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Do the effects of substrate complexity influence the emergence position of microalgae on streams?

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ABSTRACT

Do the effects of substrate complexity influence the emergence position of microalgae on streams?

The spatial distribution of stream algae on substrates may be molded by the spatial arrangement of surface features. The variation of surface complexity on stream bottom may represent the availability of suitable areas for algal growth. Here we showed that different levels of surface complexity, at the scale used, did not affect the abundance of microalgae, however, we did note that specific areas of substrates seem to be more appropriate for initial algal establishment. Our results indicate that scale is fundamental to assess the effects of substrate on spatial distribution of benthic lotic microalgae and this may help us better understand how the different types of structural changes created by human activities in streams can affect algal colonization.

Key words: stream substrate, surface complexity, habitat architecture, benthic microalgaea

RESUMO

Do the effects of substrate complexity influence the emergence position of microalgae on streams?

A distribuição espacial de algas de ribeiros em substratos pode ser moldada pelo arranjo espacial das características da superfície. A variação da complexidade da superfície no leito de ribeiros pode representar a disponibilidade de áreas adequadas para o crescimento de microalgas. Aqui mostramos que diferentes níveis de complexidade de superfície, na escala utilizada, não afetaram a abundância de microalgas, no entanto, observamos que áreas específicas dos substratos parecem ser mais apropriadas para o seu estabelecimento inicial. Nossos resultados indicam que a escala é fundamental para avaliar os efeitos do substrato na distribuição espacial das microalgas lóticas bentônicas e isso pode nos ajudar a compreender melhor como os diferentes tipos de alterações estruturais criadas pelas atividades humanas nos riachos podem afetar a colonização de algas.

Palavras chave: *substrato de riachos, complexidade superficial, arquitetura de habitat, microalgas bentônicas*

INTRODUCTION

One of the main challenges in ecology is understanding the inner mechanisms of organisms' distribution in their habitats. The mechanisms that shape their spatial occupation remains not totally clarified, especially for stream dwellers (DeNicola et al., 2021 and references cited). Lotic environments exhibit a great heterogeneity of habitats and are characterized by many specific environmental conditions. For instance, benthic algae from streams can be strongly influenced by: light, which is essential for their growth and development, as it is directly related to their photosynthetic performance (Tonetto et al., 2012b, Oliveira et al., 2013); nutrients such as phosphorus and nitrogen from the decomposition of leaves and animals and from eutrophication processes (Dodds et al., 2002; Ferragut & Bicudo, 2010; Geng et al. 2022; Salk et al., 2022); and water velocity that is crucial to the permanence of algae on the streams or rivers substrates (Tonetto et al., 2014a). More specifically, it seems that environmental characteristics, at micro-habitat scales, is a great factor that may lead to the rise of algae in specific areas (Branco et al., 2009, Tonetto et al., 2014a).

The substrate surface may represent one of the fundamental elements of the micro-habitat's complexity, providing the characteristics that may influence the development of algae in lotic environments. Several approaches regarding the effects of stream substrate have been studied. The surface texture, for instance, has been related to algal establishment (Branco et al., 2010, Scardino et al., 2006, Murdock & Dodds, 2007) and rougher surfaces can provide the accumulation of algae owing to sedimentation (Johnson, 1994), cellular adherence (Scardino et al., 2006) and protection against drag forces of water flow (Dudley & D'Antonio, 1991, Tonetto et al., 2014a, Tonetto et al., 2015, Schneck & Melo, 2012). Pits or crevices may function as shelters for small algae against herbivorous activities (Bergey & Weaver, 2004, Thomaz et al., 2008) and habitat structure (pits, cracks, and shelves, Downes et al., 1998) exhibits an influence on algal growth, but depends on assessed spatial scale (Downes et al., 1998).

