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NATUREZA

Layla Mayer Fonseca

**Ecological stoichiometry in planktonic communities of inland waters: anthropic
influences and spatial gradients**

Juiz de Fora

2022

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Dissertação apresentada ao Programa de Pós-graduação em Biodiversidade e Conservação da Natureza, da Universidade Federal de Juiz de Fora, como requisito parcial à obtenção do título de Mestre em Biodiversidade e Conservação da Natureza. Área de concentração: Processos ecológicos e Conservação da Natureza.

Orientador: Prof. Dr. André Megali Amado

Coorientador: Prof. Dr. Ng Haig They

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Dedico este trabalho para meus pais, José e Edméa.

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“Educar-se é impregnar de sentido cada momento
da vida, cada ato cotidiano.” (PAULO FREIRE)

ABSTRACT

Ecological stoichiometry is the field of study that relates the chemical composition of organisms to the availability of elements in the environment. Most studies in this field deal with Carbon, Nitrogen and Phosphorus due to their great importance in the composition of organisms, metabolic functions and for their important biogeochemical role. Alfred Redfield, in 1930, associated the chemical composition of marine plankton with the availability of nutrients in the ocean, establishing the Redfield constant of 106 C: 16 N: 1 P. Ecological Stoichiometry is an important approach for the understanding of microbial metabolism, as well as functioning of ecosystems, since bacteria are the basis of trophic relationships and are also connected to the availability of organic matter in the environment, as well as to nutrient cycling. The nutritional composition of bacteria is strongly influenced by the growth rate of these organisms, and therefore, phenomena capable of regulating bacterial metabolism are central to the functioning of aquatic ecosystems. Luminosity, temperature and precipitation are environmental factors capable of affecting the metabolism of organisms that present wide variation with latitude (e.g. increase in average temperature with decreasing latitude). Hence, differences in microbial stoichiometry can be expected at different latitudes in response to these environmental variables gradient. This work aims first to address how Ecological Stoichiometry can explain the functioning of natural aquatic ecosystems, focusing on bacterial communities and seston and also how this science can be used to understand the ecological functioning of ecosystems facing anthropic impacts, such as climate change and excessive nutrient input. Then, we investigated how the latitude in which ecosystems are located and their trophic status can influence the chemical composition of seston and bacteria and how each compartment behaves in different environmental situations established by latitude, such as luminosity and temperature and the availability of nutrients such as N and P, which determine the trophic status of the system. For this, the amounts of nutrients (C, N and P) present in the seston and in the bacterial fractions of 55 lakes along the Americas were determined. The seston C: N, C: P and N: P ratio decreased at higher latitudes, which was not observed for bacteria. When analyzed separately by trophic status, the bacterial and seston C: N decreased with the latitude in eutrophic environments, but not in oligotrophic environments. The C:P ratio of both seston and bacteria did not vary with both latitude and trophic status. The seston N: P ratio in oligotrophic environments decreased with latitude, and the opposite occurs in eutrophic environments. This study highlights the interplay between latitude and trophic state in regulating seston and bacterial stoichiometry.

Keywords: Ecological Stoichiometry. Bacterioplankton. Latitude. Trophic Status. Seston.

