

Left Running head: R. A. Cohen et al. 04-S03-JA\_8-31-09\_Productivity\_and\_Nutrients\_Cohen-T4

Right Running head: Productivity and nutrients in SFE wetlands

Primary productivity rates and nutrient availability in natural and restoring wetlands of the northern San Francisco Estuary.

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## 1 ABSTRACT

2 High rates of primary productivity within estuaries and wetlands largely result from the diversity  
3 of autotrophs present. Not only are there are many sources of organic carbon in estuarine  
4 wetlands, but the rates of production for each type of producer differs due to a number of  
5 interacting factors, including water and sediment chemical characteristics. This study was  
6 designed to obtain some of the first direct measures of water nutrient concentrations and rates of  
7 productivity for multiple groups of autotrophs in both natural and restoring wetlands of the  
8 northern San Francisco Estuary (SFE). Water nutrient concentrations and carbon fixation rates of  
9 phytoplankton, benthic microalgae, submerged aquatic vegetation (SAV) and low marsh  
10 emergent vegetation were measured in two natural reference and 4 restoring estuarine wetlands  
11 over two growing seasons (2004 and 2005). Water nutrient concentrations were generally highest  
12 in spring and decreased as the growing season progressed. Nutrient availability in the water was  
13 an important predictor of rates of production of phytoplankton and benthic diatoms. Sediment  
14 nitrogen and organic content, and interstitial nutrient concentrations influenced productivity of  
15 the low marsh vegetation. Low marsh vegetation had the overall highest rates of production,  
16 followed by SAV, benthic microalgae and phytoplankton. Productivity rates of low marsh  
17 vegetation were also higher in natural compared to restoring marshes early in the growing  
18 season, but in general rates of primary production appeared to be a function of the physical  
19 conditions and location of each wetland rather than restoration stage.

20

21 Key Words: carbon fixation, estuary, nutrients, phytoplankton, *Spartina*, wetland

22

## 22 INTRODUCTION

23           The high productivity of estuarine systems is typically due to a combination of riverine  
24 nutrient and organic inputs, and autochthonous carbon fixation by multiple groups of autotrophs,  
25 including phytoplankton, benthic microalgae, macroalgae, and vascular plants (Cloern 1987,  
26 Jassby & Cloern 2000). Rates of primary production in estuarine wetlands may therefore be  
27 affected by a number of physical and chemical factors such as water nutrient concentrations,  
28 salinity, and sediment characteristics. Inorganic nutrients, in particular  $\text{NO}_3$ ,  $\text{NH}_4$ ,  $\text{Si}(\text{OH})_4$  and  
29  $\text{PO}_4$  are essential to primary production in the water column (Wilkerson et al. 2006, Dugdale et  
30 al. 2007), benthic mudflats (Colijn & de Jonge 1984), and the terrestrial components of wetlands  
31 (Boyer et al. 2000). Salinity can change producer community composition and also rates of  
32 production, for both phytoplankton assemblage and vascular plants (Pearcy & Ustin 1984,  
33 Lehman 2007). Sediment characteristics, including grain size, organic and nutrient content may  
34 also account for changes in productivity of benthic microalgae, rooted submerged and emergent  
35 vegetation (Lindau & Hossner 1981, Craft et al. 1988, Currin et al. 1996, Piehler et al. 1998,  
36 Boyer et al. 2000).

37           The physical and chemical factors that affect the productivity rates and ultimately the  
38 relative contribution of each type of autotroph to estuarine wetland production largely depends  
39 on the characteristics of the estuary and adjacent river systems. The San Francisco Estuary (SFE)  
40 is large and turbid, with generally non-limiting nutrient concentrations consisting of 2 distinct  
41 sections; the well-mixed South Bay with little freshwater influence and the river dominated,  
42 partially to well-mixed North Bay (Conomos et al. 1985). The most important contributor of  
43 organic carbon for food web support to the SFE is generally thought to be phytoplankton (Jassby  
44 et al. 1993, Sobczak et al. 2002). Phytoplankton productivity has been well studied in the main

45 body of the SFE, and it was found that rates and biomass were most affected by light availability  
46 (Cole & Cloern 1984, Cloern 1987). In the shoals of the SFE where depths are usually less than 2  
47 m, light often penetrated to the substrate and resulted in higher rates of primary production (Cole  
48 & Cloern 1984). The SFE also has many wetland areas surrounded by shallow water and tidal  
49 channels where water depth becomes low and light penetration can be high. A recent analysis has  
50 shown that these relatively shallow coastal areas tend to have highly variable patterns in  
51 productivity that are not predictable with season (Cloern & Jassby 2008), suggesting that factors  
52 besides climate and light availability, such as nutrients may become important in determining  
53 phytoplankton productivity rates.

54 Benthic diatom productivity can be the dominant source of carbon to grazers in the  
55 shallow areas and along mudflats of estuarine wetlands (Riznyk et al. 1978, Gould & Gallagher  
56 1990, Jassby et al. 1993). In many cases, benthic production rates have been found to be very  
57 high, exceeding rates of phytoplankton production in some estuaries (Leach 1970, Varela &  
58 Penas 1985). Dominant benthic primary producers are typically diatoms and cyanobacteria  
59 (Colijn & de Jonge 1984), and the presence of diatoms is indicated by a golden brown sheen on  
60 the surface of the sediment at low tide (Gould & Gallagher 1990) in the SFE. While the  
61 importance of benthic diatom productivity in the SFE has been estimated (Jassby et al. 1993), to  
62 our knowledge, no direct measurements of benthic productivity have been performed in the  
63 estuarine wetlands of the northern SFE. Direct measures are essential to understanding the  
64 importance of benthic diatom productivity, due to the high spatial and temporal variability in  
65 benthic microalgal distribution (Pinckney et al. 2003).

66 Submerged aquatic vegetation (SAV) including macroalgae and rooted macrophytes are  
67 potentially important producers in estuarine systems, often exceeding productivity rates of

68 phytoplankton (Josselyn & West 1985). However, macroalgal biomass is low in the SFE  
69 (Josselyn & West 1985) and generally not considered major contributor to estuarine production  
70 (Jassby et al. 1993). Seaweeds and seagrasses are typically absent in the Delta (Jassby & Cloern  
71 2000), but there are increasing numbers of locations where invasive submerged rooted  
72 macrophytes, including *Egeria densa* (Grimaldo & Hymanson 1999, Brown 2003a) and  
73 *Cabomba caroliniana* (Tu & Randall 2001, Hickson & Keeler-Wolf 2007) are extremely  
74 abundant. Although there are records of channels and shallow areas completely overgrown with  
75 invasive submerged aquatic macrophytes, it can be very difficult to estimate biomass of these  
76 invasive macrophytes due to seasonal fluctuations, how recently the invader appeared, and  
77 whether populations have been treated with herbicide (Jassby & Cloern 2000). Estimations of  
78 *Egeria* productivity have been calculated based on coverage in aerial photographs (Jassby &  
79 Cloern 2000), but direct measures of production for invasive SAV have not been reported.

80         In the low marshes bordering mudflats, the largest contributors to primary productivity in  
81 adjacent estuaries are considered to be stands of vascular plants, such as cordgrass (*Spartina*  
82 spp.) (Pomeroy et al. 1981, Smart 1982). Numerous studies of *Spartina* productivity exist for  
83 other regions, and rates can be highly variable even within a region (Smart 1982). Productivity  
84 has been related to nutrient availability and tidal flushing (Cramer et al. 1981), sediment stability  
85 (Smart 1982) and salinity regime (Percy & Ustin 1986). However, relatively little is known  
86 about low marsh productivity rates in the estuarine wetlands of the northern SFE, and the data  
87 that exist are based on biomass estimates of productivity rather than direct in situ rates of carbon  
88 fixation (e.g. Callaway et al. 2007). Direct measures of physiological rates or photosynthetic  
89 rates are important to gain understanding of variability in production over the course of a  
90 growing season and between wetland sites in the same region.

91 California's estuarine wetlands are currently the focus of numerous restoration efforts  
92 (Orr et al. 2003); nearly 90% of the state's wetlands have been altered or destroyed, and these  
93 losses are primarily responsible for decreased species diversity and reduced water quality (Zedler  
94 1996). Restoration efforts have the potential to impact inorganic nutrient sources entering SFE  
95 (Bucholz 1982, Cloern 1983), water and sediment characteristics (Burdick et al. 1989, Zedler  
96 1996, Zedler 2005), which in turn influence the primary producers that support higher trophic  
97 levels, but the effects of restoration stage (age) on primary productivity in SFE are largely  
98 unknown. Obtaining data on estuarine wetland productivity rates is essential to implement  
99 appropriate restoration and management strategies. The present study arose from a unique  
100 opportunity to examine both natural and restored wetlands across the northern SFE. Our  
101 objectives were to 1) obtain some of the first measured water nutrient concentrations and rates of  
102 productivity for multiple groups of producers in estuarine wetlands of the northern SFE, and 2)  
103 gain understanding of the conditions that may affect these rates in both reference and restored  
104 wetlands. To accomplish these goals, water nutrient concentrations and productivity rates of  
105 phytoplankton, benthic microalgae, submerged aquatic vegetation and low marsh emergent  
106 vegetation were measured in two natural reference and 4 restoring estuarine wetlands in the  
107 northern SFE over two growing seasons.

108

## 109 MATERIALS AND METHODS

110

### **Study Locations**

111 Primary productivity, water nutrient concentrations and sediment characteristics were  
112 measured at six wetland sites in the SFE (Figure 1). Three were located in the Napa River (two

113 restoring and one natural reference), two were in Suisun Bay (one restoring and one natural  
114 reference) and one was located in the Petaluma River (restoring) (Table 1).

115 Bull Island (38° 13.277N, 122° 18.471W) is a 108-acre restored site located upstream of  
116 Coon Island on the Napa River. The site is vegetated, and has exposed areas of mudflat at low  
117 tide. Coon Island (38° 11.706N, 122° 19.178W) is a 400-acre natural reference site located 9.5  
118 miles upstream from the mouth of the Napa River. The site is also vegetated with associated  
119 mudflat at low tide. Pond 2A (38° 09.111N, 122° 18.860W) is a 532-acre restored site located  
120 closest to the mouth of and to the west of the Napa River within the Napa-Sonoma salt  
121 pond/marsh complex. The marsh is vegetated, but mudflat area is limited due to steep, nearly  
122 vertical, channel sides. Carl's Marsh (38° 07.379N, 122° 30.566W) is a 48-acre vegetated  
123 restored site with mudflat located near the mouth of the Petaluma River. The site was restored in  
124 1994 and contains limited channel network complexity. Browns Island (38° 02.320N, 121°  
125 52.178W) is a natural brackish marsh. The 848-acre site is vegetated, but lacks developed  
126 mudflat. Sherman Lake (38° 02.785N, 121° 49.032W) is a 3, 279-acre restored brackish tidal  
127 marsh with similar vegetation to Browns Island and little to no mudflat area.

128

129

### **Sampling Design**

130 In each wetland at the coordinates listed above, a permanent 15 m transect was  
131 established parallel to the water at the border between the high and low marsh vegetation zones.  
132 Sampling occurred at 3 random points along each transect within the low marsh zone, on the  
133 mudflat and in the adjacent water column once monthly on an incoming tide during the growing  
134 season (from March through October 2004 and 2005). At each of the three points, low marsh  
135 vegetation (n=5) and benthic diatom productivity (n=3) were sampled within 0.25 m<sup>2</sup> quadrats,

136 aboveground submerged aquatic vegetation was sampled using a 0.1 m<sup>2</sup> quadrat, surface water  
137 salinity was determined using a refractometer, and water samples for nutrient concentrations and  
138 phytoplankton productivity were collected as close to the transect as possible.

139

140

### **Nutrients**

141 Water adjacent to the permanent transects was sampled and analyzed for nitrate (NO<sub>3</sub>),  
142 silicate (Si(OH)<sub>4</sub>), phosphate (PO<sub>4</sub>) and ammonium (NH<sub>4</sub>) using hand-held sampling bottles.  
143 Interstitial water was collected from permanent sippers installed at each of the three sampling  
144 points (Yorty 2006). Replicate 20 ml water samples for NO<sub>3</sub>, Si(OH)<sub>4</sub> and PO<sub>4</sub> were frozen until  
145 analysis with a Bran and Luebbe AutoAnalyzer II [NO<sub>3</sub> and PO<sub>4</sub> according to Whitledge et al.  
146 (1981), Si(OH)<sub>4</sub> using Bran and Luebbe Method G-177-96 (Bran & Luebbe, 1999)]. Frozen  
147 samples were thawed 24 hours prior to analysis to avoid polymerization effects on Si(OH)<sub>4</sub>  
148 measurements and poor reproducibility (MacDonald et al. 1986). Typically, water samples for  
149 the AutoAnalyzer do not need pre-filtering due to the tubing dimensions and small volumes  
150 required for the chemical analyses. For NH<sub>4</sub> analyses, water was filtered through pre-combusted  
151 GF/F filters before analysis to remove any sediment, which yields anomalously high NH<sub>4</sub> values.  
152 Filtered samples were then treated with phenol reagent (Solorzano, 1969) and held at 4°C for 24  
153 h until analysis using a Hewlett Packard Model 8452A diode array spectrophotometer.

154

155

### **Phytoplankton productivity**

156 Five replicate 1 L water samples were collected and brought back to the lab in a dark  
157 cooler. Upon return from the field, 50 ml from each replicate was filtered onto a GF/F glass  
158 fiber filter for chlorophyll *a* analysis. Chlorophyll *a* from each filter was extracted in 8 ml of



159 90% acetone at 0°C in the dark for 24 h and fluorescence was measured on a Turner Designs 10  
160 AU fluorometer. The <sup>14</sup>C light-dark bottle JGOFS protocol (IOC 1996) was modified to measure  
161 SFE phytoplankton primary productivity. Incubations of collected baywater were prepared by  
162 adding 0.8 µCi of <sup>14</sup>C bicarbonate to each 250 ml polycarbonate bottle. After incubating for 24  
163 hours in a flow-through water table at simulated in situ baywater temperatures under 50% light  
164 conditions, 100 ml from each bottle was filtered onto a Whatman GF/F glass fiber filter and <sup>14</sup>C  
165 incorporation was determined by placing the filter in OptiPhase scintillation cocktail and  
166 counting in a low-background liquid scintillation counter (PerkinElmer Winspectral Guardian  
167 LSC). The chlorophyll *a* content was then used to calculate photosynthetic activity (assimilation  
168 number) per unit biomass. Since many of the sample sites were in relatively low salinity water,  
169 the dissolved inorganic carbon content (required for calculating C fixation) was determined with  
170 a Li-Cor TCO<sub>2</sub> analyzer (Friederich et al. 2002, Parker et al. 2006). Samples were also collected  
171 for phytoplankton identification and enumeration. Briefly, replicate 50 ml water samples were  
172 preserved with Lugols solution, and cells concentrated by centrifugation (Sukhanova 1978).  
173 Phytoplankton were then identified at least to the genus level and quantified with a Sedgwick  
174 Rafter chamber (Guillard 1978) at 200X.

175

### 176 **Mudflat productivity**

177 Benthic primary productivity was measured using a <sup>14</sup>C technique developed for marsh  
178 sediments (modified from VanRaalte *et al.* 1974). From each sampling site, 5 cores (2.5 cm  
179 diameter, 0.5 cm depth (Admiraal et al. 1982)) were collected from each random point at low  
180 tide and the golden-brown sheen on the surface of the sediments suggested that benthic diatoms  
181 were the dominant producers (Gould & Gallagher 1990). The cores were incubated intact and

182 upright in 30 ml clear polycarbonate sealed containers in a flow-through water table under one  
183 layer of fiberglass window screening to reduce light levels by 50% to ensure optimal light-  
184 saturated production without light inhibition (Lorenzi 2006). The surface of each core was  
185 covered with 10 mL of solution containing GF/F filtered water from the collection site and 0.4  
186  $\mu\text{Ci}$  of  $^{14}\text{C}$  bicarbonate. After the 24 h incubation, cores were killed in 2% formalin to stop all  
187 photosynthetic activity and rinsed with dilute hydrochloric acid to remove  $^{14}\text{C}$  that was not  
188 incorporated. The core was then digested using nitric acid to release labeled, fixed  $^{14}\text{C}$  into  
189 solution and the activity measured using liquid scintillation counting. The chlorophyll *a* content  
190 of the benthic diatoms in the mudflat core was determined by grinding and extraction in 90%  
191 acetone and read on a Turner Designs 10 AU fluorometer.

192

### 193 **Submerged Aquatic Vegetation (SAV) and macroalgal productivity**

194 At Sherman Lake and Brown's Island, SAV sampled was exclusively *Cabomba*  
195 *caroliniana*, while SAV at the Napa sites consisted of green macroalgae, putatively *Ulva* spp.  
196 Productivity of SAV was determined using oxygen evolution method and equations of Littler &  
197 Littler (1985). Replicate SAV samples were collected when present and brought back to the lab  
198 for incubation under the same temperature and light conditions as the phytoplankton and benthic  
199 diatom core samples. Tissue was rinsed to remove epiphytes, invertebrates and debris and spun  
200 in a lettuce spinner for 1 min to remove excess water. One-gram wet-weight samples were  
201 placed into each 300 ml BOD bottle with baywater from the collection site. Four light and two  
202 dark bottles were incubated in a flow-through water table under appropriate light conditions.  
203 After one hour, dissolved oxygen was measured using a WTW 197i meter with self-stirring  
204 probe. Oxygen evolution was then converted to carbon fixed using the equations of Littler &

205 Littler (1985). The chlorophyll *a* content of the SAV was determined by grinding and extraction  
206 in 90% acetone and read on a Turner Designs 10 AU fluorometer.

