1   Influence of mussel culture on the vertical export of phytoplankton

2   carbon in a coastal upwelling embayment (Ría de Vigo, NW Iberia)

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25 ABSTRACT

26 The goal of this paper is to find out whether suspended mussel culture affects the

27 vertical fluxes of biogenic particles in the Ría de Vigo on a seasonal scale. With this

28 aim, vertical fluxes of particulate organic carbon (POC), and the magnitude and

29 composition of vertical export of phytoplankton carbon (Cphyto) collected in sediment

30 traps, were examined by comparing data obtained inside a mussel farming area (RaS),

31 with those found at a reference station (ReS) not affected by mussels. Our results

32 indicate that mussel farming has a strong impact on sedimentation fluxes under the

33 rafts, not only increasing POC flux, but also altering the magnitude and composition of

34 Cphyto fluxes. Average POC flux at RaS (2564 ± 1936 mg m^{-2} d^{-1}) was 4 times higher

35 than at ReS (731 ± 276 mg m^{-2} d^{-1}), and much of this increase was due to biodeposit

36 fluxes (Cbiodep) which accounted for large proportion of POC flux (35–60%). Indeed,

37 because of this high Cbiodep flux, only a small proportion of the POC flux was due to

38 Cphyto flux (3 –12 %). At the same time, we observed an increased sedimentation of

39 phytoplankton cells at RaS that could be explained by a combination of mechanisms:

40 less energetic hydrodynamic conditions under mussel rafts, ballast effect by sinking

41 mussel feces and diatoms aggregates. Moreover, mussel farming also altered the quality

42 of the Cphyto flux by removing part of the predatory pressure of zooplankton, and thus

43 matching diatom composition in water column and sediment traps.

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1. INTRODUCTION

Mussels are filter-feeders that clear large amounts of phytoplankton and other organic and inorganic particles suspended in the water column, repacking them into rapidly sinking fecal pellets (Jaramillo et al. 1992). This feeding behavior enhances the sedimentation in farming areas (Dahbläck and Gunnarsson 1981), diverting primary production and energy flow from planktonic to benthic food webs (Dame 1996; Cranford et al. 2003) and potentially enriching the underlying sediments with organic matter (Callier et al. 2006; Giles et al. 2006; Cranford et al. 2009). Quantifying this sedimentation flux and knowing its plankton composition is necessary to improve our management of coastal areas with significant mussel farming activity.

The Rías Baixas are four coastal embayments located on the NW Iberia (Fig. 1), where mussel is cultured on intensive scale (Tenore et al. 1982; Blanton et al. 1987; Figueiras et al. 2002). For these coastal inlets influenced by upwelling, it has been observed a strong connection between size structure and metabolic balance of the microbial plankton community, so that the autotrophy degree of the Rías was higher with greater contribution of larger phytoplankton (Cermeño et al. 2006; Arbones et al. 2008). The dominance of microplankton (> 20 μm), especially diatoms, for much part of the year is associated with high values of net community production (NCP), which implies a high export capacity of biogenic carbon outside the microbial community (Tremblay and Legendre 1994; Smith and Kemp 1995; Buesseler 1998). But under mussel rafts, the lower irradiance that cause the decrease in gross primary production (GPP), and the consumption of large sizes of microbial plankton by mussels (Froján et al. 2014) has been related with the decrease in NCP in the raft area (Froján et al. submitted). This ability of mussel culture to affect primary production and metabolic balance of the microbial community would presumably result in a reduction in the

75 export capacity of the microbial plankton community as a consequence of mussel
76 farming.

77   To date, most studies about sedimentation of organic matter in the NW Iberian
78 upwelling region (Bode et al. 1998; Olli et al. 2001; Varela et al. 2004; Alonso–Pérez et
79 al. 2010) focused on the magnitude of vertical fluxes of particulate organic carbon
80 (POC). Recently, Zúñiga et al. (2011) showed that phytoplankton carbon flux (Cphyto)
81 accounted for up to 49 % of total POC flux in the Ría de Vigo during the summer
82 upwelling, supporting the hypothesis that sedimentation of phytoplankton living cells
83 may become an important component of POC flux (Fowler and Knauer 1986; Turner
84 2015). The few available studies about sedimentation under mussel rafts in the Galician
85 Rías showed vertical fluxes of POC significantly higher than those outside the mussel
86 influence zone (Cabanas et al. 1979; Tenore et al. 1982; Alonso–Pérez et al. 2010;
87 Zúñiga et al. 2014). Moreover, Zúñiga et al. (2014) found a strong relationship between
88 seasonal variability in biodeposition of mussels and variability in sedimentation rates
89 under the rafts in the Ría de Ares–Betanzos. However, mussel culture influence on
90 phytoplankton sedimentation in the Rías remains unknown. At this stage, the working
91 hypothesis is that mussel farming may alter the natural sedimentation rates at the raft
92 area, not only by increasing POC flux by mussel biodeposition, but also by reducing
93 Cphyto flux due to mussel grazing.

94   In this regard, our study aims to evaluate for the first time how mussel culture
95 influences the quality of POC fluxes in the Ría de Vigo. To this end, we examined the
96 magnitude and composition of Cphyto fluxes collected in sediment traps, in relation to
97 the quantity and quality of the phytoplankton community in the water column. The
98 results from this study provide new information about the role played by mussel culture
99 on the carbon cycle in this coastal upwelling region.

2. MATERIALS AND METHODS

2.1. Characterization of the water column and vertical export

In the framework of the Spanish project RAFTING (Impact of mussel raft culture on the benthic-pelagic coupling in a Galician Ría), 24 oceanographic cruises were carried out between 2007 and 2008, covering the four seasonal periods characteristic of the region, autumn (September 17 to October 4), winter (January 28 to February 14), spring (April 14 to May 01) and summer (June 26 to July 14). During these sampling periods, **daily water column observations were carried out on board R/V 'Mytilus' at 2 stations** in the Ría de Vigo (Fig. 1): a reference station (ReS) and a raft station (RaS). The ReS was positioned in the central channel of the Ría (42 m maximum depth), well outside of the mussel farming area, a position that has been well-established as a reference site for studies concerning short-term and seasonal variability in the Ría de Vigo (e.g. Nogueira et al. 2000; Nogueira and Figueiras 2005; Crespo et al. 2006). The RaS was located slightly inwards in the Ría, within a raft polygon (group of rafts). Mussel rafts have an area of 500 m^2 which are 100 m apart and from its wooden structure hang a maximum of 500 ropes 12 m long with mussels attached. Under these conditions, mussels grow fast and are able to reach the commercial size (70 to 95 mm) within a relatively short period of time (16–18 months; Pérez-Camacho et al. 2013). At both sampling stations water samples were collected at nominal depths (surface, 5, 10, 15 and 20 m), using a CTD SBE 9/11 (SeaBird) fitted to an oceanographic rosette equipped with 12 Niskin bottles, for determining particulate organic carbon (POC), chlorophyll a (chl a) and phytoplankton biomass. Concentration values of POC, chl a and phytoplankton biomass in the water column, are integrated over the first 12 m depth, coinciding with the length

123   of the ropes where mussels grow. Integration was done at 1 m intervals from sea surface

124   down to 12 m depth.

125   Vertical fluxes of particulate matter were measured by means of a sediment trap

126   system MULTITRAP, with 4 cylindrical collectors with a height/diameter ratio of 10.8.

127   At both stations, collectors were placed at a depth of 13 m, without adding any

128   preservative and filled with a saline solution (5 psu in excess) to prevent water exchange

129   with outside waters. Sediment traps remained deployed for 24 h at ReS and 3 h at RaS,

130   to avoid silting the collectors due to expected high vertical fluxes under the raft. The

131   sediment trap efficiency depends on the flow velocity. Baker et al. (1988) estimated that

132   with currents less than 12 cm s^{-1}, the fluxes of matter collected by a sediment trap are

133   equivalent to those collected by a drifting trap. In our study, current meters at the study

134   sites recorded speeds below 12 cm s^{-1} for more than 90 % of the mooring time for the

135   trap depths (Villacieros–Robineau, pers. comm.). Thus, we assume that potential biases

136   in sedimentation fluxes are very low.

137   Samples for the analysis of POC, both in the water column (250 ml) and sediment

138   traps (200 ml), were filtered through GF/F Whatman filters (0.7 μm pore size),

139   previously weighed and combusted at 450 ºC (4 h). Filters, after being dried overnight,

140   were stored frozen until analysis. POC final concentrations were obtained using a

141   PERKIN_ELMER 2400 CNH elemental analyzer, including daily acetanilide standards.

142   The accuracy of the method is ± 0.3 μmol C l^{-1}.

143   Chl *a* concentration was determined by filtering samples of water column (250 ml)

144   and sediment traps (200 ml) trough GF/F Whatman filters. Immediately after filtration,

145   filters were frozen (–20 ºC) until analysis. Prior to analysis, the filters were immersed in

146   90 % acetone, leaving them for 24 h in darkness at 4 ºC for pigment extraction. The

147 final concentration of chl *a* was determined by measuring the fluorescence of the

148 extracted pigments using a Turner Designs Fluorometer calibrated with pure chl *a*

149 (Sigma Chemical).

