Catastrophic shifts in the aquatic primary production revealed by a small low-flow section of tropical downstream after dredging

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(With 5 Figures)

Abstract
Dredging is a catastrophic disturbance that directly affects key biological processes in aquatic ecosystems, especially in those small and shallow. In the tropics, metabolic responses could still be enhanced by the high temperatures and solar incidence. Here, we assessed changes in the aquatic primary production along a small section of low-flow tropical downstream (Imboassica Stream, Brazil) after dredging. Our results suggested that these ecosystems may show catastrophic shifts between net heterotrophy and autotrophy in waters based on three short-term stages following the dredging: (I) a strongly heterotrophic net primary production -NPP- coupled to an intense respiration -R- likely supported by high resuspended organic sediments and nutrients from the bottom; (II) a strongly autotrophic NPP coupled to an intense gross primary production -GPP- favored by the high nutrient levels and low solar light attenuation from suspended solids or aquatic macrophytes; and (III) a NPP near to the equilibrium coupled to low GPP and R rates following, respectively, the shading by aquatic macrophytes and high particulate sedimentation. In conclusion, changes in aquatic primary production could be an important threshold for controlling drastic shifts in the organic matter cycling and the subsequent silting up of small tropical streams after dredging events.

Keywords: primary production, catastrophic shifts, dredging, tropical streams.

Mudanças catastróficas na produção primária aquática revelada por uma pequena seção de baixa vazão a jusante de um riacho após dragagem

Resumo
Dragagem é um distúrbio catastrófico que afeta diretamente processos biológicos chave nos ecossistemas aquáticos, especialmente naqueles pequenos e rasos. Nos trópicos, as respostas metabólicas podem ser ainda mais intensificadas pelas altas temperaturas e incidência solar. No presente estudo, avaliamos mudanças na produção primária aquática ao longo de uma pequena seção de um riacho tropical após uma dragagem (riacho Imboassica, Brasil). Nossos resultados sugeriram que estes ecossistemas podem apresentar mudanças catastróficas desde heterotrofia à autotrofia líquida na água, baseadas em três etapas de curto prazo após a dragagem: (I) uma produção primária líquida -PPL- fortemente heterotrófica associada a uma intensa respiração -R-, provavelmente sustentada por sedimentos orgânicos e nutrientes advindos do fundo; (II) uma PPL fortemente autotrófica associada a uma intensa produção primária bruta -PPB-, favorecida pelos elevados níveis de nutrientes e baixa atenuação da luz solar pelos sólidos em suspensão ou macrofitas aquáticas; e (III) uma PPL próxima ao equilíbrio associada às reduzidas taxas de PPB e R seguindo os sombreamento pelas macrofitas aquáticas e elevada sedimentação de particulados. Como conclusão, mudanças na produção primária aquática poderiam ser um importante limiar para controlar drásticas alterações na ciclagem da matéria orgânica e no subsequente assoreamento de pequenos rios tropicais após eventos de dragagem.

Palavras-chave: produção primária, mudanças catastróficas, dragagem, rios tropicais.
1. Introduction

The overall imbalance between gross primary production (GPP) and respiration (R) is commonly reported in ecosystems around the world, resulting in severe implications for the global carbon (C) cycling (Chapin III et al., 2006). The sum between C fixation by GPP and organic degradation by R is named net primary production (NPP), which may be highly dynamic in natural waters following natural or anthropogenic processes. Fluctuations in ecological conditions, such as temperature (Wohlers et al., 2009) and salinity (Hartzell and Jordan, 2012), or resources, such as solar radiation (Williamson et al., 1999), organic substrates (Azam, 1998; Ram et al., 2003) and nutrients (Duarte and Agusti, 1998; Biddanda et al., 2001), determine substantial changes in pelagic metabolic rates over space and time. Previous studies at low latitudes have found out that both magnitude and variation of biological processes involved in the organic matter cycling in inland waters are potentially enhanced by higher temperatures (Marotta et al., 2009b, 2010b; Dillon et al., 2010).

