

## Patterns in nutrient limitation and chlorophyll *a* along an anthropogenic eutrophication gradient in French Mediterranean coastal lagoons

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**Abstract:** A cross-ecosystem comparison of data obtained from 20 French Mediterranean lagoons with contrasting eutrophication status provided the basis for investigating the variables that best predict chlorophyll *a* (Chl *a*) concentrations and nutrient limitation of phytoplankton biomass along a strong nutrient enrichment gradient. Summer concentrations of dissolved inorganic nitrogen (DIN) and phosphorus (DIP) comprised only a small fraction of total nitrogen (TN) and total phosphorus (TP). On the basis of inorganic nutrient concentrations, the most oligotrophic lagoons appeared to be phosphorus-limited, with a tendency towards the development of nitrogen limitation as eutrophication increased, as evidenced by decreasing DIN:DIP ratios. A weak but significantly positive relationship was found between dissolved silicate (DSi) and Chl *a*, reflecting DSi accumulation in the water column along the trophic state gradient and implying a progressive shift away from potential Si limitation of phytoplankton growth. Observed concentrations of Chl *a* were far better explained by TN and TP than by DIN and DIP concentrations, suggesting that a total nutrient based approach is likely to be the most appropriate for managing eutrophication in Mediterranean lagoons and other coastal waters. These results give credence to the idea that marine and freshwater environments respond in a similar fashion to nutrient enrichment.

**Résumé :** Une comparaison inter-sites des concentrations de nutriments et de chlorophylle *a* (Chl *a*) issues de 20 lagunes de Méditerranée française de degrés divers d'eutrophisation a été menée afin de rechercher la meilleure variable expliquant le niveau de Chl *a* et d'explorer la limitation de la production primaire par les nutriments au long d'un fort gradient d'enrichissement en azote et phosphore. En été, l'azote et le phosphore inorganiques dissous (DIN et PID respectivement) constituaient une faible fraction des concentrations d'azote et de phosphore totaux (TN et TP respectivement). Sur la base des concentrations en nutriments inorganiques, la plupart des lagunes oligotrophes semblaient limitées par le phosphore avec une tendance vers des rapports DIN:DIP décroissants, et donc une limitation par l'azote, lorsque l'eutrophisation augmentait. Une corrélation positive mais faible a aussi été obtenue entre les concentrations de silicates (DSi) et Chl *a*, indiquant une accumulation de DSi dans la colonne d'eau et donc une diminution de la limitation de la croissance du phytoplancton par la silice au fur et à mesure que l'eutrophisation augmentait. Le fait que Chl *a* était beaucoup mieux expliquée par TN et TP que par DIN et DIP suggère même que l'approche limnologique basée sur l'ensemble des nutriments est vraisemblablement la meilleure pour gérer l'eutrophisation dans les lagunes méditerranéennes et dans d'autres écosystèmes marins côtiers. Ces constats renforcent l'idée que les écosystèmes marins et d'eau douce répondent de façon similaire à l'enrichissement en nutriments.

## 56 **Introduction**

57 The over-enrichment of lakes, inland water courses and coastal waters with nitrogen (N)  
58 and phosphorus (P) has been one of the major effects of human activity on aquatic ecosystems  
59 during the past fifty years (Nixon 1995; Cloern 2001). Cultural eutrophication presents a  
60 major problem for most of Europe's regional seas, including the Mediterranean (Ignatiades  
61 2005). However, most eutrophication-related problems in the Mediterranean region currently  
62 are confined to limited areas, rather than being widespread phenomena (European  
63 Environment Agency 1999). For example, Mediterranean coastal lagoons exhibit a wide range  
64 of trophic states, and reductions in anthropogenic N and P inputs will be necessary in order to  
65 attain the desired levels of water quality that have recently been specified by the Water  
66 Framework Directive for European water bodies (European Economic Community 2000).

67 Historically, N has been considered to be the primary growth-limiting nutrient in marine  
68 ecosystems (Ryther and Dustan 1971), and phosphorus to be the principal limiting nutrient in  
69 lakes (Schindler 1977). However, this paradigm has been increasingly called into question in  
70 recent years as evidence has accumulated for widespread occurrences of both N and P  
71 limitation in lakes and streams (Elser et al. 1990; Elser et al. 2007; Lewis and Wurtsbaugh  
72 2008), as well as frequent phosphorus limitation in the oceans (Downing et al. 1999; Elser et  
73 al. 2007). Downing et al. (1999) have observed through bioassay experiments that phosphorus  
74 limitation was strongest in unpolluted ecosystems, while limitation due to N was more  
75 frequent in relatively polluted coastal waters.

76 In marine waters, measurements of dissolved inorganic nitrogen, phosphorus and silicate  
77 concentrations (DIN, DIP and DSi respectively) are often used as a measure of eutrophication  
78 status, and ratios between dissolved nutrients have long been used to indicate which of these  
79 three nutrients is likely to be growth-limiting (Fisher et al. 1995; Justić et al. 1995). In  
80 contrast, total nitrogen (TN) and phosphorus (TP) are considered to be the best indicators of

81 eutrophication status and nutrient limitation in freshwater lakes and rivers (Dodds 2003).  
82 However, this more limnological approach using relationships between phytoplankton  
83 biomass and total nutrients has been applied to marine waters with success to predict  
84 eutrophication (Downing 1997; Meeuwig et al. 2000; Smith 2003), suggesting a common  
85 response of marine and freshwater systems to nutrient enrichment (Guildford and Hecky  
86 2000; Smith 2006). A water quality database developed for 20 Mediterranean coastal lagoons  
87 exhibiting a wide range of external nutrient loading provided the basis for a comparative  
88 assessment of nutrient limitation and the controls of algal biomass along this eutrophication  
89 gradient, using both the marine (dissolved inorganic nutrients) and the limnological approach  
90 (total forms of N and P).

## 91 **Materials and Methods**

### 92 **Studied sites**

93 A database was developed during 1998-2002 for 18 lagoons in the Languedoc-Roussillon  
94 (LR) Region of France and 2 lagoons in Corsica (Fig. 1). All marine water bodies (median  
95 salinity in summer > 20 psu) presenting an annually persistent water volume of  $\geq 0.5 \times 10^6 \text{ m}^3$   
96 were included in the database (Table 1). Some lagoons were divided into sectors  
97 corresponding to hydrodynamic boxes empirically defined on the basis of their bottom  
98 contours and depth. The aim was to individualize sectors belonging to the same lagoon but  
99 displaying significant differences (see BS, BM and BN in Bages lagoon, Fig. 1). Depending  
100 on the lagoon size and shape, 1 to 3 stations (Stns) were located in the middle of each sector.