RESUMO

Estequiometria Ecológica é o campo de estudo que relaciona a composição química de organismos com a disponibilidade dos elementos no ambiente. A maioria dos estudos neste campo versam sobre Carbono, Nitrogênio e Fósforo devido a sua grande importância na composição dos organismos para funções metabólicas e por seu importante papel biogeoquímico. Alfred Redfield, em 1930, associou a composição química do plancton marinho à disponibilidade de nutrientes no meio. Estabeleceu-se assim a constante de Redfield 106 C: 16 N: 1 P esta proporção entre a composição química dos microrganismos e seu meio foi utilizada durante muito tempo nos estudos de Estequiometria Ecológica, sobretudo no meio aquático, mas com o avanço das pesquisas percebeu-se que a constante não era válida para todos os tipos de ecossistemas aquáticos, principalmente os dulcícolas devido a várias características físicas e químicas que os diferem dos oceanos. Em estudos microbianos, a Estequiometria Ecológica é uma importante ferramenta no entendimento do metabolismo desses organismos, assim como na compreensão do funcionamento dos ecossistemas, pois bactérias são a base das relações tróficas e estão conectadas também com a disponibilização de matéria orgânica para o meio, assim como na ciclagem de nutrientes. A composição nutricional das bactérias é fortemente influenciada pela taxa de crescimento desses organismos. Por isso, fenômenos capazes de regular o metabolismo bacteriano são centrais para o funcionamento dos ecossistemas aquáticos. A luminosidade, temperatura e precipitação são fatores ambientais capazes de afetar o metabolismo dos organismos e apresentam ampla variação com a latitude (e.g. aumento da temperatura média com a diminuição da latitude). Portanto, comunidades microbianas em diferentes latitudes devem apresentar diferentes composições químicas. Este trabalho visa, primeiramente, abordar como a Estequiometria Ecológica pode explicar o funcionamento dos ecossistemas aquáticos naturais, com foco nas comunidades bacterianas e no séston e também como esta ciência pode ser utilizada na compreensão do funcionamento ecológico dos ecossistemas frente a impactos antrópicos, como as mudanças climáticas e descarga excessiva de nutrientes. Depois, investigamos como a latitude em que os ecossistemas se encontram e seu estado trófico podem influenciar na composição química de séston e bactérias e como cada compartimento desse se comporta em diferentes situações ambientais estabelecidas pela latitude, como luminosidade e temperatura e a disponibilidade de nutrientes como N e P, que determinam o estado trófico do sistema. Para isso, as quantidades de nutrientes (C, N e P) presentes no séston e nas bactérias foram determinadas em todas as frações filtradas por meio de análise no TOC-V (Shimadzu + SSM) e por espectrofotometria. Espera-se

encontrar maiores razões C: nutrientes em ambientes de baixas latitudes, devido às condições associadas (maior luminosidade e temperatura), em comparação com ambientes de alta latitude.

Palavras-chave: Estequiometria Ecológica. Bacterioplancton. Latitude. Estado trófico. Seston.

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1. GENERAL INTRODUCTION

In aquatic environments, environmental characteristics that vary with latitude, such as temperature, solar radiation, and nutrient availability, affect communities at the base of the food web, such as phytoplankton (one of the main components of seston) and bacterioplankton (ANESIO et al., 2005; APPLE; DEL GIORGIO, 2006; EDWARDS et al., 2016). One response of these communities to those factors is the variation in the elemental composition of their biomass, especially carbon (C), nitrogen (N) and phosphorus (P). In oceanic environments, for example, the seston carbon C: P ratio increases with latitude, as a function of global variations in temperature, nutrients, and biological diversity (MARTINY et al., 2013).

The stoichiometric ratios C:N:P have been widely studied since the 1930s, when Alfred Redfield demonstrated in the oceans a constant ratio of 106:16:1, which he attributed to a conditioning of the chemistry of the water by plankton organisms promoted by the long residence time of the oceans (REDFIELD, 1934; 1958). In inland waters, however, classic Redfield proportions are rarely achieved due to a number of fundamental differences: i) water residence time; ii) differences in the quantity and quality of autochthonous and allochthonous organic matter; iii) taxonomic differences; iv) intrinsic differences in metabolism, such as growth rates (COTNER et al., 2010; THEY et al., 2017).

Compared to the oceans, inland waters have a greater contribution of allochthonous organic matter (GROEGER; KIMMEL, 1984). In addition, Stets e Cotner (2008) demonstrated that the greater availability of C increases the capacity of P uptake by bacteria in these ecosystems. Bacteria that grow in P-limited environments may have high C: P ratios in their biomass (GODWIN, COTNER, 2015), or have high respiration rates in order to balance the amount of organic C through the release of CO₂, thus maintaining P at adequate concentrations (CIMBLERIS; KALF, 1998; THEY et al., 2017).

The trophic state is a factor that also exerts great influence on the stoichiometry of microorganisms. Bacteria that thrive in P-rich environments have high growth rates and a low C: P ratio in their biomass (COTNER et al., 2010). High growth rates, determined by both higher concentrations of nutrients and higher temperatures, are related to a large allocation of P to the cellular machinery in the production of ribosomal RNA for protein synthesis, as stated by the Growth Rate Hypothesis (GRH) (ELSER et al., 1996).

