pioneer adherent taxa (Morin et al., 2012a), in particular by *Achnanthidium minutissimum* (Kützing) Czarnecki (Tapia, 2008; Luís et al., 2011; Olenici et al., 2017; Lavoie et al., 2019; Sivarajah et al., 2019; Pandey, 2020) but also *Lemnicola exigua* (Grunow) Kulikovskiy, Witkowski & Pliński in Pliński & Witkowski (*Achnanthes exigua* Grunow) (Pandey, 2020). However, many studies recognized as tolerant taxa also motile species such as nitzschioid diatoms (Pandey & Bergey, 2018), *Navicula cincta* (Ehrenberg) Ralfs (Guasch et al., 2012), *Nitzschia palea* (Kützing) W. Smith or *Mayamaea atomus* (Kützing) Lange-Bertalot (Kim Tiam et al., 2019), high-profile species such as *G. pseudoaugur* (Gautam et al., 2017) or *Hygropetra balfouriana* (Grunow ex Cleve) Krammer & Lange-Bertalot in Krammer (Lavoie et al., 2019). Generally, teratological forms in these kinds of resistant communities are rare (Cattaneo et al., 2004; Ferreira da Silva et al., 2009; Lavoie et al., 2012), even if exceptions sometimes occurred (Cantonati et al., 2014; Olenici et al., 2017). *Achnanthidium minutissimum* is one of the most frequent and abundant species, encountered worldwide (Wojtal et al., 2011 and references herein; Novais et al., 2015). Over the last decades, many researchers have been questioning the reliability of this taxon as a biological indicator, apparently due to its wide ecological range. Actually, the name *A. minutissimum* hides a complex of species, rarely distinguished in the past (Ector, 2011; Cantonati et al., 2014) due to its small dimensions and the few morphological characters useful for its identification. Recently, many attempts have been carried out to settle boundaries within this complex, also with the aim to strengthen the ecological information provided during the biomonitoring process (Novais et al., 2015). Indeed, this complex has been reported from alkaline to acidic, oligo- to hyper-trophic waters (Potapova & Hamilton, 2007) and its tolerance to trace metal contamination is clearly documented (Kim et al., 2008; Falasco et al., 2009a, b; Tlili et al., 2011; Morin et al., 2012a; Cantonati et al., 2014; Leguay et al., 2016; Tolotti et al., 2019). The dominance of *A. minutissimum* in contaminated rivers, distinguished by its high reproduction rates and small dimensions, often led to wrong ecological status classification and unsuitable results when diatom indices are applied (Lainé et al., 2014).

At individual scale, trace metals can lead to impairments of the cell metabolism, photosynthesis and homeostasis, which delay or inhibit diatom growth (Morin et al., 2012a; Mu et al., 2017); it can lead to a decrease of diatom biomass production, gene expression modification, impacts on the mitochondrial metabolism and formation of radical oxygen species (Morin et al., 2012a). Last but not least, and subject of this review, trace metals lead to individual morphological abnormalities, i.e. teratological forms. In our previous review (Falasco et al., 2009a), we already cited several studies which highlighted the existing relationship between trace metal contamination and the presence of teratological forms, and these results have been strengthened in the following years up to date (Tapia, 2008; Ferreira da Silva et al., 2009; Sierra & Gómez, 2010; Ciszewski et al., 2011; Corcoll et al., 2012; Lavoie et al., 2012, 2018, 2019; Pandey et al., 2014, 2015, 2018b; Renzi et al., 2014; Laird et al., 2015; Salusso & Moraña, 2015; Cichoń, 2016; Pandey & Bergey, 2016, 2018; Sienkiewicz & Gąsiorowski, 2016; Gautam et al., 2017; Mu et al., 2017; León et al., 2018; Simić et al., 2018; Kim Tiam et al., 2019). However, in many of the above-cited studies, the relationship between metal concentrations and teratology frequencies or abundances was not statistically corroborated, even when trace metal contamination appeared as the only potential cause of valve deformation. Indeed, especially under field conditions, the high variability, unpredictability and interaction of the environmental or chemical parameters can mask and confuse the linearity of such response of the diatom community. Moreover, multiple stressors can have cumulative (synergic or additive) effects, which can impair specific and different cellular functions, and not only the metabolic pathway involved in the valve formation. In addition, water chemistry (such as pH, hardness, alkalinity and dissolved organic carbon) affects metal bioavailability (Fernández et al., 2018). Consequently, the same trace metal concentration can lead to different responses under different river chemical conditions, rendering the interpretation of the results difficult. Finally, species deformation proneness has to be taken into account during the interpretation of the results (Lavoie et al., 2017), and even within the same species, intraspecific variability can lead to different responses at the individual level (Santos et al., 2016) since natural selection in metal chronically contaminated areas can drive towards a more tolerant progeny. In a trace metal-contaminated site, teratological forms possibly appear already few days after the first contamination begins, confirming their potential as early detection biomarkers (Arini et al., 2013; Pandey et al., 2015; Kim Tiam et al., 2018; Pandey & Bergey, 2018; Gonçalves et al., 2019).

Diatom teratological forms have been recently used in the assessment of nanoparticles toxicity in freshwater environments (Jia et al., 2019). This study conducted on *Nitzschia frustulum* (Kützing) Grunow in Cleve & Grunow revealed that both titanium dioxide (TiO_2) and multi-walled carbon nanotubes (MWCNTs) have significant effects on cell growth. TiO_2-NPs, in particular, resulted more effective than MWCNTs, inhibiting chlorophyll *a* production and inducing the formation of teratological forms. These two materials have been largely used in different fields, finding application in contemporary industrial products from agricultural to medical and pharmaceutical, up to electronic ones. Consequently, tons of TiO_2-NPs and CNTs have been recently released into the aquatic environment, with growing expected amounts in the future.

Multiple stress

Multiple stressors are among the most difficult kind of impact to study. Especially in lowland rivers, biological communities provide integrated responses over time to many environmental and chemical variables (such as nutrients and toxic compounds), resulting faster and cheaper than a blind chemical screening for a wide range of contaminants (Pandey et al., 2018a, b). In such environments, to discern the effect of a single pollutant is almost impossible. Recently, the composition of diatom assemblages and the presence of teratological forms were used to assess the presence of pharmaceutical compounds (mainly analgesics, anti-inflammatories and antibiotics) in hydrologically unstable Mediterranean rivers (Tornés et al., 2018). In such environments, the combined effect of sewage inputs and hydrological alterations can be deleterious for the diatom communities, due to the low dilution capacity of these systems (Tornés et al., 2018). Under these conditions, diatom community tend to be homogeneous (regardless the river typology or geology) and composed of similar pollution tolerant taxa. Tornés et al. (2018) observed that even if abnormal diatoms were also found in unpolluted sites, possibly due to the hydrological stress, significantly higher percentage of deformed valves were related to the urban pollution. Similar results were obtained when testing the effects of olive mill wastewaters in Mediterranean streams subject to different degrees of hydrological alterations (Smeti et al., 2019). Olive mills wastewater consists in high phenolic content, as well as organic matter, ammonium, inorganic phosphorous, trace metals, suspended solids and low pH. In these ecosystems, the hydrological intermittency plays an important role in the pollutants availability, which accumulate in the sediments with significant consequences on the biota, i.e. the production of high percentages of teratological valves in many diatom species, with particular regard to *Fragilaria rumpens* (Kützing) G.W.F. Carlson (Smeti et al., 2019). Also in this study, as already observed in previous ones, the unpolluted sites subject to hydrological stress were interested by teratological forms production, even though to a less extent.

In a recent review, multiple and not very clear causes such as trace metal pollution, boron (B) presence and anoxia were recognized as the main drivers of teratology development in several diatom samples collected in Russia (Barinova, 2017). Large amounts of teratological forms in diatom and green algae communities were detected in the Rudnaya River, one of the most polluted rivers in the Primorsky region (Russia; Medvedeva et al., 2012). In South Africa, teratological forms were detected in urban sites characterized by closeness to mine areas and high levels of COD (chemical oxygen demand; Walsh & Wepener, 2009).

Many teratological diatoms were recorded under the extreme conditions characterizing the hypersaline lake of Laguna Blanca (South American Andean Mountains; Cabrol et al., 2007) or the thermo-mineral springs of Sardinia (Italy; Lai et al., 2019). In the first case, the combination of high UV radiation, high salt content (three times higher than sea water), the geothermal flux and the large supply of nutrients (N and P) are the possible causes of teratological form development within the diatom community (Cabrol et al., 2007). In the case of Italian thermo-mineral springs, the causes have been identified as a combination of low discharge, high temperatures and salinity (Lai et al., 2019).