101 Salses-Leucate (L), the second largest LR lagoon after Thau (T), has permanent karstic  
102 water inputs (Boutière et al. 1982). La Palme lagoon (LP) also features a karstic watershed but  
103 its inputs from karst aquifers are weaker than at L (Wilke and Boutière 2000). The Bages-  
104 Sigean (B) lagoon is made up of several smaller basins and has only one opening to the sea at  
105 the southernmost end (Jacques et al. 1975). Ayrolle (AY) is directly connected to the sea

106 while Gruissan (GR) is connected to the sea by a 2.5 km channel that can receive freshwater  
107 from a diversion canal. Vendres (VE) is a complex wetland-like system whose hydraulic  
108 management is made difficult by marine water inflows and the Aude river flash floods (Aloisi  
109 and Gadel 1992).

110 The Thau (T) lagoon is the largest and deepest LR lagoon (Souchu et al. 2001). The  
111 digging of the Sète to Rhone canal has split in half 4 lagoons located to the east of T (Ingril to  
112 Méjean/Grec). These 8 lagoons are called “palavasian” due to their proximity to the coastal  
113 resort of Palavas-les-Flots. Lagoons located landward (Ingril North: IN, Vic: VC, Arnel: AR,  
114 Mauguio: M) are bordered by wetlands and can communicate with seafront lagoons (Ingril  
115 South: IS, Pierre Blanche: PB, Prévost: PR, Grec: GE) through numerous openings into the  
116 Sète to Rhone canal. Or (O), is bordered by a wetland with a steady supply of freshwater from  
117 the northeast. The Ponant (PO) lagoon receives freshwater inflow all year round. The small  
118 Médard (MD) lagoon is an old feed pond for salt marshes. The 2 Corsican lagoons Diana (D)  
119 and Urbino (U), which have a maximum depth of 10 m and mean depth  $\geq 4$  m, could be  
120 classified as “deep lagoons” as well as T (Frisoni et al. 1983).

121 Field observations also allowed us to assign to each lagoon a trophic status (Figure 1)  
122 according to their phanerogam-macroalgae and/or phytoplankton succession (Duarte 1995,  
123 Schramm 1999). The oligotrophic lagoons corresponded to transparent waters with a  
124 dominance of marine phanerogams with associated macroalgae. The mesotrophic lagoons  
125 included climax species but also proliferating macroalgae. The eutrophic lagoons exhibited a  
126 disappearance of Phanerogams, but proliferating macroalgae could still develop. The  
127 hypertrophic lagoons exhibited quasi-exclusive dominance by phytoplankton.

## 128 **Data collection**

129 This study was focused on the summer period during which primary production is  
130 maximum. The 29 Stns (Table 1) were sampled in June, July and August 1999, 2001 and

131 2002 except for 10 Stns in 1999 and 4 Stns in 2001. Periods of temporary sediment  
132 resuspension were avoided by not sampling for three days following any period of wind speed  
133 exceeding  $25 \text{ m}\cdot\text{s}^{-1}$ . Temperature and salinity were measured with a WTW LF 197 field  
134 sensor (precision  $\pm 0.5\%$ ) calibrated monthly with salinity standards (IAPSO 38H5 Ocean  
135 Scientific). Subsurface water samples were taken by boat between 10 AM and 4 PM with 2  
136 liter polypropylene bottles pre-washed with 1 N acid and then copiously rinsed with deionized  
137 water.

138 In the laboratory, water was pre-filtered less than 3 hours after sampling through  $200 \mu\text{m}$   
139 mesh to remove most zooplankton. The pre-filtered water was transferred to ashed ( $450 \text{ }^\circ\text{C}$   
140 for 6 h) Pyrex bottles and stored at  $-20 \text{ }^\circ\text{C}$  for further analyses of total nitrogen (TN) and total  
141 phosphorus (TP, see below). For analyses of dissolved inorganic nutrients, the pre-filtered  
142 water was filtered through Whatman GF/F membranes with an all-glass filtering system and a  
143 vacuum of less than 10 cm Hg. The whole apparatus and the membrane were pre-rinsed twice  
144 before filtration. Ammonium concentrations ( $\text{NH}_4^+$ ) were measured according to the manual  
145 method of indophenol blue (Aminot and K erouel 2004). Nitrate ( $\text{NO}_3^-$ ), nitrite ( $\text{NO}_2^-$ ) and  
146 dissolved inorganic phosphorus (DIP) samples were frozen at  $-20 \text{ }^\circ\text{C}$  in Pyrex bottles before  
147 their analyses on a segmented flow analyzer (Tr eguer and Le Corre 1975). Dissolved  
148 inorganic nitrogen concentration was expressed as  $\text{DIN} = \text{NH}_4^+ + \text{NO}_3^- + \text{NO}_2^-$ . Samples for  
149 dissolved silicate analysis (DSi) were stored at  $4 \text{ }^\circ\text{C}$  in polycarbonate bottles and analysed on  
150 a segmented flow analyzer according to Tr eguer and Le Corre (1975) in the following weeks.  
151 DSi was analyzed only during annual cycles. Although the filtration of water through  
152 Whatman GF/F membranes and with an all-glass filtering system potentially could lead to  
153 overestimates of DSi, the similarity of these results to those obtained from 2003 to 2006 using  
154 nitrate cellulose filter filtration and an all-polycarbonate filtering system leads us to believe  
155 that our glass-filtered DSi data are valid.

156 Concentrations of TN were measured on the pre-filtered water by chemical oxidation with  
157 potassium persulfate in hot alkaline medium in Teflon vials (adapted from Raimbault and  
158 Slawyk 1991). 5 mL of reagent mix was added to 40 mL of sample then autoclaved in Teflon  
159 vials at 120 °C (1 bar) for 1 h. The various N forms (except N<sub>2</sub>) were oxidized to nitrate that  
160 was then measured according to Tréguer and Le Corre (1975). For analyses of TP, the  
161 potassium persulfate oxidation was carried out in acid medium according to Menzel and  
162 Corwin (1965). DIP concentrations were then measured according to Tréguer and Le Corre  
163 (1975). Measurements of TP in Corsican lagoons were limited to the summer of 2002 due to  
164 the use of faulty vials during annual cycle sampling. However, results of TP measurements in  
165 2002 were confirmed by those obtained between 2003 and 2006 (Laugier et al. unpublished).

166 Chlorophyll *a* concentrations (Chl-*a*), described in Bec et al. (unpublished data), were  
167 analyzed on all samples. Upon return to the laboratory, 5 to 50 mL (depending on the  
168 phytoplankton abundance) were filtered under a vacuum < 10 cm Hg on Whatman GF/F  
169 membranes and stored at -20 °C in glass tubes. Filters were ground in acetone (90%) and  
170 extracted during 24 h in the dark at 4 °C. Pigments were measured by spectrofluorimetry  
171 (Neveux and Lantoiné 1993) and are expressed in µg·L<sup>-1</sup> (precision ± 5%).