150 From every depth of the water column and from two of the four sediment trap

151 collectors, 100 ml samples were collected to estimate the carbon biomass of living

152 phytoplankton cells in the water column and in the sediment traps. Samples were

153 preserved in iodine solution and depending on chl *a* concentration, between 5 and 100

154 ml of sample were settled using sedimentation chambers. An inverted microscope was

155 used for counting and identification of phytoplankton cells, reaching the species level

156 whenever possible. For simplicity, we apply the term phytoplankton to denote the set of

157 autotrophic and heterotrophic microplankton (20 – 200 μm) identified by this means.

158 Chain-forming diatoms (< 20 μm) were also ascribed to microplankton. The smaller

159 species (< 20 μm) were counted doing one or two perpendicular transects with 400x

160 magnification, medium individual (20 – 50 μm) were counted in one or two

161 perpendicular transects using 200x magnification and larger organisms within

162 phytoplankton (> 50 μm) were counted by scanning across the board with 100x

163 magnification. At least 500 cells were counted in each sample. Cell biovolumes were

164 calculated as recommended by Hillebrand (1999) and the biovolumes of diatoms and

165 dinoflagellates were converted into carbon biomass according to Strathmann (1967).

166 However, the estimation of cell carbon in *Noctiluca scintillans* was conducted by

167 applying the correction suggested by Tada et al. (2000). Cellular carbon in flagellates,

168 other than dinoflagellates, was estimated according Verity et al. (1992) and in ciliates

169 according Putt and Stoecker (1989). Unfortunately, due to technical problems

170 encountered during autumn sampling, we do not have the data set of chl *a* flux at ReS

171 station, nor chl *a* and Cphyto flux at RaS during this period.

172   2.2. Ekman transport and Runoff

173   We analyzed the intensity of upwelling based on the upwelling index, which was

174   estimated using the component ($-Q_x$, m^3 s^{-1} km^{-1}) of the Ekman transport, that is

175   perpendicular to the coast and hence equivalent to the surface water outflow from the

176   Ría, following Bakun (1973):

177                    $-Q_{x=} -[(\rho_a C|V|)/(f \rho_{sw})] V_y$ (1)

178   where ρ_a is the air density (1.22 kg m^{-3}) at 15 ºC, C is an empirical coefficient of drag

179   (1.3×10^{-3}, dimensionless), $|V|$ is the daily mean value of the module of the wind stress

180   (m s^{-1}) of northerly component (V_y) registered by the Silleiro buoy deployed on the

181   **shelf in front of the Ría de Vigo by 'Puertos del Estado',** f is the Coriolis parameter

182   (9.95×10^{-5} s^{-1}) at 43 ºN and ρ_{sw} is the density of seawater (1025 kg m^{-3}). Positive

183   values of $-Q_x$ indicate the predominance of northerly winds responsible for upwelling

184   within the Ría, while negative values are related to downwelling induced by southerly

185   winds.

186   Continental runoff into the inner part of the Ría de Vigo (Q_r, m^3 s^{-1}) is dominated by

187   the discharge from the river Oitavén–Verdugo (Fig. 1). Daily flows were provided by

188   **'Aguas de Galicia' (the company in charge of the management of urban waters).** The

189   natural component of the flow per unit area was calculated according to the empirical

190   equation of Ríos et al. (1992).

191   2.3. Statistical analysis

192   To detect the significant differences between the observed sedimentation fluxes at

193   ReS and at RaS, the non–parametric analysis of variance (Kruskal–Wallis test) was used.

194   Statistical analysis was performed using the statistical software SPSS.

195   3. RESULTS

196   3.1. Biogeochemical properties of the water column at ReS

197   The observed variability in integrated POC, chl *a* and Cphyto concentrations at ReS

198   for the four study periods (Fig. 2, Table 1) was closely linked with the hydrographic

199   changes previously analyzed in detail by Froján et al. (2014). The highest seasonal

200   average POC concentration occurred in autumn (3531 ± 803 mg m^{-2}, Table 1), when

201   transition from upwelling to downwelling conditions took place (Fig. 2a).

202   Concentrations of Cphyto and chl *a* followed a similar pattern to POC and the

203   contribution of Cphyto amounted on average about a half of POC (55 ± 32 %). Diatoms

204   were the largest biomass contributors to Cphyto (66 ± 22 %), with an outstanding

205   presence of *Chaetoceros socialis* (Fig. 4).

206   During winter, the studied variables recorded annual minimum concentrations.

207   Average POC in winter (1923 ± 443 mg m^{-2}) was almost half of average POC obtained

208   for the other three sampling periods (Table 1). Along with low chl *a* concentration (17 ±

209   5 mg m^{-2}), phytoplankton biomass also decreased, so its contribution to POC (11 ± 4 %)

210   was considerably reduced. Diatoms continued to be the major component of

211   phytoplankton community (53 ± 8 %). The most prominent representative was the

212   chain‑forming species S*keletonema* cf. *costatum* (Fig. 4).

213   During spring, Cphyto (2294 ± 1057 mg m^{-2}) and chl *a* (66 ± 30 mg m^{-2})

214   concentrations reaching the highest average values of all periods (Fig. 2b). Under these

215   conditions, POC was largely made up of Cphyto (67 ± 20 %). Diatoms biomass

216   dominated (67 ± 14 %). *Detonula pumila* was the species that contributed the most in

217   the first half of the period, under low wind–high mixing conditions, while *Chaetoceros*

218   *curvisetus* flourished after the strong river discharge (Fig. 4).

219   In summer, the three biogeochemical variables followed a similar evolution

220   modulated by alternation of upwelling and relaxation events. Average concentrations

221   and Cphyto:POC ratio were lower than in autumn and spring. Dinoflagellates provided

222   most of the biomass (62 ± 13 %) due to the contribution of the oversized dinoflagellate

223   *Noctiluca scintillans* (Fig. 4).

224   3.2. Sedimentation flux at ReS

225   Flux of POC barely fluctuated during autumn (640 ± 100 mg m^{-2} d^{-1}; Table 2) despite

226   changes in upwelling conditions (Fig. 3). Similarly, Cphyto flux was high and steady,

227   being the largest contribution to POC for the four studied periods (23 ± 12 %). Diatoms

228   accounted for 49 ± 15 % of biomass collected in the sediment traps. *Chaetoceros*

229   *socialis*, *Chaetoceros curvisetus* and *Asterionellopsis glacialis* provided most of the

230   biomass while the upwelling lasted. However, ciliates, dinoflagellates cysts and

231   *Thalassiosira* sp. accounted for more than a half of the phytoplankton biomass after the

232   strong downwelling (Fig. 3c, 4).

233   The POC flux during winter (633 ± 183 mg m^{-2} d^{-1}) hardly differed from the autumn

234   one, but it reached minimum seasonal values for Cphyto (55 ± 15 mg m^{-2} d^{-1}) and chl *a*

235   (4 ± 1 mg m^{-2} d^{-1} ; Table 2). Therefore, Cphyto content in POC flux (10 ± 4 %) was also

236   low during this period. More than half of phytoplankton cells collected in the traps was

237   diatoms (57 ± 27 %), mainly *Skeletonema* cf. *costatum* (Fig. 4).

238   Average POC flux in spring (924 ± 445 mg m^{-2} d^{-1}) was the annual highest (Fig. 3b).

239   Chl *a* flux showed greater variability than Cphyto flux, which was relatively low and

240 constant. Precisely, given the large POC flux of this period, Cphyto:POC ratio was

241 similar to that found in winter (11 ± 6 %). Moreover, there was a high contribution of

242 diatoms biomass (60 ± 20 %). *Detonula pumila* and *Leptocylindrus danicus* were the

243 species that provided more biomass at the beginning, under mixing conditions, while

244 the diatom *Chaetoceros curvisetus* thrived associated to large river input (Fig. 4).

245 Average summer POC flux was high (728 ± 185 mg m^{-2} d^{-1}), though not as much as

246 the spring one (Fig. 3b). However, average Cphyto flux (115 ± 84 mg m^{-2} d^{-1}) was

247 slightly higher than in the previous sampling, resulting in a Cphyto:POC ratio

248 considerably higher (18 ± 17 %). Dinoflagellates became more important during this

249 period, contributing 38 ± 22 % of the biomass flux (Table 2), mostly due to *Noctiluca*

250 *scintillans* (Fig. 4).

251 3.3. Biogeochemical properties of the water column at RaS

252 During autumn, suspended POC concentration at RaS (2526 ± 666 mg m^{-2}) was on

253 average 27 ± 17 % lower than at ReS (Fig. 5, Table 1), being the only period with

254 significant differences in POC concentration between the two sampling stations

255 (Kruskal–Wallis test, $p < 0.05$). Likewise, Cphyto (508 ± 369 mg m^{-2}) and chl *a* (28 ±

256 19 mg m^{-2}) concentrations at RaS were significantly lower than at ReS. These changes

257 resulted in a considerable reduction in the Cphyto:POC ratio at RaS (20 ± 11 %).