In a recent paper, Millan et al. (2020) found very high percentage of teratological forms (up to 26%) in mineral springs affected by natural radioactivity (namely La Montagne and Mariol) in the French Massif Central. Radon concentration and the percentage of teratological forms in the communities were highly correlated; however, authors did not exclude a possible additive or synergic effect of other factors such as trace metal presence or the high salinity levels characterizing the sampling sites. In the Tiquina Strait at San Pablo de Tiquina (Los Andes Province, Bolivia), a mixture of oil, gasoline and solid waste contaminants in the water were recognized as the cause responsible for the presence of diatom teratological forms. One of the species illustrated in the paper, *Ulnaria titicacaensis* E. Morales, Ector & P.B. Hamilton in Morales et al., showed abnormal striation pattern; however, only less than 1% of the population showed teratological valves (Morales et al., 2014).

Artificial growth conditions

It is already known that artificial growth conditions can induce teratological form development in many diatom species. Falasco et al. (2009b) analysed 17 long-term monospecific culture strains, belonging to different genera, and observed different proneness to teratology among the different species. The authors recognized *A. minutissimum* as one of the few species not producing teratological forms under these growth conditions, hypothesizing its possible use as target species for ecotoxicological tests (Falasco et al., 2009b). A more recent research conducted by Windler et al. (2014) rejected that hypothesis, showing that also *A. minutissimum* produces abnormal cells in long-term cultures, under certain conditions. The authors observed differences in cell morphology of strains cultivated in xenic and axenic conditions. In particular, both *A. minutissimum* and *Cymbella affiniformis* Krammer strains developed teratological individuals when cultivated in axenic conditions, hypothesizing a mutualistic role of bacteria on the diatom reproduction and/or valve synthesis. Suboptimal cultural conditions and long-term cultivation were, once more, recognized as the main cause of teratological form appearance in *Frustulia curvata* Kulichová & Urbánková in Urbánková et al. (2015), *Gomphonema gracile* Ehrenberg (Cerisier et al., 2019; Coquillé & Morin, 2019), *Nitzschia* sp. aff. *dubiformis* Hustedt and *Nitzschia* sp. aff. *laevis* Hustedt (Stachura-Suchoples et al., 2016) strains. The appearance of teratological individuals under artificial growth conditions represents an important limit to the laboratory ecotoxicological tests, since it represents a significant background noise masking the species response to a certain contaminant (Kim Tiam et al., 2019). For this reason, further research is needed to improve and optimize the conditions for long-term diatom cultivations.

Physical stress

In general, harsh conditions and unstable environments favour the development of teratological forms. This is the case of *Nupela troglophila* Falasco, C.E. Wetzel & Ector in Falasco et al., an aerophilous species described for the first time in the touristic cave of Bossea Cave (NW Italy) (Falasco et al., 2015) and *Humidophila gallica* (W. Smith) R.L. Lowe, Kociolek, Q. You, Q. Wang & J. Stepanek (*Diadesmis gallica* W. Smith), found in the Valporquero Cave (León, NW Spain) (Borrego-Ramos et al., 2018) and both showing teratological individuals. Subterranean environments present extreme conditions for the growth of the biofilm covering walls and speleothems that strictly depend on both artificial light systems and high percentages of humidity.

The peculiar features which characterize extreme environments such as high-altitude Andean lakes (i.e. very high levels of total solar and UV irradiation; Albarracín et al., 2015) or fumaroles (Angel et al., 2018) were identified as the possible responsible cause of diatom teratology formation. Extreme environmental conditions are also typical of brackish marshes and saline lakes, where physical parameters such as low current velocity and high light intensity might affect silica deposition on the valve surface, producing abnormal forms in the genus *Cocconeis* Ehrenberg and *Mastogloia* Thwaites ex W. Smith (Al-Handal & Abdullah, 2010; Al-Handal et al., 2016).

Moreover, Clarson et al. (2009) observed that abnormal diatoms can also be induced by turbulence. Physical disturbance, such as shallow and transparent waters and the consequent high temperature, were the main hypothesized causes of the malformations observed in the epizoic diatom *Falcula hyalina* Takano (Donadel & Torgan, 2016).

Acid Mine Drainage

Acid Mine Drainage (AMD) is considered one of the most harmful ecosystem issue related to trace metal pollution. Indeed, the tailing of the abandoned mines (such as pyrite, galena or sphalerite) usually encompasses high percentages of sulphide minerals containing reduced forms of sulphur. When exposed to water and air, these wastes release acid leaches (due to the transformation of sulphides into sulphuric acid) and trace metals, which easily percolate over and through the soil to reach watercourses. As a consequence, the sites affected by AMD present very low pH values (pH 2–4), very high ionic strength and high dissolved metal loads, which can induce the production of diatom teratological forms (Luís et al., 2011, 2013, 2016; Jones et al., 2018). In order to quantify AMD impact, in 2018 Fernández et al. developed a new index based on diatom community (namely ICM, Índice de Contaminación por Metales), starting from the statement that AMD promotes the same pool of species independently of the geographical location of the studied area. The index formula took into account species tolerance to trace metal and species reliability as ecological indicators, obtained by using trace metal bioavailability and not trace metal concentration by itself. The authors found that some assemblages were significantly recurrent in sites affected by the highest AMD levels (with *Pinnularia aljustrelica* Luís, S.F.P. Almeida & Ector in Luís et al. and *P. acidophila* G. Hofmann & Krammer in Krammer as characteristic species). *Pinnularia subcapitata* W. Gregory and *Eunotia exigua* (Brébisson ex Kützing) Rabenhorst were found in heavily polluted waters, while *A. minutissimum* and *Brachysira vitrea* (Grunow) R. Ross in Hartley were typical of intermediate trace metal pollution. It is hard to discern whether these assemblages were driven by the low pH levels or trace metal contaminations, however, this goes beyond the final aim of the index. The authors also tested the efficiency of including the percentages of teratological forms into the index calculation but they found out that the inclusion of this metric does not improve its accuracy. The authors justify this result with the different proneness of the species to deform under stress. This could be due to the adaptation of certain species to the AMD, which is generally considered a long-term disturbance. For instance, *P. aljustrelica* probably developed efficient resistance mechanisms for detoxification (such as trace metal exclusion and/or chelation), which prevent the formation of teratologies. Recently, Luís et al. (2019) detected a significantly low diatom diversity and the presence of specific bioindicators of acid- and metal-contaminated waters, such as *P. aljustrelica*, in sites affected by AMD (Alentejo Province, south of Portugal). Again, diatom species richness and diversity was very low in the acidic lakes located in the Łuk Mużakowa along the Polish–German border (Sienkiewicz & Gąsiorowski, 2017). In these communities, many teratological valves of *Eunotia* spp. and *Pinnularia gibba* (Ehrenberg) Ehrenberg were recorded (Sienkiewicz & Gąsiorowski, 2017, 2019).

pH

Low pH levels were recognized as the single possible cause of teratological form development in a study conducted at vent sits in the Aeolic Islands (Rogelja et al., 2016), as well as in a small dystrophic lake in Poland (Grabowska et al., 2014). In a recent past, diatom teratological forms have also been used for identifying and tracking those areas affected by acid precipitations, such as the Great Smoky Mountains National Park (USA) (Furey et al., 2009). Indeed, many headwater streams in this area, even if free from any type of pollution from sewage or industry wastes, received atmospheric pollution from acid precipitations. In sites characterized by low pH and high levels of aluminium (Al), barium (Ba) and manganese (Mn), the percentages of deformed *Eunotia subarcuatoides* Alles, Nörpel & Lange-Bertalot were particularly high, creating growing interest of the researchers monitoring the phenomenon.

Organic loading and eutrophication

Toxic compounds are not the only responsible factor of teratological forms development, but from 2009 only two studies hypothesized nutrients as the main responsible of abnormal diatom production. Straub et al. (2014) found significant percentages of teratological forms mainly related to the intensive agriculture and urbanization, which characterize some area in the Vaud County (Switzerland). Again, Beauger et al. (2016) found abnormal *Sellaphora labernardierei* Beauger, C.E. Wetzel & Ector in Beauger et al. in samples collected in a spring characterized by slightly acidic pH, high conductivity, calcium and nitrates derived from agricultural activities. Even though trace metal concentrations were not measured during that study, the authors hypothesized that nutrients were the most probable factor inducing teratologies.