An interesting aspect about the substrate surface is its level of complexity (Tokeshi & Arakaki, 2012, Dwyer et al., 2021). The concept of fractal geometry, for instance, has been used to measure the surface complexity (Taniguchi & Tokeshi 2004; Tonetto et al., 2014a, 2015). In general, more complex substrates tend to exhibit greater abundance of organisms (Kovalenko et al., 2012) and this has been reported for several stream organisms such as invertebrates (Taniguchi & Tokeshi, 2004) or algae (Tonetto et al., 2014a). One of the explanations for this kind of response is related to the accumulation of debris and the hydraulic conditions associated with the type of surface (Buffington & Montgomery, 1999, Taniguchi & Tokeshi, 2004). For example, the combination of water flow with different substrate morphologies can create small hydraulic conditions that are perceived by stream organisms (Brooks et al., 2005). Therefore, small geometric variations on a surface can lead the spatial distribution of benthic organisms like algae (Tonetto et al., 2014a).

Although there are several studies relating substrate variation and algal growth, the effects of complexity have been scarcely investigated so far, especially for freshwater ecosystems (considering the surface architecture, in millimeter to centimeter scales) (Tonetto et al., 2014a, 2014b, for stream macroalgae; Osório et al., 2019, for periphytic community). In this context, we aimed to assess the influence of different complexity levels of artificial substrates on the colonization of lotic microalgae. More specifically, we intended to check if the type of substrate affects precisely the initial growth of those organisms, and consequently how are the areas where they are more abundant. Lastly, it is expected that more complex substrates provide greater algal growth and that particular surface areas of these substrates exhibit better conditions for the establishment of microalgae, which would explain the typical mosaic spatial distribution of these organisms in streams.

METHODOLOGY

Study Area

The study was conducted at Guapeva Stream located in Jundiaí city, São Paulo State (23° 13' 00.8" S, 46° 52' 29.8" W). We selected this river

Figure 1. Illustration of the surfaces used in the experiment. Top and side view of the plates. The black spots illustrate the peaks and the white spots the valleys. The letter D indicates the fractal dimension of each surface. *Ilustração das superfícies utilizadas no experimento. Vista superior e lateral das placas. As manchas pretas ilustram os picos e as manchas brancas os vales. A letra D indica a dimensão fractal de cada superfície.*

for the experiment owing to specific characteristics: abundant presence of benthic algae (deep enough for the immersion of artificial substrates), predominance of pebbles and boulders at the river bottom and full exposition to sun light. These characteristics were previously analyzed to avoid unwanted influences on the experiment.

The region is located in the geomorphological Province of Atlantic Plateau (Saka, 2009). The relief has mountainous with average altitude approximately of 762 m but with higher peaks of up to 1200/1300 m. The predominant climate in the region is Cfa and Cfb (Köppen's international system), which means hot and humid climates, without a dry season, and rainfall above 30 mm in the driest periods (Cardoso-Leite et al., 2002).

Experimental design

We created different fractal surfaces for algal colonization (adapted from Taniguchi & Tokeshi, 2004, Tonetto et al., 2014a). All artificial substrates were made of glass fragments creating peaks and valleys arranged in a chequerboard pattern. All glass fragments (peaks) exhibited 3 mm of height and were placed on a glass base (76 x 26 x 3 mm) in order to create three complexity levels: C1 – plane surface, without peaks and valleys; C2 – surface with peaks and valleys with 38 x 13 mm each; and C3 – surface with peaks and valleys with 19 x 13 mm each (Fig. 1 and Fig. S1 (see Supplementary material, available at http://www.limnetica.net/en/limnetica)). We calculated the fractal dimension for all surfaces by using grid method (Williamson & Lawton, 1991, Tokeshi & Arakaki, 2012, software Fractalyse, version 2.4, Besançon, France). The fractal dimension varied from 1.258 to 1.402 (Fig. 1).

The study was carried out in a block design complete randomized (Sokal & Rohlf, 2000, Gotelli & Ellison, 2004). One set of the three complexity surfaces was installed in 7 riffles areas of the stream, 100 meters distant from each other (Schneck & Melo, 2012). The experiment was conducted during autumn-winter period, the most suitable for algal growth in streams owing to low precipitation indices (Branco et al. 2009, for subtropical regions). In order to avoid substrate loses we anchored the surfaces on a concrete plate (20 x 20 cm) and fastened all system to a near and heavy boulder.

The artificial substrates kept submerged for 21 days, enough for algal colonization in glass slides (Tonetto et al., 2012). We visited the samplers at three days in order to remove eventually leaves or small tree boughs attached to the concrete plates.