172 Median values for the above water quality parameters were calculated for the pooled data  
173 from each lagoon, or from each individual sector of lagoons within which the sector median  
174 water quality was found to differ significantly (Kruskal-Wallis, *p* < 0.05). Individual sectors  
175 were then kept for B and M lagoons whose between-Stn differences were significant for both  
176 TN and TP.

## 177 **Results**

178 All DIN concentrations were close to 1 µmol·L<sup>-1</sup> except for lagoons GE and MD (Fig. 2),  
179 and the contribution of DIN to TN remained below 6% except at D. DIP concentrations  
180 ranged from low values of ≤0.12 µmol·L<sup>-1</sup> in oligotrophic lagoons L, LP, BS, AY, D and U to

181 much higher values of  $>1 \mu\text{mol}\cdot\text{L}^{-1}$  in hypertrophic lagoons VE and MW (Figure 2). The  
182 contribution of DIP to TP remained below 15% except at BM, BN, T and PO. DSi ranged  
183 between  $0.5 \mu\text{mol}\cdot\text{L}^{-1}$  at D and  $204 \mu\text{mol}\cdot\text{L}^{-1}$  at VE. DSi individual concentrations remained  
184  $<2 \mu\text{mol}\cdot\text{L}^{-1}$  in 11% of samples (16 out of 144 samples). Reflecting the strong eutrophication  
185 gradient in these lagoons, TN varied from  $16 \mu\text{mol}\cdot\text{L}^{-1}$  at D to  $452 \mu\text{mol}\cdot\text{L}^{-1}$  at VE, whereas  
186 TP varied from  $0.14 \mu\text{mol}\cdot\text{L}^{-1}$  at D to  $28 \mu\text{mol}\cdot\text{L}^{-1}$  at VE. Salinity ranged from 21.3 psu at O  
187 to a maximum value of 40.1 psu at PB. DIP, TN and TP were inversely correlated with  
188 salinity (Table 2: Eq. 1 to 5).

189 DIN:DIP ratios varied from 1.1 by moles at VE and PO, to 40 at D. No significant  
190 correlation was found between the DIN:DIP ratio and DIN; the observed variability in  
191 DIN:DIP instead was largely explained by variations in DIP (Table 2: Eq. 9 and 10; Fig. 2).  
192 DIN:DIP was inversely correlated with both TN and TP (Table 2: Eq. 12 and 13). Similarly,  
193 DIN:DIP was inversely correlated with DSi (Table 2: Eq. 11), reflecting the almost significant  
194 correlation between DIP and DSi (Table 2: Eq. 7). DSi:DIN ratios ranged from 0.5 at D to  
195 267 at VC, but D was the only lagoon with a DSi:DIN ratio  $<1$ . DSi:DIP ratios ranged from  
196 17 at BM to 1640 at L.

197 A strong positive relationship was found between TN and TP (Table 2, Eq. 14). TN:TP  
198 ratios decreased from about 75 in the less eutrophic lagoons ( $\text{TP} < 0.80 \mu\text{mol}\cdot\text{L}^{-1}$ ) to the  
199 Redfield ratio (16:1 by moles) in the most eutrophic systems (Fig. 3; Table 2, Eq. 15 and 16).  
200 There was also a significant and positive covariance between TN:TP and DIN:DIP (Table 2:  
201 Eq. 17; Fig. 4).

202 Chl-a varied along the eutrophication gradient from  $<2 \mu\text{g}\cdot\text{L}^{-1}$  at L, LP, BS and AY, to  
203  $>270 \mu\text{g}\cdot\text{L}^{-1}$  at VE. There was no significant correlation between DIN and Chl-a (Table 2: Eq.  
204 18; Fig. 5). However, both DIP and DSi exhibited weak but significant correlations with Chl-a  
205 (Table 2: Eq. 19 and 20; Fig. 5). In contrast, both TN and TP were very strongly correlated

206 with Chl-a, with much higher coefficients of determination than for dissolved nutrients (Table  
207 2: Eq. 21 and 22; Fig. 6).

## 208 **Discussion**

### 209 **Nutrient limitation assessments using dissolved inorganic nutrients**

210 Inorganic nutrient concentrations in coastal waters reflect the integrated sum of riverine,  
211 sewage, atmospheric, and oceanic inputs, uptake, sorption, grazing, sedimentation,  
212 regeneration, burial, etc. (Fisher et al. 1992). We found that summer DIN remained at low  
213 concentrations in virtually all lagoons, while DIP and DSi varied largely along a range of  
214 concentrations resembling those typically found in coastal and oceanic waters (Nixon 1982;  
215 Ragueneau et al. 2002).

216 When compared to the dissolved nutrient-based criteria for nutrient limitation that have  
217 been suggested by Justić et al. (1995),

218

219 (1) N limitation:  $\text{DIN} < 1 \mu\text{mol}\cdot\text{L}^{-1}$ ;  $\text{DIN:DIP} < 10$ ; and  $\text{DSi:DIN} > 1$

220

221 (2) P limitation:  $\text{DIP} < 0.1 \mu\text{mol}\cdot\text{L}^{-1}$ ;  $\text{DIN:DIP} > 22$ ; and  $\text{DSi:DIP} > 22$

222

223 (3) Si limitation:  $\text{DSi} < 2 \mu\text{mol}\cdot\text{L}^{-1}$ ;  $\text{DSi:DIN} < 1$ ; and  $\text{DSi:DIP} < 10$

224

225 the consistently high DIN:DIP ratios observed in the oligotrophic lagoons (range: 11 to 40 by  
226 moles, Fig. 4) suggest that P was most likely to be the primary limiting nutrient for algal  
227 growth in these systems. This conclusion is consistent with the data of Souza et al. (2003) for  
228 the oligotrophic Araruama Lagoon (Brazil), as well as the conclusions of Murrell et al. (2006)  
229 and Johnson et al. (2006) for several coastal waters in Florida. These general conclusions also  
230 are consistent with Downing et al. (1999), who suggested that the role of P in primary



231 production limitation in non-polluted coastal waters may have been underestimated. Summer  
232 limitation by nitrogen alone seemed to become apparent above a certain level of  
233 eutrophication in the studied lagoons (Fig. 4). Experimental nutrient enrichment bioassays  
234 carried out in parallel with this study confirmed that both nitrogen and phosphorus limit  
235 summer pelagic primary production in the oligotrophic lagoon L (Bec et al. unpublished data),  
236 and that nitrogen alone was limiting in the mesotrophic lagoon T (Fouilland et al. 2002).