Pesticides

The response of diatom communities to pesticide contamination was particularly active field of research in the first years of the 2000s. In a review published in 2010, Debenest et al. (2010) examined the effects of pesticides on diatom communities at different levels: from the intracellular toxic effects involving the organelles, to the impairments of the cell metabolism, from the effects on diatom growth, to the community composition alterations. The response of diatoms to these toxic compounds can vary depending on both the herbicide mechanism of action and community composition, with different sensitivity levels depending from species to species, and the presence of a sort of community adaptation, when the exposure to the herbicide is chronic (Larras et al., 2012). Recently, noteworthy percentages of diatom teratological forms were observed in communities exposed to thiram (35 and 170 µg l^{-1}) and a hydrocarbon emulsion (0.01, 0.4, 2, 20 mg l^{-1}) during ecotoxicological studies performed in outdoor mesocosms (Bayona et al., 2014).

New insights in the mechanisms involved in cell formation and teratological forms development

In a recent review, Hildebrand et al. (2018) investigated the process of diatom cell wall formation exploring both the spatio-temporal dynamics and interactions among components. Cell walls are composed of amorphous silica, a physically robust structure. Depending on the external environmental concentration, silicic acid can pass across cell membranes through free diffusion or by means of silicon transporters (SITs). Valve formation consists of two steps: first, the formation of a 2D structure composed of a very flexible basal layer; second the thickening of the valve through a 3D deposition of silica. In general, the first step is very fast and can be completed in 8–15 min depending on the species (Hazelaar et al., 2005). In this phase major features of ornamentation can be sketched, but still present an irregular shape;

these elements are finally better defined during the second step (Hildebrand et al., 2018). The formation of the silica structures is located in the silica deposition vesicles (SDV) that are surrounded by a membrane called silicalemma composed of silica-associated proteins and long chain polyamines. SDV are strictly associated to the cytoskeleton, which provides a rigid path for SDV expansion and defines the correct positioning of the components within the valve. It has been hypothesized that SDV are kept in position not only through microtubules connections, but also to the participation of transmembrane proteins called cingulins (Tesson et al., 2017; Bedoshvili et al., 2018). Valve morphogenesis is a complex process, which can be described as a combination of micro- and macromorphogenesis. The micromorphogenesis controls the development of pore fields and areolae velum and should be mainly related to the SDV content, silicalemma and neighbouring plasmalemma. Macromorphogenesis is mediated by cytoskeleton (and as a consequence by the SDV position) and internal organelles.

The mechanisms involved in the teratological form development are, nowadays, still unknown, but they likely involve both cytoskeleton alterations and/or the impairment of the silicon metabolic pathway. As already discussed in our previous paper, abnormal frustule formations could be the result of nuclear alterations (such as dislocation, micronucleus formation, nucleus fragmentation and nucleus membrane breakage) which can be induced through the exposition to toxic compounds and can present significantly higher percentage of occurrence in strongly impacted urban sites (Nicolosi Gelis et al., 2020). Based on the hypotheses of Debenest et al. (2008), nucleus alterations would disrupt part of the diatom cytoskeleton involved in the migration of important components for cell wall formation, leading to the development of teratological forms. Recently, these results were in part contradicted by Licursi & Gómez (2013), who observed a significant correlation between abnormal nucleus location and membrane breakage in microcosms treated with hexavalent chromium, but they did not observe teratological forms at all. However, the role of cytoskeleton in the valve morphogenesis has been highlighted by many experiments conducted with microtubule inhibitors, which generally impede macromorphogenesis (Bedoshvili & Likhoshway, 2019). Cells treated with microtubule inhibitors, such as colchicine, showed abnormal ornamentation patterns, anomalies in the valve outline, curved or displaced raphe, and unusual raphe channel (see Bedoshvili et al., 2018; Bedoshvili & Likhoshway, 2019 and references within). Cytoskeleton inhibitors can also affect finer structures of the valve such as fultoportulae or areolae.

Recent studies pointed out that polycyclic aromatic hydrocarbon (PAH), and in particular Benzo[a]pyrene, impairs silicon metabolic pathway of the diatom *Thalassiosira pseudonana* Hasle & Heimdal through a decreasing expression of two genes involved in the frustule formation (the silicon transporter 1 and silaffin 3), which leads to the decrease of the available silica into the cells (Carvalho et al., 2011). These results were also confirmed by Kim Tiam et al. (2018) who showed a strong down regulation of the silicon transporter (*sit*) under Cd contamination, which would lead to a decrease in the silica uptake. Olenici et al. (2018, 2019) proposed two different hypotheses to explain the mechanisms involved in the production of a new type of teratology involving the valvocopulae (see "Identification and classification of the diatom teratologies" section). The first dealt with the weak extent of silicification of the girdle bands and the related problems arising during the vegetative reproduction (which generally lead to valve size reduction under trace metal contamination). The second hypothesis dealt with the above-cited cingulins, since mediated by a zinc-dependent system. When Zn exceeds into the water, it may affect the metabolic pathway related to the silica, damaging girdle bands.

Reproduction capacity and viability of teratological cells

Another important issue deals with the viability and reproductive success of teratological individuals. In recent years, Cox (2010) discussed on the importance of the valve morphogenesis and wall structures in diatom systematics. The author underlined that while some structural features of the diatom valve are highly consistent among groups, other features are more often subject to variation in response of particular environmental changes, and these changes likely confer success to the species under such conditions. In our previous review, we hypothesized that cells affected by abnormalities are probably disadvantaged in natural environment and doomed to disappear. We supposed that viability of abnormal diatoms could be also related to the type of teratology involved. For instance, raphe disruption could lead to lower viability and reproductive capacity, especially in natural environment where adhesion ability of the cell is essential (Falasco et al., 2009b); contrarily, striae and mixed deformations probably enable cells to survive and reproduce (Arini et al., 2013). Some evidence supported our thesis and showed that during a decontamination process, the percentages of teratological forms in samples affected by the highest levels of Cd were less abundant, than those collected in the less impacted ones (Arini et al., 2013). The authors hypothesized that populations exposed to higher trace metal contaminations were more damaged and, likely, less viable than the other ones. Contrarily to our idea, a recent experiment carried out on culture strains of *G. gracile* led to different results (Coquillé & Morin, 2019). Under the same artificial conditions, teratological strains of *G. gracile* showed growth rates similar to normal individuals and presented comparable photosynthetic efficiency and mobility. As presented in Lavoie et al. (2017), results from unpublished studies suggest that teratological individuals of *Asterionella formosa* Hassall under artificial condition did not seem to have a reduced fitness.

Pandey & Bergey (2016) observed lower motility rate in species colonizing severely polluted sites (contaminated by Cu and Zn) than less polluted ones; in addition, diatoms in the less contaminated site followed straight curved or sigmoid paths, while erratic and random under higher pollution. However, as evidenced in a recent paper, parameters related to motility are difficult to be interpreted since highly variable even within the same genus (Nicolosi Gelis et al., 2020). Even though, culture conditions offer a less harsh environment than natural rivers and streams, where flow plays a key selective role, these studies recently suggested the evolutionary success of the teratological forms. Considering this, a question arises: why are the percentages of abnormal individuals so low in natural conditions? Indeed, especially during decontamination processes, we should expect a similar reproductive success of normal and teratological cells. The answer is likely related to the continuous contribution of normal diatoms drifting from the upstream sections, serving as a source, and that can mask the presence of teratological individuals at the polluted site just downstream (Coquillé & Morin, 2019). Indeed, diatom migration, especially from drift, has been recognized as one of the main mechanisms involved in the diatom community recovery or colonization process (Morin et al., 2012b; Falasco et al., 2018a).