207

### 208 **Low marsh plant productivity**

209 To assess net productivity in low marsh vegetation (*Spartina foliosa* at all Napa sites and  
210 Carl's Marsh, *Carex* spp. at Brown's), we measured CO<sub>2</sub> uptake using an infrared gas exchange  
211 technique (Geider & Osborne 1992). Measurements of photosynthesis were made at monthly  
212 intervals throughout the growing season (March-October). Blades of the intact living plants were  
213 placed within a chamber with flow-through CO<sub>2</sub> gas flow between the chamber and an infrared  
214 gas analyzer (CIRAS-1, PP Systems). Carbon fixation was measured directly as the decrease in  
215 CO<sub>2</sub>. We sampled replicate (n=5 per plot) plants at peak light intensity (points between 10 am  
216 and 2 pm) to determine C fixation m<sup>-2</sup> μg chlorophyll *a*<sup>-1</sup>. The chlorophyll *a* content of the plant  
217 tissue within the chamber was determined by grinding and extraction in 90% acetone and read on  
218 a Turner Designs 10 AU fluorometer.

219

### 220 **Sediment methods**

221 To relate productivity to sediment characteristics, replicate sediment samples were  
222 collected from each wetland along the permanent transects in May of 2005. Cores were 15 cm  
223 depth, which is the approximate depth of *Spartina* rhizosphere (Teal et al. 1979). Sediment grain  
224 size was determined by measuring changes in suspension using a hydrometer (Sheldrick & Wang  
225 1993), % total N was quantified by first combusting samples to convert inorganic compounds to  
226 gases, and then separating the gases using gas chromatography and thermal conductivity  
227 detection (AOAC 1997), and organic matter was measured using a modified Walkey-Black

228 procedure in which organic carbon is reduced with potassium dichromate followed by  
229 spectrophotometric measurement (Nelson & Sommers 1982). All sediment physical and  
230 chemical analyses were performed at UC Davis.

231

### 232 **Statistical Analysis**

233 Data were tested for normality with the Shapiro-Wilk W Goodness of Fit test and  
234 homogeneity of variances using Levene's test. Sediment characteristics, including interstitial  
235 water nutrient concentrations did not meet assumptions of parametric analyses, therefore  
236 correlative relationships between sediment variables and plant primary productivity were  
237 examined using nonparametric Spearman's  $\rho$  tests. All statistical tests were performed using  
238 JMP 7.0.1 (SAS).

239

## 240 **RESULTS**

241 Water nutrient concentrations, with the exception of  $\text{NO}_3$ , were high and non-limiting at  
242 all six wetland sites in both growing seasons (Figures 2-5).  $\text{NO}_3$  concentrations appeared to  
243 decrease by the end of spring and then increase again in late summer or early fall at all sites with  
244 the exception of Sherman Lake, where concentrations were extremely low throughout the  
245 growing season (Figure 2). In the Napa River,  $\text{NO}_3$  concentrations were consistently higher at  
246 Bull and Coon Islands than at Pond 2A throughout both 2004 and 2005, which reflected the  
247 upstream position and proximity to one another of Coon and Bull relative to Pond 2A (Figure 2  
248 A, B, C). Values at the Napa River sites were greatest in March, and all sites showed a reduction  
249 to potentially limiting levels (i.e.  $< 6 \mu\text{M}$ ) by May in 2004 and June in 2005. Carl's Marsh in the  
250 Petaluma River showed a similar pattern of high  $\text{NO}_3$  in the early spring followed by a reduction,

251 however concentrations were, with the exception of May 2004 and 2005, > 10  $\mu\text{M}$  over the  
252 course of both growing seasons. The Suisun sites had lower  $\text{NO}_3$  than the other areas, with  
253 concentrations < 25  $\mu\text{M}$  at Browns Island, and < 2.5  $\mu\text{M}$  at Sherman Lake.

254 In general,  $\text{Si}(\text{OH})_4$  concentrations were consistently high (generally >100  $\mu\text{M}$ ) at all  
255 sites (Figure 3). As with  $\text{NO}_3$ , at the Napa sites, the highest concentrations of  $\text{Si}(\text{OH})_4$  were  
256 observed at Bull and Coon Islands in the early spring, followed by a decrease in the summer, and  
257 concentrations were greater when compared to Pond 2A throughout both 2004 and 2005.  
258 Interestingly, both Bull and Coon Islands showed differences in years with higher concentrations  
259 in 2005 compared to 2004.  $\text{Si}(\text{OH})_4$  concentrations at Carl's Marsh in both 2004 and 2005  
260 exhibited a similar pattern of decrease from spring to early summer (Figure 3F). Concentrations  
261 at Browns and Sherman were relatively similar (~300  $\mu\text{M}$ ) and consistent over the course of the  
262 growing season in both 2004 and 2005 (Figure 3 D, E), although there was a slight downward  
263 trend over the growing season at Browns Island whereas at Sherman Lake, the low  $\text{NO}_3$  site,  
264 levels of  $\text{Si}(\text{OH})_4$  stayed around 300  $\mu\text{M}$ .

265  $\text{PO}_4$  concentrations were generally non-limiting (i.e. > 1  $\mu\text{M}$ ) over all sites and both  
266 seasons, and patterns were similar in each site in both 2004 and 2005 (Figure 4). However, in  
267 2005 values were particularly low in July at Bull Island and below detection in March at Pond  
268 2A (Figure 4A, C). The three sites in the Napa River generally exhibited highest  $\text{PO}_4$   
269 concentrations in late summer and early fall (Figure 4 A, B, C). In Suisun, concentrations were  
270 higher in spring and declined at Sherman Lake, whereas there was no pattern in  $\text{PO}_4$   
271 concentrations at Browns (Figure 4D, E). The highest water column  $\text{PO}_4$  concentrations in both  
272 seasons were observed in the Petaluma River near Carl's Marsh (Figure 4F) with a maximum  
273 concentration of 12.29  $\mu\text{M}$  in April 2004.

274 Water column  $\text{NH}_4$  concentrations at the Napa River locations generally followed a  
275 pattern of high concentrations in the spring and fall with reduced concentrations in the late spring  
276 or early summer months in both years (Fig. 5 A-C). In addition, spring and fall concentrations  
277 were lower at Pond 2A, the most downstream location, than either Coon or Bull Islands.  
278 Concentrations at Browns Island in Suisun Bay were consistently below  $5 \mu\text{M}$  with the exception  
279 of a  $10 \mu\text{M}$  peak in August 2004 (Fig 5D) while concentrations at Sherman peaked in April ( $> 10$   
280  $\mu\text{M}$ ) in both 2004 and 2005, though concentrations were generally higher in 2004 than 2005  
281 (Fig. 5E).  $\text{NH}_4$  concentrations at Carl's Marsh remained high until late summer when  
282 concentrations dropped to near zero in July and August before peaking again in the fall (Fig. 5F).

283 Comparisons of water column chlorophyll and nutrient concentrations showed a trend of  
284 higher chlorophyll *a* concentrations associated with low  $\text{NO}_3$  concentrations (Fig. 2, 6). It  
285 appears that  $\text{NH}_4$  concentration was reduced early in the growing season, followed by depletion  
286 of  $\text{NO}_3$ , after which chlorophyll *a* increased. At Sherman where  $\text{NO}_3$  concentrations were very  
287 low throughout the season, chlorophyll peaks paralleled  $\text{NH}_4$  declines, as this source of DIN was  
288 likely fueling phytoplankton growth. At Bull and Coon Islands, there was also a trend of high  
289 chlorophyll *a* concentrations associated with decreases in  $\text{Si}(\text{OH})_4$  but this pattern was not  
290 observed at the other marshes (Fig. 3, 6).

291 Patterns of water nitrogen concentrations were associated with phytoplankton  
292 productivity during the spring bloom at the Napa River sites, but phytoplankton productivity  
293 patterns across sites and later in the season were more complex (Fig. 2, 5, 7 A-C). For example,  
294 the decline in  $\text{NO}_3$  concentrations throughout the spring (Fig. 2) corresponded to a general trend  
295 of increased phytoplankton productivity at all three sites (Figs 7 A,B,C) in the early spring. In  
296 May of 2004 and June of 2005, the evident decrease in productivity rates at Coon, Bull and Pond

297 2A was consistent with the depletion of  $\text{NO}_3$  in the water column (Figures 2A-C, 7A-C).  
298 However, while the greatest  $\text{NO}_3$  concentrations were observed in the spring near Bull and Coon  
299 Island (Fig. 2 A, B), the highest rates of spring productivity occurred at Pond 2A, along with  
300 decreased light attenuation, in both years (Table 2). As the growing seasons progressed, there  
301 were additional peaks of productivity without concurrent nutrient or increased light availability.  
302 Productivity rates in the summer and fall were much higher at Pond 2A, the newer restored site,  
303 than at either of the other two sites, when chlorophyll *a* concentrations were lowest, likely due to  
304 changes in phytoplankton community composition with distance downriver (Table 3).

305 The relationships between water nitrogen concentrations and phytoplankton productivity  
306 were not straightforward at the Suisun Bay and the Petaluma River sites (Fig 2, 5, 7 D-F). At  
307 Browns, only a fall peak in productivity was observed in 2004, but there were spring and  
308 summer peaks present in 2005 (Fig 7D). In contrast, productivity rates were generally low at  
309 Sherman in both years, which is consistent with the low  $\text{NO}_3$  concentrations in both years (Fig 2,  
310 7 E). The highest rates of productivity at Carl's Marsh occurred in fall of 2004 and summer of  
311 2005, as also occurred at Browns Island when  $\text{NO}_3$  concentrations were below  $25 \mu\text{M}$  and  
312 chlorophyll *a* was below  $5 \mu\text{g L}^{-1}$  (Fig 2, 6, 7 E).

313 Benthic diatom primary productivity rates were an order of magnitude greater than water  
314 column phytoplankton productivity rates, and appeared to follow water  $\text{NO}_3$  concentrations more  
315 closely than pelagic phytoplankton rates (Fig 6, 8). Diatom productivity rates generally peaked in  
316 the spring and seemed to decrease with time across all sites over the growing season in 2004 (Fig  
317 8), which followed the concurrent trend of decreasing water column  $\text{NO}_3$ . Spring benthic  
318 diatom productivity at Sherman exceeded the rates at all other sites by an order of magnitude,  
319 even though this marsh had the lowest water column  $\text{NO}_3$  levels throughout the season. The peak

320 in benthic production in Sherman Lake in April matched a peak in  $\text{NH}_4$  concentration. However,  
321 during the 2005 season, most sites had consistently low productivity throughout the entire  
322 growing season. Only the benthic productivity rates at Coon Island followed the 2004 pattern of  
323 high to low values with season progression (Fig 8B), despite the similarities across all sites in  
324 water column  $\text{NO}_3$  concentration patterns with the previous year (Fig 2, 8).

325 Submerged aquatic vegetation or macroalgae were generally rare at all sites except  
326 Sherman Lake. Green macroalgae (*Ulva* spp.) were occasionally observed at the Napa sites,  
327 most often at Bull Island, which had the coarsest sediment (Table 4, 5). In 2004, macroalgal  
328 productivity rates at Bull Island were highest from May to August, with a  $\geq 50\%$  decline in the  
329 fall, while rates were more consistent throughout the growing season in 2005 (Table 5). No  
330 macroalgae were found at Carl's marsh in either growing season. At Sherman Lake, submerged  
331 vegetation, putatively *Cabomba caroliniana*, grew extensively over the course of each growing  
332 season, and corresponded to a general increase in productivity over the course of the growing  
333 season in both 2004 and 2005 (Table 5). *C. caroliniana* was present at Browns Island only in  
334 July of 2004, but occurred throughout the summer in 2005, with similar rates of production to  
335 those measured for Sherman Lake SAV.

336 The Petaluma and Napa sites have extensive areas of mudflat that slope upward toward  
337 the low marsh vegetation, which was comprised of monospecific stands of *Spartina foliosa*  
338 plants. Productivity rates for *S. foliosa* were highest in spring and decreased through the fall in  
339 both 2004 and 2005 (Fig 9 A-D). With only a few exceptions, rates were higher in 2004 than in  
340 2005 similar to the observed  $\text{NO}_3$  concentrations. In contrast, Browns Island had very low  
341 salinities (Table 6) and little mudflat area. The bank rose nearly vertically at the sides of the  
342 tidal channel. The closest vegetation to the channel edge at the study site was *Carex* spp.



343 Despite these differences, like *S. foliosa*, *Carex* spp. exhibited the highest rates of productivity in  
344 spring with declining rates over time, and higher rates in 2004 than 2005 (Fig 9E). Finally, there  
345 was no *Carex* spp at the Sherman site (only *Scirpus* spp, which was characteristic of the zone  
346 located adjacent to and upland of *S. foliosa* and *Carex* spp. at the other sites), but the site  
347 vegetation was dominated by the submerged *C. caroliniana*.

348         Of the four sites with *S. foliosa* as the dominant low marsh vegetation, the highest rates of  
349 productivity occurred at Coon, followed by Pond 2A and Carl's Marsh, and rates were lowest at  
350 Bull. Coon was the only one of the four sites that was a reference site, but both Carl's Marsh and  
351 Pond 2A were restored in the mid-1990's, while Bull Island was restored much earlier, in the  
352 1950's. Differences in *S. foliosa* productivity were likely due to sediment characteristics, rather  
353 than restoration age. Detailed sediment analyses performed in May 2005 revealed significant  
354 correlative relationships between sediment percent organic content and productivity rates, and  
355 between sediment percent total nitrogen and productivity (Fig 10). In addition, there were weak  
356 but significant positive correlations between plant productivity and interstitial nutrient  
357 concentrations of  $\text{NH}_4$  and  $\text{PO}_4$  (Fig. 11). There was a general absence of measurable interstitial  
358  $\text{NO}_3$  concentrations at all sites (Table 7). Though there was no significant relationship between  
359 productivity and sediment grain size, sediment at Bull had 3-8 times higher percent sand content  
360 than any of the other three sites (Table 3), and coarse grain size can indicate low nutrient  
361 retention capacity.

362

## 363 DISCUSSION

364         Water nutrient concentrations and rates of productivity for the different types of  
365 autotrophs varied widely across estuarine wetlands of the northern SFE, likely due in part to their

366 different locations rather than restoration stage. However, some similar patterns emerged for all  
367 sites except for the restored Sherman Lake marsh in the western Delta. The water column  
368 concentration of inorganic nutrients, especially  $\text{NO}_3$ , was related to both phytoplankton biomass  
369 and productivity, and overall chlorophyll concentrations were similar to those in Argentina's  
370 Parana Basin, where nutrient concentrations were in the same range as ours (Izzaguirre et al.  
371 2001, Unrein 2002, Vicari et al. 2002, Table 8). Water  $\text{NO}_3$  concentrations were highest in the  
372 spring, and then exhibited a smaller peak in the fall, which was consistent with increased  
373 phytoplankton production in the spring and in the late summer/early fall. Spring peaks in  
374 phytoplankton productivity rates at the three Napa sites, Carl's Marsh and Browns Island  
375 appeared to be related to nutrient draw-down in the water. Also, there were peaks in  $\text{Si}(\text{OH})_4$   
376 concentrations at Bull and Coon in 2005 when salinities were particularly low, and an associated  
377 peak in chlorophyll *a* concentration, suggesting that the bloom consisted mainly of diatoms. In  
378 the Seine River drainage, which had silica concentrations similar to what we observed (~70-500  
379  $\mu\text{M}$ , Table 8), phytoplankton blooms occur in April to May when river discharge decreases and  
380 light availability increases. Then, silica concentrations decrease dramatically and the  
381 phytoplankton assemblage becomes dominated by diatoms (Garnier et al. 1995).

382         Although DIN concentrations were highest upriver and decreased with distance  
383 downriver in the Napa River, productivity rates were generally highest over the entire sampling  
384 period at Pond 2A, the most downriver location. This finding suggested that productivity rate  
385 might not be entirely related to nutrient concentration because the concentrations of all nutrients  
386 measured were lower at Pond 2A than either Bull or Coon Islands. It is generally accepted that  
387 light limits phytoplankton productivity in the well-mixed, turbid SFE, but in the shallow tidal  
388 channels light can potentially penetrate all the way to the substrate, particularly at low tide

389 (Cloern 1987). In addition, the observed productivity rates were probably not due to restoration  
390 age, since Pond 2A is at an earlier restoration age than Bull, and Coon is the natural reference  
391 site.

392 Our data suggest that factors other than nutrient concentrations, such as phytoplankton  
393 community composition, contributed to the observed patterns in primary productivity.  
394 Differences in phytoplankton productivity due to shifts in phytoplankton species composition  
395 along the gradient from upstream to downstream are common (Garnier et al. 1995, Lehman  
396 2007). Similar to Lehman's (2007) findings in the San Joaquin River in the upper SFE, we also  
397 observed high downstream chlorophyll specific productivity along a riverine to freshwater tidal  
398 gradient in the Napa River, and our data supported a shift in phytoplankton community  
399 assemblage from diatoms and green algae upstream to more flagellates downstream. The  
400 changes in phytoplankton community composition along a salinity gradient also suggest that the  
401 differences in productivity rates were due to position in the Napa River rather than restoration  
402 stage.