Sampling procedure

Some environmental characteristics of each stretch were measured before taking out the samples from the stream: water velocity obtained by floating object (time passage in 10 m); depth measured by regular ruler (at the area where samplers were installed); and a 500 mL sample of stream water was collected to obtain its physicochemical data. This sample was sent to the quality laboratory of Jundiaí Department of Water and Sewage. Table 1 lists the environmental variables measured in the studied river.

At laboratory, we immediately quantify the microalgae attached to artificial surfaces by using

Table 1. Environmental variables of the studied stream (Mean ± SD). *Variáveis ambientais do riacho estudado (Média ± DP).*

Guapeva River	
Turbidity (µT)	15±1.2
Color (µH)	72±4
pH	7.1±0.4
Condutivity (µS)	210±12
Total Nitrogen (mg/L)	3.4±0.8
Total Phosphorus (mg/L)	0.36±0.05
Phosphate (mg/L PO4-)	0.33±0.1
Deep (m)	0.19±0.09
Velocity (m/s)	0.8±0.3
Illumination	Sunny

an optic microscopy (Olympus CX31). In each surface we used a gridded film, with squares of 2 x 2 mm, for counting the amount of algal individuals and its total density. More specifically, all individuals were counted independently of taxonomic group and the density was obtained dividing the number of individuals counted by the area assessed (number of squares counted). A total of 10 thousand squares were counted during quantification. Finally, we counted individuals from peaks and valleys separately on the C2 and C3 surfaces. In each of them, for instance, the individuals present in each peak and valley were counted to compose density values for these particular regions. In addition, the occupation position where microalgae were growing on each surface was also recorded. For this purpose, we used a paper with a checkered illustration of each surface (a representation of the surfaces in the microscopy). Thus, when microalgal individuals appeared, during counting procedure, we wrote down the exactly position where they were observed painting the squares in the illustration. In this way, it was possible to map the spatial distribution of algae on artificial substrates.

Statistical analyses

A randomized block ANOVA was used with each stretch of the stream representing blocks (Tonetto et al., 2012, 2014a, Schneck & Melo, 2012). This type of analysis has been widely used in other experiments involving heterogeneous environments, as its adjusts for differences in treatments under comparison (Gotelli & Ellison, 2004). All analyzes were performed using Bioestat 5.0.

RESULTS

We found mostly representants of diatoms (different species of Gomphonema, Eunotia, Navicula and Fragilaria) and few green algae (mainly species of Closterium and Cosmarium) colonizing the artificial substrates (Table S1, see Supplementary material, available at http://www.limnetica.net/en/limnetica). In general, we found no differences on microalgal densities among complexity levels.

Regarding total density of C1, C2 and C3 surfaces, ANOVA registered no difference among them ($F = 0.10$, $p = 0.89$, Fig. 2A). When densities of Peaks and Valleys were compared separately no differences between these regions were observed either. More specifically, the densities of C1 x Peaks C2 x Peaks C3 ($F = 0.45$, $p = 0.43$, Fig. 2B), C1 x Valleys C2 x Valleys C3 ($F = 0.49$, $p = 0.41$, Fig. 2C) and Peaks C3 x Valleys C3 ($F = 0.29$, $p = 0.58$, Fig. 2D). Only one exception was observed, the Valleys of C2 surface registered densities values significantly higher than Peaks ($F = 9.45$, $p = 0.0059$, Fig. 2E).

Although there were no great differences among complexity levels, the mapping of microalgal spatial position revealed two main trends: i – in general, on peaks, algae accumulated on the initial portion of this area (against water flow) and, ii - on valleys, groups of diatoms were frequently present on periphery of these surface areas (Fig. 3). These trends were observed independently of surface complexity.