Identification and classification of the diatom teratologies

As already pointed out in our previous review, an important issue for the inclusion of teratological forms in the application of diatom indices is related to the subjectivity of the analysts and the microscopical resolution involved in the determination whether an individual can be considered normal or deformed. To overlook teratological individuals and to exclude them from the inventories can lead to significant mistakes in watercourses quality assessment and classification. To confirm this, a recent study carried out by Olenici et al. (2020) demonstrated that specific pollution index (SPI) can be significantly overestimated when teratological individuals are excluded from the counting (up to 8 units in samples where abnormalities are abundant) masking the environmental pressures impacting the sampling sites. The mistaken identity of a teratological form can also lead to significant errors such as the description of new species. This was the case of *Planothidium victori* Novis, Braidwood & Kilroy whose valves were described as "rotationally asymmetric to a variable degree [..], from almost linear to slightly curved near one pole to incised near one pole to form a hook" while they were just teratological individuals belonging to the genus *Planothidium* Round & Bukhtiyarova (Novis et al., 2012; Wetzel et al., 2019b). Recently, some authors tried to overcome identification mistakes by means of specific tools such as the geometric morphometric analyses. For instance, Cerisier et al. (2019) demonstrated that a simplified approach (i.e. by using a limited numbers of landmarks, just six, optimally positioned on the valve outline) was sufficient to preserve the discriminating power of the geometric morphometric analysis, that resulted in a statistically significant method for the discrimination of normal/abnormal valves. Moreover, for some species it was possible to detect a gradient of deformations generally associated to the increasing level of Zn contamination. This approach could potentially be employed in the diatom automated identification which is currently under development.

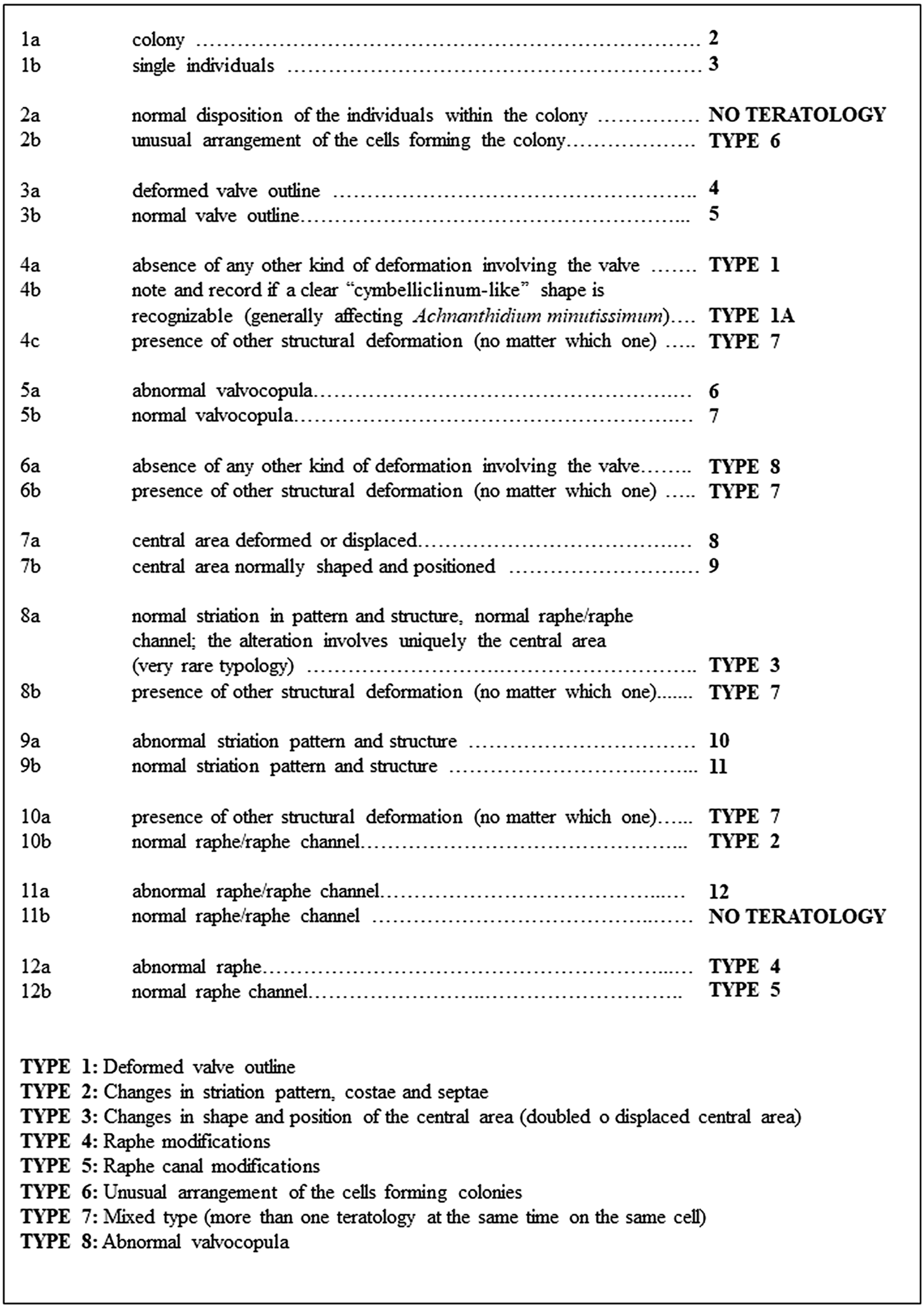
Similar results were obtained by Olenici et al. (2017) who found the geometric morphometric approach to be a good discriminatory analysis to distinguish abnormal and normal frustules of *A. minutissimum* and *Achnanthidium macrocephalum* (Hustedt) Round & Bukhtiyarova.

A first attempt to classify teratologies was proposed by Falasco et al. (2009b). In that study, seven different types of teratologies were recognized and described basing on the results obtained from field and laboratory experiments. The authors observed that the most frequent and abundant teratology recorded under natural conditions was the deformation of the valve outline. Many other structural deformations were observed, but mainly in cultures. Abnormal valve outline, indeed, is easily transmitted through generations as the mother valve serves as a template for the following generations; on the contrary, any other alterations involving the ornamentation patterns are not. Moreover, the authors hypothesized that teratologies affecting ornamentations probably need more time to develop, and this could be the reason of the minor frequency of records in natural environments.

The attempt to classify teratological forms arose from the need to answer the question if deformities are toxicant specific or not. Lavoie et al. (2017) tried to solve this question and observed that trace metals exposure, such as herbicide, generally induce valve deformations, while other non-toxic causes can also lead to high percentages of mixed teratologies. Olenici et al. (2017) noticed that species belonging to *A. minutissimum* sensu stricto and *A. macrocephalum*, presented a different type of teratology when exposed to the same trace metal contamination (mainly Zn and Cu). In particular, while abnormal individuals of *A. minutissimum* presented deformities involving mainly the apices, *A. macrocephalum* abnormalities involved the whole outline. In both laboratory and field studies, Pandey et al. (2015) and Pandey & Bergey (2016) observed a dominance of type 4 teratology (affecting raphe slit) in periphytic communities exposed to Cu and Zn, while Pandey et al. (2014, 2015) reported prevalence of abnormal striations and mixed deformities under Zn stress. Recently, Kim Tiam et al. (2019) observed that raphe related deformities (which they classified as "early morphogenesis deformities") generally affected Cd tolerant species, such as *N. palea* and *M. atomus*, that appeared more resistant to valve outline deformation or striae alterations. Contrarily, mixed teratologies were mainly observed in Cd sensitive species, i.e. *Pinnularia mesolepta* (Ehrenberg) W. Smith. After the publication of Falasco et al. (2009b), many researchers started to group teratological forms in the proposed types, even though some authors moved constructive criticisms to this classification, observing that type 3 of teratology (abnormal or displaced central area) should be included in type 2 (abnormal striation pattern) since they are strictly dependent on one another (Pandey et al., 2014; Pandey & Bergey, 2016). Considering the promising results obtained with this classification, we use the present publication to try to better define the type of teratologies through an identification key (Fig. 2).

Most types of teratology are fully described in Falasco et al. (2009b). Type 1 involves valve outline, which can result as more or less deformed and lose its typical symmetry/asymmetry depending on the species. In the present paper we want to pose the attention on the so-called "cymbelliclinum-like" teratology, mainly involving *A. minutissimum* sensu lato, and likely induced by the contamination of two trace metals (copper and zinc) and one metalloid (antimony) (Cantonati et al., 2014). Valves presenting this kind of deformation show one or even both bent off apices (Fig. 3). A similar species has been recently described by Wetzel et al. (2019a) and named *Achnanthidium peetersianum* C.E. Wetzel, Jüttner & Ector in Wetzel et al.