258 Despite the general decline in Cphyto, diatoms continued to dominate (59 ± 15 %), with

259 an important presence of *Chaetoceros socialis* (Fig. 4, 5c).

260 During winter, POC (1650 ± 344 mg m^{-2}), Cphyto (130 ± 41 mg m^{-2}) and chl *a* (11 ±

261 3 mg m^{-2}) concentrations in the water column at RaS reached the annual minima and

262 were generally lower than at ReS. Furthermore, Cphyto:POC ratio at RaS (8 ± 3 %) was

263 even lower than at ReS (Table 1). Also, the proportion of diatom biomass at RaS

264 decreased (48 ± 10 %), though *Skeletonema* cf. *costatum* remained the most important

265 species (Fig. 4).

266 The highest concentrations of POC (3111 ± 427 mg m^{-2}), Cphyto (1575 ± 941 mg

267 m^{-2}) and chl *a* (54 ± 19 mg m^{-2}) at RaS were reached in the spring sampling. Under

268 these conditions, about half of POC was attributable to Cphyto (49 ± 26 %), a

269 contribution slightly lower than that observed at ReS, with diatoms accounting for > 70

270 % of the biomass. Similarly to ReS, *Detonula pumila* and *Chaetoceros curvisetus* were

271 the most important species during this period (Fig. 4).

272 During summer, the Cphyto concentration at RaS (739 ± 520 mg m^{-2}) was

273 significantly lower (by 48 ± 21 %) than at ReS (Kruskal–Wallis test, $p < 0.05$). Besides,

274 Cphyto:POC ratio in the water column at RaS (35 ± 26 %) was lower than at ReS. The

275 proportion of dinoflagellates at RaS was high, and as observed at ReS, *Noctiluca*

276 *scintillans* was the most important species during this period (Fig. 4).

277 3.4. Sedimentation flux at RaS

278 Average POC flux at RaS during autumn (2507 ± 2031 mg m^{-2} d^{-1}) far exceeded the

279 flux recorded at ReS (Table 2). Maximum POC flux values were recorded at the

280 beginning of the period, and decreased to four times its value for the second half (Fig.

281 6b). Unfortunately, we only have data of Cphyto and chl *a* fluxes at RaS for the first

282 autumn sampling day.

283 In winter, average POC flux (1203 ± 975 mg m^{-2} d^{-1}) at RaS (Fig. 6b, Table 2) was

284 the lowest of the year and showed no significant differences with ReS (Kruskal–Wallis

285 test, $p > 0.05$). Nor we did find significant differences in chl *a* flux, which was very

286   similar at the two stations. Nevertheless, Cphyto flux at RaS (22 ± 14 mg m^{-2} d^{-1}) was

287   significantly lower than at ReS (Kruskal–Wallis test, $p < 0.05$) and its contribution to

288   POC (3 ± 4 %) was also substantially lower. Although *Skeletonema* cf. *costatum* was

289   the species with the highest biomass in the water column (Fig. 4), more than half of the

290   biomass flux at RaS (54 ± 23 %) was due to dinoflagellates and dinoflagellates cysts

291   (Table 2, Fig. 4).

292   During spring, the highest seasonal average fluxes of POC (3958 ± 1871 mg m^{-2} d^{-1}),

293   Cphyto (412 ± 269 mg m^{-2} d^{-1}) and chl *a* (125 ± 101 mg m^{-2} d^{-1}) were recorded, being

294   significantly higher than at ReS (Kruskal–Wallis test, $p < 0.05$). Cphyto contribution to

295   POC flux (12 ± 5 %) was relatively low during this period and similar to ReS. In terms

296   of biomass, diatoms were the main contributors to Cphyto flux (77 ± 15 %), with

297   *Detonula pumila* and *Chaetoceros curvisetus* frequently appearing in the sediment traps

298   at RaS (Fig. 4).

299   In summer, POC flux (2590 ± 2026 mg m^{-2} d^{-1}) was highly variable at RaS and

300   significantly higher than at ReS (Kruskal–Wallis test, $p < 0.05$). However, Cphyto flux

301   at RaS (182 ± 135 mg m^{-2} d^{-1}) was not significantly different from ReS. Consequently,

302   Cphyto:POC ratio at RaS was lower (10 ± 12 %). As at ReS, diatoms provided an

303   important part of the biomass collected in sediment traps (39 ± 26 %), especially the

304   species *Chaetoceros curvisetus*, *Lauderia annulata, Leptocylindrus danicus* and

305   *Coscinodiscus* sp. Dinoflagellates maintained a high biomass flux at RaS (49 ± 23 %),

306   higher than at ReS (38 ± 22 %), whose foremost representative remained *Noctiluca*

307   *scintillans* (Fig. 4).

308

309 4. DISCUSSION

310 4.1. Vertical export of phytoplankton carbon

311 Considering that the structure and composition of the microbial community in the
312 ocean involves a certain degree of autotrophy of the system and therefore a certain
313 export capacity (Smith and Kemp 2001; Cermeño et al. 2006; Arbones et al. 2008), in
314 this study we focused on unravelling to what extent changes in quantity and quality of
315 phytoplankton biomass in the water column can modulate the vertical export of organic
316 carbon outside the photic layer, and how this export is modified by the presence of
317 mussel farming.

318 The present study showed that the seasonal variability of suspended POC (Fig. 7a,
319 Table 1) was not reflected in the magnitude of POC vertical flux, since it remained
320 relatively constant with an annual average of 731 ± 276 mg m^{-2} d^{-1}, and with no
321 significant differences between periods (Fig. 7b, Table 2). However, we did find
322 variability in the composition of POC collected in the traps, due to variability in Cphyto
323 flux (Fig. 7b, c). In this way, between 9 and 31 % of POC flux at ReS was due to
324 Cphyto flux, similar to previously published results for the Ría de Pontevedra and Vigo
325 (2 − 26%), (Varela et al. 2004; Zúñiga et al. 2011). Likewise, diatom contribution to
326 vertical Cphyto flux varied over the different periods (35 − 69 %). This seasonal
327 variation in quantity and quality of Cphyto points to a vertical flux modulated by the
328 different composition of phytoplankton community in the water column and the
329 changing oceanographic scenarios (Fig. 8).

330 In fact, during our study year the two contrasting situations regarding export capacity
331 of phytoplankton living cells corresponded to the autumn and winter cruises. The largest

332   Cphyto fluxes at ReS were achieved during the upwelling to downwelling autumn

333   transition, associated with the presence of large and chain–forming diatoms, responsible

334   for the high export capacity of the system. In this way, initial upwelling conditions

335   favored diatoms bloom followed by subsequent sinking of chain–forming species

336   (*Chaetoceros socialis*, *Chaetoceros curvisetus* and *Asterionellopsis glacialis*; Fig. 8).

337   By contrast, during the winter mixing, annual minimum levels of Cphyto in the water

338   column resulted in the lowest Cphyto fluxes of the year. Nevertheless, the proportion of

339   diatoms in the traps (57 ± 27 %) reflected Cphyto composition in the water column (Fig.

340   7a, b), where long chains of the diatom *Skeletonema* cf. *costatum* were vertically

341   exported (Fig. 8).

342   In between these two contrasting cases of Cphyto flux, minimum for winter and

343   maximum for autumn, the intermediate export capacities for the spring and summer

344   cruises also responded to prevailing hydrographic conditions (higher or lower degree of

345   stratification) and the composition of the microbial community. Under the well mixed

346   water column of the spring sampling, long chains of diatoms predominated (*Detonula*

347   *pumila* and *Leptocylindrus danicus*) (Fig. 8a). These large and chain–forming species

348   present a high export capacity, being identified in the sinking material together with

349   dinoflagellates cysts, which indicated the occurrence of surface sediment resuspension

350   (Fig. 8b). The subsequent thermohaline stratification resulted in the proliferation of the

351   chain–forming diatom *Chaetoceros curvisetus* (Fig. 8a) with relatively low contribution

352   to the settling material (9 ± 6 %, Fig. 7b). This low share could be related with the

353   morphologically favored buoyancy of *Ch. curvisetus* (Margalef 1978; Tilstone et al.

354   2000; Acuña et al. 2010), but also with intense water column stratification that hinders

355   vertical flux, and favors the potential horizontal offshore advection as a result of the

356   positive circulation reinforced by river discharge (Varela et al. 1991; Castro et al. 1994).

357 On the other hand, the buoyancy or swimming ability of *Noctiluca scintillans* (Fermín

358 et al. 1996) likely favored the accumulation of this oversized heterotrophic

359 dinoflagellate during the summer sampling (Fig. 8a). However, the contribution of

360 Cphyto to POC in sediment traps (18 ± 17 %, Fig. 7b), was relatively low compared

361 with water column (54 ± 33 %, Fig. 7a), indicating that an important part of the fixed

362 carbon was not vertically exported, being probably consumed by *Noctiluca scintillans*

363 (Kiørboe et al. 1998; Tiselius and Kiørboe 1998).