403 Sherman Lake conditions differed from the other northern SFE wetlands in that water  
404 NO<sub>3</sub> concentrations were consistently low throughout the sampling period, which coincided with  
405 overall low rates of phytoplankton production. Another key difference between Sherman Lake  
406 and all other sites was abundance of invasive submerged aquatic vegetation throughout the  
407 growing season in both years. It is well known in the limnology literature that lakes tend to exist  
408 in alternate stable states, and be either phytoplankton or macrophyte dominated (Peckham et al.  
409 2006). Thus in the extremely shallow channels of Sherman Lake, the low phytoplankton  
410 productivity can likely be attributed to the high biomass of submerged aquatic vegetation  
411 competing for DIN, along with the very high benthic productivity rates which were an order of

412 magnitude greater there than for rates at the other sites. However, small peaks in chlorophyll *a*  
413 were associated with peaks in water NH<sub>4</sub> concentration. Macrophytes can contribute NH<sub>4</sub> to the  
414 water column to support increases in phytoplankton abundance during natural senescence  
415 (Landers 1982). Thus it is not surprising that increases in NH<sub>4</sub> and chlorophyll were observed at  
416 Sherman Lake during times with high *C. caroliniana* abundance. In addition the degrading  
417 macrophyte tissue may have also released DON (not measured in this study), which has been  
418 shown to be a potential source of nutrients for phytoplankton (Bronk et al. 2006).

419         Benthic diatom productivity rates were an order of magnitude greater than phytoplankton  
420 productivity rates, suggesting that the benthic algal community is an important contributor to  
421 wetland productivity in the SFE (Table 8, 9, 10). Our observations were similar to those of  
422 Varela & Penas (1985), who found a 10-fold difference in between benthic and water column  
423 phytoplankton production rates. Benthic productivity rates peaked in the spring across all 6 sites  
424 in 2004 (Table 8, 9), but in 2005 only Coon Island had a spring peak, and there were no major  
425 peaks in productivity at any of the other sites (Table 8, 10). Van Raalte et al. (1976) also found  
426 peaks in benthic production in the early spring in a temperate marsh in the northeastern U.S.

427         Benthic productivity rates appeared to be related to nutrient availability rather than  
428 restoration stage, which is not surprising given that Zheng et al. (2004) found no relationship  
429 between benthic algal production and restoration stage in 1-28 yr old marshes in North Carolina  
430 due to high variability in productivity rates. In 2004, primary production rates across sites  
431 appeared to relate to water column NO<sub>3</sub> concentrations, although the high spring benthic  
432 productivity at Sherman Lake was associated with a peak in water column NH<sub>4</sub> concentration.  
433 However, only Coon followed this pattern of high benthic production in the early spring in 2005.  
434 Colijn & de Jonge (1984) suggested that microphytobenthos productivity rates might be affected

435 by nutrient availability in both overlying and interstitial water. When we examined interstitial  
436 water nutrient concentrations (2005 only),  $\text{NO}_3$  concentrations were highest in early spring at all  
437 sites and became limiting as the growing season progressed with the exception of Bull Island,  
438 which had no measurable  $\text{NO}_3$  at the start of the growing season (Table 5). This finding was also  
439 not surprising given that  $\text{NO}_3$  concentrations are typically low in marsh sediments (Reeburgh  
440 1983) due to low oxygen availability (Boon 1986) and rapid denitrification (Seitzinger et al.  
441 1991). The only site for which interstitial  $\text{NO}_3$  was predictive of high rates of benthic  
442 productivity was Coon Island. In contrast, at all sites,  $\text{NH}_4$ , the dominant form of DIN in marsh  
443 sediments (Chambers et al. 1992), increased in availability through the summer followed by  
444 declines in the fall without concurrent changes in benthic productivity rates. High temporal and  
445 spatial variability in benthic production (Van Raalte et al. 1976, Zheng et al. 2004) provide some  
446 explanation for the lack of a relationship between interstitial nutrient availability and benthic  
447 productivity rates.

448         Our measured rates of benthic productivity were generally low compared to rates  
449 measured in other temperate estuaries (Colijn & de Jonge 1984). Although the other studies also  
450 used  $^{14}\text{C}$  to measure productivity, methodological differences in incubations, sampling processes  
451 and calculations make direct comparisons challenging. We are aware of the potential problems  
452 associated with the nitric acid digestion method that we employed (Colijn & de Jonge 1984,  
453 Gould & Gallagher 1990), however, we are confident that our measured values are useful for  
454 cross-site comparisons.

455         Macroalgae (Ulvales, Chlorophyta) were only occasionally present in the Napa sites,  
456 predominantly at Bull Island. When macroalgae were present, their rates of productivity were  
457 high, exceeding those for phytoplankton (Table 8, 9, 10), but biomass was very low. Thus

458 macoralgae are not likely to be major contributors to wetland productivity in the SFE due to low  
459 biomass and patchy and inconsistent distribution, likely due to absence of suitable substrate  
460 (Josselyn & West 1985). In contrast, the Suisun sites often contained submerged macrophytes,  
461 predominantly the invasive fanwort *Cabomba caroliniana*. At Sherman Lake, *Cabomba* was a  
462 dominant producer, filling shallow channels almost completely by mid summer. Production  
463 rates for SAV were similar in magnitude to the majority of the benthic production measurements  
464 (Table 5). The generally high SAV production rates may have importance for these wetland  
465 systems as food and habitat for fish and invertebrate species (Hester et al. 2005), however, there  
466 is the concern that the invasive SAV habitat is not used by native species (Brown 2003b,  
467 Nobriga et al. 2005).

468 All sites with emergent low marsh vegetation exhibited the same pattern of high  
469 productivity rates in the spring, followed by a decline in productivity rates over the remainder of  
470 the growing season in both years. Of the sites where *Spartina* sp. was found (Napa River and  
471 Petaluma River sites), rates of primary productivity were the highest at Coon Island. One  
472 explanation could be that Coon was the natural reference site, and the other four locations  
473 sampled were restoring. However, by this reasoning, the restoring sites should have increasing  
474 productivity rates with increasing time since restoration, and we observed all three restoring sites  
475 to have similar rates and patterns of productivity. Thus it is more likely that plant productivity  
476 rates were associated with characteristics due to location of the wetland (Howe & Simenstad  
477 2007). For example, differences in productivity rates may have been due to salinity effects.  
478 Percy & Ustin (1984) also measured direct CO<sub>2</sub> uptake by intact *Spartina foliosa* and found  
479 productivity rates declined with increasing salinity. Although Coon generally had lower  
480 salinities than Pond 2A and Carl's Marsh, Bull Island had the lowest salinities measured yet did

481 not have the highest productivity rates (Table 2, 5). Also, none of the sites had water column  
482 salinity exceeding 27 psu, suggesting salinity stress was an unlikely explanation for the observed  
483 differences in productivity.

484 Characteristics specific to a given wetland, such as sediment grain size, organic and  
485 nutrient content have been found to be associated with changes in marsh vegetation productivity  
486 (Lindau & Hossner 1981, Craft et al. 1988, Currin et al. 1996, Piehler et al. 1998, Boyer et al.  
487 2000), and may help to explain our observed patterns in productivity rates. We found that Bull  
488 Island sediments had highest sand content, and corresponded to some of the lowest productivity  
489 rates. Although no significant relationship between plant productivity rates and sediment grain  
490 size across sites with *S. foliosa* emerged, differences in grain size were likely related to amount  
491 of organic matter and nitrogen content (Craft 2001). In general we found productivity to be  
492 positively correlated with increased sediment and interstitial water nutrients, though these  
493 relationships were highly variable. We also found increased interstitial NH<sub>4</sub> concentrations  
494 associated with higher productivity rates. That NO<sub>3</sub> was only present in interstitial water in  
495 March suggests that the high concentrations of available NH<sub>4</sub> are important in maintaining plant  
496 productivity throughout the growing season (Simas & Ferreira 2007).

497 In conclusion, water nutrient concentrations were highest in spring and decreased as the  
498 growing season progressed. Nutrient availability was an important predictor of rates of  
499 production of phytoplankton and benthic diatoms in shallow wetlands of SFE, where light  
500 availability is potentially high. The data also showed the potential importance of benthic  
501 production to wetland productivity in SFE marshes. Sediment nitrogen and organic content,  
502 interstitial nutrient concentrations, and to a lesser extent, grain size, influenced productivity of  
503 the low marsh vegetation. Low marsh vegetation has the overall highest rates of production

504 compared to the other groups of autotrophs, but its contribution is most likely primarily to the  
505 detrital food chain and to export from the wetland, while phytoplankton and the  
506 microphytobenthos contribute organic carbon directly to zooplankton and benthic grazers.  
507 Although the natural marsh in the Napa River typically had higher *Spartina* productivity rates  
508 than nearby restoring sites, both water nutrient concentrations and production by the other groups  
509 of autotrophs studied appeared to be a function of the physical conditions and location of each  
510 wetland rather than restoration age. The exception was the restored marsh in the western Delta;  
511 Sherman Lake was very different from the other sites in terms of low water NO<sub>3</sub> availability,  
512 high benthic and SAV productivity rates, possibly due to alteration by invasive species rather  
513 than either restoration stage or marsh location. This study provides an initial step in  
514 understanding the complex factors that affect primary productivity rates in estuarine wetlands.

515

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524

#### 525 LITERATURE CITED

526 Admiraal W, Peletier H, Zomer H (1982) Observations and experiments on the population  
527 dynamics of epipelagic diatoms from an estuarine mudflat. Est Coast Shelf Sci 14:471-487



- 528
- 529 AOAC Method 972.43. Official Methods of Analysis of AOAC International, 16th  
530 Edition (1997), AOAC International, Arlington, VA
- 531
- 532 Boon PI (1986) Uptake and release of nitrogen compounds in coral reef and seagrass, *Thalassia*  
533 *hemprichii* (Ehrenb.) Aschers., bed sediments at Lizard Island, Queensland. Aust J Mar Freshw  
534 Res 37:11-19
- 535
- 536 Boyer KE, Callaway JC, Zedler JB (2000) Evaluating the progress of restored  
537 cordgrass (*Spartina foliosa*) marshes: Belowground biomass and tissue nitrogen. Estuaries  
538 23:711-721
- 539
- 540 Bran Luebbe AutoAnalyzer Applications (1999) AutoAnalyzer Method No. G-177-96 Silicate in  
541 water and seawater. Bran Luebbe, Inc. Buffalo Grove, IL
- 542
- 543 Bronk DA, See JH, Bradley P, Killberg L (2006) DON as a source of bioavailable  
544 nitrogen for phytoplankton. Biogeosciences Discussions 3:1247-1277
- 545
- 546 Brown LR (2003a) An introduction to the San Francisco Estuary tidal wetlands restoration  
547 series. San Francisco Estuary and Watershed Science 1:1-10.
- 548
- 549 Brown LR (2003b) Will tidal wetland restoration enhance populations of native fishes? San  
550 Francisco Estuary and Watershed Science 1:10-54.

551

552 Bucholz JW (1982) Nitrogen flux between a developing salt marsh and South San Francisco  
553 Bay. MA thesis, San Francisco State University, San Francisco, CA

554

555 Burdick DM, Mendelsohn IA, McKee KL (1989) Live standing crop metabolism of  
556 the marsh grass *Spartina patens* as related to edaphic factors in a brackish mixed marsh  
557 community in Louisiana. *Estuaries* 12:195-204

558

559 Callaway JC, Parker VT, Vasey MC, Schile LM (2007) Emerging issues for the  
560 restoration of tidal marsh ecosystems in the context of predicted climate change. *Madroño*  
561 54:234-248

562

563 Chambers RM, Harvey JW, Odum WE (1992) Ammonium and phosphate dynamics  
564 in a Virginia salt marsh. *Estuaries* 15:349-359.

565

566 Cloern JE (1983) Tidal Mixing, Fresh-Water Inflow, and Phytoplankton Dynamics in South  
567 San-Francisco Bay, California. *Estuaries* 6:322-323

568

569 Cloern JE (1987) Turbidity as a control on phytoplankton biomass and productivity in  
570 estuaries. *Cont Shelf Res* 7:1367-1381

571

572 Cloern JE, Jassby AD (2008) Complex seasonal patterns of primary producers at  
573 the land–sea interface. *Ecol Lett* 11:xxx-xxx

- 574
- 575 Cole BE, Cloern JE (1984) Significance of biomass and light availability to phytoplankton  
576 productivity in San Francisco Bay. *Mar Ecol Prog Ser* 17:15-24
- 577
- 578 Colijn F, de Jonge VN (1984) Primary production of microphytobenthos in the Ems-  
579 Dollard Estuary. *Mar Ecol Prog Ser* 14:185-196
- 580
- 581 Conomos TJ, Smith RE, Gartner JW (1985) Environmental setting of San Francisco  
582 Bay. *Hydrobiologia* 129:1-12
- 583
- 584 Craft CB (2001) Soil organic carbon, nitrogen and phosphorus as indicators of recovery in  
585 restored *Spartina* marshes. *Ecological Restoration* 19:87-91
- 586
- 587 Craft CB, Broome SW, Seneca ED (1988) Nitrogen, phosphorus and organic carbon  
588 pools in natural and transplanted marsh soils. *Estuaries* 11:272-280
- 589
- 590 Cramer GW, Day JW, Conner WH (1981) Productivity of four marsh sites  
591 surrounding Lake Pontchartrain, Louisiana. *Am Midland Nat* 106:65-72.
- 592
- 593 Currin CA, Joye SB, Paerl HW (1996) Diel rates of N<sub>2</sub>-fixation and denitrification in a  
594 transplanted *Spartina alterniflora* marsh: Implications for N-flux dynamics. *Est Coast Shelf*  
595 *Sci* 42:597-616
- 596

- 597 Dugdale RC, Wilkerson FP, Hogue VE, Marchi A (2007) The role of ammonium and  
598 nitrate in spring bloom development in San Francisco Bay. *Est Coast Shelf Sci* 73:17-29.  
599
- 600 Friederich GE, Walz PM, Burczynski MG, Chavez FP (2002) Inorganic carbon in the central  
601 California upwelling system during the 1997-1999 El Niño – La Niña event. *Prog Oceanogr*  
602 54:185-203.  
603
- 604 Garnier J, Billen G, Coste M (1995) Seasonal succession of diatoms and Chlorophyceae in the  
605 drainage network of the Seine River: Observations and modeling. *Limnol Oceanogr* 40:750-765.  
606
- 607 Geider RJ, Osborne BA (1992) *Algal photosynthesis*. Chapman & Hall, New York  
608
- 609 Gould DM, Gallagher ED (1990) Field measurement of specific growth rate, biomass,  
610 and primary production of benthic diatoms of Savin Hill Cove, Boston. *Limnol Oceanogr*  
611 35:1757-1770.  
612
- 613 Grimaldo L, Hymanson Z (1999) What is the impact of the introduced Brazilian waterweed  
614 *Egeria densa* to the Delta ecosystem? *Interagency Ecological Program Newsletter* 12:43-45  
615
- 616 Guillard RRL (1978) Counting slides. In: Sournia A (ed) *Phytoplankton manual-*  
617 *monographs on oceanographic methodology*. UNESCO, Paris, France.  
618
- 619 Hester MW, Spalding EA, Franze CD (2005) *Biological resources of the Louisiana coast: Part 1.*

- 620 An overview of coastal plant communities of the Louisiana Gulf shoreline. *J Coast Res* 44:134-  
621 145  
622
- 623 Hickson D, Keeler-Wolf T (2007) Vegetation and land use classification and map of the  
624 Sacramento-San Joaquin River Delta. California Department of Fish and Game. 283 pp.  
625
- 626 Howe ER, Simenstad CA (2007) Restoration trajectories and food web linkages in San  
627 Francisco Bay's estuarine marshes: a manipulative translocation experiment. *Mar Ecol*  
628 *Prog Ser* 351:65-76  
629
- 630 IOC (Intergovernmental Oceanographic Commission) (1996) JGOFS Report 19. Protocols for  
631 the Joint Global Ocean Flux Study (JGOFS) Core Measurements  
632
- 633 Izaguirre I, O'Farrell I, Tell G (2001) Variation in phytoplankton composition and  
634 limnological features in a water-water ecotone of the Lower Parana Basin (Argentina).  
635 *Freshw Biol* 46:63-74  
636
- 637 Jassby AD, Cloern JE, Powell TM (1993) Organic carbon sources and sinks in San  
638 Francisco Bay: variability induced by river flow. *Mar Ecol Prog Ser* 95:39-54  
639
- 640 Jassby AD, Cloern JE (2000) Organic matter sources and rehabilitation of the  
641 Sacramento-San Joaquin Delta (California, USA). *Aquat Conserv: Mar Freshw Ecosyst* 10:323-  
642 352