After its description, the same teratology has been recognized by other authors (Cerisier et al., 2019; Tolotti et al., 2019) and associated to trace metal contamination. In many cases, the analysed assemblages showed also a very low biodiversity, and few accompanying species were detected (mainly belonging to the genus *Fragilaria* Lyngbye, that also deformed). Despite involving the valve outline, we strongly believe this kind of teratology should be considered as a reliable and sure marker of trace metal contamination, since our idea has been supported by many personal observations (record of this specific teratology in river flowing in mining areas, unpublished data). For this reason, we divided it from the type 1 teratology, creating a specific sub-class. Type 2 affects pattern and structure mainly of striae and costae, which can appear disordered in their orientation and organization, as well as constitution (loss or unusual shape of the areolae forming the striae). Type



1a	colony ……………………………………………………………	**2**
1b	single individuals ………………………………………………………	**3**
2a	normal disposition of the individuals within the colony ……………	**NO TERATOLOGY**
2b	unusual arrangement of the cells forming the colony………………	**TYPE 6**
3a	deformed valve outline ………………………………………………..	**4**
3b	normal valve outline………………………………………………...	**5**
4a	absence of any other kind of deformation involving the valve …….	**TYPE 1**
4b	note and record if a clear “cymbelliclinum-like” shape is recognizable (generally affecting *Achnanthidium minutissimum*)….	**TYPE 1A**
4c	presence of other structural deformation (no matter which one) …..	**TYPE 7**
5a	abnormal valvocopula……………………………………………..…	**6**
5b	normal valvocopula……………………………………………….…	**7**
6a	absence of any other kind of deformation involving the valve……..	**TYPE 8**
6b	presence of other structural deformation (no matter which one) …..	**TYPE 7**
7a	central area deformed or displaced……………………………..…	**8**
7b	central area normally shaped and positioned ……………………..…	**9**
8a	normal striation in pattern and structure, normal raphe/raphe channel; the alteration involves uniquely the central area (very rare typology) ………………………………………………..	**TYPE 3**
8b	presence of other structural deformation (no matter which one).......	**TYPE 7**
9a	abnormal striation pattern and structure ……………………………	**10**
9b	normal striation pattern and structure ………………………………..	**11**
10a	presence of other structural deformation (no matter which one)…...	**TYPE 7**
10b	normal raphe/raphe channel…………………………………………...	**TYPE 2**
11a	abnormal raphe/raphe channel……………………………………..…	**12**
11b	normal raphe/raphe channel …………………………………..……	**NO TERATOLOGY**
12a	abnormal raphe……………………………………………………..…	**TYPE 4**
12b	normal raphe channel…………………..………………………..	**TYPE 5**

TYPE 1: Deformed valve outline
TYPE 2: Changes in striation pattern, costae and septae
TYPE 3: Changes in shape and position of the central area (doubled o displaced central area)
TYPE 4: Raphe modifications
TYPE 5: Raphe canal modifications
TYPE 6: Unusual arrangement of the cells forming colonies
TYPE 7: Mixed type (more than one teratology at the same time on the same cell)
TYPE 8: Abnormal valvocopula

Fig. 2 Key for the identification of the diatom teratologies

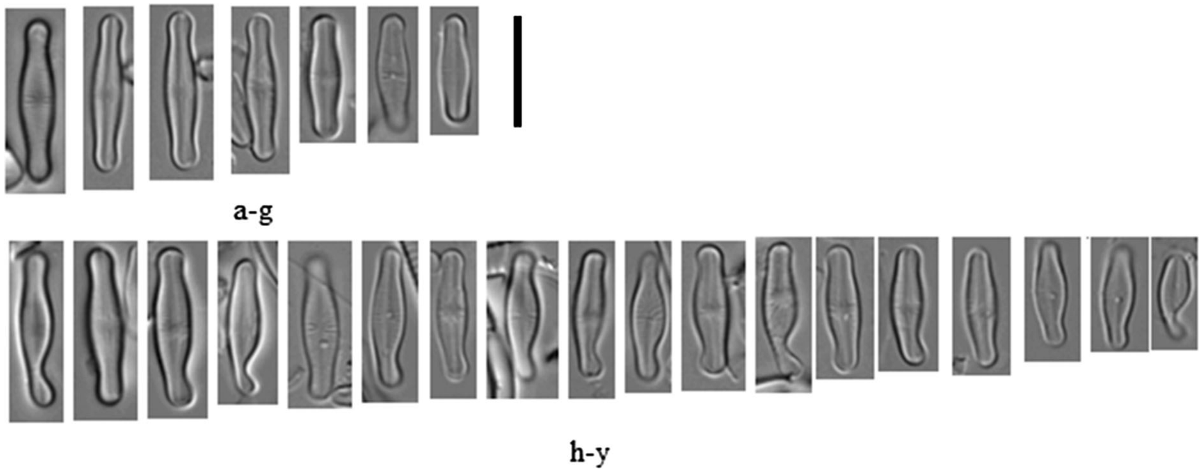


Fig. 3 Normal (**a**–**g**) and abnormal (**h**–**y**) individuals of *Achnanthidium minutissimum* sensu lato displaying the "cymbelliclinum-like" teratology. Samples were collected in the Saint Marcel River (Aosta Valley, NW Italy), that flows in Saint Marcel Valley, known to host in the past several Cu and Mn mines

3 is quite rare and affects central area of the valve, leaving the pattern of striation normal. This is mainly the case of *Planothidium* species, for which the central area often appear deformed, displaced, or doubled. In some cases, the number of teratological diatoms bearing this type of alteration was so high and the modification so constant in its structure, that some authors identified the teratological individuals as new species. This is the case of *Achnanthes lanceolata* var. *bimaculata* described by Hustedt in 1950, which presents a doubled central area with a doubled hood. The same species was identified as an initial cell of *A. lanceolata* (Brébisson ex Kützing) Grunow in Cleve & Grunow by Geitler in 1977. Finally, it was described again as a new taxon by Bukhtiyarova in 2017, under the name of *Planothidium bilensis* Bukhtiyarova. However, type 3 teratology can also affect *Ulnaria* (Kützing) Compère or *Fragilaria* species, where central area is sometimes displaced and moved towards the apex. Type 4 and 5 respectively involve raphe slit and raphe channel, which appear displaced, interrupted, doubled or forked. Type 6 is recorded when an unusual disposition of the cells forming a colony is observed. Type 7 is the "mixed" category, including two or more teratologies affecting the same valve at the same time. In the present paper, we add to these previously described typologies also the type 8. Recently recognized and described by Olenici et al. (2018, 2019) this new type 8 of teratology involves the cingulum and was observed in some individuals belonging to the *A. minutissimum* complex. In particular, the valvocopula of these individuals appeared undulated.

After the analysis of the existing relationships between type of teratology and type of contamination (Lavoie et al., 2017), in the present paper we propose the hypothesis that the type of teratology could have a relation with the structure of the valve itself. To do this, basing on the literature analysis, we pose the attention on which types of teratologies affect each diatom genera (see Electronic Supplementary Material 1). Figure 4 shows the most frequently recorded genera and relative proportions of the types of teratologies observed.

We start with a simple consideration, i.e. the more complex the valve structure, the greater type of deformations can potentially be involved. Indeed *Stephanodiscus* Ehrenberg, with its simple radial symmetry and ornamentation, just shows two types of deformations including outline and striation pattern. Araphid diatoms, such as *Diatoma* Bory, *Fragilaria*, *Staurosira* Ehrenberg, *Tabularia* (Kützing) D.M. Williams & Round and *Ulnaria* present mainly three types of deformations, involving the outline (TYPE 1), the pattern of striation (TYPE 2) or both of them at the same time (TYPE 7). Displaced longitudinal or central area were also observed, but in few cases. Based on our literature data, no unusual shape of the colonies