Temporal changes in metabolic pathways may be intense, but are still poorly understood in aquatic environments due to constraints to assess them over short- (Staehr and Sand-Jensen, 2007) and long- (Engstrom et al., 2000) term periods. An alternative to reduce constraints for ecological studies throughout the time is by using the chronosequence scale in the space, which represents a series of sites varying in age since surface formation or catastrophic disturbance, but with all other extrinsic driving factors being relatively constant (Wardle et al., 2004). Although restricted to peculiar sites, ecologists have used chronosequences since pioneer papers (Cowles, 1899; Lowrie, 1948) and currently for terrestrial (Lichter, 1998; Wardle et al., 2004; Zona et al., 2010) and aquatic (Engstrom et al., 2000; Nislow and Lowe, 2006) environments.

In the watershed, the human land use has increased substantially nutrient inputs (Knoll et al., 2003; Schindler, 2006) and deforestation (Davidson et al., 2012), drivers positively related with sediment load to the aquatic ecosystems. The subsequent depth reduction followed by water quality and biodiversity loss has made shallow streams particularly sensitive to these anthropogenic disturbances (Casatti et al., 2006; Röig et al., 2007). Also, the silting up of shallow inland waters may be still intensified by the growth of aquatic primary producers (Moreira-Turcq et al., 2004), especially under eutrophic conditions (Marotta et al., 2009a). In this way, dredging is a common man-made intervention to mitigate silting up processes (Benvenuti et al., 2005; Jiang and Shen, 2006). This catastrophic disturbance causes intense metabolic changes following a drastic sediment removal and resuspension (Lohrer and Wetz, 2003). Here, we assessed changes in the pelagic NPP along a short chronosequence after dredging in a small section of low-flow tropical downstream.

2. Methods

2.1. Study area

The Imboassica Stream (22° 25’ S e 42° 55’ W) is a small fourth order tropical stream with low flow and about 14 km in length, the main tributary of the Imboassica Lagoon watershed (area = 55 km²; Marotta et al., 2009a) in the North of Rio de Janeiro state (Southeast of Brazil, Figure 1). The low flow of this stream reflects the low altitudinal gradient from the spring to the mouth, as 90% of the extension is between 0 and 40 m (maximum altitude 120 m). We studied the downstream section next to its mouth into the lagoon, a mesotrophic coastal ecosystem receiving anthropogenic nutrient inputs (Marotta et al., 2010a). The predominant land use in the whole Imboassica Lagoon watershed is abandoned pasture fields with fragments of native Atlantic Forest, although lowlands are dominated by the urban use. The mean temperature of this area ranges from 21 °C in July and 26 °C in February (INMET, 1992). Despite highly variable among years (Carnouze et al., 1991), the minimum and maximum monthly rainfall are typically observed in August (38 mm) and December (182 mm; INMET, 1992).

Before the dredging activities, the mouth of the Imboassica Stream into Imboassica Lagoon had showed an intermittent water column and dense colonization by the emergent aquatic macrophyte Typha domingensis Pers (Marotta et al., 2009a). From June to September 2002, a dredging removed the T. domingensis stand together with a large amount (4-5 m height and 8-10 m width) of peat sediments (Figure 2). This dredging resulted in a perennial water column, with a depth of 0.9 m and a very low flow not detected by the 2031H flowmeter (water flow < 0.1 m s⁻¹).

2.2. Study design and sampling stations

During 120 days before the sampling, the very low flow and turbulence coupled to the absence of rainfall and affluent inputs contributed to form a short-term aquatic chronosequence in the section of Imboassica Stream near to Imboassica Lagoon. Different conditions at this fluvial section (as nutrient and suspended solid in waters) were mainly a result of the progressive changes through time following the dredging. A strong rainfall homogenized all extension of the Imboassica downstream by increasing the fluvial flow, ending with the studied chronosequence, only ten days after our sampling.