237 The observed accumulation of DIP along the eutrophication gradient and the inverse  
238 correlation between DIP and salinity could be explained by invoking progressively lower N:P  
239 supply ratios that reflect an increasing influence of sewage inputs on the total nutrient load  
240 (Downing and McCauley 1992). However, nowadays, sewage can be richer in N than in P  
241 because of a more effective removal of P as it is the case for the 8 Palavasian and O lagoons  
242 (Table 3). Moreover, the range of N:P loading ratios to the 13 lagoons for which N and P  
243 loading data are available is narrower than the ranges of DIN:DIP and TN:TP in the water  
244 column. We tentatively conclude that the observed increase of DIP along the eutrophication  
245 gradient is better explained by the P content of lagoon sediments than by salinity, and that  
246 recycling processes strongly affect inorganic nutrient concentrations in the water column  
247 (Souchu et al. unpublished data).

248 Egge and Aksnes (1992) have shown that diatoms often dominate the phytoplankton  
249 community when DSi concentrations exceeded  $2 \mu\text{mol}\cdot\text{L}^{-1}$ . However, few samples in the  
250 pooled database exhibited DSi concentrations  $<2 \mu\text{mol}\cdot\text{L}^{-1}$  (13%). Moreover, based the  
251 empirical criteria in Eq. 1-3 above, the relatively high observed ratios of DSi:DIN (range: 0.5  
252 to 267 by moles) and DSi:DIP (range: 17 to 1640 by moles) together suggest that DSi was  
253 very unlikely to limit algal growth in the studied lagoons, even at extreme levels of nutrient  
254 enrichment. The trend for DSi to accumulate along the eutrophication gradient was  
255 unexpected because DSi typically is not increased by any significant extent during

256 anthropogenic N and P enrichment (Conley et al. 1993). Indeed, several authors have reported  
257 a pattern of species shifts towards phytoplankton species other than diatoms as a consequence  
258 of DSi depletion in nutrient-enriched waters (Anderson et al. 2002; Turner 2002). However,  
259 phytoplanktonic proliferation induces an accumulation in sediments of diatom frustules,  
260 whose dissolution can lead to summer DSi maxima (Aller and Benniger 1981). The similarity  
261 of DIP and DSi relationships with Chl-a (see below), which suggest the accumulation of both  
262 dissolved nutrients along the eutrophication gradient, could potentially result from the  
263 recycling of phytoplankton at the water-sediment interface in the studied lagoons (Bec et al.,  
264 unpublished data; Souchu et al. unpublished data.).

### 265 **Nutrient limitation assessments using total nutrients**

266 Guildford and Hecky (2000) proposed the following criteria for N and P limitation  
267 assessment in lake and ocean waters, using molar ratios of total nitrogen and total phosphorus  
268 (Eq. 4–6):

269

270 (4) N limitation:  $TN:TP < 20$

271

272 (5) N and P limitation:  $TN:TP = 20-50$

273

274 (6) P limitation:  $TN:TP > 50$

275

276 Based upon these empirical thresholds, we conclude that the most oligotrophic lagoons in  
277 this study were consistently limited by P (Fig. 4). For a majority of the studied lagoons, the  
278 phytoplankton production was likely limited by both N and P ( $TN:TP = 20-50$ ). The three  
279 lagoons having  $TN:TP < 20$  (VE, MW and PO) were also those for which the median summer  
280 DIP concentration was in excess ( $>1 \mu\text{mol}\cdot\text{L}^{-1}$ ; see Fig. 2), providing additional evidence that

281 P was unlikely to limit net primary production in these low N:P ratio systems. Summer  
282 limitation of algal growth by N thus may only occur in more mesotrophic Mediterranean  
283 coastal lagoons, with a tendency towards increasingly likelihood of N-limitation as  
284 eutrophication increases; consequently, transitions from limitation by P to limitation by N  
285 may be considered as an indication of anthropogenic eutrophication in these systems.

286 The convergence of the limnological and marine approaches in lagoons is evident from  
287 the positive and high correlation between DIN:DIP and TN:TP (Table 2, Eq. 17). The  
288 relationship suggests that  $TN:TP = 45$  when  $DIP:DIN$  is 16, a value that is close to the  
289 empirical TN:TP threshold proposed by Guilford and Hecky (2000). However, if the decrease  
290 of DIN:DIP along the eutrophication gradient (Table 2, Eq. 13) is clearly due to DIP  
291 accumulation, the TN:TP ratio decrease (Table 2, Eq. 16) is more difficult to explain since TN  
292 and TP are a mixture of inorganic nutrients, dissolved organic matter (DOM) and seston. In  
293 the study lagoons, regarding to the low contribution of inorganic nutrients to TN and TP (ca.  
294 10%), TN and TP can be considered as essentially made of seston and DOM. The N:P ratios  
295 in DOM are largely higher than Redfield ratio (Hopkinson and Vallino 2005) while TN:TP  
296 ratios in sestonic organic matter would display values closer to the Redfield ratio (Hall et al.  
297 2005). As Chl-a concentrations increase, TN and TP are increasingly determined by the N and  
298 P content of the phytoplankton cells (see Wetzel 2001 for DON and PON in lakes). This trend  
299 may help to explain why TN:TP ratios move closer to the Redfield ratio as eutrophication  
300 increases (Fig. 3). In hypertrophic lagoons (VE in Fig. 3), the planktonic biomass is high  
301 enough that TN:TP ratios are close to 16.

### 302 **Nutrient controls of algal biomass**

303 The predictive power of using a total nutrient-based approach for the prediction of  
304 summer median algal biomass is strongly evident in the lagoons studied here: total N and total  
305 P-based regression models for summer median Chl-a were consistently much superior to

306 comparable DIN- and DIP-based models (compare Figs. 5 and 6). There was in fact no  
307 correlation between concentrations of DIN and Chl-a (Table 2: Eq. 18), and both DIP and DSI  
308 exhibited only weak correlations with Chl-a (Table 2: Eq. 19 and 20). It is also very important  
309 to note that the simple regression model reported here for summer median TP and Chl-a in  
310 coastal Mediterranean lagoons

311

312 (7)  $\log \text{Chl-a} = 0.690 + 1.08 \log \text{TP}, r^2 = 0.78$

313

314 confirms the strongly positive relationship observed by Knoppers et al. (1991; data not  
315 shown) for annual average TP and Chl-a in six coastal lagoons in Brazil:

316

317 (8)  $\log \text{Chl-a} = 0.017 + 2.02 \log \text{TP}, r^2 = 0.92,$

318

319 as well as that observed between annual median TP and summer median Chl-a in 15 coastal  
320 embayments in Germany (Sagert et al. 2008, data not shown):

321

322 (9)  $\log \text{Chl-a} = 0.601 + 1.24 \log \text{TP}, r^2 = 0.83.$

323

324 A similarly strong relationship has been found between summer mean concentrations of TP  
325 and Chl-a in the hypertrophic Vistonis Lagoon, Greece (Gikas et al. 2006; data not shown):

326

327 (10)  $\log \text{Chl-a} = 0.300 + 2.367 \log \text{TP}, r^2 = 0.92,$

328

329 as well as in numerous other comparative analyses of freshwater and marine ecosystems  
330 (Prairie et al. 1989; Champion and Currie 2000; Smith 2006).