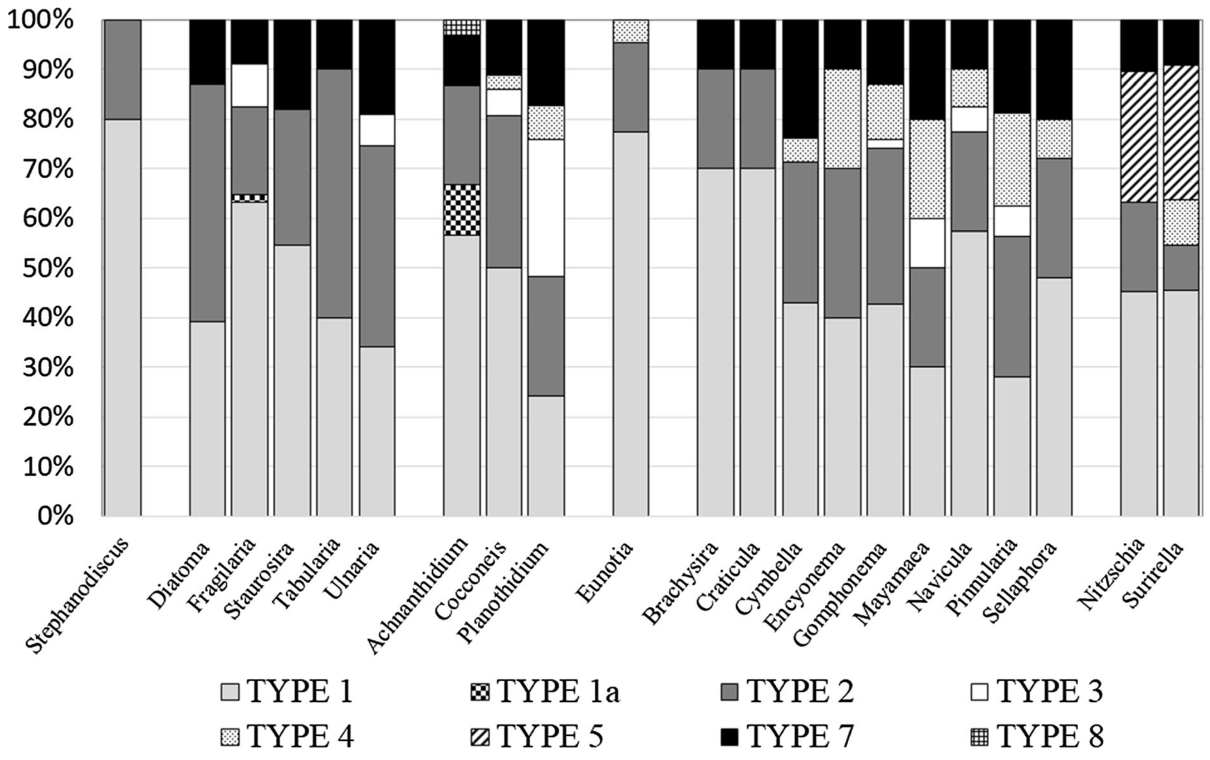


Fig. 4 Most common diatom genera and types of teratology affecting them, based on literature data (Falasco et al., 2009a and the present paper). Teratology type 6 is excluded from the figure since none of the examined genera presented an unusual arrangement of the individuals forming a colony

has been ever observed in these genera. Monoraphid taxa, such as *Achnanthidium* Kützing, *Cocconeis* and *Planothidium*, display different behaviour. In *Achnanthidium* type 1, type 2 and type 7 teratologies have been observed and only recently abnormal valvocopulae (TYPE 8) have been recorded. No aberration involving the raphe slit have been recorded in *Achnanthidium* probably due to the small dimensions of the individuals and the difficulties encountered in the observation of this kind of alteration in light microscopy (LM). *Cocconeis* is generally prone to deform in natural environment (personal observations) and 50% of the teratologies recorded in literature involve the valve outline. *Planothidium* is a heterovalvar genus with a more complex valve structure. The rapheless valve can present a hood (called cavum) or a rimmed depression (called sinus) on the internal surface. It is especially in those species bearing the cavum that the type 3 teratology has been observed (i.e. displaced or doubled central area; Rimet et al., 2004; Morin & Coste, 2006; Arini et al., 2013). In this genus, raphe slit is also subject to abnormalities. *Eunotia* is a biraphid diatom whose raphe slits lie on the valve mantle and it is characterized by absent longitudinal and central areas. In the literature, the only teratologies encountered in *Eunotia* species are those involving valve outline, striation patterns and raphe; no mixed typology has ever been observed. Finally, biraphid diatoms display the most of the described type of teratologies. Interestingly, in these genera, the alteration of the raphe slit or, when present, the raphe canal, have been often recorded. In *Nitzschia*, type 5 teratology involving the raphe canal is much more frequent than type 4 (abnormal raphe slit) in all the other genera, where the keel is absent.

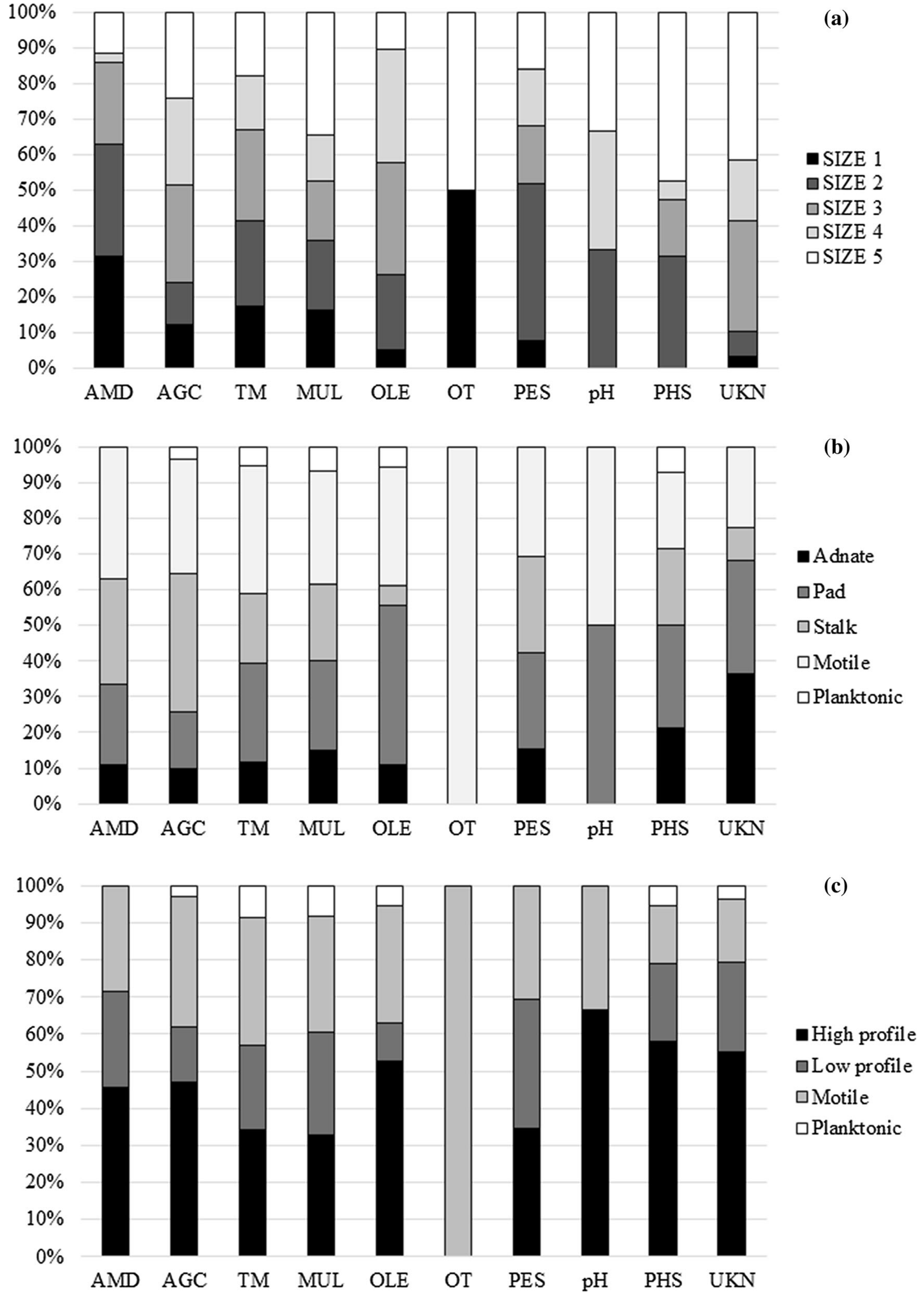
Functional responses at community level

In recent years, many authors obtained encouraging results and advantages by using a functional approach (i.e. exploring the response of several metrics, such as diatom cell size, growth forms and ecological guilds) for the evaluation of the ecological status of water bodies (Rimet & Bouchez, 2012; Falasco et al., 2018b; Nicolosi Gelis et al., 2020). The evidence, herein, led us to take into consideration the approach in the framework of contamination assessment and the consequent production of teratological forms. In particular, in this review, we tried to answer the following questions: is there a size dependency in teratological form development? Does a specific environmental stress preferentially induce teratological forms in a certain group of diatom class size and/or life forms and/or ecological guilds?