- 643
- 644 Josselyn MN, West JA (1985) The distribution and temporal dynamics of the estuarine  
645 macroalgal community of San Francisco Bay. *Hydrobiologia* 129:139-152
- 646
- 647 Landers DH (1982) Effects of naturally senescing aquatic macrophytes on nutrient chemistry  
648 and chlorophyll *a* of surrounding waters. *Limnol Oceanogr* 27:428-439
- 649
- 650 Lehman P (2007) The influence of phytoplankton community composition on primary  
651 productivity along the riverine to freshwater tidal continuum in the San Joaquin River,  
652 California. *Estuaries and Coasts* 30:82-93
- 653
- 654 Lindau CW, Hossner LR (1981) Substrate characterization of an experimental marsh and  
655 three natural marshes. *Soil Science Society of America Journal* 45:1171-1176
- 656
- 657 Littler MM, Littler DS (1985) *Ecological Field Methods: Macroalgae*. Littler MM, Littler DS  
658 (eds) *Handbook of phycological methods*. Cambridge Univ. Press, New York
- 659
- 660 Lorenzi A (2006) Primary Productivity and *rbcL* gene expression in Central San Francisco Bay.  
661 MS thesis, San Francisco State University, San Francisco, CA
- 662
- 663 MacDonald RW, McLaughlin FA, Wong CS (1986) The storage of reactive silicate  
664 samples by freezing. *Limnol Oceanogr* 31:1139-1142
- 665

- 666 Nelson DW, Sommers LE (1982) Total carbon, organic carbon and organic matter. In:  
667 Page AL (ed) *Methods of soil analysis: Part 2. Chemical and microbiological properties.*  
668 *ASA Monograph Number 9, 539-579*  
669
- 670 Nobriga ML, Feyrer F, Baxter RD, Chotkowski M (2005) Fish community ecology in  
671 an altered river delta: Spatial patterns in species composition, life-history strategies, and  
672 biomass. *Estuaries* 28:776-785  
673
- 674 Orr M, Crooks S, Williams PB (2003) Will restored tidal marshes be sustainable? In:  
675 Brown LR (ed) *Issues in San Francisco Estuary tidal wetlands restoration.* San Francisco  
676 *Estuary and Watershed Science.* 1:Article 5.  
677
- 678 Parker AE, Fuller J, Dugdale RC (2006) Estimating dissolved inorganic carbon  
679 concentrations from salinity in San Francisco Bay for use in <sup>14</sup>C-primary production studies.  
680 *Interagency Ecological Program for the San Francisco Estuary.* 19:17-22  
681
- 682 Percy RW, Ustin SL (1984) Effects of salinity on growth and photosynthesis of three  
683 California tidal marsh species. *Oecologia* 62:68-73  
684
- 685 Peckham SD, Chipman JW, Lillesand TM, Dodson SI (2006) Alternate stable states and the  
686 shape of lake trophic distribution. *Hydrobiologia* 571:401-407  
687
- 688 Piehler MF, Currin CA, Cassanova R, Paerl HW (1998) Development and N<sub>2</sub>-fixing

689 activity of the benthic microbial community in transplanted *Spartina alterniflora* marshes in  
690 North Carolina. *Restoration Ecology* 6:290-296  
691

692 Pinckney JL, Carman KR, Lumsden SE, Hymel SN (2003) Microalgal-meiofaunal  
693 trophic relationships in muddy intertidal estuarine sediments. *Aquat Microb Ecol* 31:99-108  
694

695 Pomeroy LR, Darley WM, Dunn EL, Gallage, JL, Haines EB, Whitney DM (1981) Primary  
696 production. In: Pomeroy LR, Wiegert RG (eds) *The Ecology of a Salt Marsh*. Springer-Verlag,  
697 Berlin.  
698

699 Reeburgh WS (1983) Rates of biogeochemical processes in anoxic sediments. *Annu Rev*  
700 *Earth Planet Sci* 11:269-298  
701

702 Riznyk RZ, Edens JI, Libby RC (1978) Production of epibenthic diatoms in a southern  
703 California impounded estuary. *J Phycol* 14:273-279  
704

705 Seitzinger SP, Gardner WS, Spratt AK (1991) The effect of salinity on ammonium  
706 sorption in aquatic sediments: Implications for benthic nutrient cycling. *Estuaries* 14:167-174  
707

708 Sheldrick BH, Wang C (1993) Particle-size Distribution. In: Carter MR  
709 (ed) *Soil Sampling and Methods of Analysis*, Canadian Society of Soil Science, Lewis  
710 Publishers, Ann Arbor, MI  
711



- 712 Smart RM (1982) Distribution and environmental control of productivity and growth form of  
713 *Spartina alterniflora* (Loisel.). *Tasks for Vegetation Science* 2:127-142  
714
- 715 Simas TC, Ferreira JG (2007) Nutrient enrichment and the role of salt marshes in the  
716 Tagus estuary (Portugal). *Est Coast Shelf Sci* 75:393-407  
717
- 718 Sobczak WV, Cloern JE, Jassby AD, Muller-Solger AB (2002) Bioavailability of  
719 organic matter in a highly disturbed estuary: The role of detrital and algal sources. *Proc Nat*  
720 *Acad Sci* 99:8101-8105  
721
- 722 Solorzano L (1969) Determination of ammonia in natural waters by the phenolhypochlorite  
723 method. *Limnol Oceanogr* 14:799-801  
724
- 725 Sukhanova IN (1978) Settling without the inverted microscope. In: Sournia A (ed)  
726 *Phytoplankton Manual*, United Nations Educational, Scientific and Cultural Organization, Paris  
727
- 728 Teal JM, Valiela I, Berlo D (1979) Nitrogen fixation by rhizosphere and free-living bacteria in  
729 salt marsh sediments. *Limnol Oceanogr* 24:126-132  
730
- 731 Tu M, Randall JM (2001) 2001 red alert! New expansions into and around California.  
732 *California Exotic Pest Council* 9:4-5.  
733
- 734 Unrein F (2002) Changes in phytoplankton community along a transversal section of the Lower

- 735 Parana floodplain, Argentina. *Hydrobiologia* 468:123-134
- 736
- 737 U.S. Salinity Laboratory Staff (1954) pH reading of saturated soil paste. In: Richards, L
- 738 A (ed) *Diagnosis and improvement of saline and alkali soils*. USDA Agricultural Handbook
- 739 60. U.S. Government Printing Office, Washington, D.C.
- 740
- 741 Van Raalte C, Stewart WC, Valiella I, Carpenter EJ (1974) A  $^{14}\text{C}$  technique for
- 742 measuring algal productivity in salt marsh muds. *Bot Mar* 17:186-188
- 743
- 744 Van Raalte CD, Valiella, I, Teal JM (1976) Production of epibenthic salt marsh
- 745 algae: Light and nutrient limitation. *Limnol Oceanogr* 21:862-872
- 746
- 747 Varela M, Penas E (1985) Primary production of benthic microalgae in an intertidal sand
- 748 flat of the Ria de Arosa, NW Spain. *Mar Ecol Prog Ser* 25:111-119
- 749
- 750 Vicari RL, Fischer S, Madanes N, Bonaventura SM, Pancotto V (2002) Tiller
- 751 population dynamics and production on *Spartina densiflora* (Brong) on the floodplain of the
- 752 Parana River, Argentina. *Wetlands* 22:347-354
- 753
- 754 Whitley TE, Malloy SC, Patton CJ, Wirick CD (1981) Automated Nutrient
- 755 Analysis in Seawater, Report BNL 51398. Brookhaven National Laboratory, Upton NY, 216 pp.
- 756
- 757 Wilkerson FP, Dugdale RC, Hogue VE, Marchi A (2006) Phytoplankton blooms and

- 758 nitrogen productivity in San Francisco Bay. *Estuaries and Coasts* 29:401-416  
759
- 760 Yorty J (2007) Nitrogen Fixation at Six San Francisco Bay Tidal Wetlands. MS thesis, San  
761 Francisco State University, San Francisco, CA  
762
- 763 Zedler JB (1996) Tidal wetland restoration: a scientific perspective and southern California  
764 focus. La Jolla, CA: California Sea Grant College System, University of California.  
765
- 766 Zedler JB (2005) Restoring wetland plant diversity: a comparison of existing and adaptive  
767 approaches. *Wetlands Ecology and Management* 13:5–14.  
768
- 769 Zedler J, Callaway J, Desmond J, Vivian-Smith G, Williams G, Sullivan G, Brewster A,  
770 Bradshaw B (1999) Californian salt-marsh vegetation: an improved model of spatial pattern.  
771 *Ecosystems* 2:19-35  
772
- 773 Zheng L, Stevenson RJ, Craft C (2004) Changes in benthic algal attributes during salt  
774 marsh restoration. *Wetlands* 24:309-323  
775  
776

776 Table 1. Estuarine wetland sites monitored as part of the Integrated Regional Wetland  
 777 Monitoring Pilot Project (IRWM). Restoring sites were originally estuarine wetland, and had  
 778 tidal flushing returned following breaching of levees in the year listed.

779

780	<u>Site</u>	<u>Location</u>	<u>Size (ac)</u>	<u>Condition</u>
781	Bull Island	Napa River	108	Restoring (1950's)
782	Coon Island	Napa River	400	Natural reference
783	Pond 2A	Napa River	532	Restoring (1995)
784	Sherman Lake	Suisun Bay	3,279	Restoring (1920's)
785	Browns Island	Suisun Bay	848	Natural reference
786	Carl's Marsh	Petaluma River	48	Restoring (1994)

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790 Table 2. Light attenuation (%) from water surface to 15 cm depth at Bull Island, Coon Island and  
 791 Pond 2A in 2004 and 2005. Asterisks indicate no data available.

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Month	2004			2005		
	Bull	Coon	Pond 2A	Bull	Coon	Pond 2A
March	*	*	36	28	43	16
April	35	29	20	24	39	50
May	16	22	17	66	35	23
June	42	10	23	33	33	31
July	28	22	20	17	35	23
August	23	18	21	16	27	18
September	25	25	18	8.0	22	19
October	25	20	25	17	15	33

793

793 Table 3. Phytoplankton community composition and abundance (cells L<sup>-1</sup>) in June 2005.

794 Asterisks indicate absence of cells.

Taxonomic Group	Genus	Bull Island	Coon Island	Pond 2A
Desmid	<i>Ankistrodesmis</i>	1334	4660	*
Diatom	<i>Amphiprora</i>	1779	3330	444.7
Diatom	<i>Chaetoceros</i>	444.7	*	*
Diatom	<i>Cyclotella</i>	2223	*	*
Diatom	<i>Cylindrotheca</i>	3113	666.7	444.7
Diatom	<i>Nitzschia</i>	*	13330	*
Diatom	<i>Pleurosigma</i>	889.3	*	*
Dinoflagellate	<i>Gyrodinium</i>	*	*	889.3
Flagellate	Multiple Cryptomonads	3113	9330	16452

795

796

796 Table 4. Mean sediment characteristics (% dry weight) in May 2005. Numbers in parentheses are  
 797 standard error of the mean.

798

	% Sand	% Silt	% Clay	% Organic	% Total N
Bull Island	69 (1.2)	13 (1.0)	18 (0.3)	0.91 (0.14)	0.068 (0.014)
Coon Island	8.0 (0.0)	54 (0.3)	38 (0.3)	3.41 (0.15)	0.206 (0.007)
Pond 2A	17 (2.9)	40 (3.7)	43 (1.2)	5.60 (0.18)	0.316 (0.009)
Carl's Marsh	8.0 (0.6)	44 (0.3)	48 (0.3)	2.14 (0.06)	0.186 (0.002)
Browns Island	44 (17)	35 (10)	21 (6.7)	5.97 (3.20)	0.326 (0.075)
Sherman Lake	17 (0.9)	56 (1.2)	28 (0.3)	7.58 (0.69)	0.358 (0.033)

799

799 Table 5. Mean macroalgal and SAV productivity rates (mg C mg Chl-a<sup>-1</sup> h<sup>-1</sup>). Numbers in  
 800 parentheses are standard error of the mean and asterisks indicate no data available.

		March	April	May	June	July	August	September	October
Bull	2004	*	*	0.049 (0.010)	0.063 (0.010)	*	0.032 (0.004)	0.018 (0.002)	0.017 (0.001)
	2005	0.021 (0.002)	*	0.043 (0.008)	0.040 (0.003)	0.013 (0.001)	0.037 (0.003)	0.049 (0.008)	*
Coon	2004	*	*	*	0.091 (0.027)	*	*	0.001 (0.0)	*
	2005	*	*	*	*	*	*	*	*
Pond 2A	2004	*	*	*	*	*	*	*	*
	2005	*	*	*	0.047 (0.006)	*	*	*	*
Browns	2004	*	*	*	*	0.019 (0.002)	*	*	*
	2005	*	*	*	0.013 (0.0)	0.009 (0.002)	0.014 (0.0)	0.013 (0.001)	*
Sherman	2004	0.010 (0.001)	0.010 (0.001)	0.015 (0.002)	0.014 (0.003)	0.018 (0.002)	0.013 (0.002)	0.018 (0.001)	0.013 (0.001)
Sherman	2005	0.005 (0.000)	0.013 (0.001)	0.002 (0.000)	0.008 (0.001)	0.010 (0.001)	0.017 (0.002)	0.021 (0.001)	0.011 (0.001)

801

802



802 Table 6. Water column salinity in A) 2004 and B) 2005 at all sites.

803

804 A) 2004

	March	April	May	June	July	August	September	October
Bull	0	4	6	9	15	13	20	20
Coon	0	5	7	14	18	19	18	22
Pond 2A	5	10	14	17	20	19	21	20
Carl's	0	10	12	21	22	24	27	26
Browns	0	0	0	0	0	0	1	3
Sherman	0	0	0	0	0	0	1	1

805

806 B) 2005

	March	April	May	June	July	August	September	October
Bull	0	1	0	0	4	12	14	16
Coon	0	5	1	0	5	10	16	14
Pond 2A	4	6	8	4	10	15	18	18
Carl's	2.5	4	9	10	15	17	22	24
Browns	0	0	0	0	0	0	0	0
Sherman	0	0	0	0	0	0	0	0

807

808 Table 7. Interstitial water nutrient concentrations ( $\mu\text{M}$ ) (mean and standard error).

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810

Site	Nutrient	March	April	May	June	July	August	September	October
Bull Island	NO <sub>3</sub>	0.0	0.1 (0.1)	0.0	0.0	0.0	0.0	0.0	0.8 (0.1)
	Si(OH) <sub>4</sub>	298.9 (29.5)	187.2 (14.1)	322.0 (16.8)	369.9 (31.9)	304.0 (7.9)	211.6 (10.6)	192.0 (13.1)	212.9 (9.7)
	PO <sub>4</sub>	6.5 (1.0)	0.5 (0.1)	0.6 (0.1)	4.1 (1.3)	7.8 (3.1)	0.1 (0)	0.0	0.2 (0.1)
	NH <sub>4</sub>	14.4 (2.1)	137.0 (10.7)	151.0 (19.6)	164.9 (18.4)	79.7 (15.3)	24.5 (4.8)	10.9 (2.6)	10.2 (2.2)
Coon Island	NO <sub>3</sub>	7.2 (3.7)	0.0	0.0	0.0	0.0	0.0	0.0	*
	Si(OH) <sub>4</sub>	360.3 (23.2)	163.9 (14.7)	504.1 (5.3)	471.5 (9.4)	290.4 (34.2)	287.9 (10.0)	267.8 (14.2)	*
	PO <sub>4</sub>	8.0 (1.7)	0.6 (0.2)	42.6 (6.2)	47.4 (9.2)	1.7 (0.6)	19.3 (6.0)	11.5 (4.3)	*
	NH <sub>4</sub>	54.1 (4.5)	113.0 (28.2)	217.7 (4.4)	247.1 (60.1)	256.6 (10.9)	146.0 (27.4)	160.4 (42.3)	*
Pond 2A	NO <sub>3</sub>	6.9 (2.3)	0.4 (0.1)	0.1 (0.1)	0.0	0.0	0.0	0.4 (0.2)	0.0
	Si(OH) <sub>4</sub>	391.9 (92.2)	259.8 (10.7)	279.9 (21.6)	560.1 (52.6)	399.9 (45.4)	239.8 (60.1)	381.4 (29.4)	367.9 (15.0)
	PO <sub>4</sub>	7.6 (1.4)	5.5 (1.5)	14.5 (5.7)	53.3 (13.1)	15.0 (3.8)	1.3 (0.4)	10.9 (3.2)	3.1 (1.3)
	NH <sub>4</sub>	90.2 (4.2)	198.2 (7.2)	274.2 (19.8)	413.1 (23.5)	457.1 (117.7)	109.4 (42.3)	51.4 (8.6)	56.7 (10.6)
Browns Island	NO <sub>3</sub>	4.1 (1.8)	0.0	0.0	0.6 (0.3)	1.8 (0.5)	0.4 (0.2)	0.0	0.0
	Si(OH) <sub>4</sub>	423.1 (52.6)	372.0 (11.5)	269.2 (33.7)	120.5 (22.9)	250.4 (14.4)	202.8 (5.3)	247.0 (12.1)	243.6 (13.5)
	PO <sub>4</sub>	5.8 (1.70)	3.9 (0.6)	3.0 (0.6)	2.3 (1.0)	0.6 (0.0)	0.5 (0.0)	1.2 (0.4)	0.7 (0.2)
	NH <sub>4</sub>	12.0 (4.0)	46.4 (4.6)	29.9 (4.3)	26.2 (9.8)	12.7 (0.5)	6.4 (1.2)	33.3 (10.3)	16.5 (8.1)
Sherman Lake	NO <sub>3</sub>	5.1 (2.1)	0.0	0.0	0.0	0.0	0.0	0.1 (0.0)	0.9 (0.1)
	Si(OH) <sub>4</sub>	484.7 (216.7)	178.2 (3.9)	187.7 (12.4)	141.5 (26.2)	288.9 (14.0)	312.3 (27.3)	280.5 (5.0)	268.4 (21.9)
	PO <sub>4</sub>	5.6 (1.1)	0.9 (0.1)	1.1 (0.1)	2.1 (0.7)	0.8 (0.1)	0.4 (0.1)	0.5 (0.1)	0.5 (0.2)
	NH <sub>4</sub>	35.3 (6.2)	49.6 (13.6)	39.7 (3.1)	46.0 (5.0)	46.8 (8.5)	21.3 (3.8)	29.1 (8.2)	8.5 (2.8)
Carls Marsh	NO <sub>3</sub>	5.7 (0.6)	1.7 (0.3)	0.0	0.1 (0.1)	0.0	0.0	0.7 (0.2)	*
	Si(OH) <sub>4</sub>	283.4 (11.3)	100.8 (2.6)	125.8 (3.4)	172.5 (3.8)	180.3 (12.3)	187.9 (2.1)	194.2 (27.0)	*
	PO <sub>4</sub>	10.7 (0.8)	1.5 (0.2)	0.4 (0.1)	1.5 (0.2)	1.4 (0.1)	2.8 (0.3)	5.2 (0.5)	*
	NH <sub>4</sub>	45.6 (1.7)	92.6 (2.3)	92.3 (2.60)	32.3 (4.8)	22.0 (1.6)	41.2 (6.4)	58.2 (11.7)	*

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812 Table 8. Mean range of measures for 2004 and 2005 combined.