364 Thus, the composition of phytoplankton community, together with hydrodynamic

365 processes modulates the vertical export of biogenic particles in the Ría de Vigo. The

366 largest Cphyto fluxes at ReS were achieved during the autumn transition from

367 upwelling to downwelling conditions, associated with high NCP (186 ± 67 mmol O_2 m^{-2}

368 d^{-1}; Froján et al. submitted), and the presence of large and chain–forming diatoms,

369 responsible for the high export capacity of the system. By contrast, during the winter

370 mixing we found lower Cphyto fluxes associated with a lesser degree of autotrophy (43

371 ± 22 mmol O_2 m^{-2} d^{-1}).

372 4.2. Influence of mussel farming in vertical export of phytoplankton carbon

373 Studies conducted in the Galician Rías have showed high sedimentation rates in the

374 rafts area (Cabanas et al. 1979; Tenore et al. 1982; Alonso–Pérez et al. 2010; Zúñiga et

375 al. 2014) due to mussel biodeposits flux. Our results corroborates these previous works,

376 since we have observed an average POC flux at RaS (2564 ± 1936 mg m^{-2} d^{-1}) four

377 times higher than at ReS (731 ± 276 mg m^{-2} d^{-1}). At the same time and in contrast to the

378 pattern observed at ReS, the magnitude of the POC flux at RaS varied seasonally (Fig

379 7e, Table 2). In this context, our study is the first to analyze in detail the seasonality in

380 POC sedimentation under a mussel raft.

381   If we consider that much of the POC flux collected by sediment traps in the raft area

382   was due to the contribution of biodeposits, the variability in the biodeposits flux could

383   explain the observed variability in the POC flux at RaS. In this regard, little is known

384   about the relative contribution of mussel biodeposits to vertical sedimentation fluxes,

385   despite being essential to understand the influence of mussel farming in the ecosystem.

386   Giles et al. (2006) indicated that between 6 and 14 % of the sediment flux in the

387   farming area of a bay in New Zealand was due to mussel feces. In our study, to estimate

388   the proportion of POC flux due to biodeposits at RaS, we distinguish three components

389   of the POC flux collected by the sediment traps: biodeposits flux (Cbiodep), Cphyto

390   flux measured in the sedimentation traps at RaS (Cphyto), and remaining particulate

391   organic carbon flux (Crest), which we assume the same at the two sampling stations.

392
$$FluxC_{biodep}^{RaS} = FluxPOC^{RaS} - FluxC_{phyto}^{RaS} - FluxC_{rest}^{ReS} \qquad (2)$$

393   In this way, the observed differences in POC flux between ReS and RaS would be

394   due to differences in Cphyto and Cbiodep fluxes. Based on these calculations, Cbiodep

395   flux accounted for 58 ± 32 % of the POC flux in spring, and for 60 ± 19 % in summer,

396   being related with the significant increase of the POC flux observed in RaS regarding

397   ReS in these periods (Kruskal–Wallis test, $p < 0.05$). On the contrary, during winter,

398   with a lower estimated Cbiodep flux (35 ± 39 %), we did not find significant differences

399   in the POC flux between the two sampling stations (Kruskal–Wallis test, $p > 0.05$).

400   Overall, our values are higher than those provide by Giles et al. (2006), but in line with

401   a greater mussel production in our study region.

402   Indeed because of the high Cbiodep flux in the raft area, only a small proportion of

403   the POC flux was due to Cphyto flux (3 – 17%), (Fig. 7e, Table 2). If we also consider

404   the decline in NCP at RaS observed by Froján et al. (submitted), we may expect a lower

405 Cphyto flux since it involves a smaller export capacity of the system. During winter, our

406 assumption was met, with a significant reduction in the vertical exportation of Cphyto at

407 RaS (Kruskal–Wallis test, $p < 0.05$), that would be related to the reduction in Cphyto

408 biomass in the water column as consequence of mussel feeding (Fig. 7). By contrast,

409 Cphyto flux at Ras was higher than at ReS during spring and summer (Fig. 7c, f),

410 though the differences were only significant in spring (Kruskall–Wallis test, $p < 0.05$).

411 In this context, we have identified a variety of mechanisms which would explain the

412 increase in sedimentation of Cphyto at RaS.

413 First of all, our observations lead us to think that Cphyto flux at RaS in spring and

414 summer could have been favored by the less energetic hydrodynamic conditions in the

415 raft area, due to the decrease in the current velocity when passing through culture ropes

416 (Blanco et al. 1996; Newell and Richardson 2014). Moreover, based on the fact that a

417 high Cbiodep flux occurred at RaS both in spring and summer samplings, and that the

418 average size of mussel feces exceeds 200 μm (Giles and Pilditch 2004) we suggest that

419 the settling of mussel feces could cause a ballast effect on other biogenic particles in the

420 water column (Boyd and Trull 2007; Passow and Carlson 2012), increasing Cphyto

421 fluxes. In principle, it can be expected that these mechanisms affect more those species

422 with greater tendency to settle, as occurred in summer for large (*Coscinodiscus* sp.) and

423 chain–forming diatoms (*Lauderia annulata*), that sedimented more at RaS (Fig. 4, 8d).

424 But even species, whose morphological characteristics give them some buoyancy as

425 *Noctiluca scintillans* in summer and *Chaetoceros curvisetus* in spring and summer,

426 recorded increased sedimentation at RaS (Fig 4). In the particular case of *Ch.*

427 *Curvisetus,* we think that the quietest hydrodynamic conditions in the raft area could

428 even favor the formation of aggregates (Kranck and Milligan 1988; Alldredge and

429 Gotschalk 1989), resulting from increase the adherence between cells by producing

430 exopolymers (Lancelot 1983; Kiørboe and Hansen 1993), and this could be a secondary

431 factor contributing to explain the increase of sedimentation of this species at RaS (Fig.

432 8d).

433   We also note that mussel farming not only altered the quantity of Cphyto flux, but

434 also the quality, understood as the contribution of diatoms to Cphyto flux. At RaS, the

435 proportion of diatoms in the traps was very similar to that found in the water column,

436 and both proportions were significantly correlated ($r^2 = 0.73$, $p < 0.001$). By contrast at

437 ReS, a greater variability can be seen, and it is striking the loss of the relationship

438 between proportions observed at ReS ($r^2 = 0.14$, $p < 0.05$). One possible explanation for

439 this lower variability at RaS, could be the reduction of zooplankton in the water column

440 after being consumed by mussels (Maar et al. 2008). By removing the predatory

441 pressure of zooplankton, feeding disturbance that zooplankters exerted on the

442 distribution and composition of diatoms in the water column would be reduced,

443 resulting in less variability in the composition of the vertical fluxes of diatoms collected

444 in the sediment traps with regard to those found in the water column.

445   In short, this is the first study that analyzes the Cphyto flux under a mussel raft and

446 proposes a combination of mechanisms that explain the increased sedimentation of

447 phytoplankton cells in this area. As a result of this increase at RaS, the relationship

448 between NCP and Cphyto that existed at ReS was lost. Thus, despite the decline in NCP

449 because of top–down control by mussels on phytoplankton and the light attenuation

450 under rafts (Froján et al. submitted), we observed that the export capacity increased in

451 the raft area. Hence, our results indicate that mussel farming has a strong impact on

452 sedimentation flux under the rafts, not only increasing the POC flux, but also altering

453 the magnitude and composition of Cphyto fluxes. Additional research increasing

454 temporal and spatial resolution of sampling, both inside and outside the farming areas,

455 is needed to further support our conclusions.

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678   FIGURE CAPTIONS

679

680   Fig. 1 Location map of the Ría de Vigo showing the two sampling sites (✳):

681   Reference (ReS) and raft (RaS) stations. Raft polygons are shown as blue areas. Above,

682   zoom in nearby the experimental raft showing the seawater sampling site (SW) and the

683   location used for sediment trap deployments (ST) at RaS.

684

685   Fig. 2 (a) Time series of upwelling index (UI, $m^3 \ s^{-1} \ km^{-1}$, black bars) and river

686   outflow (Q_r, $m^3 \ s^{-1}$, grey bars), (b) particulate organic carbon (POC), phytoplankton

687   carbon (Cphyto), and chlorophyll a (chl a) integrated concentrations for the first 12 m

688   of the water column at the reference station (ReS), (c) Bar plots of biomass of the main

689   phytoplankton groups in the water column. Units (mg m^{-2}).

690

691   Fig. 3 (a) Time series of upwelling index (UI, $m^3 \ s^{-1} \ km^{-1}$, black bars) and river

692   outflow (Q_r, $m^3 \ s^{-1}$ grey bars), (b) particulate organic carbon (POC), phytoplankton

693   carbon (Cphyto), and chlorophyll a (chl a) vertical fluxes at the reference station (ReS),

694   (c) Bar plots of biomass of the main phytoplankton group collected in the sediment

695   traps. Units (mg $m^{-2} \ d^{-1}$).