Preliminary results addressing the first question were already obtained by Arini et al. (2012c), who hypothesized a diatom size dependency in teratological form development. Indeed, the authors observed severe teratologies at LM involving especially large-sized diatoms [such as *Navicula lanceolata* (C. Agardh) Kützing or *N. gregaria* Donkin, more than small-sized ones (such as *E. minima* and *M. atomus*)]. However, it is also important to take into account that teratologies involving valve ornamentation or raphe system are obviously more visible in larger individuals, than in small ones, for which scanning electron microscopy (SEM) analyses is the only way to detect them. Indeed, throughout SEM analysis Morin et al. (2014) found a significant percentage of teratological forms affecting small diatom species and a decrease in cell biovolume in trace metal-contaminated sites.

In order to answer the second question, we reviewed the literature concerning diatom teratological forms and the above-cited environmental stress (see Fig. 1) under a functional perspective, i.e. by analysing data considering class sizes, life forms and ecological guilds. The results of this analysis are shown in Fig. 5. Please note that, considering the heterogeneity of the data sources, and the different statistical meaning of the relative results, we decided not to perform any statistical analysis on them, but just to draw some general considerations. Moreover, we excluded from this section species for which no sure data concerning class size and ecological guild were provided in Rimet & Bouchez (2012).

The “AMD” mostly affects small-sized taxa (SIZE 1 + SIZE 2 account together more than 60% of the cases), generally belonging to the high-profile and motile guilds (Fig. 5b). We can explain this result if we consider that AMD generally produces a long-term impact and likely favours small species and communities characterized by low total biovolume (Pandey et al., 2017 and references herein). Contrarily, “ARTIFICIAL GROWTH CONDITIONS” conditions lead higher percentages of deformations in medium-large sized diatoms (SIZE 3–4–5 accounted for the 75% of the total observations, with equal proportions), mainly belonging to the high-profile, stalk and motile guilds. Under these conditions, adnate and pad-attached species demonstrated to be resistant and do not deform; on the contrary, stalked and motile taxa were the most affected and showed teratologies. Although culture conditions can mimic natural environments, some parameters such as artificial light, nutrient depletion, metabolic wastes produced by the strain and in some case the absence of water flow, likely create a physical stress for the cell growth. Low-profile species easily adapt to these stressful conditions, especially those concerning light and low nutrients, and probably deform less in comparison to the other ecological guilds and life forms. Similar conclusions can be drawn for the stress category “PHYSICAL DISTURBANCE”. Indeed, also in this case, large species (SIZE 5 representing 47% of the observations) belonging to the high-profile guild result as the most affected classes and easily deform. On the contrary, very few observations were recorded concerning stalked diatoms, which seem to be less subject to deformation under physical disturbance than under artificial growth conditions. We can easily explain this if we consider that stalked taxa in natural environment are the most sensitive group to physical disturbance and simply disappear. Other differences in diatom response to “ARTIFICIAL GROWTH CONDITIONS” and “PHYSICAL DISTURBANCE” can be explained if we consider that most of the studies conducted under artificial conditions assume the growth of monospecific strain and excludes the interspecific competition that naturally characterizes the periphyton dynamics. The “TRACE METALS” and “MULTIPLE” stressors show the same pattern, inducing teratologies in high-profile and motile guilds more than low profile and planktonic. Few differences were observed when analysing the affected class sizes, with multiple stress inducing teratology in bigger-sized diatoms (SIZE 5). We can hypothesize that these kinds of stresses, and especially the multiple contamination, are mainly characteristic of lowland rivers


(a)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
AMD
AGC
TM
MUL
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OT
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pH
PHS
UKN
■ SIZE 1
■ SIZE 2
■ SIZE 3
□ SIZE 4
□ SIZE 5
(b)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
AMD
AGC
TM
MUL
OLE
OT
PES
pH
PHS
UKN
■ Adnate
■ Pad
■ Stalk
□ Motile
□ Planktonic
(c)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
AMD
AGC
TM
MUL
OLE
OT
PES
pH
PHS
UKN
■ High profile
■ Low profile
■ Motile
□ Planktonic

◀**Fig. 5** Percentage of teratologies induced by specific environmental causes and acting on different diatom class sizes (**a**) life forms (**b**) and ecological guilds (**c**). *AMD* Acid Mine Drainage, *AGC* artificial growth conditions, *TM* trace metals, *MUL* multiple, *OLE* organic loading and eutrophication, *OT* others, *PES* pesticides, *pH* pH, *PHS* physical stress, *UKN* unknown

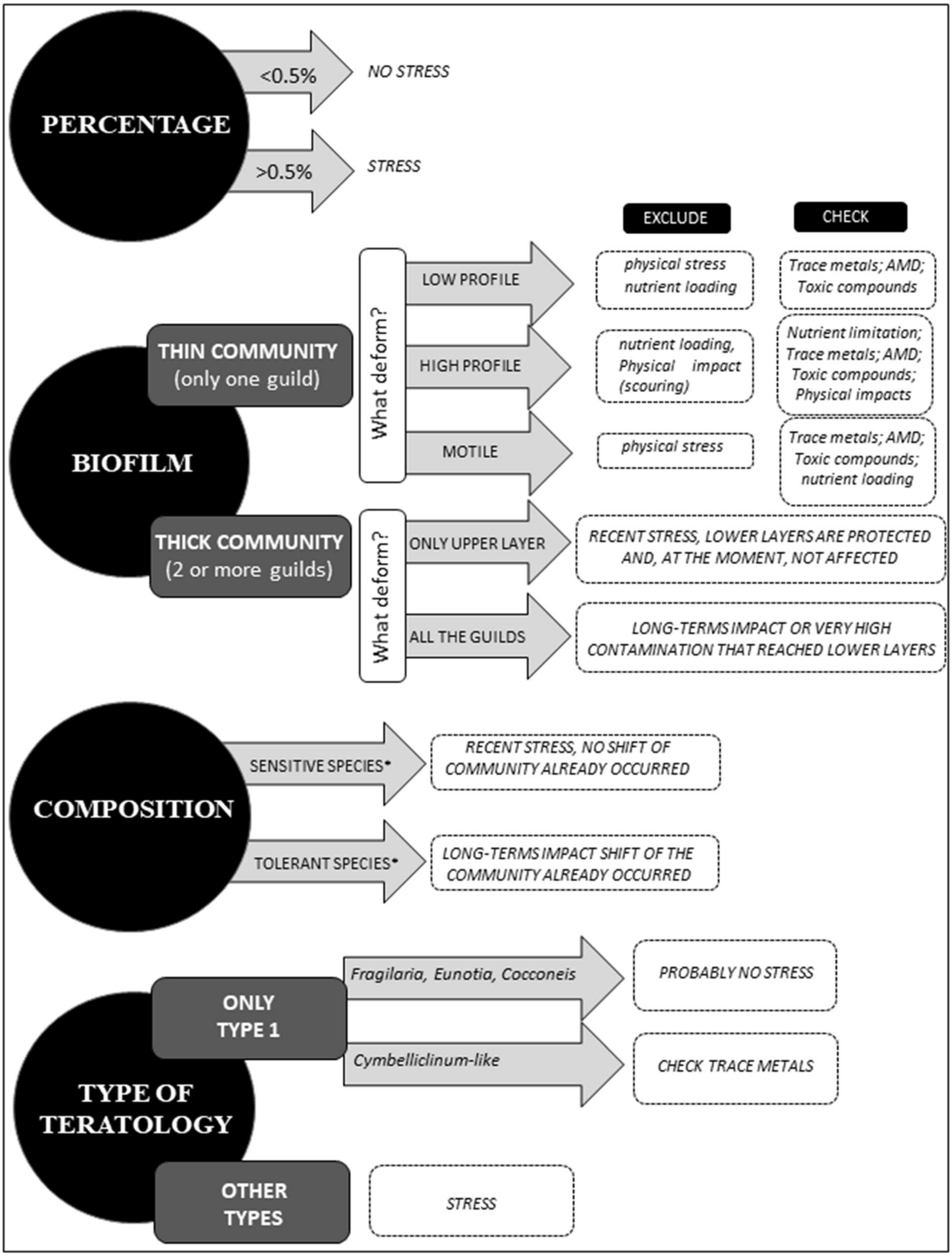
where nutrients are not a limiting factor and larger species are favoured. The category "PESTICIDES" induces deformations mainly in small-sized species (class size 2). This stress seems to affect in the same way both ecological guilds and life forms, since no differences within these two groups were observed. The "pH" category appears to affect both small and large species in the same way. However, low pH seems mainly to affect pad-attached and motile guilds, while no observation was recorded on taxa belonging to the low-profile guild, whose species never show deformations. The category "ORGANIC LOADING AND EUTROPHICATION" generally affects medium-sized diatoms, pad-attached and belonging to the high-profile and motile guilds, in accordance with the general definition of the ecological guilds. Low-profile taxa are simply disadvantaged in these kinds of environments and less represented within the community, so they deform less.