331 Moreover, Boynton et al. (1996) found significant relationships between annual TN  
332 loading rates and average TN and Chl-a concentrations for Maryland coastal bays, even  
333 without making any adjustments for hydraulic residence time. We found very significant  
334 relationships between annual total N and P loading rates and median TN and TP  
335 concentrations for the 13 lagoons with well-defined watersheds (Table 3), without making any  
336 adjustments for their hydraulic residence time ( $r^2 = 0.85$  and  $0.94$  for N and P respectively,  
337 ANOVA  $p < 0.05$ ; Dupré unpublished data). Søballe and Kimmel (1987) have suggested that  
338 algal production per unit P in water increases in the sequence: rivers<impoundments<natural  
339 lakes, and suggested that we view aquatic systems as occupying positions along a continuum  
340 ordered by water residence time. The Mediterranean lagoons studied here appear to behave  
341 very similarly to lakes because they have relatively long hydraulic residence times due to their  
342 low tidal amplitudes (Bacher et al. 1995).

#### 343 **Implications for eutrophication management**

344 As noted by Rabalais et al. (2009), coastal water quality is currently on the decline, and  
345 excessive exports of nutrients from the land to the world's coastal oceans will almost certainly  
346 continue to occur unless societal intervention or changes in human culture are successfully  
347 pursued. Our cross-system comparison of Chl-a and nutrients from 20 coastal Mediterranean  
348 lagoons suggests that the identity of the primary limiting growth-limiting nutrient in these  
349 systems may shift from P alone in oligotrophic lagoons, to N alone as eutrophication  
350 proceeds. We tentatively conclude that, like most unenriched freshwater systems, pristine  
351 coastal French Mediterranean lagoons may typically be P-limited.

352 A critical need remains for water resource managers to reduce nutrient loads, in order to  
353 reduce the negative effects of global eutrophication and to prevent further degradation  
354 (Rabalais et al. 2009). The management of eutrophication will require careful assessments of  
355 whether N, P, or both N and P should be controlled in order to develop successful and cost-

356 effective strategies for the control of coastal zone eutrophication. We note, however, that  
357 Elser et al. (2007) found that while enrichment by either N or P can increase autotroph  
358 production, a simultaneous increase in *both* nutrients leads to dramatically higher levels of  
359 production in nearly all situations. We surmise that the converse response also can be  
360 expected to occur (i.e., simultaneous reductions in both N and P will minimize algal  
361 production), and we thus favor joint N and P loading control to protect estuarine and coastal  
362 marine environments. However, such management decisions will need to be based upon  
363 careful syntheses of current and historical data (e.g., Conley et al. 2009; Paerl 2009), as well  
364 as quantitative and objective frameworks for the assessment of coastal zone water quality.

365 Strong relationships between Chl-a and total nutrient, and empirical models predicting in-  
366 lake P concentrations as a function of annual P load have been essential tools for management  
367 of eutrophication in lakes for more than three decades (Vollenweider 1976; OECD 1982). We  
368 concur with Hoyer et al. (2002) that an approach using total nutrients is similarly valid for  
369 eutrophication modeling in marine systems, and as shown by the data presented here, it is in  
370 fact superior to approaches that rely upon concentrations and ratios of dissolved inorganic  
371 nutrients. However, Cloern (2001) has suggested that differences between the eutrophication  
372 response of lakes and coastal waters to eutrophication potentially may result from system-  
373 specific attributes that act as filters that may modulate their respective responses to  
374 enrichment. We thus urge other researchers worldwide to test the utility of this empirical  
375 approach in coastal waters that exhibit a wide range of physicochemical, biological, and  
376 hydrological characteristics in order to confirm if the tools and methods that have been so  
377 very successful in the management of freshwater eutrophication, are also broadly applicable  
378 to coastal marine ecosystems.

### 379 **Acknowledgments**

380 This paper uses unpublished raw data from the Lagoon Monitoring Network (Réseau de  
381 Suivi Lagunaire) financed by Agence de l'Eau, Région Languedoc-Roussillon and Ifremer.  
382 This paper also was supported in part by NSF DMS-0342239 to Val H. Smith. We thank the  
383 staff of the Ifremer laboratories in Corsica and Languedoc-Roussillon, the Parc Naturel  
384 Régional de la Narbonnaise. The authors are grateful to anonymous reviewers for their  
385 comments on the paper. This paper is dedicated to Nicolas Dupré (1978-2008).  
386

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- 539

539 **Table 1.** Summary characteristics of the 20 studied lagoons.

Lagoon	Label	Mean depth (m)	Area (km <sup>2</sup> )	Volume (× 10 <sup>6</sup> m <sup>3</sup> )	Station	Station Depth (m)
Salse-Leucate	<b>L</b>	2.0	54	90	<b>LS</b>	3.0
					<b>LN</b>	2.6
La Palme	<b>LP</b>	0.5	6.0	3.3	<b>LP</b>	1.5
					<b>BS</b>	1.3
					<b>BM</b>	2.0
Bages-Sigean	<b>B</b>	1.3	37	49	<b>BN</b>	2.1
					<b>AY</b>	0.9
Ayrolle	<b>AY</b>	0.5	13.2	9.0	<b>AY</b>	0.9
Gruissan	<b>GR</b>	0.5	1.4	1.0	<b>GR</b>	0.7
Vendres	<b>VE</b>	0.9	4.8/10	1.4/3.0	<b>VE</b>	0.8
Thau	<b>T</b>	4.0	75	260	<b>TW</b>	5.5
					<b>TE</b>	9.0
<b>Palavasian</b>						
South-Ingril	<b>IS</b>	0.6	3.6	2.2	<b>IS</b>	1.0
North-Ingril	<b>IN</b>	0.6	3.2	1.9	<b>IN</b>	1.0
Pierre-Blanche	<b>PB</b>	0.4	3.7	1.5	<b>PB</b>	0.9
Vic	<b>VC</b>	1.2	11.5	13.8	<b>VC</b>	1.6
Prévost	<b>PR</b>	0.75	3.8	2.9	<b>PRW</b>	0.8
					<b>PRE</b>	0.9
Arnel	<b>AR</b>	0.40	4.7	1.9	<b>AR</b>	0.7
Grec	<b>GE</b>	0.30	2.7	0.7	<b>GE</b>	0.7
Méjean	<b>M</b>	0.75	5.5	4.1	<b>MW</b>	0.8
					<b>ME</b>	0.9
Or (Mauguio)	<b>O</b>	0.8	32	24	<b>OW</b>	1.2
					<b>OE</b>	1.2
Ponant	<b>PO</b>	2.7	2.0	5.4	<b>PO</b>	3.5
Médard	<b>MD</b>	0.6	1.4	0.9	<b>MD</b>	0.8
<b>Corsican</b>						
Diana	<b>D</b>	6.0	5.7	10.2	<b>DS</b>	8.0
					<b>DN</b>	7.0
Urbino	<b>U</b>	5.0	7.6	33	<b>US</b>	7.5
					<b>UN</b>	7.5

540

540 **Table 2.** Empirical models and summary statistics for the relationships between salinity,  
 541 nutrients and Chl-a in the 20 studied lagoons. n: sample size;  $r^2$ : coefficient of determination;  
 542 p: significance level of r; NS: not significant ( $p \geq 0.05$ ).