696

697   Fig. 4 Average integrated biomass of the main phytoplankton species in the water

698   column (up bars, mg C m^{-2}), and in the sediment traps (down bars, mg C $m^{-2} \ d^{-1}$), at

699   reference (ReS, black bars) and raft (RaS, gray bars) stations, for each sampling period

700   (autumn, winter, spring and summer)

701

702   Fig. 5 (a) Time series of upwelling index (UI, $m^3 s^{-1} km^{-1}$, black bars) and river

703   outflow (Q_r, $m^3 s^{-1}$, grey bars), (b) particulate organic carbon (POC), phytoplankton

704   carbon (Cphyto), and chlorophyll a (chl a) integrated for the first 12 m of the water

705   column at raft station (RaS), (c) Bar plots of the biomass of the main phytoplankton

706   groups in the water column. Units (mg m^{-2}).

707

708   Fig. 6 (a) Time series of upwelling index (UI, $m^3 s^{-1} km^{-1}$, black bars) and river

709   outflow (Q_r, $m^3 s^{-1}$, grey bars), (b) particulate organic carbon (POC), phytoplankton

710   carbon (Cphyto), and chlorophyll a (chl a) fluxes at raft station (RaS), (c) Bar plots of

711   the biomass of the main phytoplankton group collected in the sediment traps. Units (mg

712    $m^{-2} d^{-1}$)

713

714   Fig. 7 Stacked bars plot showing the relative contribution of diatoms (striped blue,

715   % blue number) to Cphyto (solid blue), and the relative contribution of Cphyto (%

716   white number) to POC (solid gray), both in the water column (mg C m^{-2}) at reference (a,

717   ReS) and raft (d, RaS) stations, and in the sediment traps (mg C $m^{-2} d^{-1}$) at reference (b,

718   ReS) and raft (e, RaS) stations. Below (c, ReS) and (f, RaS) zoom on the relative

719   contribution of diatoms flux to Cphyto flux. The stacked bars correspond to the

720   different oceanographic scenarios: the first half of autumn (aut–1), the second half of

721   autumn (aut–2), winter (win), the first half of spring (spr–1), the second half of spring

722   (spr–2), and summer (sum)

723

724   Fig. 8 Schematic evolution of the phytoplankton annual cycle with the major

725   phytoplankton species in biomass for each sampling period, both in the water column

726　(a, ReS), (b, RaS) and in the sediment traps (c, ReS), (d, RaS). Redrawn according to

727　the seasonal scheme provided by Figueiras et al. (2002)
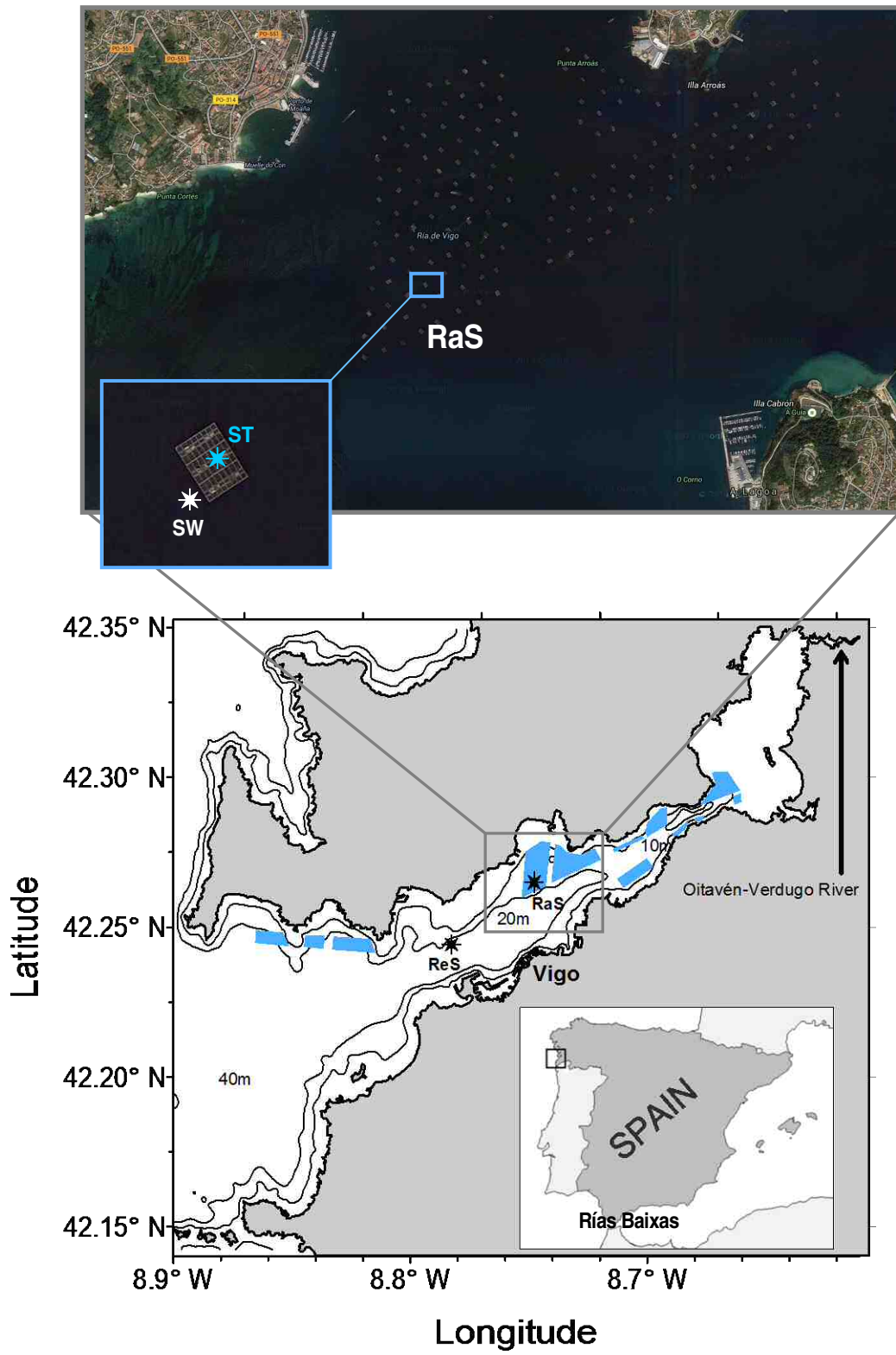
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Figure 1
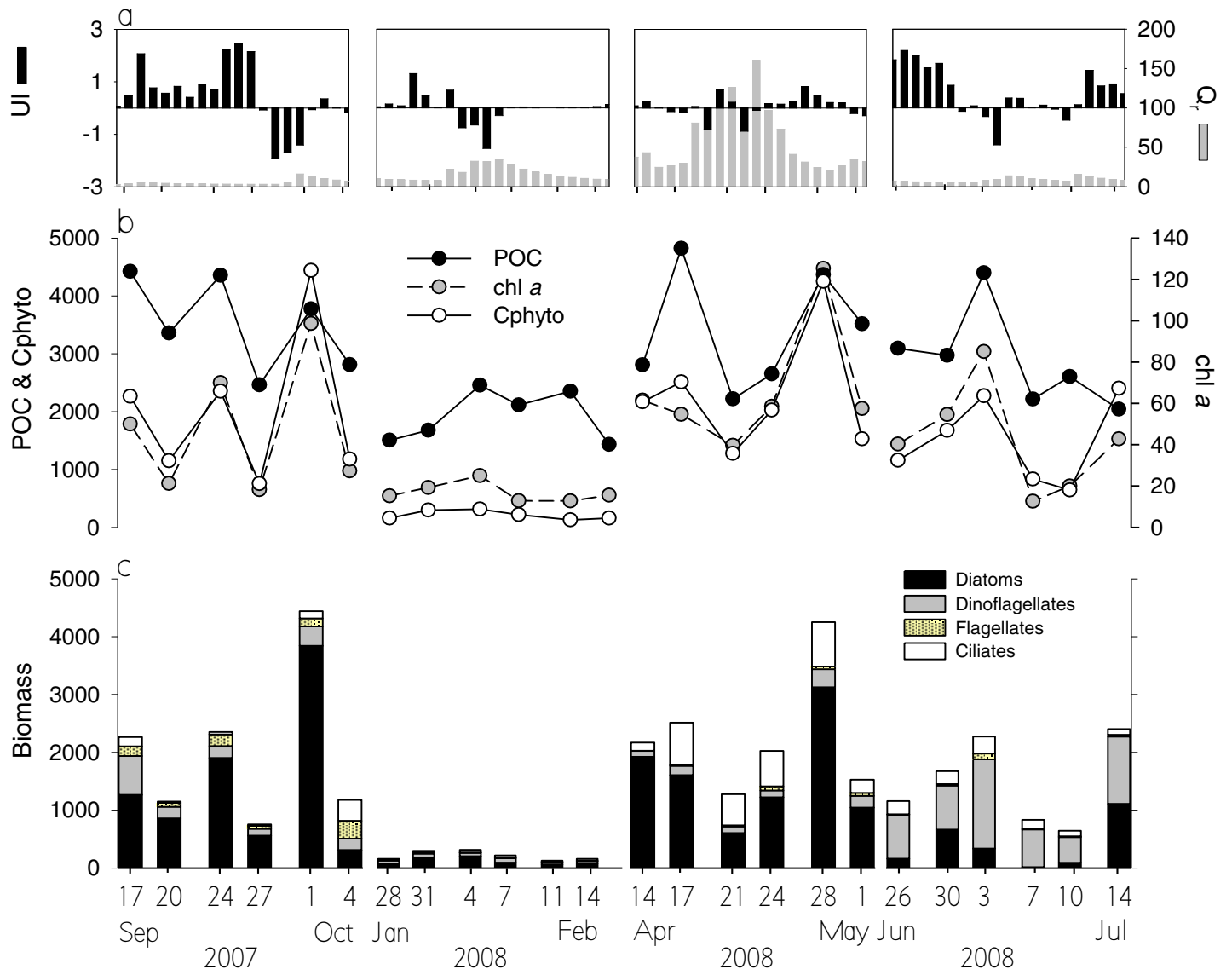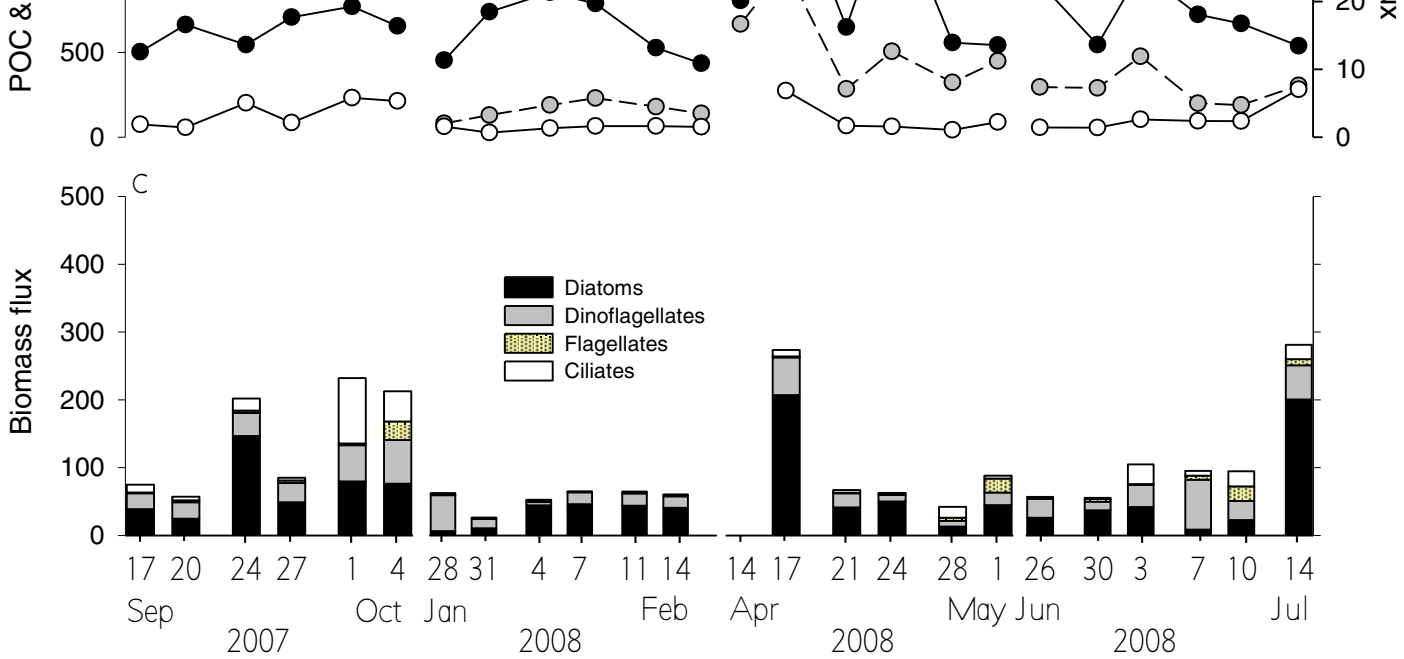