Factors that can determine differences in stoichiometry between marine and continental environments and that also vary with latitude, can determine changes in the stoichiometry of

aquatic microorganisms. Water temperature, sunlight, availability of nutrients such as N and P, composition of organic matter and predation by other microorganisms are the most commonly reported regulatory factors of bacterial activity (COTNER; BIDDANDA, 2002; HALL; COTNER, 2007; BERGGREN et al., 2010). For example, the higher the temperature and the availability of nutrients, the higher the metabolic rates of bacterioplankton, i.e., bacterial growth and respiration rates (e.g. BERGGREN et al., 2010).

In addition to the factors that influence the stoichiometry of seston and bacteria mentioned above, we also need to talk about human pressures on aquatic ecosystems, which end up impacting chemistry and ecosystem functioning. Anthropogenic activities have accelerated biogeochemical cycles and increased aquatic pollution worldwide (QUADRA et al., 2019). Pollution can be understood as a manifestation of a stoichiometric imbalance. For instance, the nutrient concentrations and ratios of N: P, C: N, and C: P have been changing due to eutrophication, driven primarily by agriculture, untreated sewage, and human population growth, with important implications for aquatic metabolism and biological interactions (DODDS & COLE 2007; WELTI et al., 2017).

In this work, we first review how the most diverse human activities can change the chemistry of aquatic environments, and consequently the stoichiometry of bacteria and seston. Then, we aim at investigating the stoichiometric composition of seston and bacterioplankton in inland waters from the Americas along a latitudinal gradient. Our hypotheses are that: (1) seston will have higher C:P ratios in low latitude environments compared to high latitude environments, and (2) bacterioplankton will also have higher C:N:P ratios in low latitude environments due to the stoichiometry of features seston, a fraction bacteria depend on.

2. CHAPTER 1: AQUATIC ECOSYSTEMS FROM THE LENS OF ECOLOGICAL STOICHIOMETRY: FROM THEIR NATURAL FUNCTIONING TO ANTHROPIC IMPACTS

2.1. INTRODUCTION

2.1.1. Ecological Stoichiometry and aquatic ecosystem functioning

Ecological stoichiometry (ES) is a body of theory that focuses on ecosystem functioning targeting nutrients ratios and how they mediate the relationships between consumers (biological requirements) and resources (availability) (STERNER; ELSER, 2002). Alfred Redfield was one of the first researchers to make the connection between organisms, the quality and ratios of resources and the ecosystems functioning by establishing the classic and conservative “Redfield ratio”, which is the relative abundance of carbon (C) to nitrogen (N) and to phosphorus (P); i.e. C: N: P of 106:16:1 in planktonic organisms of the ocean (REDFIELD, 1934; 1958). One of the most important key points from Redfield's work was that it made it clear that planktonic organisms are essentially able to manipulate the marine environment to reflect their biomass composition. The relative uniformity of biomass composition, that Redfield highlighted, and the long residence times of water in the oceans leads to a feedback mechanism whereby the carbon and nutrient pools reflect the elemental composition of the plankton.

However, these feedbacks work much less efficiently in freshwater systems that can have residence times on the order of weeks to decades rather than hundreds of years to millenia in the oceans (THEY et al., 2017). Consequently, there can be greater stoichiometric imbalances in these systems especially when these short residence times are coupled with ecological stressors (WELTI et al., 2017). Imbalances in C: P and N: P ratios can occur among different trophic levels or among organisms and the environment (STERNER et al., 1998; STERNER; ELSER, 2002), which has important ecological consequences for population dynamics, nutrient cycling and, finally, for ecosystem metabolism (ELSER; URABE, 1999; STERNER; ELSER, 2002).

The first axiom in ES examines relationships between organismal chemical composition and their resource chemical composition (STERNER; ELSER, 2002). For instance, homeostatic organisms have the ability to keep their chemical composition relatively uniform, despite changes in the environment or resource, while non-homeostatic organismal composition varies with the composition of their resources (KOOILMAN, 1995). In the real world, it is also

common to observe different degrees of homeostasis among different organisms (GODWIN; COTNER, 2015).