Equation	Regression Model	n	$r^2$	p
1	$\log_{10}\text{DIN}$ on $\log_{10}\text{Sal}$	23	NS	0.29
2	$\log_{10}\text{DIP} = 4.8 - 3.7 \log_{10}\text{Sal}$	23	0.39	0.001
3	$\log_{10}\text{DSi} = 5.8 - 3.1 \log_{10}\text{Sal}$	23	NS	0.12
4	$\log_{10}\text{TN} = 5.3 - 2.3 \log_{10}\text{Sal}$	23	0.25	0.01
5	$\log_{10}\text{TP} = 5.8 - 3.7 \log_{10}\text{Sal}$	23	0.30	0.006
6	$\log_{10}\text{DIN}$ on $\log_{10}\text{DIP}$	23	NS	0.08
7	$\log_{10}\text{DIN}$ on $\log_{10}\text{DSi}$	23	NS	0.38
8	$\log_{10}\text{DSi}$ on $\log_{10}\text{DIP}$	23	NS	0.05
9	$\log_{10}\text{DIN:DIP}$ on $\log_{10}\text{DIN}$	23	NS	0.56
10	$\log_{10}\text{DIN:DIP} = 0.30 - 0.69 \log_{10}\text{DIP}$	23	0.76	0.0001
11	$\log_{10}\text{DIN:DIP} = 1.24 - 0.34 \log_{10}\text{DSi}$	23	0.19	0.04
12	$\log_{10}\text{DIN:DIP} = 1.67 - 0.47 \log_{10}\text{TN}$	23	0.20	0.03
13	$\log_{10}\text{DIN:DIP} = 0.97 - 0.45 \log_{10}\text{TP}$	23	0.34	0.003
14	$\log_{10}\text{TN} = 1.64 + 0.65 \log_{10}\text{TP}$	23	0.92	0.0001
15	$\log_{10}\text{TN:TP} = 2.2 - 0.37 \log_{10}\text{TN}$	23	0.52	0.0001
16	$\log_{10}\text{TN:TP} = 1.63 - 0.30 \log_{10}\text{TP}$	23	0.77	0.0001
17	$\log_{10}\text{TN:TP} = 1.24 + 0.34 \log_{10}\text{DIN:DIP}$	23	0.48	0.0003
18	$\log_{10}\text{Chl-a}$ on $\log_{10}\text{DIN}$	23	NS	0.22
19	$\log_{10}\text{Chl-a} = 1.60 + 0.72 \log_{10}\text{DIP}$	23	0.27	0.001
20	$\log_{10}\text{Chl-a} = -0.23 + 0.70 \log_{10}\text{DSi}$	23	0.23	0.02
21	$\log_{10}\text{Chl-a} = -1.96 + 1.62 \log_{10}\text{TN}$	23	0.81	0.0001
22	$\log_{10}\text{Chl-a} = 0.69 + 1.08 \log_{10}\text{TP}$	23	0.78	0.0001

543



543 **Table 3.** Contribution of sewage to total inputs of N and P in 13 lagoons for which the  
 544 watershed is well defined (Dupré et al., unpublished data). N:P ratios (by moles) in sewage  
 545 and inputs are compared with ratios in lagoon waters. For Bages (B) and the 8 Palavasian  
 546 lagoons, N:P ratios in the water correspond to pooled data from all stations.

Lagoons	% contribution of sewage to total inputs		TN:TP in sewage	TN:TP in total inputs	DIN:DIP in water	TN:TP in water
	N	P				
Bages	39	12	26.5	33.1	4.9	41
La Palme	37	14	3.4	16.0	11.4	85
Leucate	39	21	8.9	16.5	36.5	46
Or	49	55	24.0	27.4	11.5	29
Palavasian (8)	87	77	26.2	23.0	7.7	29
Thau	34	46	10.7	14.7	2.2	21

547

547 **Figure captions**

548 **Fig. 1.** Location of sampling Stns and limits of sectors (dotted line) in oligotrophic (□),  
549 mesotrophic (△), eutrophic (■) and hypertrophic (▲) LR and Corsica lagoons.

550 **Fig. 2.** Log scaled plot of DIN on DIP in oligotrophic (□), mesotrophic (△), eutrophic (■)  
551 and hypertrophic (▲) LR and Corsica lagoons.

552 **Fig. 3.** Relationship between TN and TP in oligotrophic (□), mesotrophic (△), eutrophic  
553 (■) and hypertrophic (▲) LR and Corsica lagoons. The dotted line corresponds to the  
554 Redfield ratio (16:1 by moles). See Table 2 for regression parameters.

555 **Fig. 4.** Relationship between TN:TP and DIN:DIP in oligotrophic (□), mesotrophic (△),  
556 eutrophic (■) and hypertrophic (▲) LR and Corsica lagoons. The solid and the dotted lines  
557 correspond respectively to the ratios used by Justić et al. (1995) for dissolved inorganic  
558 nutrients, and by Guildford and Hecky (2000) for total nutrients, to discriminate phosphorus  
559 limitation from nitrogen limitation. See Table 2 for regression equations.

560 **Fig. 5.** Relationships between Chl-a and DIN, DIP and DSi in oligotrophic (□), mesotrophic  
561 (△), eutrophic (■) and hypertrophic (▲) LR and Corsica lagoons. See Table 2 for  
562 regression equations.

563 **Fig. 6.** Relationships between Chl-a, and TN and TP in oligotrophic (□), mesotrophic (△),  
564 eutrophic (■) and hypertrophic (▲) LR and Corsica lagoons. See Table 2 for regression  
565 equations.