Fig. 1
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Figure 2

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Fig. 3
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Figure 4
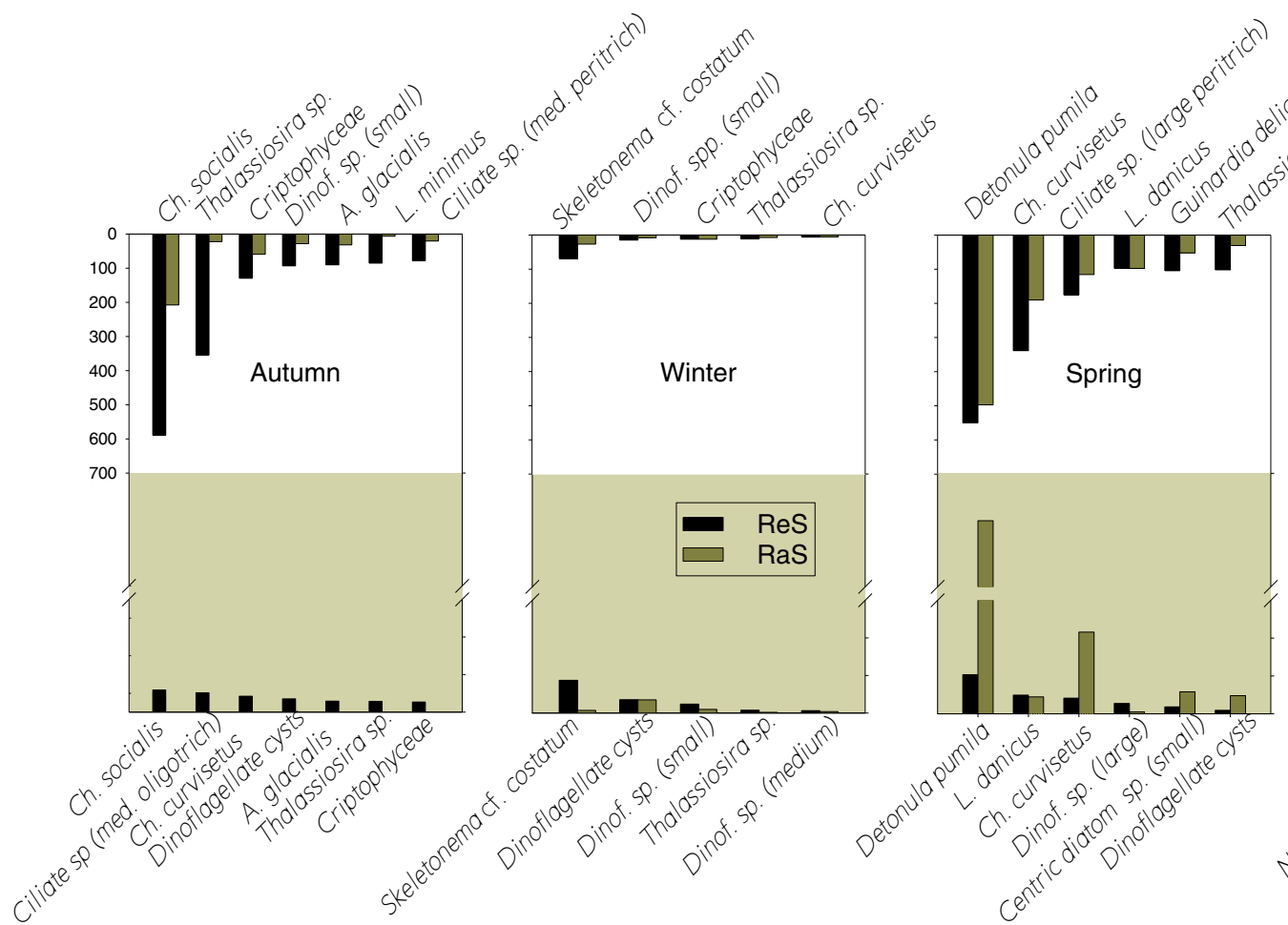
Figure 5