Most ecological stoichiometry studies are currently related to C, N, and P, yet living organisms typically require more than 20 elements and much less is known about some of these other chemical elements such as Zn, Fe and Cu (JEYASINGH et al., 2017). Very similar to N and P, when they are low in terms of their relative abundance, they can exert control on ecosystem function. A good example of this is the Southern Ocean where N and P are found in excess in relation to the needs of plankton but Fe limits primary production (BEHRENFELD; KOLBER, 1999). But unlike N and P and due to the fact that trace elements are much less prevalent in biomass, when the concentrations of these elements are in excess, it can be toxic to many organisms. For instance, several marine cyanobacteria species had reduced reproduction due to high copper (Cu) and Cadmium (Cd) concentrations (BRAND et al., 1986; and for more recent review see SUNDA, 2012).

It is important to keep in mind that toxicity of these elements reflects a stoichiometric imbalance. Whereas aquatic ecosystems with an excess of N and P typically respond with excess growth, due to the central role of these elements in growth, excesses of trace elements typically result in toxicity. Lately, anthropogenic activities have been increasing the concentration of several of trace elements in surface waters, bringing up consequences for ecosystem services (KAYAMURA; ESPOSITO, 2010; RAI; SINGH, 2020; COTNER, 2019).

2.2. Aquatic ecosystems under anthropic pressures and Ecological Stoichiometry

Anthropogenic activities have accelerated biogeochemical cycles and increased aquatic pollution worldwide (QUADRA et al., 2019). In fact, one could think of the word 'pollution' as a manifestation of a stoichiometric imbalance. For instance, the pollution of the world's waterways with N and P is problematic because the imbalance of these nutrients contributes to increased abundance of harmful algal blooms (HABs). The nutrient concentrations and ratios of N: P, C: N and C: P have been changing due to eutrophication, driven primarily by agriculture, untreated sewage and human population growth, with important implications for aquatic metabolism and biological interactions (DODDS, COLE, 2007; WELTI et al., 2017). When N and P occur in high concentrations in aquatic ecosystems and out of stoichiometric balance with other nutrients, they can favor the rapid proliferation of fast-growing microorganisms. In fact, the Growth Rate Hypothesis (GRH) is the stoichiometric theory which

connects the nutritional needs of organisms to these elements which are disproportionately represented in nucleic acids which are a central feature of organismal growth (ELSER et al., 2000). Fast-growing organisms require large amounts of N and especially P because nucleic acids are required and this results in low N: P, C: N and C: P ratios, that supports the high rates of protein synthesis necessary for rapid growth rates (ELSER et al., 1996; 2000; STERNER; ELSER, 2002). Organisms favored by these factors are usually connected to ecological imbalances such as harmful algae that could cause serious damage to the ecosystems functioning and biodiversity (GLIBERT; BURKHOLDER, 2011).

Important metrics to understand ecosystems functioning are the net ecosystem production, nutrient flow through ecosystems and energy flow through the trophic chain. Eutrophication and stoichiometry have been extensively studied (see DE SENERPONT DOMIS et al., 2014). A recent study highlights the role of nutrient flow and stoichiometry using the 'pipe model' approach (MARANGER et al., 2018) and some attempts were made to understand how anthropogenic changes may affect the trophic chain in aquatic ecosystems under the stoichiometric view (KOVALENKO, 2019). However, it is a hard task to find studies referring ES theories to the effects of human interventions on aquatic ecosystems, even though it was recently shown to be a powerful tool to look at ecosystem functioning (WELTI et al., 2017).

2.3. Spatial conditions and Stoichiometry in aquatic ecosystems

2.3.1. Climatic differences and stoichiometry

Aquatic environments located in different parts of the planet are subject to the most varied climatic conditions (ROOTS, 1989). Spatial conditions such as luminosity, temperature and nutrient availability are responsible, together with chemical factors, for controlling the metabolism of organisms that live in these environments, as well as the functioning of ecosystems (BIDDANDA et al., 2001; BERGGREN et al. 2010; D'ANDRILLI et al. 2019). The metabolic theory of ecology stipulates that organisms living in conditions of elevated temperatures exhibit higher metabolic rates than those subjected to milder temperatures (BROWN et al., 2004). In tropical environments, that is, of low latitude, the light incidence is more pronounced than in temperate environments (high latitude) (LEWIS, 1996; STERNER et al., 2008). Thus, this causes photosynthetic rates to be higher in tropical environments than in temperate ones, also influencing the availability and quality of dissolved organic matter and

nutrients such as N and P and primary production, which is directly related to the stoichiometry of the resources and communities present (LEWIS, 1996).