566

# FIGURE 1

566

567

568

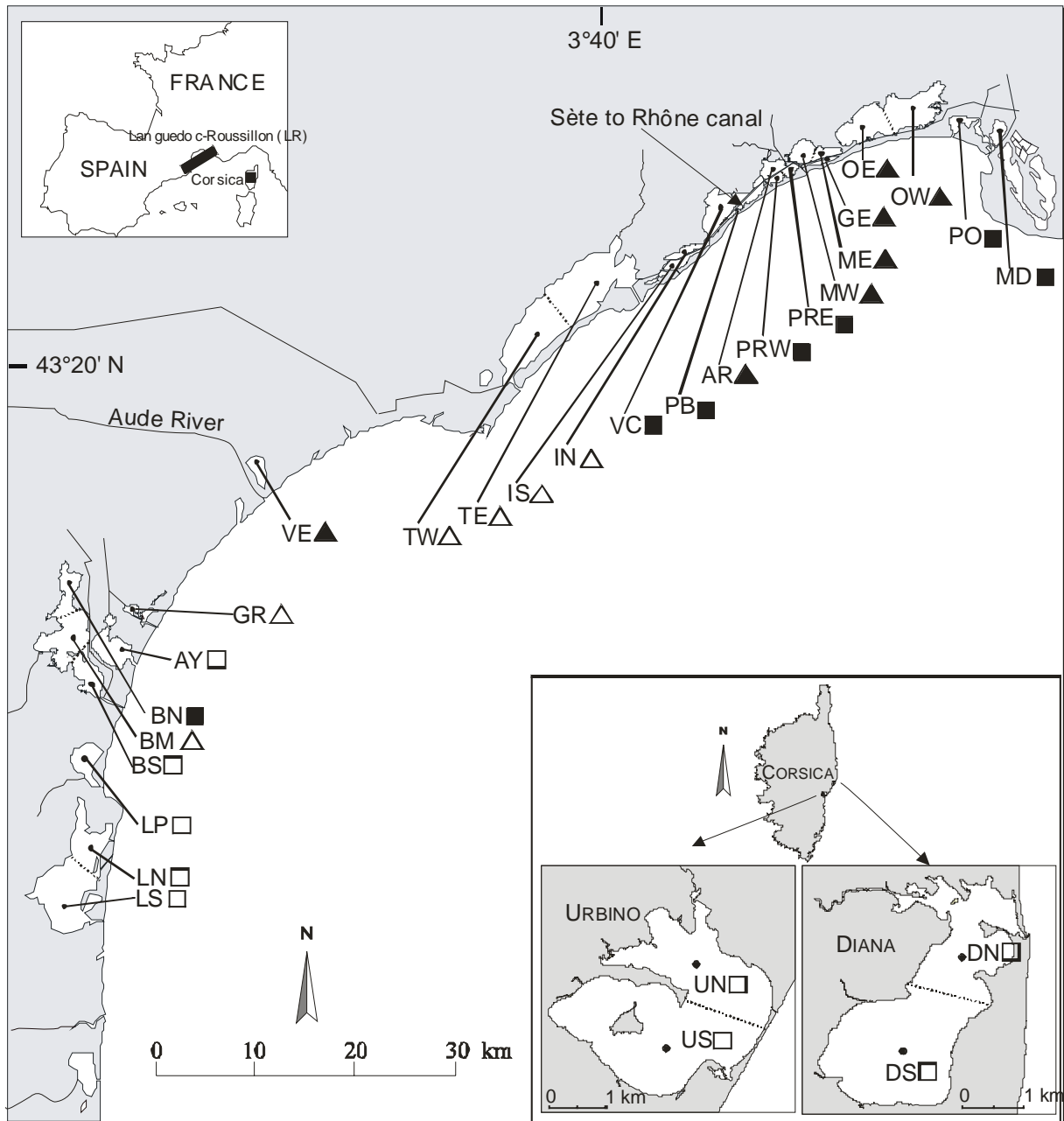


FIGURE 2

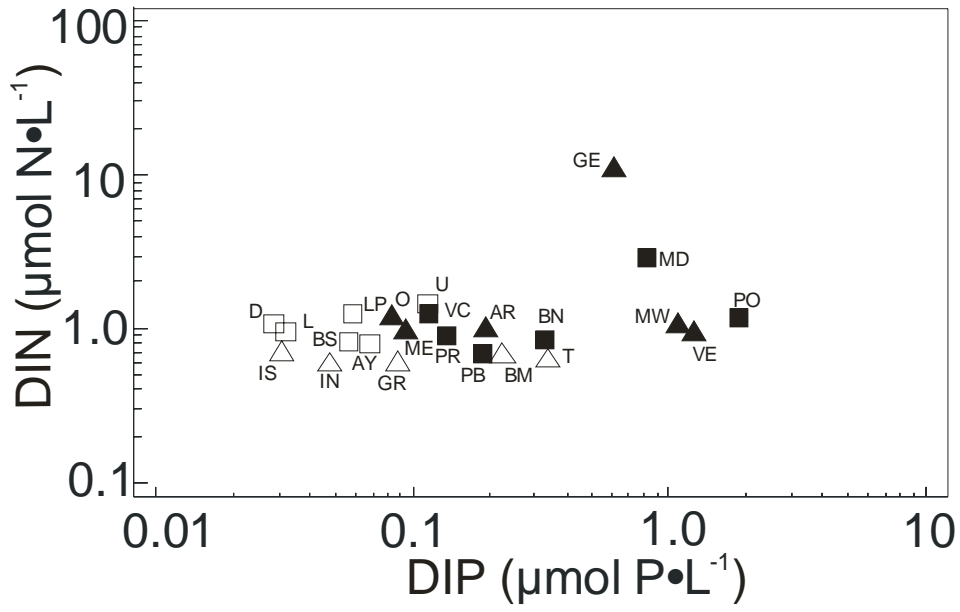


FIGURE 3

569

570

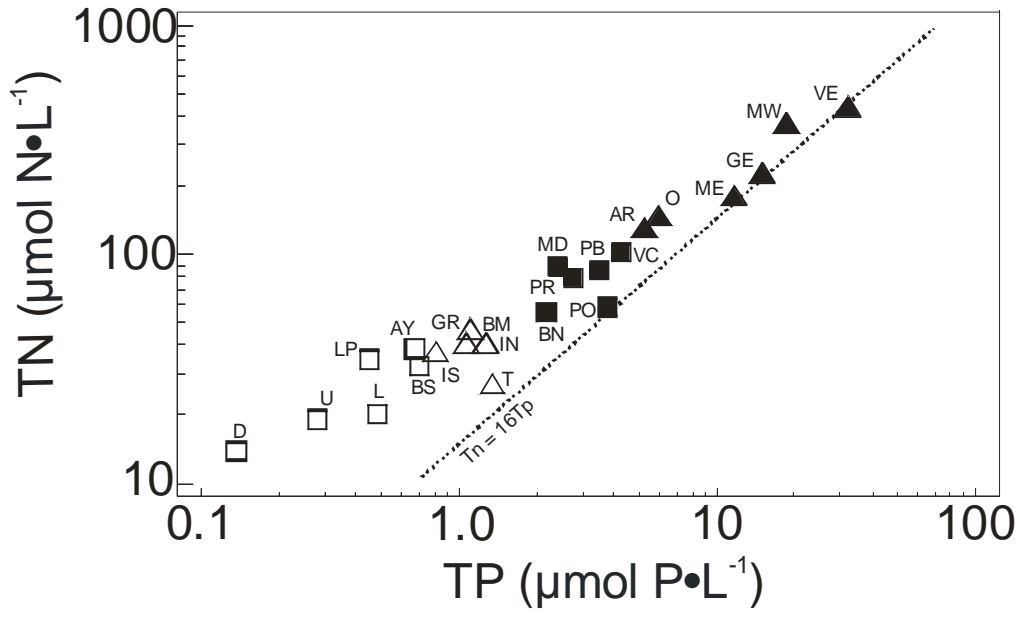