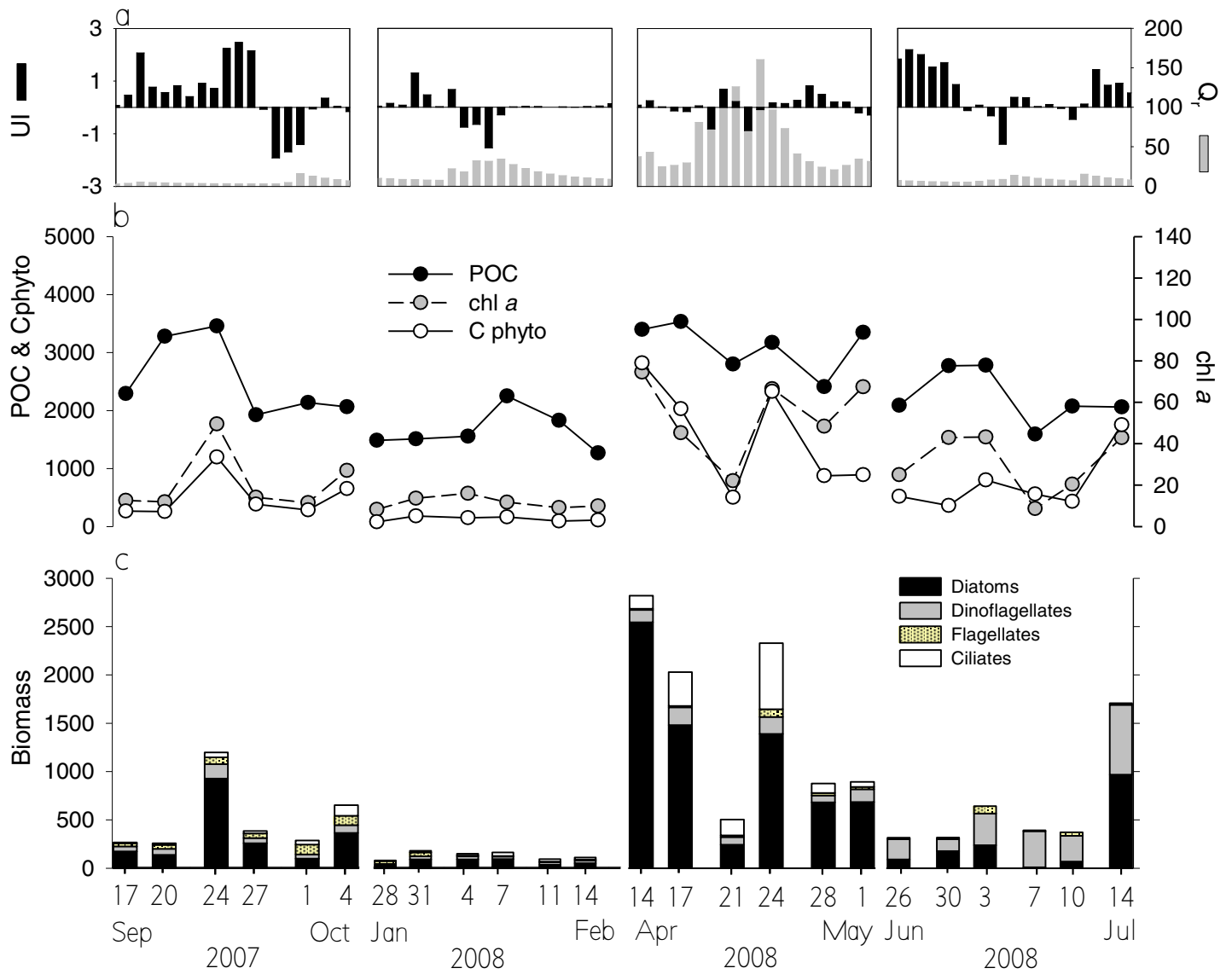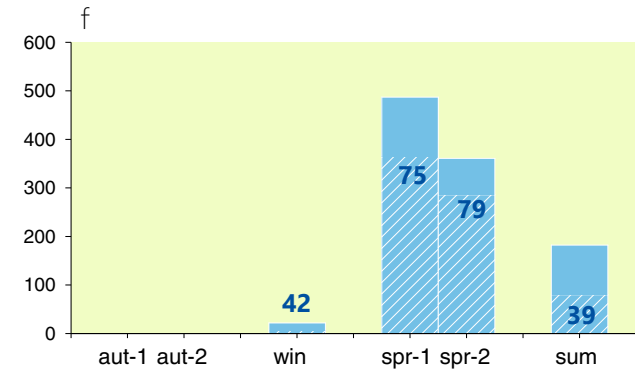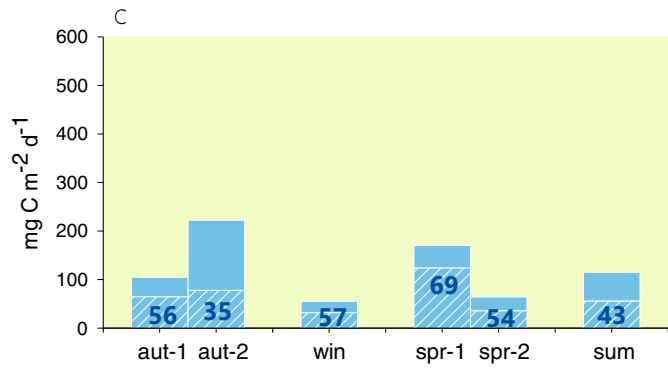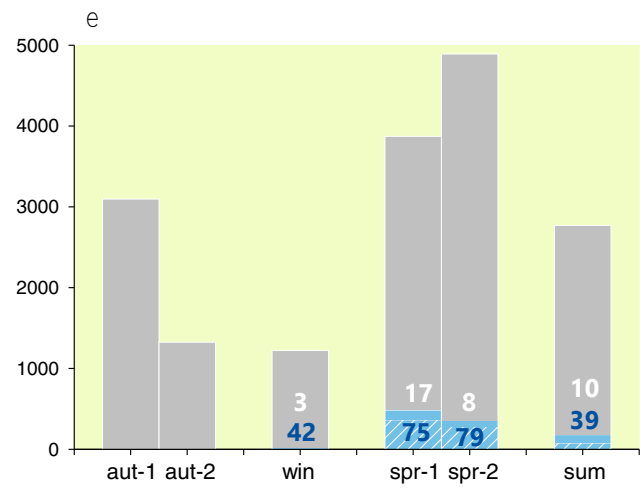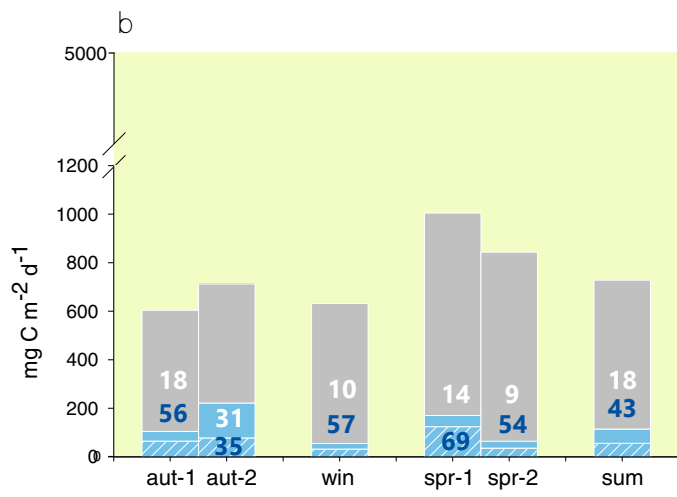

Fig. 5
Froján et al.

Figure 6
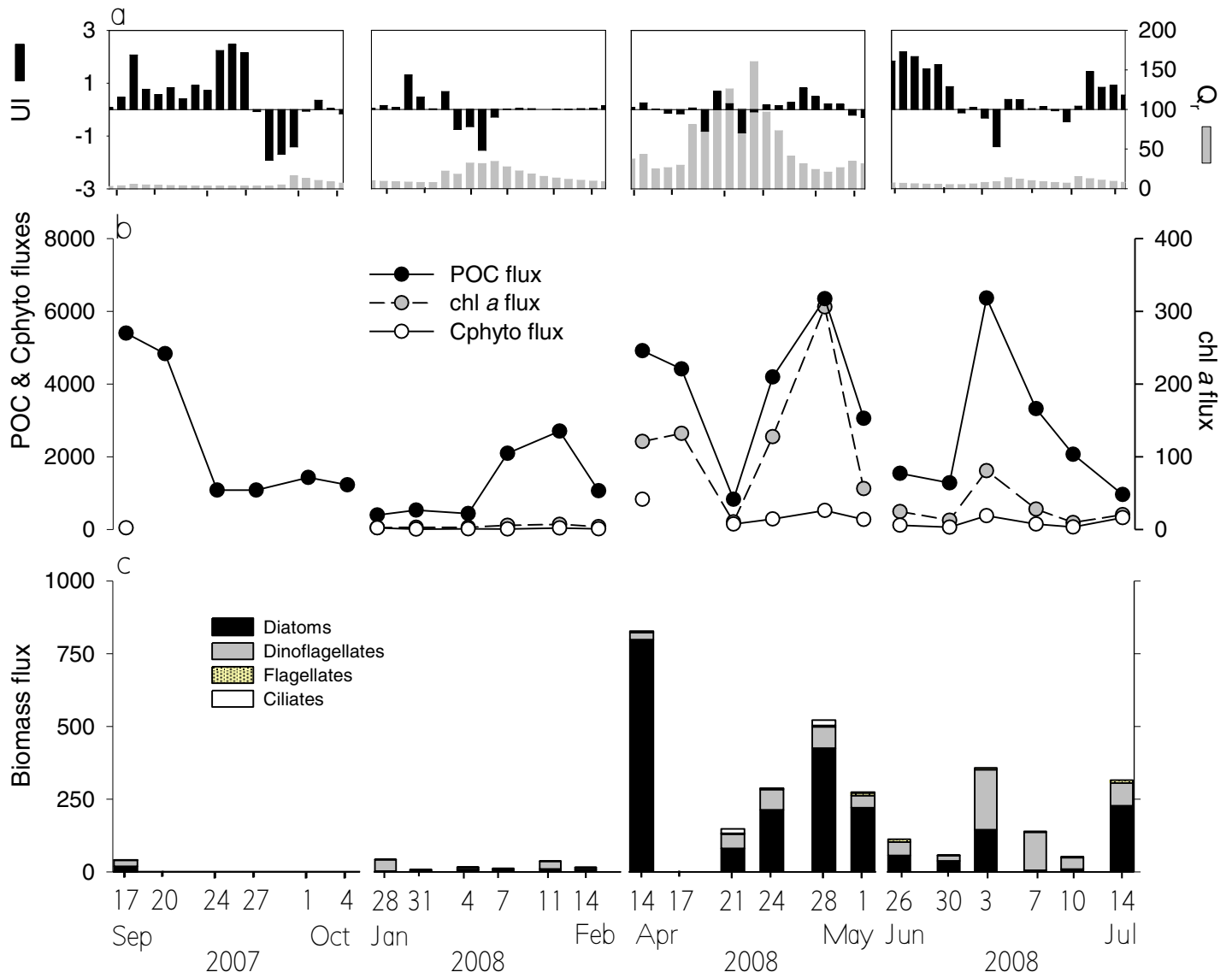
Fig. 6
Froján et al.