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	Bull Island	Coon Island	Pond 2A	Carl's Marsh	Browns Island	Sherman Lake
Restored/Natural	Restored	Natural	Restored	Restored	Natural	Restored
NO <sub>3</sub> (µM)	0-79.99	1.96-61.17	0.01-9.75	8.33-53.58	2.05-19.27	0-1.80
NH <sub>4</sub> (µM)	1.98-13.62	2.55-17.98	3.84-9.99	0.27-17.08	1.45-7.38	2.21-12.19
PO <sub>4</sub> (µM)	0.77-2.52	1.04-4.04	0.86-4.55	5.34-10.58	1.38-3.14	2.64-5.31
Si(OH) <sub>4</sub> (µM)	67.62-547.66	92.42-410.48	89.02-200.17	143.69-275.48	167.71-299.86	266.27-332.81
Chl a (µg L <sup>-1</sup> )	2.0-12.4	2.2-14.3	1.7-9.7	1.9-14.0	0.9-4.5	1.9-7.6
Phytoplankton PP (µg C µg Chl a <sup>-1</sup> h <sup>-1</sup> )	1.4-4.1	1.0-5.2	1.6-7.8	1.0-7.1	1.6-7.2	0.7-2.8
Benthic PP*10 <sup>-3</sup> (mg C mg Chl a <sup>-1</sup> h <sup>-1</sup> )	2.0-24.0	2.5-40.0	3.0-21.5	3.5-40.0	3.5-20.5	12.0-108.5
SAV PP (mg C mg Chl a <sup>-1</sup> h <sup>-1</sup> )	0-0.056	0-0.091	0-0.047	N/A	0-0.017	0.006-0.019
Vegetation PP (mg C mg Chl a <sup>-1</sup> h <sup>-1</sup> )	0.5-2.5	0.5-3.4	0.7-2.8	0.2-2.7	0.8-2.2	N/A

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825 Table 9A. Range of C fixation and chlorophyll *a* measures monthly from March-June 2004.  
 826 Phytoplankton C fixation ( $\text{mg C L}^{-1} \text{h}^{-1} * 10^{-3}$ ) and Chl-*a* ( $\text{mg L}^{-1} * 10^{-3}$ ).  
 827 Benthic C fixation ( $\text{mg m}^{-2} \text{h}^{-1}$ ) and Chl-*a* ( $\text{mg m}^{-2}$ )  
 828 SAV C fixation ( $\text{mg C g}^{-1} \text{h}^{-1}$ ), Chl-*a* ( $\text{mg g}^{-1}$ )  
 829 Low marsh vegetation (*Spartina/Carex*) C fixation ( $\text{mg m}^{-2} \text{h}^{-1}$ ) Chl-*a* ( $\text{mg m}^{-2}$ )  
 830

		March		April		May		June	
		C fixation	Chlorophyll	C fixation	Chlorophyll	C fixation	Chlorophyll	C fixation	Chlorophyll
Bull Island	Phyto	7.2-9.4	3.7-5.0	2.1-3.4	1.6-2.2	23.0-34.3	6.6-9.4	13.4-15.3	3.6-4.8
	Benthic	*	0.0-9.9	0.0-5.6	60.9-378.7	0.6-2.7	9.8-93.6	0.7-2.1	41.9-208.2
	SAV	*	*	*	*	1.15-1.39	18.2-36.6	1.04-1.31	11.5-23.3
	Spartina	*	*	99.4-177.1	55.2-298.9	393.1-794.9	157.6-226.1	177.1-717.1	78.3-235.9
Coon Island	Phyto	8.1-10.3	6.1-9.2	10.1-14.2	3.4-4.1	6.6-11.3	5.8-7.0	14.0-15.7	4.0-4.6
	Benthic	0.9-1.3	19.7-35.1	0.7-2.4	35.8-139.8	0.0-1.7	29.4-104.8	0.5-2.1	41.9-188.7
	SAV	*	*	*	*	*	*	1.04-1.21	6.8-28.1
	Spartina	129.6-544.3	26.6-153.3	570.2-786.2	89.1-293.5	423.4-643.7	33.9-211.9	492.5-794.9	59.2-320.6
Pond 2A	Phyto	9.9-16.5	6.2-10.8	22.4-26.5	4.2-5.2	8.4-13.0	2.1-5.7	6.1-9.1	1.3-2.1
	Benthic	1.9-4.1	101.3-236.7	3.3-4.7	47.4-466.8	1.3-3.1	40.8-160.7	0.6-1.4	31.0-92.2
	Spartina	432.0-669.6	159.8-367.4	116.6-453.6	72.8-318.5	77.7-743.0	213.0-489.1	116.6-1019.5	252.2-400.0
Browns Island	Phyto	1.8-4.7	2.1-3.3	3.8-4.6	2.3-3.4	8.5-10.6	3.9-8.8	3.7-4.1	1.9-3.3
	Benthic	1.3-10.2	53.7-1301.3	2.1-2.7	17.5-121.6	0.7-1.6	41.8-360.5	0.7-1.5	32.3-307.4
	Carex	*	*	445.0-682.6	147.8-326.1	155.5-652.3	93.5-278.2	341.3-557.3	9.8-258.7
Sherman Lake	Phyto	2.4-3.5	2.1-2.7	4.9-7.5	3.2-4.5	10.7-15.3	5.4-7.4	11.6-15.2	5.5-6.7
	Benthic	0.8-3.6	46.3-101.3	1.9-5.5	8.7-124.4	1.0-2.4	12.9-103.4	2.1-3.1	36.3-283.7
	SAV	0.23-0.24	16.5-27.6	0.28-0.37	21.9-63.0	0.45-0.54	21.8-41.4	0.49-0.61	25.1-56.4
Carls Marsh	Phyto	5.5-13.2	5.2-7.4	31.0-44.5	9.1-25.6	8.3-12.9	8.1-21.0	4.1-5.9	2.3-2.8
	Benthic	*	*	1.3-3.3	15.0-102.0	1.1-2.9	15.7-79.1	0.5-1.5	37.9-89.4
	Spartina	453.6-777.6	122.8-305.4	319.7-833.8	201.1-372.8	354.2-829.4	33.7-238.0	263.5-894.2	117.4-296.7

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832 Table 9B. Range of C fixation and chlorophyll *a* measures monthly from July-October 2004.

833 Phytoplankton C fixation ( $\text{mg C L}^{-1} \text{h}^{-1} * 10^{-3}$ ) and Chl-*a* ( $\text{mg L}^{-1} * 10^{-3}$ ).

834 Benthic C fixation ( $\text{mg m}^{-2} \text{h}^{-1}$ ) and Chl-*a* ( $\text{mg m}^{-2}$ )

835 SAV C fixation ( $\text{mg C g}^{-1} \text{h}^{-1}$ ), Chl-*a* ( $\text{mg g}^{-1}$ )

836 Low marsh vegetation (*Spartina/Carex*) C fixation ( $\text{mg m}^{-2} \text{h}^{-1}$ ) Chl-*a* ( $\text{mg m}^{-2}$ )

		July		August		September		October	
		C fixation	Chlorophyll	C fixation	Chlorophyll	C fixation	Chlorophyll	C fixation	Chlorophyll
Bull Island	Phyto	15.1-20.9	5.2-6.1	8.4-9.7	2.1-3.1	4.3-8.3	0.6-4.9	8.3-11.4	3.4-6.5
	Benthic	1.6-2.4	69.2-262.7	0.9-3.4	160.7-698.7	0.2-1.5	124.4-322.8	1.5-2.9	141.5-300.0
	SAV	*	*	1.21-1.83	31.7-52.7	1.46-1.73	52.7-108.3	0.98-1.06	52.7-76.1
	Spartina	177.1-842.4	148.9-322.8	86.4-216.0	243.5-450.0	73.4-254.9	200.0-506.5	133.9-436.3	302.3-527.6
Coon Island	Phyto	13.8-18.0	2.7-3.2	9.7-15.5	2.2-2.7	5.0-9.1	2.1-4.7	2.4-7.1	2.4-5.0
	Benthic	2.0-2.6	195.7-303.3	1.0-2.2	188.7-409.5	1.8-3.3	211.4-409.1	0.0-0.3	61.4-187.5
	SAV	*	*	*	*	0.11-0.15	87.0-114.8	*	*
	Spartina	492.5-1006.6	209.8-335.8	207.4-449.3	204.3-379.3	406.1-1049.8	340.7-588.6	90.7-436.3	357.9-652.2
Pond 2A	Phyto	17.8-26.4	2.1-3.2	5.0-12.8	2.6-4.0	6.3-12.1	1.3-1.9	5.9-15.2	3.4-6.0
	Benthic	0.2-1.7	39.0-415.1	1.7-3.2	89.4-272.5	0.7-1.9	190.9-354.6	0.1-1.2	184.1-323.9
	Spartina	540.0-959.0	175.0-311.9	241.9-877.0	178.2-406.5	177.1-846.7	165.7-506.4	99.4-285.1	222.7-527.6
Browns Island	Phyto	2.0-3.0	1.6-2.1	1.3-2.2	0.7-1.1	4.7-6.2	0.5-1.3	2.8-6.0	0.8-1.4
	Benthic	0.4-1.3	67.9-349.4	0.7-1.6	258.5-536.6	0.9-1.6	94.3-335.8	0.1-3.6	20.6-216.5
	SAV	0.92-1.01	44.3-66.0	*	*	*	*	*	*
	Carex	276.5-406.1	108.7-313.0	181.4-432.0	129.3-310.8	181.4-622.1	147.2-424.2	38.9-358.6	135.2-426.9
Sherman Lake	Phyto	9.1-18.5	6.1-6.2	2.2-3.3	3.3-4.1	1.6-2.8	1.6-2.4	2.7-8.4	4.7-10.1
	Benthic	2.1-3.5	69.9-130.0	2.2-3.8	104.8-190.1	1.8-3.4	85.2-398.9	1.2-4.6	31.4-356.3
	SAV	0.72-0.80	31.1-59.3	0.48-0.67	27.1-52.2	0.73-1.06	44.6-67.3	0.47-0.71	10.7-49.0
Carls Marsh	Phyto	6.1-7.5	2.2-2.8	2.9-5.1	3.0-5.4	4.6-5.8	0.3-1.4	4.8-6.5	0.8-4.0
	Benthic	0.3-1.4	39.1-102.0	0.0-0.3	46.4-65.7	0.0-0.2	32.6-47.7	0.0-0.2	35.8-69.9
	Spartina	449.3-747.4	207.6-552.1	185.8-622.1	241.3-443.4	77.8-138.2	168.4-450.7	86.4-272.2	140.3-543.5

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839

840 Table 10A. Range of C fixation and chlorophyll *a* measures monthly from March-June 2005.  
 841 Phytoplankton C fixation ( $\text{mg C L}^{-1} \text{h}^{-1} * 10^{-3}$ ) and Chl-*a* ( $\text{mg L}^{-1} * 10^{-3}$ ).  
 842 Benthic C fixation ( $\text{mg m}^{-2} \text{h}^{-1}$ ) and Chl-*a* ( $\text{mg m}^{-2}$ )  
 843 SAV C fixation ( $\text{mg C g}^{-1} \text{h}^{-1}$ ), Chl-*a* ( $\text{mg g}^{-1}$ )  
 844 Low marsh vegetation (*Spartina/Carex*) C fixation ( $\text{mg m}^{-2} \text{h}^{-1}$ ) Chl-*a* ( $\text{mg m}^{-2}$ )  
 845

		March		April		May		June	
		C fixation	Chlorophyll	C fixation	Chlorophyll	C fixation	Chlorophyll	C fixation	Chlorophyll
Bull Island	Phyto	5.1-5.9	3.7-4.5	7.6-11.6	4.3-7.8	5.7-8.5	2.1-3.0	16.0-24.5	13.9-21.4
	Benthic	0.4-2.2	214.8-531.8	1.5-2.5	356.3-859.1	0.7-2.0	117.6-681.8	2.0-3.2	68.2-521.6
	SAV	0.64-0.75	28.6-33.4	*	*	1.39-1.50	21.4-51.2	1.34-1.66	34.4-48.3
	Spartina	181.4-488.2	217.4-354.0	470.9-816.5	119.3-307.6	263.5-643.7	129.9-297.0	194.4-756.0	161.7-351.3
Coon Island	Phyto	7.4-15.6	4.8-7.9	4.6-7.5	4.8-8.6	13.4-25.4	4.0-4.5	15.5-41.2	12.2-15.6
	Benthic	3.1-37.5	185.8-334.1	0.1-2.9	76.7-254.0	0.4-2.2	58.0-129.6	0.1-0.9	59.7-150.0
	Spartina	367.2-825.1	129.9-388.4	626.4-911.5	183.0-391.1	406.1-807.8	177.6-335.4	388.8-777.6	145.8-335.4
Pond 2A	Phyto	12.1-26.1	6.9-13.3	20.3-40.1	9.4-12.3	17.5-21.7	2.7-3.7	6.2-8.6	3.1-4.6
	Benthic	1.9-2.5	192.6-335.8	1.6-3.2	168.8-422.7	1.3-2.8	155.1-296.6	0.8-3.0	119.3-381.8
	Spartina	349.9-656.6	330.1-403.0	453.6-829.4	192.2-360.6	479.5-920.2	177.6-424.2	*	205.5-411.0
Browns Island	Phyto	5.3-14.7	1.8-2.6	5.9-6.8	1.6-3.6	2.3-2.7	0.8-1.0	3.4-4.5	1.9-2.3
	Benthic	0.8-1.8	175.6-613.7	1.0-1.7	90.3-458.5	0.5-2.0	98.2-354.6	1.2-1.9	67.2-347.7
	SAV	*	*	*	*	*	*	0.69-0.79	38.4-60.7
	Carex	380.2-721.4	245.3-438.8	423.4-652.3	262.5-369.9	237.6-470.9	157.8-347.3	133.9-423.4	153.8-346.0
Sherman Lake	Phyto	4.1-9.5	2.6-2.7	2.8-4.3	3.2-4.8	5.2-6.9	3.2-4.9	5.2-15.1	5.6-14.7
	Benthic	3.6-4.2	110.8-351.1	1.7-4.0	80.1-248.9	1.4-3.1	76.7-327.3	1.6-2.5	24.9-247.2
	SAV	0.23-0.35	44.2-79.7	0.47-0.52	34.5-46.8	0.07-0.14	41.5-66.6	0.30-0.45	42.3-51.2
Carls Marsh	Phyto	13.8-24.1	9.7-15.5	9.1-20.7	11.7-15.1	2.6-8.1	1.7-3.9	7.4-11.7	2.5-5.5
	Benthic	0.4-1.4	49.4-179.0	0.8-2.3	73.3-236.9	0.2-1.4	58.0-218.2	0.3-2.1	38.0-109.1
	Spartina	544.3-937.4	194.9-380.5	332.6-738.7	189.6-327.5	380.2-591.8	184.3-438.8	388.8-691.2	66.3-384.5

846 Table 10B. Range of C fixation and chlorophyll *a* measures monthly from July-October 2005.

847 Phytoplankton C fixation ( $\text{mg C L}^{-1} \text{h}^{-1} * 10^{-3}$ ) and Chl-*a* ( $\text{mg L}^{-1} * 10^{-3}$ ).