DISCUSSION

The results showed that the variation in surface complexity did not significantly influence the microalgae abundance. Thus, we rejected our initial hypothesis, but the way in which microalgae grow on the substrate may explain this result (Tonetto et al., 2014a, Schneck & Melo, 2012). In general, due to their smaller size, microscopic algae are

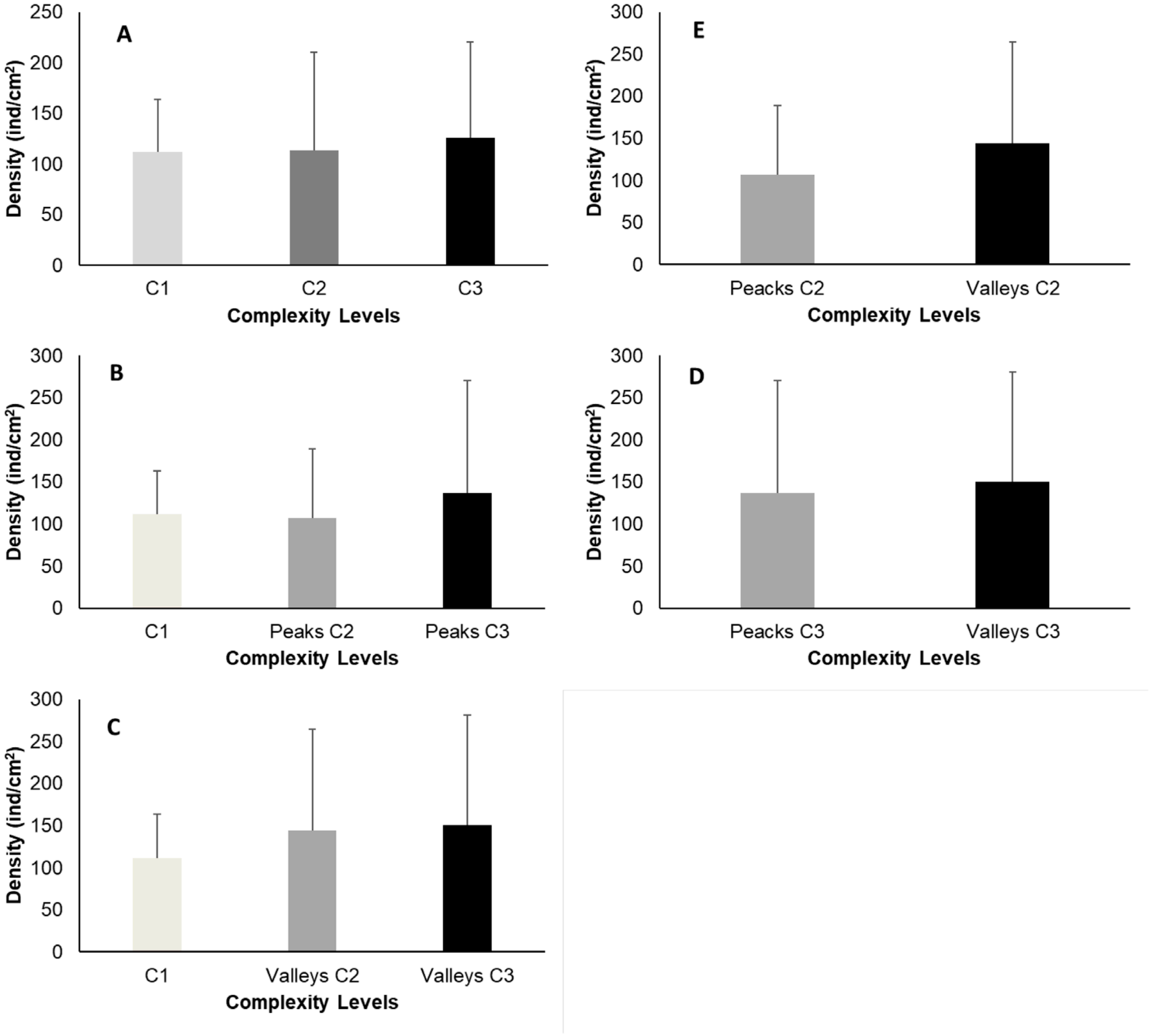

Figure 2. Graphics illustrating the density of algae in each treatment. *Ilustração gráfica da densidade de algas em cada tratamento.*

typically inserted in the boundary layer of the water column. The boundary layer refers to a space of lesser water turbulence between the substrate and the natural flow of stream current (Tonetto et al., 2015). Therefore, this microenvironment may be little influenced by changes caused by the substrate's architecture, so the conditions for microalgal growth did not change enough to exhibit significant differences in the colonization of these substrates (regardless of the level of complexity created in the study).