Fig. 7
Froján et al.

Figure 8

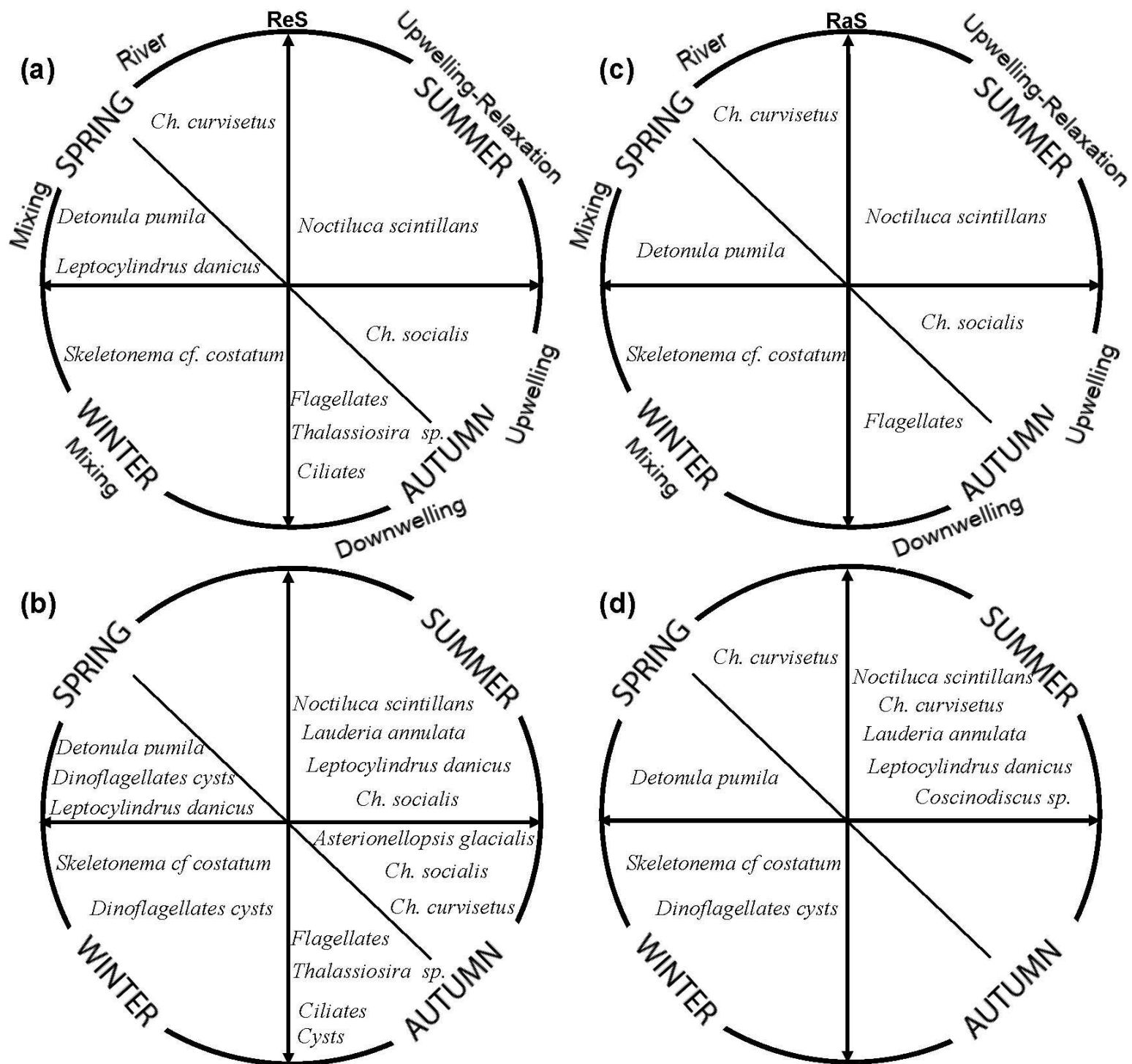
Fig. 8
Froján et al.

Table 1

Table 1 Average (± SD) of integrated POC, Cphyto and chl *a* concentrations (mg m^{-2}) in the upper 12 m of the water column, the average (± SD) of integrated Cphyto contribution (%) to integrated POC and the average (± SD) of integrated biomass contribution of diatoms, dinoflagellates, flagellates and ciliates (%) to integrated Cphyto, during each sampling period (autumn, winter, spring and summer) at reference (ReS) and raft (RaS) stations.

	ReS				RaS			
	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer
POC	3531 ± 803	1923 ± 443	3397 ± 1027	2888 ± 846	2526 ± 666	1650 ± 344	3111 ± 427	2229 ± 464
Cphyto	2023 ± 1348	213 ± 79	2294 ± 1057	1498 ± 740	508 ± 369	130 ± 41	1575 ± 941	739 ± 520
chl *a*	61 ± 27	17 ± 5	66 ± 30	43 ± 26	28 ± 19	11 ± 3	54 ± 19	31 ± 15
% Cphyto:POC	55 ± 32	11 ± 4	67 ± 20	54 ± 33	20 ± 11	8 ± 3	49 ± 26	35 ± 26
% Diatoms	66 ± 22	53 ± 8	67 ± 14	22 ± 17	59 ± 15	48 ± 10	71 ± 15	28 ± 21
% Dinoflagellates	16 ± 8	27 ± 6	8 ± 3	62 ± 13	17 ± 5	22 ± 4	10 ± 4	48 ± 13
% Flagellates	10 ± 8	7 ± 4	2 ± 1	2 ± 1	16 ± 10	14 ± 13	2 ± 1	5 ± 4
% Ciliates	8 ± 11	13 ± 5	24 ± 13	14 ± 6	9 ± 6	17 ± 8	17 ± 12	20 ± 13

Table 2

Table 2 Average (± SD) POC, Cphyto and chl *a* fluxes (mg m^{-2} d^{-1}), average (± SD) Cphyto contribution (%) to POC flux and average (± SD) biomass contribution of diatoms, dinoflagellates, flagellates and ciliates (%) to Cphyto flux, during each sampling period (autumn, winter, spring and summer) at reference (ReS) and raft (RaS) stations.

	ReS				RaS			
	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer
POC flux	640 ± 100	633 ± 183	924 ± 455	728 ± 185	2507 ± 2031	1203 ± 975	3958 ± 1871	2590 ± 2026
Cphyto flux	144 ± 79	55 ± 15	107 ± 95	115 ± 84		22 ± 14	412 ± 269	182 ± 135
chl *a* flux		4 ± 1	13 ± 7	7 ± 3		4 ± 2	125 ± 101	29 ± 26
% Cphyto:POC	23 ± 12	10 ± 4	11 ± 6	18 ± 17		3 ± 4	12 ± 5	10 ± 12
% Diatoms	49 ± 15	57 ± 27	60 ± 20	43 ± 24		42 ± 22	77 ± 15	39 ± 26
% Dinoflagellates	29 ± 9	38 ± 27	21 ± 6	38 ± 22		54 ± 23	18 ± 11	49 ± 23
% Flagellates	4 ± 4	3 ± 3	8 ± 10	7 ± 8		4 ± 5	2 ± 1	4 ± 3
% Ciliates	17 ± 13	2 ± 2	11 ± 15	12 ± 11		1 ± 1	3 ± 4	8 ± 7