In the case of aquatic communities, bacteria are important from the point of view of ecosystem functioning, due to their importance in the remineralization of organic matter, nutrient cycling and also for being the base organisms of trophic relationships (AZAM et al., 1983; DEL GIORGIO; COLE, 1998). Understanding the regulatory mechanisms of bacterial metabolism and chemical composition is of fundamental importance to understand the ecosystem functioning as a whole (LENNONS; PFAFF, 2005). There are several regulatory factors for bacterial metabolism, including water temperature, availability of nutrients and even the stoichiometry of the organic matter used by them (FARJALLA et al., 2002; 2006; HALL; COTNER, 2007; BERGGREN et al., 2010; VIDAL et al., 2011; SARMENTO, 2012; SARMENTO; GASOL, 2012). When compared, bacteria from tropical environments showed higher respiration rates (e.g. CO₂ release), than bacteria from temperate environments, which might be directly linked to the stoichiometry of organisms, that is, bacteria from tropical aquatic environments would have a stoichiometric ratio C: nutrients lower than bacteria from temperate environments (FARJALLA et al., 2009; AMADO et al., 2013).

2.3.2. Climatic change and stoichiometry

The intense human fossil fuel burning in the last century has been causing the atmospheric accumulation of greenhouse gases, such as carbon dioxide (CO₂), methane (CH₄) among others, which in turn have been changing the planetary climatic patterns. This phenomenon is known as climate changes and it has motivated a great number of scientific studies. Climate models have systematically shown temperature increase as a major climatic response in the Brazilian territory and biomes (for instance, MARENCO et al., 2010; 2020) with great consequences to hydrology (BRITO et al., 2018) and biogeochemical cycling in inland waters (ROLAND et al., 2012). For instance, temperature increase may change organism's growth rates and affect their chemical composition (i.e. stoichiometric imbalance) and ecosystems functions as primary production or decomposition rates.

Climate changes may be affecting ecosystems stoichiometry and ecological processes in several ways. Recently, it has been shown that increased N, P and CO₂ availability may be 'diluting' micronutrients in food crops with important implications for human health (MEDEK et al., 2017; MYERS et al., 2014). Increasing CO₂, as well as N and P (from cultural

eutrophication process, another environmental global issue as discussed below) concentrations may be having a similar effect in aquatic ecosystems (COTNER, 2019), a phenomenon referred to as 'environmental obesity'; i.e., higher proportions of C would be being fixed by primary producers (i.e. higher C: nutrient ratios) due to the higher CO₂ concentrations on the atmosphere with consequences to nutrients recycling and energy flow through the aquatic food web (VAN DER WALLS et al., 2010; COTNER, 2019).

Fundamentally, this represents a stoichiometric imbalance in the availability of nutrients to ecosystems. Moreover, increasing temperatures can directly affect aquatic metabolism, as well (BROWN et al., 2004) by altering organismal growth rates. For instance, increasing temperatures have been shown to increase bacterial biomass, C: P and N: P biomass stoichiometry in P deficient conditions (PHILLIPS et al., 2017). Furthermore, if increasing temperature increases P deficit in organisms' biomass, it can also result in energy flow changes due to stoichiometric imbalance between resources and predators, such as zooplankton grazing high C: P biomass phytoplankton (as in the plankton paradox energy; STERNER et al., 1998). Besides, increasing temperature and N and P availability can change heterotrophic bacteria metabolic rates, such as respiration and biomass production (SCOFIELDS et al., 2015, BERGGREN et al., 2010), which, in turn, can increase CO₂ and nitrous oxide (N₂O) emission from freshwaters (MAROTTA et al., 2014; LIENGAARD et al., 2013).

As an indirect consequence of climate change, the hydrological and rainfall patterns changes were predicted to drastically affect ecological processes such as nutrients cycling, energy flow and spatial ecological gradients in inland waters (ROLAND et al., 2012). The reduction of the annual precipitation in the Brazilian semi-arid, for example, has caused drastic changes in water volume and resuspension of sediments reducing light availability to primary producers, but also increasing P concentrations in the water column during droughts (COSTA et al., 2019). On the one hand, these frequent and prolonged droughts can shift the phytoplankton community to the dominance of mixotrophic organisms and affect the trophic , chain energy flow (COSTA et al. 2019). On the other hand, it can also affect seston and bacterial stoichiometry by increasing water residence times in aquatic ecosystems (THEY et al., 2017). With prolonged water residence times, bacterial and the whole seston increased their nutritional quality by reducing C: P ratios, affecting nutrient cycling, such as the increase in C mineralization rates (THEY et al., 2017).