848 Benthic C fixation ( $\text{mg m}^{-2} \text{h}^{-1}$ ) and Chl-*a* ( $\text{mg m}^{-2}$ )

849 SAV C fixation ( $\text{mg C g}^{-1} \text{h}^{-1}$ ), Chl-*a* ( $\text{mg g}^{-1}$ )

850 Low marsh vegetation (*Spartina/Carex*) C fixation ( $\text{mg m}^{-2} \text{h}^{-1}$ ) Chl-*a* ( $\text{mg m}^{-2}$ )

		July		August		September		October	
		C fixation	Chlorophyll	C fixation	Chlorophyll	C fixation	Chlorophyll	C fixation	Chlorophyll
Bull Island	Phyto	14.1-19.9	5.2-7.1	2.5-13.8	4.0-4.5	7.7-11.1	0.8-2.7	8.3-10.6	0.8-3.2
	Benthic	3.3-6.9	192.6-804.6	0.3-1.1	107.4-177.3	1.9-3.3	254.0-591.5	0.4-2.7	109.1-1121.6
	SAV	0.85-1.15	60.7-80.5	0.88-1.02	22.1-31.9	0.70-1.07	13.9-24.1	*	*
	Spartina	77.8-185.8	141.9-315.5	177.1-600.5	324.8-718.5	241.9-643.7	177.6-639.0	73.4-358.6	259.8-625.7
Coon Island	Phyto	13.3-28.4	17.6-23.4	22.5-28.7	5.7-7.8	12.6-20.1	0.8-14.2	4.4-15.7	0.3-3.2
	Benthic	0.7-2.5	93.8-131.3	0.9-2.4	114.2-301.7	0.1-1.5	129.6-340.9	2.0-2.6	288.1-427.8
	Spartina	220.3-600.5	189.6-404.3	315.4-609.1	116.7-633.7	60.5-272.2	297.0-625.7	138.2-358.6	286.4-644.3
Pond 2A	Phyto	11.3-14.7	1.7-1.9	18.6-23.9	2.5-2.9	11.8-16.5	1.6-2.0	6.7-20.2	1.8-2.3
	Benthic	0.6-2.6	98.9-344.3	1.2-2.6	92.1-165.3	2.5-3.9	170.5-509.7	0.5-1.7	153.4-494.3
	Spartina	254.9-743.0	153.8-444.1	272.2-881.3	98.1-465.3	241.9-686.9	25.3-493.2	73.4-514.1	34.9-468.0
Browns Island	Phyto	18.3-20.9	1.8-2.5	4.6-5.6	1.6-2.3	3.1-3.7	1.3-1.6	1.3-5.5	0.9-1.0
	Benthic	1.2-2.1	119.3-349.4	0.7-2.3	80.1-294.9	3.3-4.9	223.3-555.7	0.7-1.8	185.8-477.3
	SAV	0.42-0.89	43.5-65.8	0.47-0.57	34.1-44.6	0.93-1.15	65.8-97.3	*	*
	Carex	77.8-341.3	110.0-298.3	69.1-267.8	103.4-257.2	73.4-453.6	88.8-340.7	155.5-358.6	190.9-360.6
Sherman Lake	Phyto	4.0-8.2	6.7-9.3	2.6-4.2	4.0-6.0	1.9-2.2	2.0-2.4	4.2-10.4	1.9-2.0
	Benthic	4.5-6.1	104.0-407.4	1.9-3.7	100.6-269.3	0.8-4.3	37.7-293.2	1.2-3.4	80.1-226.7
	SAV	0.54-0.60	39.8-61.4	0.71-0.82	32.9-53.4	0.98-1.10	43.6-57.1	0.55-0.76	48.3-77.5
Carls Marsh	Phyto	27.0-35.0	2.9-4.9	11.4-16.1	2.5-4.2	5.8-13.3	0.4-4.2	8.2-12.1	4.0-5.9
	Benthic	0.2-0.7	24.9-69.9	0.1-1.3	31.7-71.6	0.7-1.4	88.6-110.8	0.1-1.0	56.3-136.4
	Spartina	95.0-246.2	290.3-551.5	112.3-185.8	192.2-567.4	25.9-82.1	123.3-554.1	8.6-47.5	171.0-588.6

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853 Figure Captions:

854 Fig 1. Map of study sites (in black) from west to east 1) Carl's Marsh, 2) Bull Island, 3) Coon  
855 Island, 4) Pond 2A, 5) Browns Island, and 6) Sherman Lake.

856

857 Fig 2. Mean surface water  $\text{NO}_3$  concentrations ( $\mu\text{M}$ ) at each study site from March to October  
858 2004 and 2005 (n=3).

859

860 Fig 3. Mean surface water  $\text{Si}(\text{OH})_4$  concentrations ( $\mu\text{M}$ ) at each study site from March to  
861 October 2004 and 2005 (n=3).

862

863 Fig 4. Mean surface water  $\text{PO}_4$  concentrations ( $\mu\text{M}$ ) at each study site from March to October  
864 2004 and 2005 (n=3).

865

866 Fig 5. Mean surface water  $\text{NH}_4$  concentrations ( $\mu\text{M}$ ) at each study site from March to October  
867 2004 and 2005 (n=3).

868

869 Fig 6. Mean chlorophyll *a* concentration ( $\mu\text{g L}^{-1}$ ) at each study site from March to October 2004  
870 and 2005 (n=5).

871

872 Fig 7. Mean phytoplankton productivity ( $\mu\text{g C } \mu\text{g Chl-a}^{-1} \text{ h}^{-1}$ ) at each study site from March to  
873 October 2004 and 2005 (n=4).

874

875



876 Fig 8. Mean benthic productivity ( $\text{mg C mg Chl-a}^{-1} \text{ h}^{-1}$ ) at each study site from March to October  
877 2004 and 2005 (n=9).

878

879 Fig 9. Mean plant productivity ( $\text{mg C mg Chl-a}^{-1} \text{ h}^{-1}$ ) at each study site (with the exception of  
880 Sherman Lake) from March to October 2004 and 2005 (n=15). Dominant vegetation was  
881 *Spartina* spp. at Bull Island, Coon Island and Pond 2A, and *Carex* spp. at Browns Island.  
882 March/April and May/June values combined due to missing data.

883

884 Fig 10. Nonparametric Spearman's  $\rho$  correlations between plant productivity and A) sediment  
885 total N and B) sediment organic matter (% dry weight).

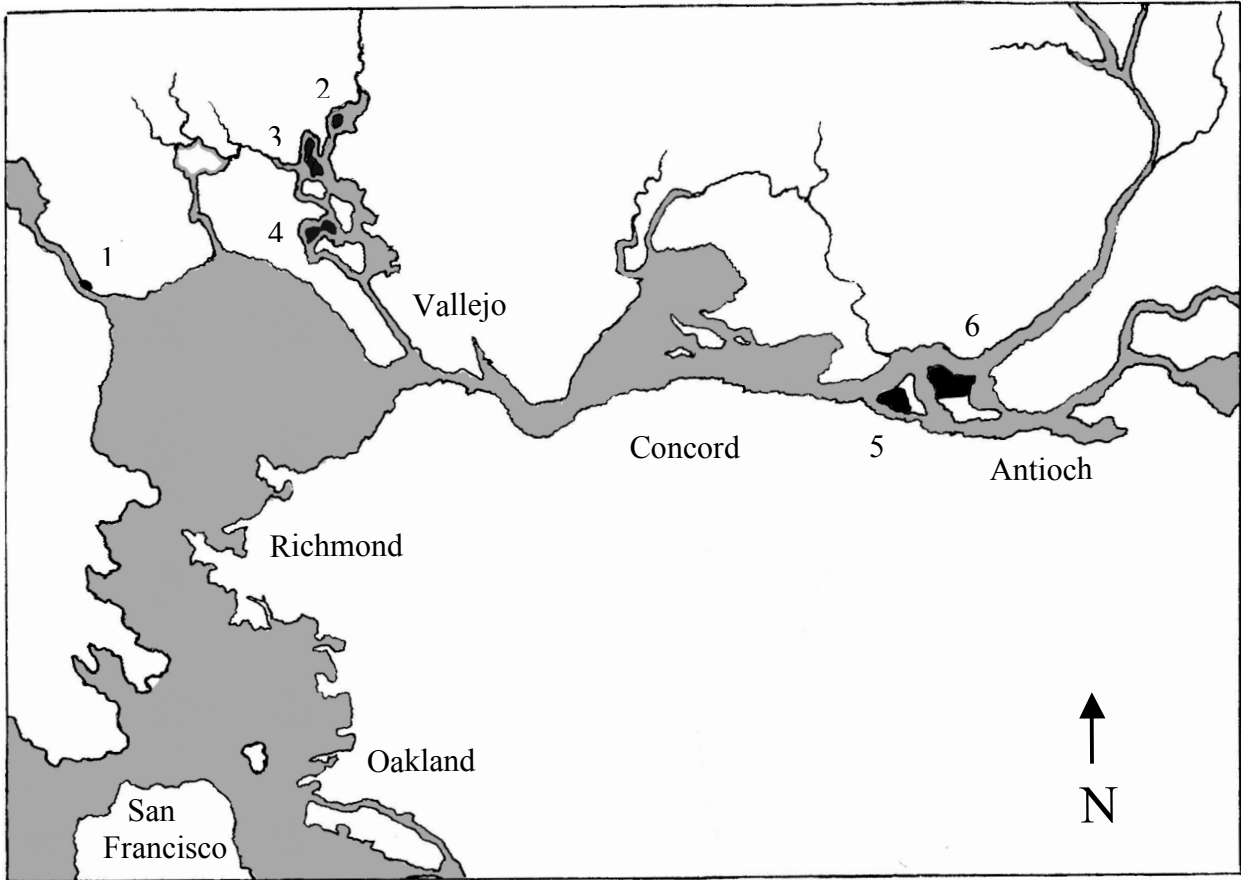
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887 Fig 11. Nonparametric Spearman's  $\rho$  correlations between plant productivity and interstitial  
888 water A)  $\text{NH}_4$  and B)  $\text{PO}_4$  concentrations ( $\mu\text{M}$ ).

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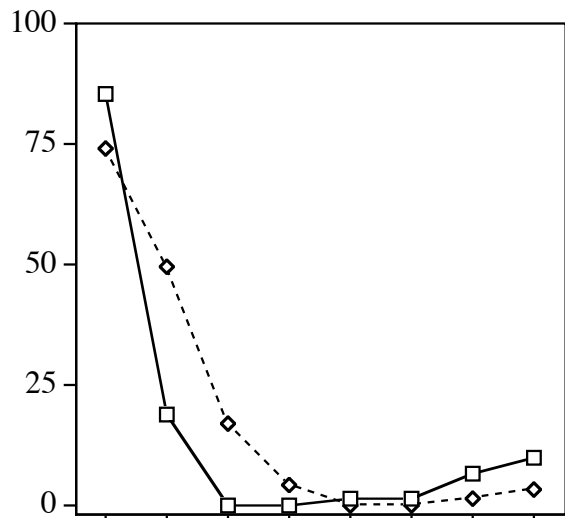
Figure 1.



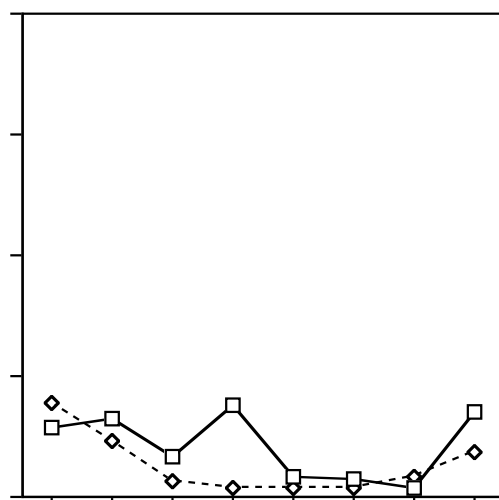
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Fig 2.

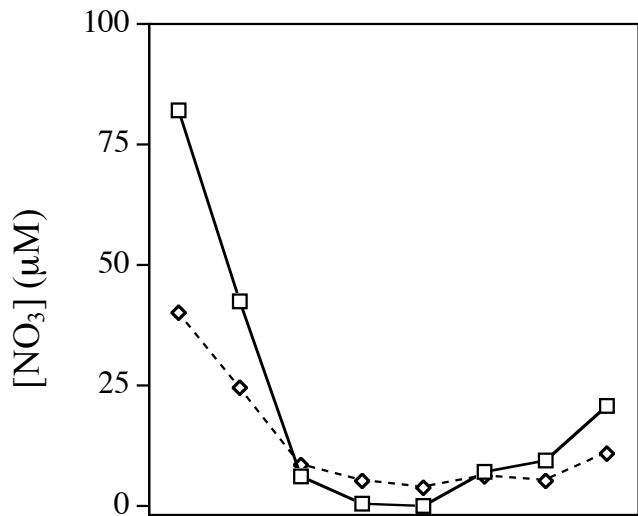
A. Bull (Restored)



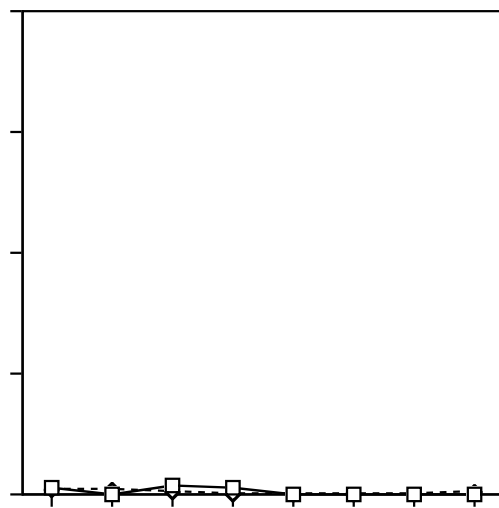
D. Browns (Natural)



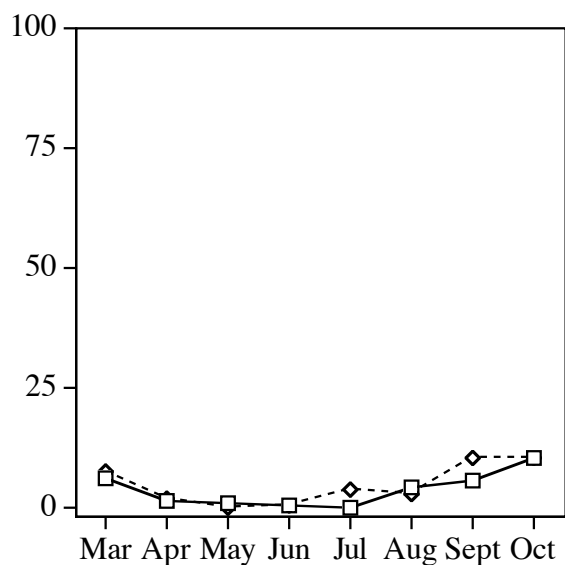
B. Coon (Natural)



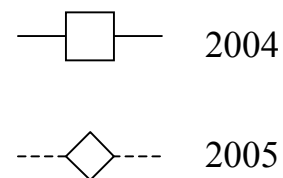
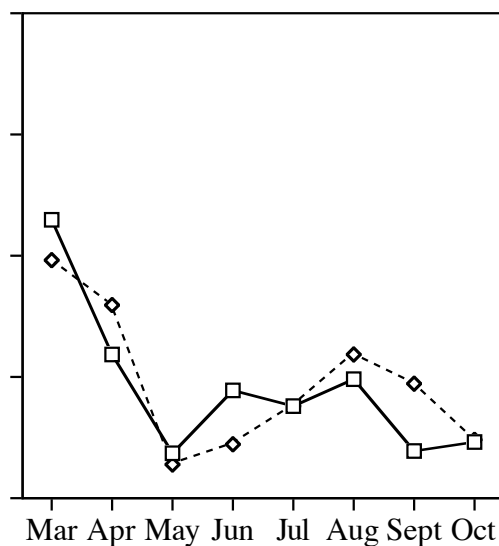
E. Sherman (Restored)



C. Pond 2A (Restored)



F. Carl's (Restored)



Time (month)

Fig 3.