FIGURE 4

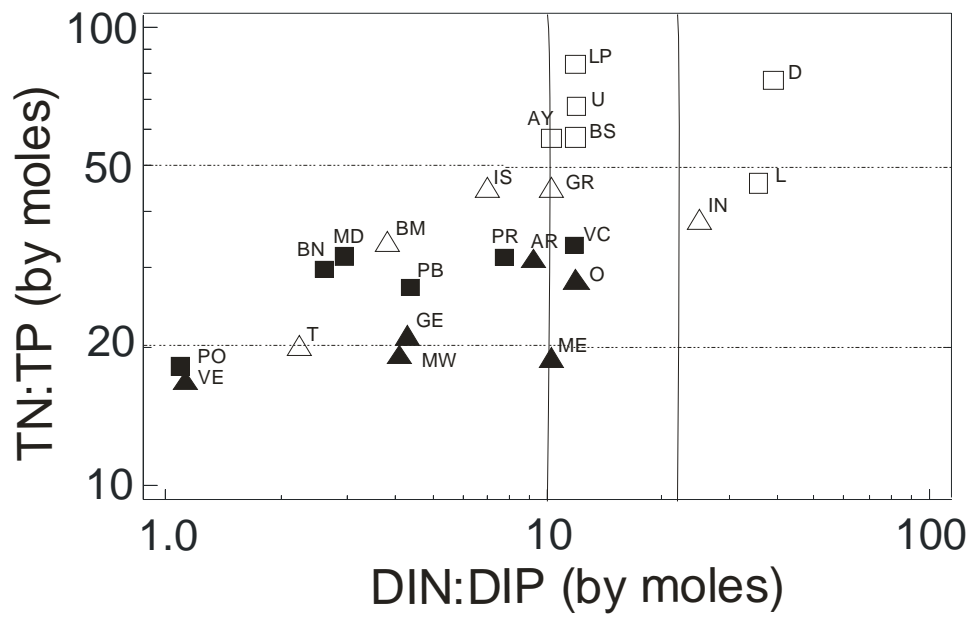
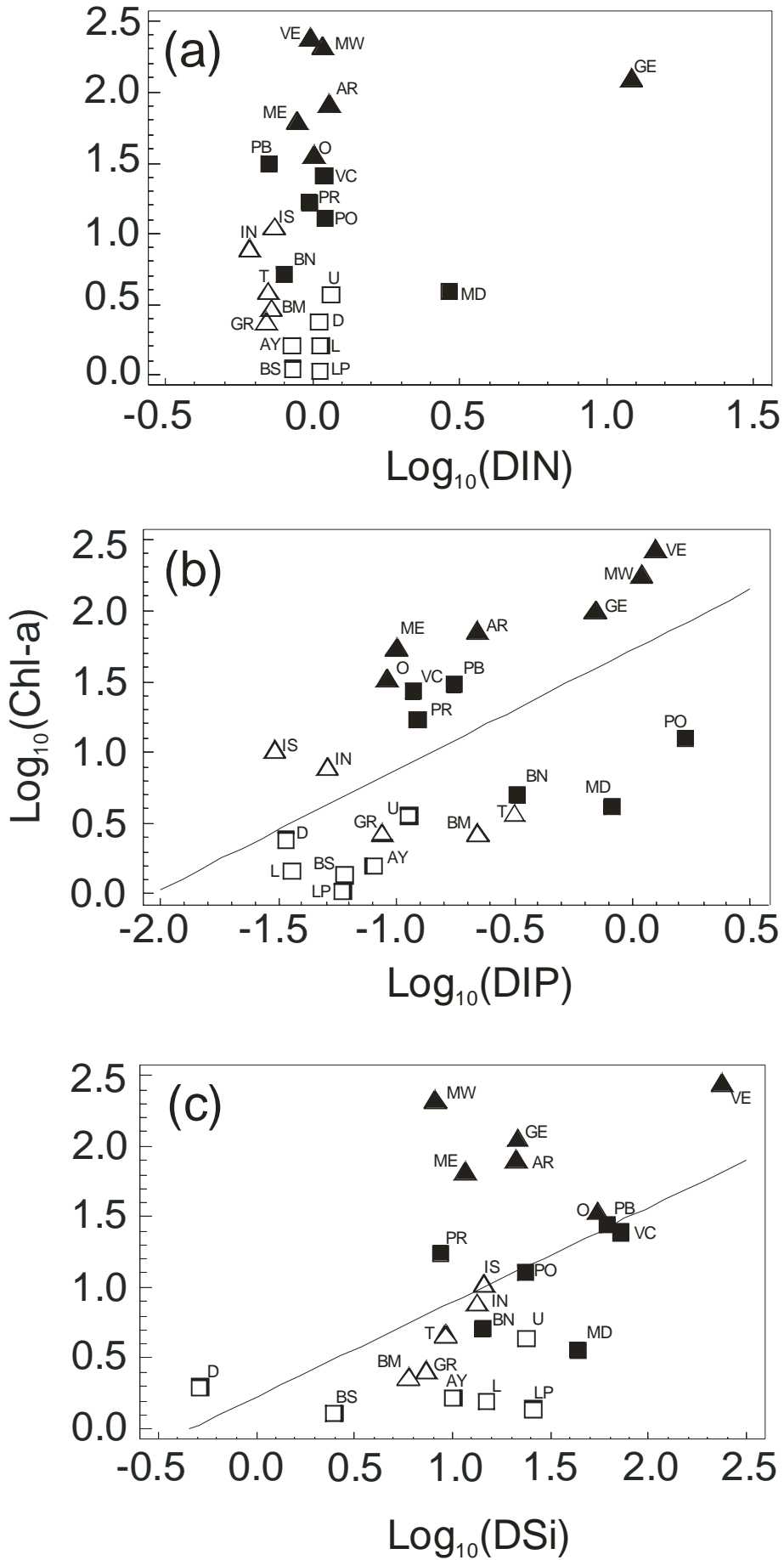


FIGURE 5

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FIGURE 6