Furthermore, the scale used in the present study may have been too large to exert a significant influence on the establishment of microalgae in the substrates. For instance, despite the different architectures, all surfaces in the study were smooth, at micrometric scale. According to Murdock & Dodds (2007), the topography of the substrate influences the growth of microalgae up to a peak of only 17 µm, and they suggested that the roughness-stimulating effect diminishes after a certain point. In our study, the created valleys were 300 µm deep in addition to the surfaces being smooth. Thus, the lack of significant differences between complexity levels may be associated with a greater effect of the micrometric scale

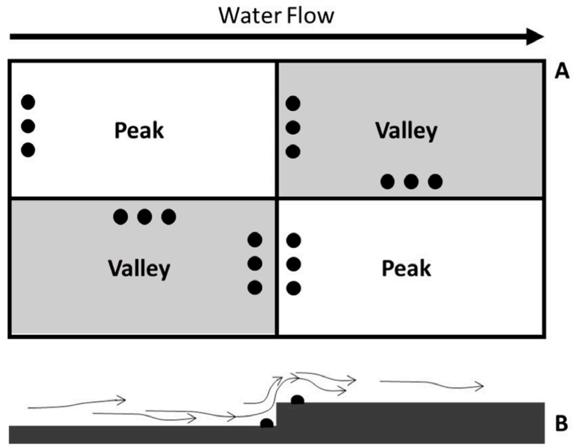

Figure 3. Illustration of artificial surface C2 as an example of surface with peaks and valleys. Black circles represent the most common position of algal colonization. Curved gray arrows indicate water flow. A represents the top view and B represents the lateral view of the surface. *Ilustração da superfície artificial C2 como exemplo de superfície com picos e vales. Os círculos pretos representam a posição mais comum de colonização de algas. As setas cinzentas curvas indicam o fluxo de água. A representa a vista superior e B representa a vista lateral da superfície.*

on algal growth than the millimeter/centimeter scale created in this study (Tonetto et al., 2012).

However, an exception was observed, the algae density was higher in the valleys of the C2 surface when compared to the peaks of the same treatment. A plausible explanation for this response may be related to a probable action of scraping herbivores (Dudley & D'Antonio, 1991). In C2 surface, the size (in area) of the valleys may be too large to function as a refuge for insect larvae (Brooks, 2005, Bergey, 2005). Therefore, perhaps the algae could grow better without the action of herbivores. On the other hand, in C3 surface (where the valleys were smaller) herbivorous insects may have found a more suitable shelter condition and thus decreased algae density in these regions, possibly masking the effect of substrate complexity. In general, taking into account the possible action of herbivores, this response may represent one of the influences of surface complexity, on the scale used in this study.

An interesting result observed in the experiment was the spatial position of microalgae on the surfaces, regardless the complexity levels. Most individuals tended to settle in the regions directly against the current flow. There, the water flow may touch the lateral surface of the peak and can swerve its direction creating a reduced flow condition at this peak's edge (Fig. 3, Tonetto et al., 2014a). Therefore, these regions create a micro hydraulic niche that can increase the accumulation of algal propagules that passively arrive from upstream and, they can serve as an initial area for the emergence of a population or community of microalgae in the substrate. In addition, some clusters of diatoms were observed in the periphery of valleys, also regardless of their complexity level. These areas may also have a more favorable hydraulic condition, as well as possibly avoiding herbivory. For instance, diatoms exhibit spatial mobility and can, actively colonize places that are more suitable for their development (Hoagland et al., 1982, Bondoc-Naumovitz & Cohn, 2021.

CONCLUSIONS

In general, the present study found that the substrate complexity, at the investigated scale, did not exert a great influence on the abundance of microalgae on the studied artificial substrates. However, it was possible to observe a possible spatial preference in their initial colonization. Thus, the surface complexity demonstrates that it can influence the establishment and development of algae in the substrates of rivers and streams. However, more studies are needed to enhance our understanding about initial settlement of algae in stream substrates. Experiments with combined factors (surface texture, complexity and herbivorous) may clarify the complex interaction between spatial distribution of algae and associated variables to surface features. Finally, knowing that surface scale may influence the algal colonization, the intensity of physical changes in the stream bottom caused by human's activities may help us better understand how algal communities could respond to habitat degradation in urban regions.

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