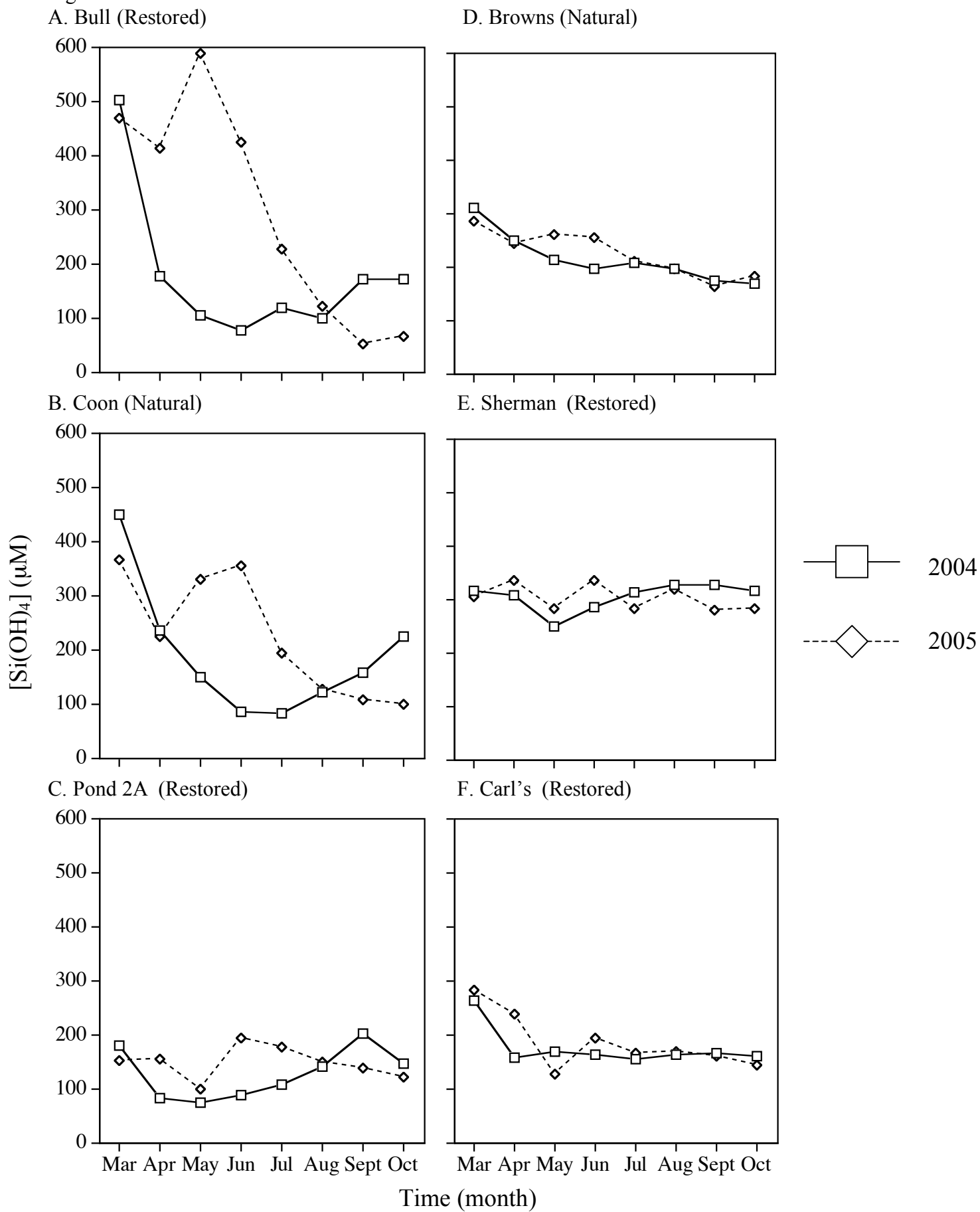
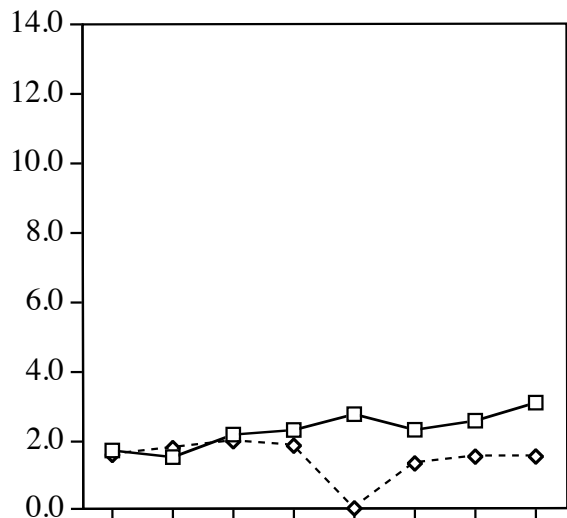
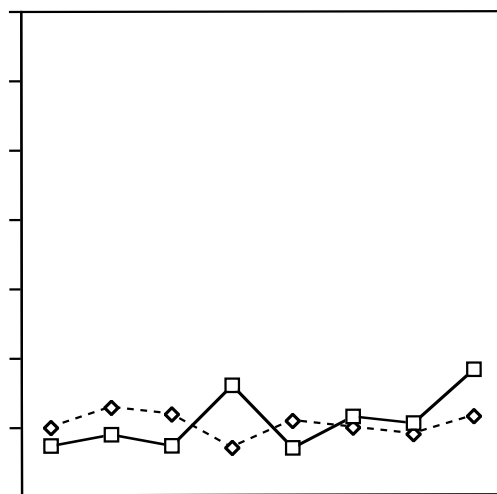


Fig 4.

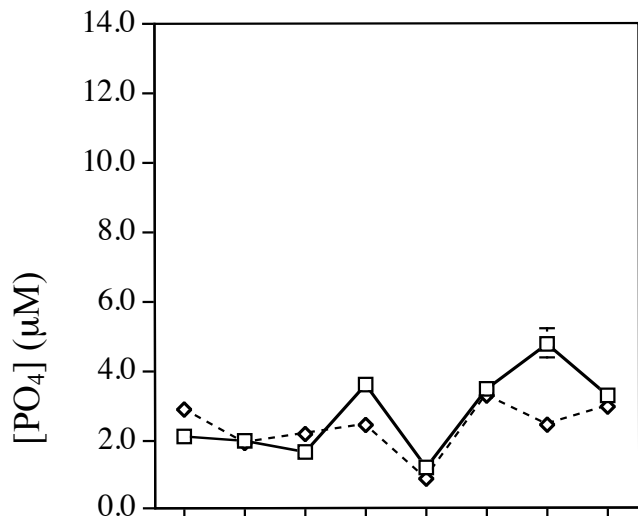
A. Bull (Restored)



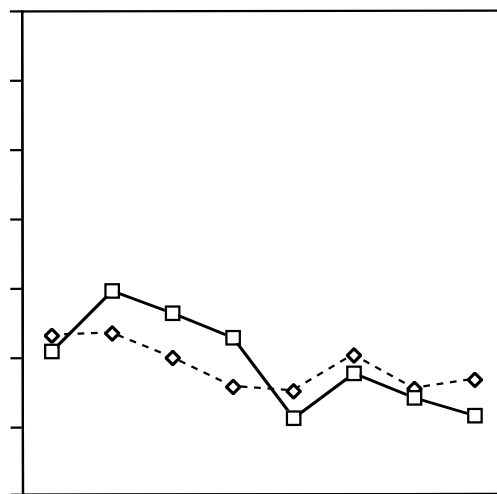
D. Browns (Natural)



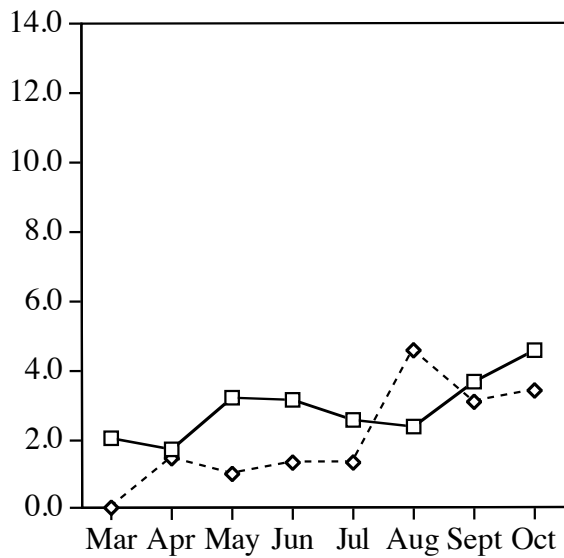
B. Coon (Natural)



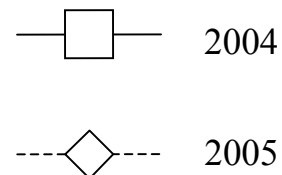
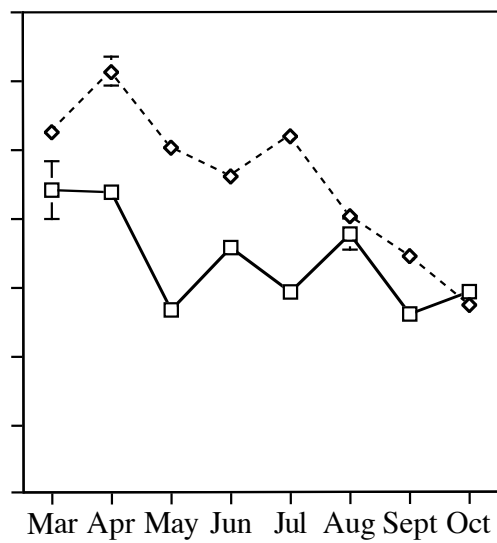
E. Sherman (Restored)



C. Pond 2A (Restored)



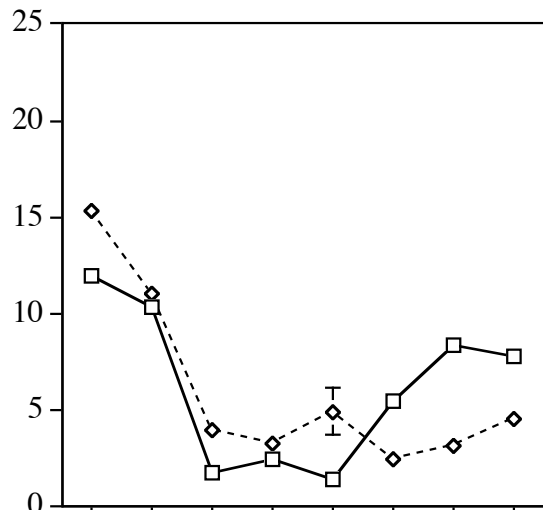
F. Carl's (Restored)



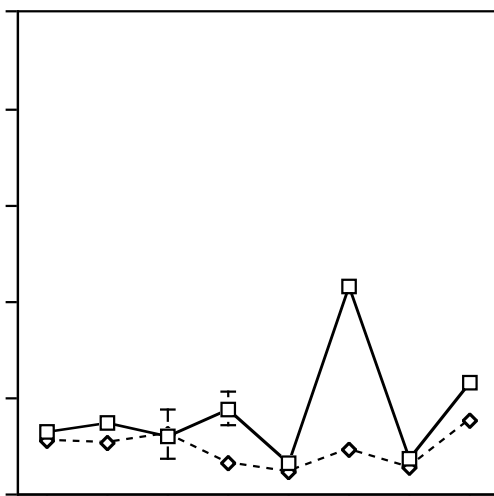
Time (month)

Fig 5.

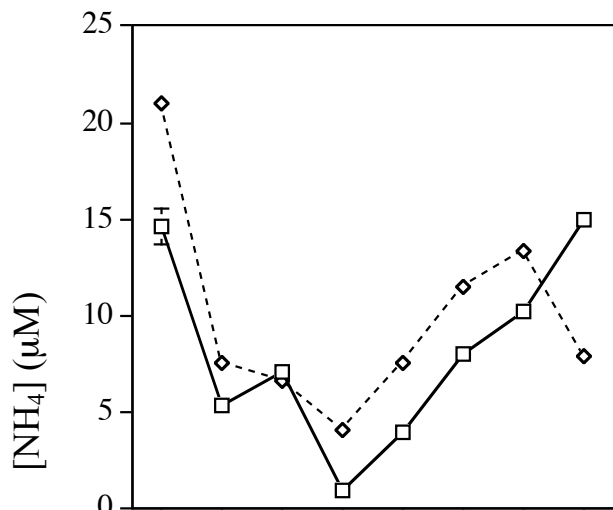
A. Bull (Restored)



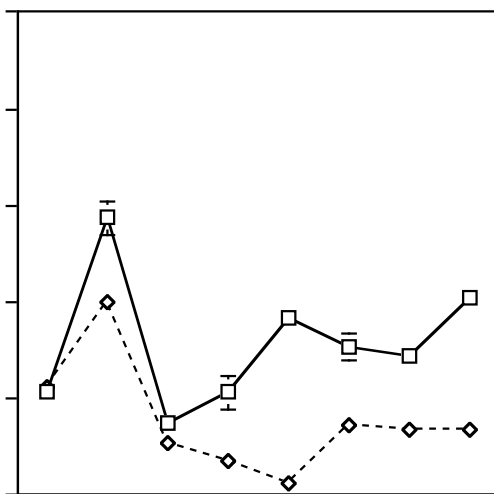
D. Browns (Natural)



B. Coon (Natural)

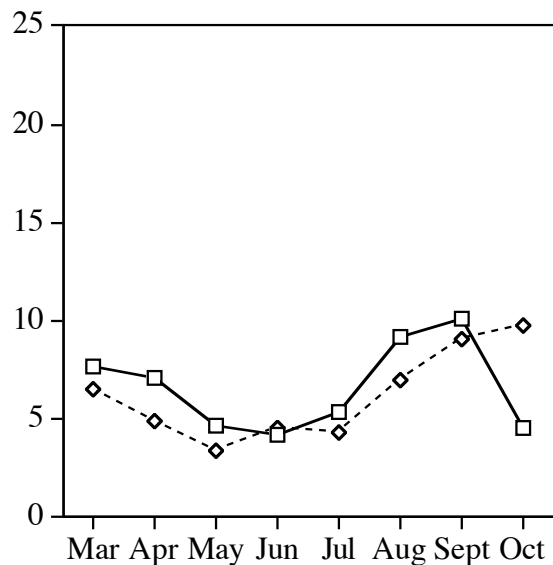


E. Sherman (Restored)

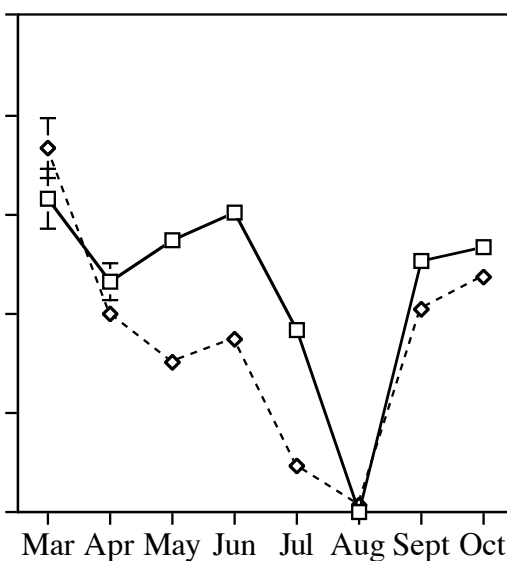


—□— 2004  
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C. Pond 2A (Restored)



F. Carl's (Restored)



Time (month)

Fig 6.

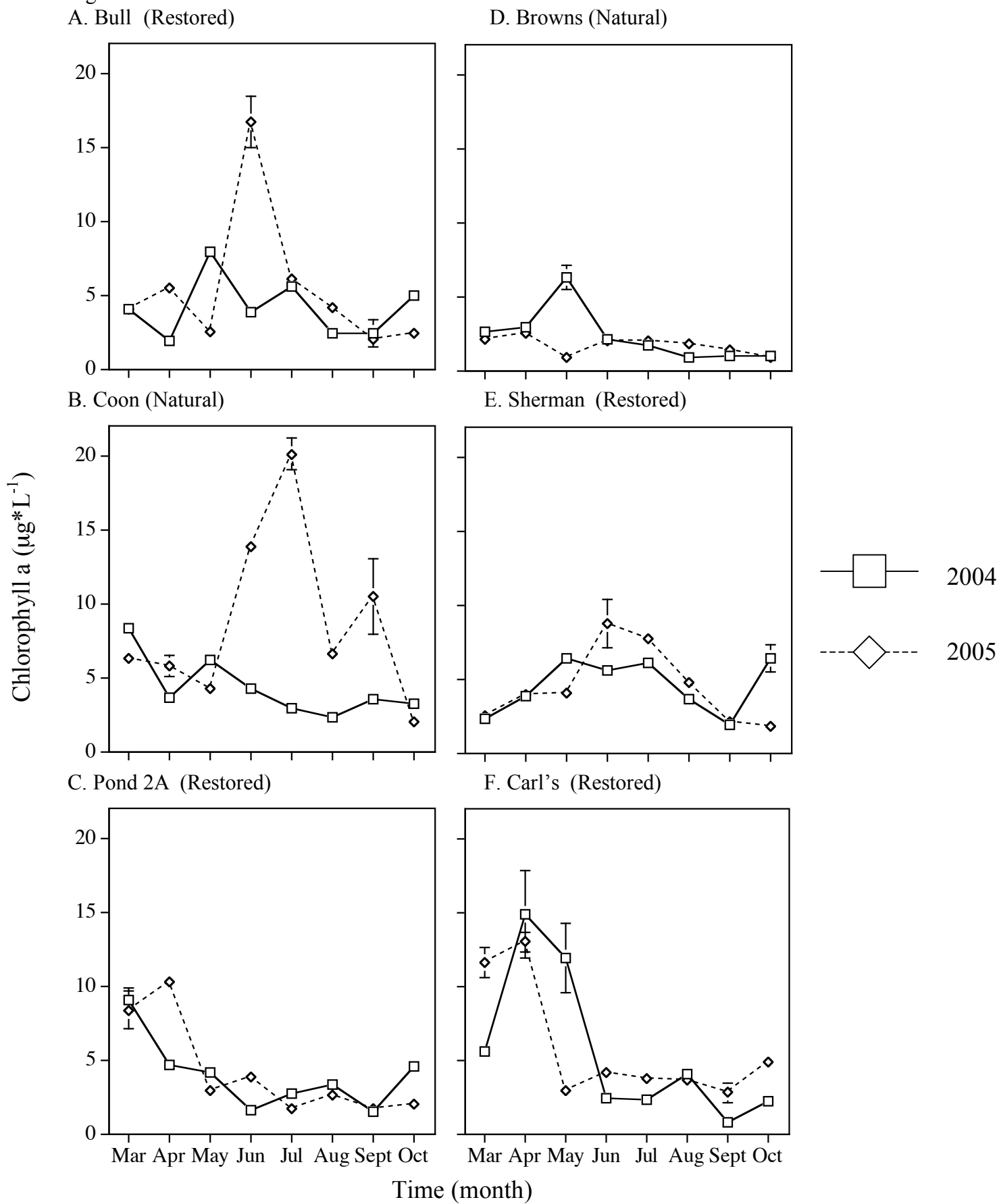


Fig 7.