A four-step procedure for data interpretation

The considerations we have just made in the previous section, on the functional responses at the community level, must be interpreted with caution and discussed taking account other aspects, such as the structure of the biofilm subject to the stress; the type and percentage of guilds showing teratological species; the species composition; and the taxa proneness to deform. The same stress likely has different effects on a pioneer community composed of only low-profile species or on a well-developed 3D mature biofilm. This is also, in our opinion, one of the reasons for which many different and, sometimes, contrasting results appear often in the literature. To focus uniquely on single species responses, appears to be insufficient. Indeed, it is already well known that a thick mature biofilm can be considered as a shelter for the lower layers (Ivorra et al., 2000; Licursi & Gómez, 2013), which can be less susceptible to trace metal contamination (Duong et al., 2010) or herbicides (Tabak et al., 2007; Franz et al., 2008). In this section, we propose a four-step procedure that, through the analysis of different scenarios, could be used by researchers to comment results deriving from future research (Fig. 6).

First, researchers have to take into consideration the **percentage** of teratological forms within a community. We have already seen in a previous section that percentages ranging from 0 to 0.5% should be considered as naturally occurring, while higher values mostly indicate an environmental stress.

Second, **biofilm structure** gives us information concerning the maturity and stability of the biofilm and, as a consequence, of the diatom community. Very thin biofilms are generally composed of only low-profile guild, and can represent either a recently settled community (a first stage of colonization after a strong perturbation events, such as flood) or a mature community resource-stressed but disturbance free (i.e. experiencing nutrient and light limitation, but resisting to physical disturbance). This is the case, for instance, of a typical community inhabiting a mountain stream (subject to both high-flow velocity and low-nutrient loads). When a contamination event affects these kinds of communities, the low-profile guild is directly involved since no upper layer is present to provide a shelter. If teratological forms appear in this context, we can probably exclude the physical stress as source of disturbance, since low-profile species are already naturally adapted to face this kind of pressure, mainly due to their growth form (adnate, prostrate, erected). We can hypothesize and we can exclude a high-nutrient load from the sources of disturbance, since low-profile species would not survive under these conditions (with the exception of few taxa). Trace metal, AMD or toxic compounds are among the most probable source of contamination. Communities composed of only high-profile or motile guilds are rare, but existing. In the case of the sole high-profile guild, the species would be resource-unlimited but disturbance-stressed. Considering this, we should add to the possible source of stress also those related to the scarcity of nutrients or to the physical disturbance, in particular grazing activities or siltation (and the consequent light limitation). We would exclude scouring since high-profile species would not survive under these conditions. Among the ecological guilds, the motile one is free from both resource limitation and disturbance stress, since it is


PERCENTAGE
<0.5%
NO STRESS
>0.5%
STRESS
EXCLUDE
CHECK
BIOFILM
THIN COMMUNITY (only one guild)
What deform?
LOW PROFILE
physical stress nutrient loading
Trace metals; AMD; Toxic compounds
HIGH PROFILE
nutrient loading, Physical impact (scouring)
Nutrient limitation; Trace metals; AMD; Toxic compounds; Physical impacts
MOTILE
physical stress
Trace metals; AMD; Toxic compounds; nutrient loading
THICK COMMUNITY (2 or more guilds)
What deform?
ONLY UPPER LAYER
RECENT STRESS, LOWER LAYERS ARE PROTECTED AND, AT THE MOMENT, NOT AFFECTED
ALL THE GUILDS
LONG-TERMS IMPACT OR VERY HIGH CONTAMINATION THAT REACHED LOWER LAYERS
COMPOSITION
SENSITIVE SPECIES*
RECENT STRESS, NO SHIFT OF COMMUNITY ALREADY OCCURRED
TOLERANT SPECIES*
LONG-TERMS IMPACT SHIFT OF THE COMMUNITY ALREADY OCCURRED
TYPE OF TERATOLOGY
ONLY TYPE 1
Fragilaria, Eunotia, Cocconeis
PROBABLY NO STRESS
Cymbelliclinum-like
CHECK TRACE METALS
OTHER TYPES
STRESS

◀**Fig. 6** Four-step procedure which includes the analysis of different biofilm features and scenarios. *See Morin et al. (2012a) and Wood et al. (2019)

able to move relatively fast and exploit most suitable habitats. This guild is usually the most representative in the epipelon. The presence of teratological forms in this kind of community would probably mean that species are tolerant to that kind of stress and the contamination is chronic.

All these considerations should be revised when the involved biofilm present a well-developed 3D architecture that, basing on several ecological and ecotoxicological papers, may exert a protective role on the deeper layers. In that case, the percentage of guilds presenting teratological individuals can provide important information concerning the time of exposure to a certain stress. From a theoretical point of view, high-profile species are the most exposed to the source of stress, extending beyond the boundary layer. Contamination would affect this guild first. Indeed, motile species can easily move through the biofilm to escape the source of disturbance. Low profile would be the last group affected by the stress, being protected by the upper layers. Therefore, time of exposure can be recent when only one guild present teratological individuals (mainly high and motile), or long term if all the guilds are affected, since possibly the source of stress was able to pass through the whole biofilm. There is a further possibility for which, among the 3D biofilm, only the low-profile guild shows deformed individuals. In this case, we could hypothesize that an acute stress took place in the past, affecting only low-profile guilds, afterwards, in the absence of stress, the colonization continues and upper layers settled. Under these conditions, low-profile species, both normal and teratological ones, continue to reproduce even though the stress has ceased. In this case, the teratology would provide a track of a past stressful event.

Community composition can also provide important information on the exposure time of the contamination, especially when the pollution concerns trace metal or herbicides for which some studies on species sensitivity already exist (see Morin et al., 2012a; Wood et al., 2019). If only sensitive species are present, and some of them deform, we can deduce the pressure is recent, since no shift in the diatom community composition towards tolerant taxa was already possible. On the contrary, when tolerant taxa are composing the community, we can hypothesize the chronic nature of the contamination.

The possible different meaning of the **type of teratologies** in the context of the environmental biomonitoring has been already explored by Lavoie et al. (2017). The authors believe that certain genera (namely *Fragilaria* and *Eunotia*, but also *Cocconeis*, personal observation also confirmed by Al-Handal & Abdullah, 2010; Al-Handal et al., 2014) are more prone to produce teratological forms than other when affected by a certain kind of disturbance and, as a consequence, they should be considered as less reliable than other taxa in the context of the environmental contamination assessment. The same authors also hypothesized that deformed valve outline (namely type 1) should be considered a less reliable teratology than other types. Abnormal valve outline, indeed, is transmitted through the generations in an easier way than the other types of teratology. In this context, we think it should be taken into account also the reproduction strategy of the different diatom genera. Indeed, if type 1 teratology could be overestimated when affecting a ruderal species with high reproductive rates, this could be less true in secondary colonizers.

Conclusions

This paper intends to give continuity to a project started in 2009 and fruitfully pursued in 2017, when several issues related to diatom teratological forms were examined throughout the collaboration of many experts (Lavoie et al., 2017). Even though an index based on teratological forms is still far from being developed, we hope the present paper can help researchers in the interpretation of the results obtained from their future research. The four-step procedure we proposed in this article is based on theoretical hypotheses, and most of the readers certainly know that natural processes are never so linear in their responses. Indeed, many other important issues necessarily need to be considered in the stress-response analysis. Among them, the interspecific competitions within diatom community and among the other primary producers inhabiting the biofilm, which could drive and shape species composition and induce the production of teratological forms. For instance, it has been recently demonstrated that allelopathic compounds produced by the cyanobacterium *Nodularia spumigena* Mertens ex Bornet & Flahault induce the development of teratological forms in *Bacillaria paxillifera* (O.F. Müller) T. Marsson (Śliwińska-Wilczewska et al., 2016). Also, the biotic interactions among diatoms and biofilm decomposers, which share resources and space becoming important under extreme environments (such as trace metal pollution) need to be considered (Guasch et al., 2012). Other important issues are the reproduction strategy of the species belonging to the different ecological guilds, and least but not last, the proneness of the single species to deform. All these aspects and many others deserve consideration and further investigations in order to be included in the procedure.

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