The sampling stations were situated along a linear 1200-m extension of the Imboassica stream near to its mouth. The dredge withdrew sediments in a constant rate of 10 m d⁻¹ during 120 days. Six sampling stations were simultaneously collected: St 02, St 15, St 30, St 60, St 90 and St 120. These stations represented a short-term chronosequence with different distances from the dredge and subsequent days after dredging (Figure 2).

2.3. Analytical methods

We estimated pelagic GPP, R and NPP from changes in dissolved oxygen (DO) concentrations by the light-dark bottle method (Wetzel and Likens, 2000). Water samples
were taken at intermediate depth in each station and enclosed in four replicates for each bottle type (transparent or opaque) and placed in situ. NPP and R were estimated from changes in DO during 24 hours in transparent and opaque bottles respectively. GPP was calculated from the sum of NPP and R during the daytime. The sampling periods to integrate daily changes in O$_2$ were: 6-10h, 10-14h, 14-18h, and 18-6h day after. DO concentrations were quantified by Winkler’s titration (Wetzel and Likens, 2000) in the field.

Water samples were transported to the laboratory and frozen for total nutrient analysis, while dissolved nutrients were determined in waters previously filtered with 0.7 μm filters (Whatman GF/F) before freezing (APHA, 1992). Nitrogen concentrations were estimated by the sum between Kjeldahl N and NOx forms (Mackereth et al., 1978), and phosphorus concentrations by the blue molybdenum reaction (Golterman et al., 1978). Ammonium and NOx forms were quantified using a Flux Injector Analyzer ASIA/ISMATEC (APHA, 1992).

Total suspended solids (TSS) and chlorophyll-$a$ concentrations were determined in the filtered fraction > 0.7 μm (Whatman GF/F filters). Chlorophyll-$a$ was used as a proxy for phytoplankton biomass, measured by the extraction with ethanol in the dark for 24h before subsequent analyses using wavelengths of 433 nm for excitation and 673 nm for emission measurements in a spectrophotometer (Nusch and Palme, 1975). The biomass of aquatic macrophytes was determined by the harvest

Figure 1. Geographic location of the sampling site in the Imboassica lagoon watershed.

Figure 2. Sampling stations along the short-term chronosequence in the Imboassica Stream.
method (N = 4 quadrats of 1 m² in each sampling station) and drying at 60 °C in the laboratory until constant weight. The index of macrophyte cover on the water surface was estimated by longitudinal transects (N = 4) in each sampling station.

2.4. Statistical approach

Data were log-transformed to meet assumptions of parametric statistical tests (Zar, 1996), including significant normal distribution (Kolmogorov-Smirnov test, p<0.05) and non-significant differences for standard deviations among sampling matrices (Bartlett test, p<0.05). Statistical differences were assessed with one-way analysis of variance (ANOVA) followed by post-hoc Tukey-Kramer multiple comparisons (significant p<0.05; Zar, 1996), using the software STATISTICA 6.0.

3. Results

The sampling station located closer to the dredge (St 02) showed the highest TSS and nutrient concentrations in our study (Tukey-Kramer, p<0.05; Table 1 and Figure 3a). TSS in St 02 were around fourfold higher than in St 15, where these values were also significantly higher than St 30, St 60, St 90 and St 120 (Tukey-Kramer, p<0.05; Figure 3a). Phosphorus and nitrogen concentrations (both total and dissolved forms) were between 3.5 and 10 times higher in St 02 (Tukey-Kramer, p<0.05; Table 1). In contrast, chlorophyll-α concentrations (proxy for phytoplankton biomass) were at least twice higher in St 30 than any other station, reaching 10 µg L⁻¹ (Tukey-Kramer, p<0.05; Figure 3a). Lastly, floating aquatic macrophytes (Salvinia auriculata) colonized only St 60, St 90 and St 120, increasing from 6 g DW m⁻² in St 60 to about 300 g DW m⁻² in St 90 and St 120 (Tukey-Kramer, p<0.05; Figure 3b). Any other species of aquatic macrophytes was not observed during this study.