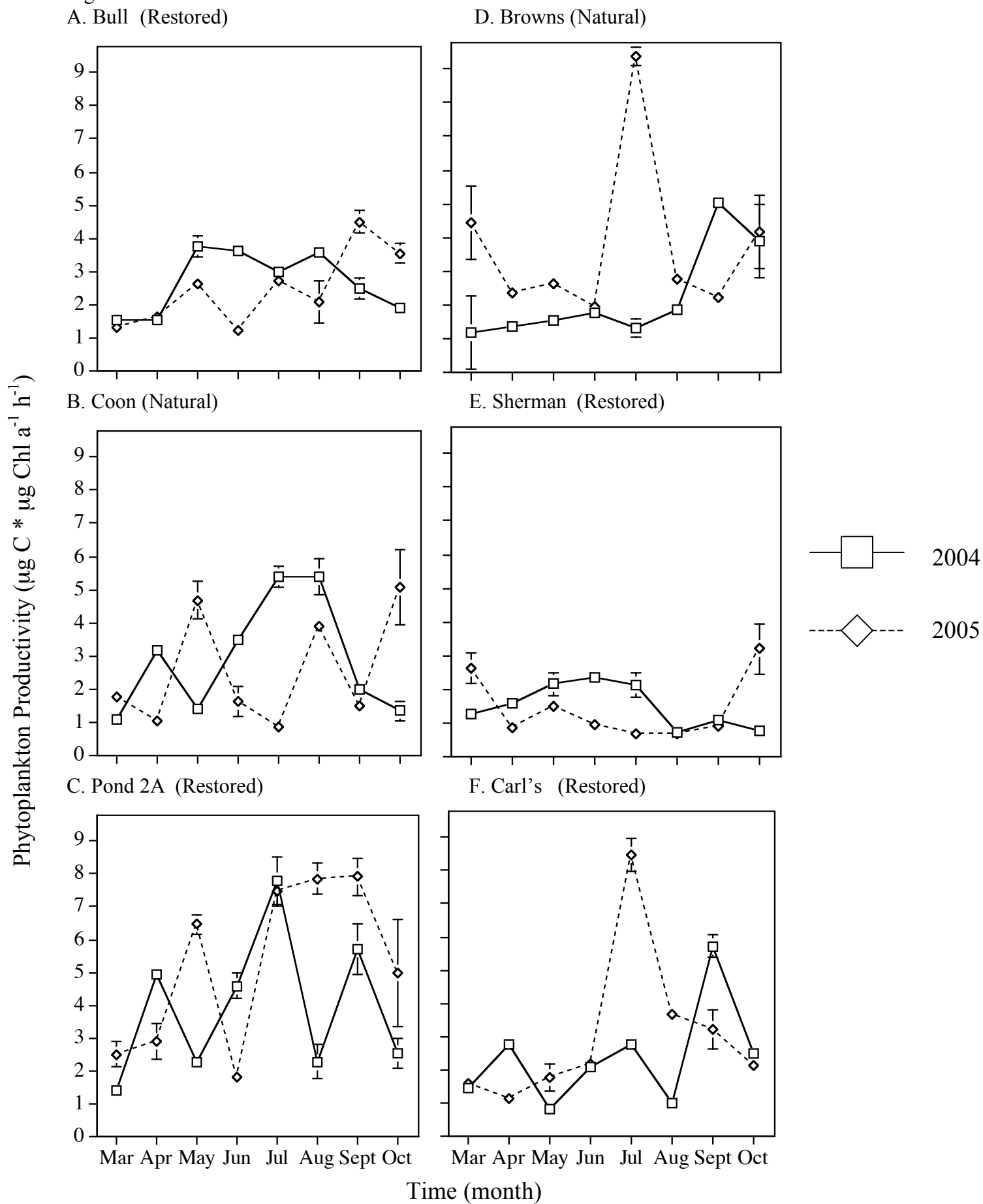
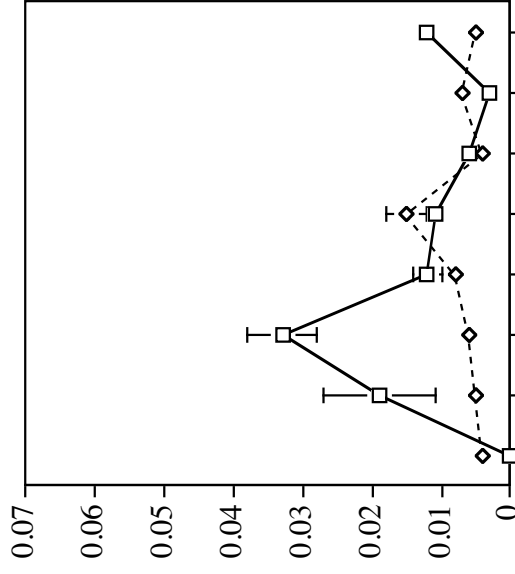


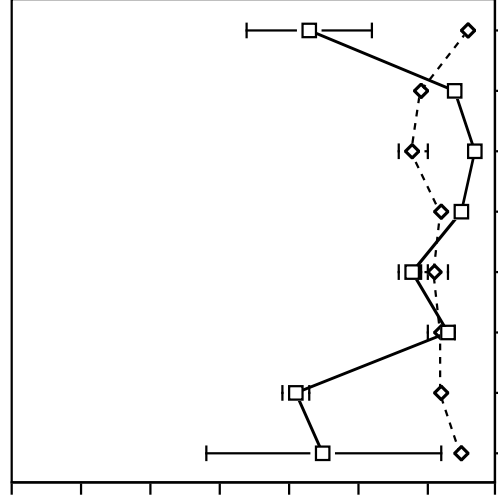


Fig 8.

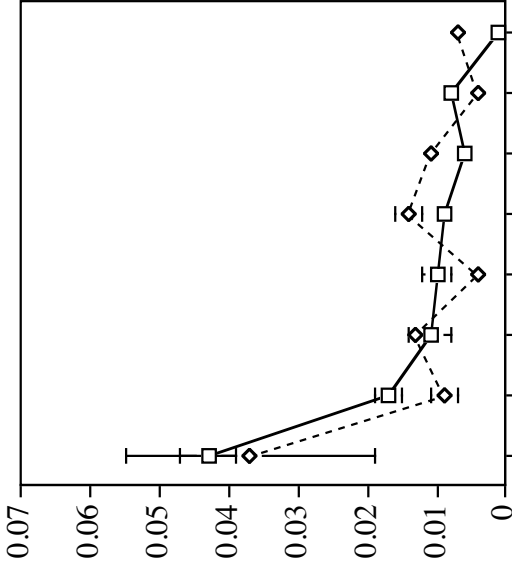
A. Bull (Restored)



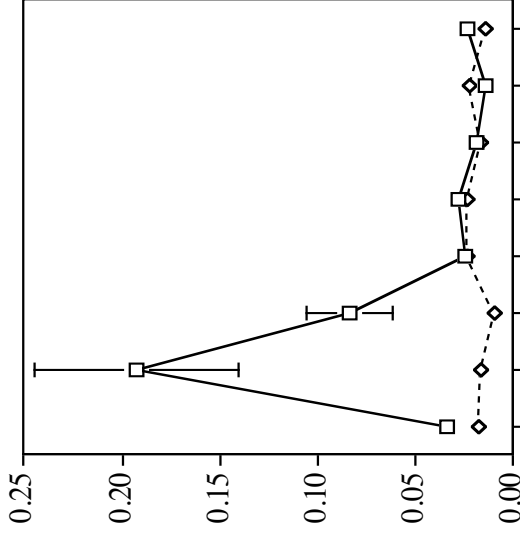
D. Browns (Natural)

Benthic Productivity ( $\text{mg C} * \text{mg Chl a}^{-1} \text{h}^{-1}$ )

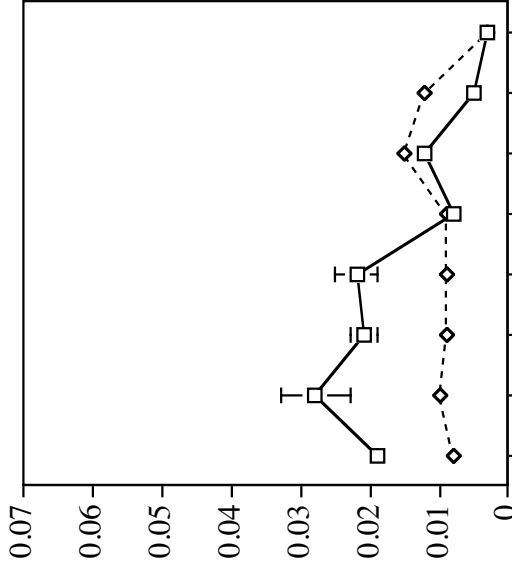
B. Coon (Natural)



E. Sherman (Restored)



C. Pond 2A (Restored)



F. Carl's (Restored)

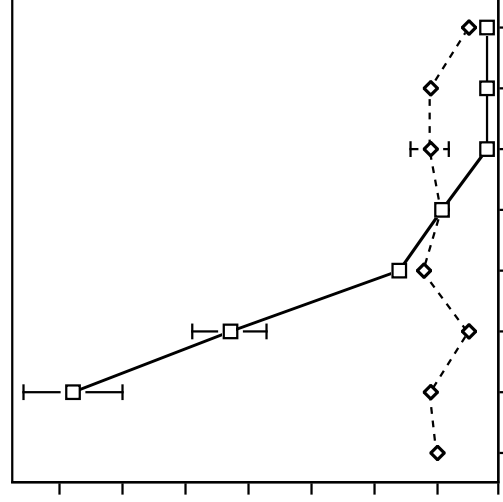
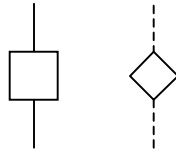
Time (month)  
Mar Apr May Jun Jul Aug Sept Oct

Fig 9.

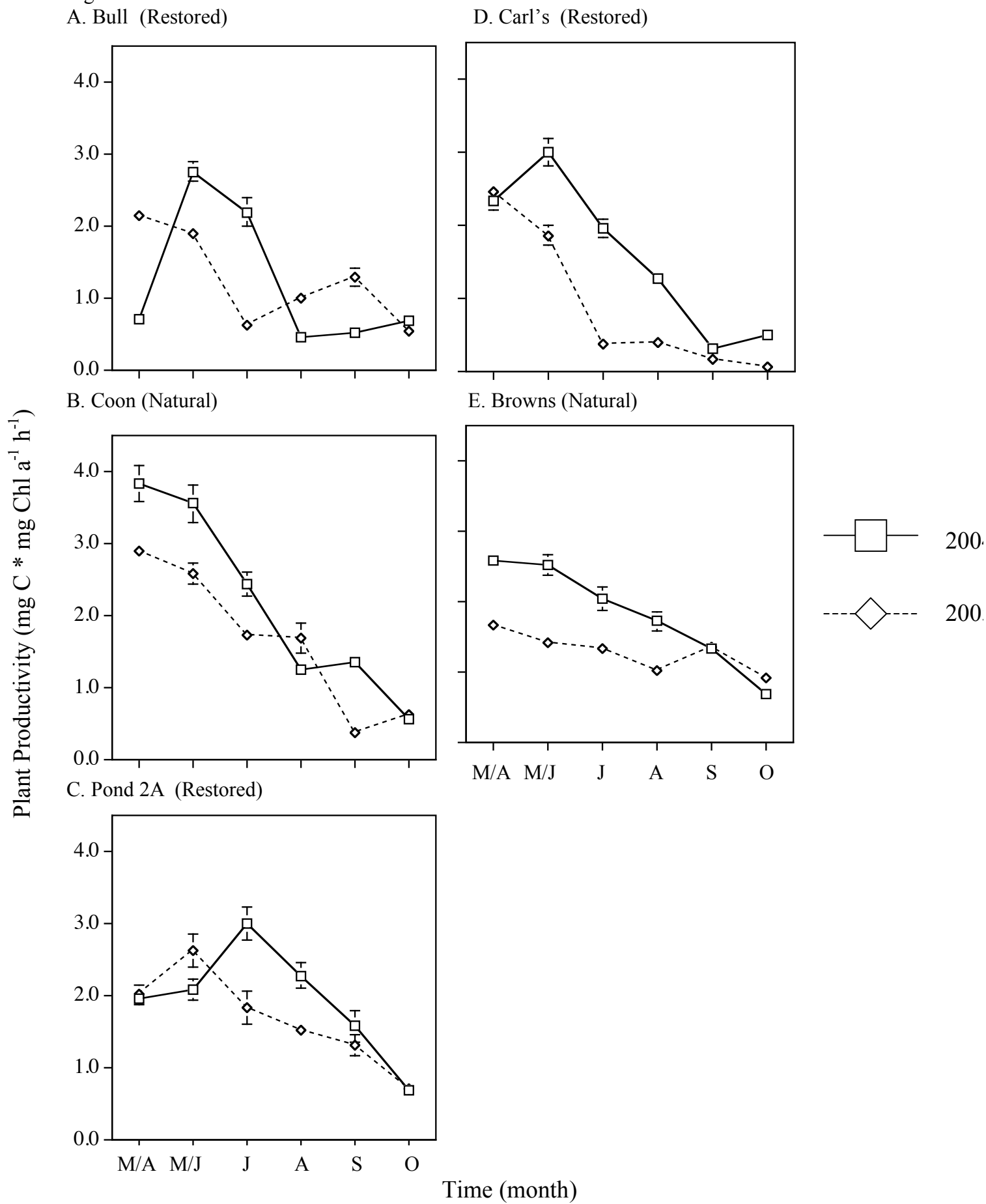


Fig 10.

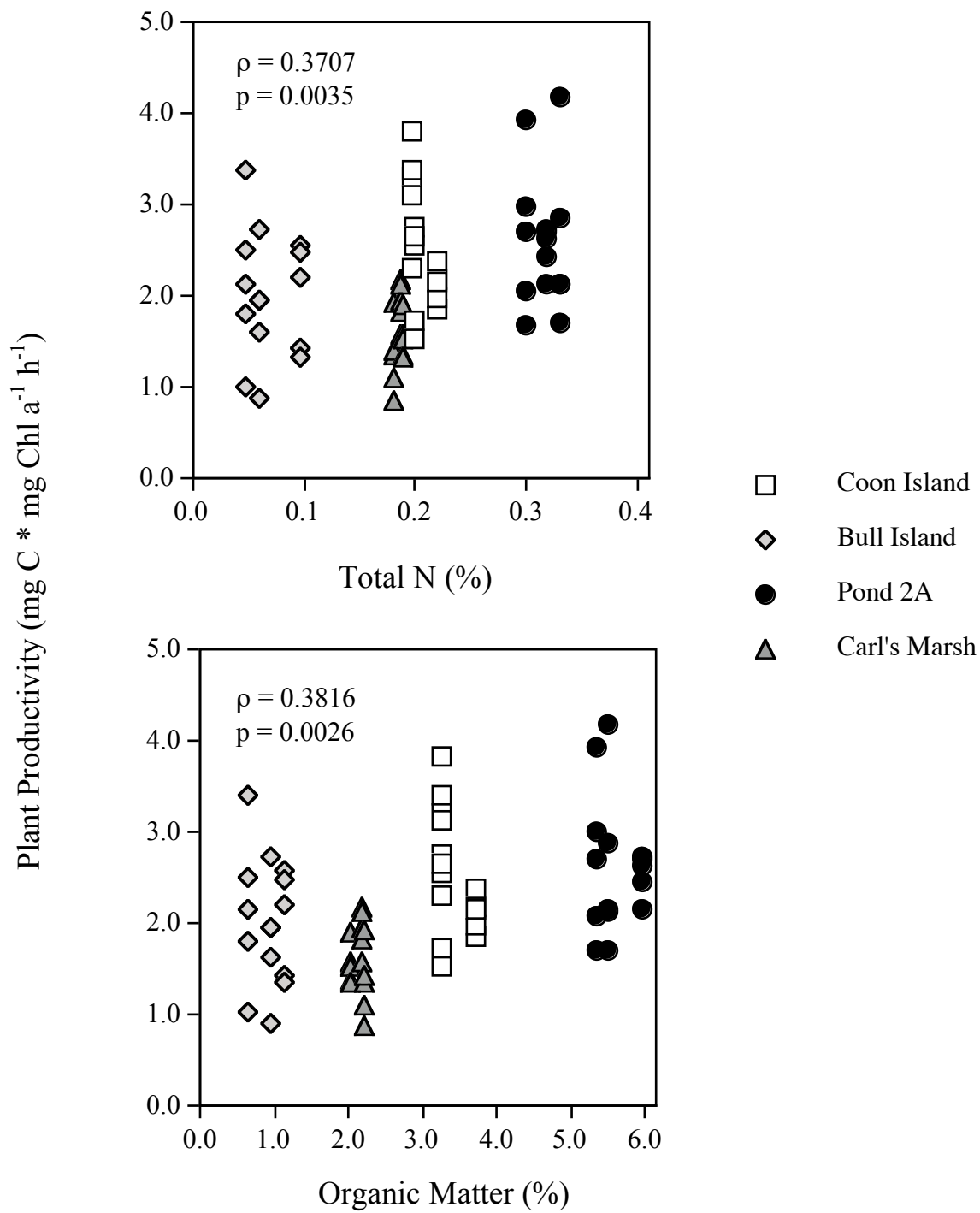


Fig 11.