The sampling station with higher values of chlorophyll-α in waters (St 30) also showed significantly higher pelagic GPP (Tukey-Kramer, p<0.05; Figure 4), while R were significantly more intense in St 02 followed by a strong decline mainly in St 60, St 90 and St 120 (Tukey-Kramer, p<0.05; Figure 4). Consequently, the pelagic NPP showed net heterotrophy in St 02 and St 15, net autotrophy in St 30 and St 60, and values next to equilibrium in St 90 and St 120 (Tukey-Kramer, p<0.05; Figure 4).

4. Discussion

Dredging activities provided drastic short-term changes in waters of the Imboassica Stream during our study, as indicated by the substantially higher values of suspended solids and nutrients soon after (St 02), and further consistent temporal variation among all sampling stations. This confirms that dredging represents a catastrophic disturbance on the water quality (Lohrer and Wetz, 2003; Bemvenuti et al., 2005), altering well-known drivers on ecosystem functioning and the organic matter cycling in aquatic environments (Cole et al., 2000, 2007). Here, the recent removal of organic-enriched sediments (Petrucio et al., 1997) from the Imboassica Stream (St 02) was also related to more intense metabolic rates, including the most heterotrophic NPP and highest R among stations. On the other hand, this contrasted with the general positive relationship between higher nutrient

Figure 3. (a) total suspended solids (TSS; unbroken line, filled square) with chlorophyll-α (dashed line, filled triangle), and (b) biomass (black bars) with cover index (dash-dot line, crosses) of floating aquatic macrophytes in waters of the downstream of the Imboassica Stream. Values are the average ± standard error (SE). The same letters indicate non-significant differences for each variable among sampling stations (n=4; Tukey-Kramer, p>0.05), and the asterisks (*) those stations showing null values in all samples for both biomass and cover index.

Table 1. Nutrient concentrations in each sampling station. Values are in µmol L⁻¹.

<table>
<thead>
<tr>
<th>Sampling Stations</th>
<th>Ammonium</th>
<th>Nitrate</th>
<th>Dissolved Nitrogen</th>
<th>Total Nitrogen</th>
<th>Dissolved Phosphorus</th>
<th>Total Phosphorus</th>
</tr>
</thead>
<tbody>
<tr>
<td>St 02</td>
<td>43.3</td>
<td>3.3</td>
<td>54.2</td>
<td>170.6</td>
<td>6.6</td>
<td>6.6</td>
</tr>
<tr>
<td>St 15</td>
<td>1.3</td>
<td>2.3</td>
<td>13.3</td>
<td>15.1</td>
<td>0.6</td>
<td>0.6</td>
</tr>
<tr>
<td>St 30</td>
<td>3.1</td>
<td>0.8</td>
<td>20.4</td>
<td>50.2</td>
<td>0.8</td>
<td>1.1</td>
</tr>
<tr>
<td>St 60</td>
<td>1.3</td>
<td>0.3</td>
<td>15.6</td>
<td>16.5</td>
<td>0.3</td>
<td>0.6</td>
</tr>
<tr>
<td>St 90</td>
<td>4.2</td>
<td>1.4</td>
<td>17.2</td>
<td>22.1</td>
<td>1.2</td>
<td>1.3</td>
</tr>
<tr>
<td>St 120</td>
<td>0.9</td>
<td>0.4</td>
<td>8.0</td>
<td>13.8</td>
<td>0.2</td>
<td>0.2</td>
</tr>
</tbody>
</table>

The same letters indicate non-significant differences for each variable among sampling stations (n=4; Tukey-Kramer, p>0.05).
levels and the net aquatic autotrophy (Duarte and Agusti, 1998; Biddanda et al., 2001), but confirmed that highly eutrophic and organic-enriched conditions may result in the persistence or even intensification of the heterotrophic status in tropical inland waters (Marotta et al., 2010a, 2012). These results might be attributed to resuspended organic matter from the bottom blocking light radiation to aquatic autotrophs (Roland and Esteves, 1998; Williamson et al., 1999) and supporting pelagic respiration, an imbalance that could explain net heterotrophy in nutrient-enriched waters (Cole et al., 2000).

Also, over time, the pelagic biological activity removes nutrients (Saunders and Kalff, 2001), while physical sedimentation plays an important role to decrease both TSS and nutrients in low-turbulence waters (Biddanda and Cotner, 2002). Further, intermediate levels of nutrients under low light attenuation by TSS and macrophytes potentially supported higher phytoplankton biomass, pelagic GPP and the subsequent net autotrophy in waters of St 30 comparing with stations more recently dredged (St 02 and St 15).

In contrast to higher algae biomass and pelagic primary production in St 30, other conditions contributed to reduce them in sampling stations where dredge had been carried out previously (St 60, St 90 and St 120). Despite similar TSS and nutrients in waters, St 60 showed a substantially lower pelagic GPP and phytoplankton biomass than St 30. The nutrient availability by sewage discharges (Marotta et al., 2009a) and absence of shading by riparian vegetation (Wallace et al., 1997) could stimulate the floating aquatic vegetation (e.g. S. auriculata), conditions that were observed in the Imboassica Stream after dredging. Floating aquatic macrophytes covered 100% of water surface in St 90 and St 120, which can intensely reduce light penetration light into waters (Scheffer et al., 2003). Indeed, the presence of S. auriculata on waters was related to the lowest pelagic chlorophyll-α and primary production in our study. In addition, the lower pelagic R observed in St 90 and St 120 may be further attributed to our sampling after the high sedimentation expected in non-turbulent waters (Roland and Esteves, 1998; Biddanda and Cotner, 2002), and below the very thin surface depth where organic matter is retained in between floating roots of the aquatic macrophytes (Mann and Wetzel, 1996). Overall, this might have contribute to changes in NPP from a net autotrophy in St 30 and a net equilibrium with floating macrophytes gradually covering the water surface in St 60, St 90 and St 120.

These results confirmed that metabolic rates in low-flow aquatic ecosystems may be highly dynamic (Staehr and Sand-Jensen, 2007; Marotta et al., 2010a), showing catastrophic shifts (Scheffer et al., 2001) among different metabolic balances stimulated under warmer tropical conditions (Marotta et al., 2010b). Small tropical downstreams might show three rapid stages for the pelagic production following the catastrophic disturbance by dredging (Conceptual Model, Figure 5): (I) a strongly heterotrophic NPP coupled to an intense respiration, probably supported by the high resuspended organic sediments and nutrients from the bottom; (II) a strongly autotrophic NPP coupled to an intense high primary production favored by high nutrient levels and low solar light attenuation by suspended solids or aquatic macrophytes; and (III) a NPP next to the equilibrium coupled to low pelagic GPP and R rates due to, respectively, shading by aquatic macrophytes and high sedimentation of particulate matter.

Therefore, floating aquatic macrophytes dominated downstream here over very short-term after dredging, representing a significant source of organic matter that could be buried in the aquatic bottom sediment (Engle et al., 2008). Other human-induced conditions of the Imboassica downstream during the study (e.g. high
nutrients availability, low flow and no light shading to algae by the absence of riparian vegetation) might also have increased the magnitude of metabolic responses after catastrophic disturbances. Our results support that small streams might show catastrophic shifts between net autotrophy and heterotrophy after dredging, reflecting potentially important implications on organic matter cycling and settling up controls in extensive inland flooded areas at low latitudes.

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