2.4. Eutrophication and Stoichiometry

2.4.1. Cultural eutrophication

Unlike Redfield's oceans where the microbiota regulates elemental cycling due to internal processing and long residence times, inland waters are externally supplied N and P from sewage, aquaculture water discharges but especially from agricultural fertilizers, which disrupt the close coupling between these elements and other required elements including C, Fe, and Zn among others. Presumably, this would lead to increased retention of these elements, but it is likely complicated by temporal and spatial complexities. For example, increased demand for micronutrients with N and P enrichment could potentially be offset by changes in water column or sediment redox potential (COTNER et al., 1990; BURGIN et al., 2011; RIEDEL et al., 2013).

Nonetheless, the effects of changing *relative* nutrient availability is likely to have important effects on ecosystem scale processes that become more or less favorable with added N and P. For example, added N and P facilitates algal biomass production (COTNER; WETZEL, 1992) but potentially chemosynthetic production (nitrification) and denitrification depending on Fe and Mn availability to these different communities (BROWNING et al., 2021). While ecologists have done an excellent job examining competition between organisms with similar metabolic strategies such as photo-synthesizers or aerobic heterotrophs, more work could be done to address how micronutrient limitation affects metabolism and processes with ecosystem-scale implications, such as competition between N-fixers and denitrifiers for Fe. The implications of these dynamics are important not only for a given freshwater system, but also downstream environments such as the ocean (MARANGER et al., 2018).

Sewage effluents can be a key source of N and P to aquatic ecosystems (JARVIE et al., 2006; XU et al., 2008; MCCRACKIN et al., 2013) contributing to eutrophication and increased growth rates of both autotrophs and heterotrophs and selecting for fast-growing P-rich species (according to the growth rate hypothesis; SMITH et al., 1999; STERNER; ELSER, 2002; SMITH, SCHINDLER, 2009; WELTI et al., 2017). At the beginning of the eutrophication process, the primary producers grow quickly and facilitate growth of the higher trophic levels, however changes in the biological and/or physico-chemical conditions, such as higher relative accumulation of P than N, can alter ecosystem behavior. Additionally, increased availability of N and P can stimulate both autotrophic and heterotrophic metabolism affecting CO₂ formation

and consumption rates in freshwaters, such as in humic and clearwater coastal tropical lagoons (PEIXOTO et al., 2013), which may represent a positive feedback to climate changes in those ecosystems (SCOFIELD et al., 2015).

It is known that the contamination of water resources with N and P has been increasing worldwide (GLIBERT, 2012). However, how this may affect the stoichiometry of organisms is still unknown and deserves more attention in future work (SARDANS et al., 2012; SITTERS et al., 2015). It is important to consider that the agricultural fertilizers and aquaculture water disposals mainly loads nutrients and organic matter, while sewage input is a complex mixture that also loads various other elements such as contaminants or trace elements to the environments (SMITH et al., 1999; JARVIE et al., 2006; SSHWARZENBACH et al., 2010; TUNDISI, 2018). Hence, it could be expected that the other elements would interact with high N and P concentrations and could express other important, but still unrevealed, features in ES. Thus, macronutrients stoichiometry may affect trace elements cycling and its use by organisms. Besides, trace elements may present important constraints to macronutrients cycling. For instance, Karimi E Folt (2006) showed that the variation of C: N: P ratios were lower among benthic macroinvertebrates, while non-essential metals (lead (Pb), mercury (Hg), and cadmium (Cd)) presented a higher variation among the same groups (KARIMI; FOLT, 2006).

Around the world, aquatic ecosystems are subject to the overexploitation of their resources and receive large discharges containing nutrients from the most diverse human activities (TORREMORELL et al., 2021). The exploitation and mismanagement of water resources leads to eutrophication of water, which increases the bloom of toxic algae (BAE; SEO, 2021). With climate change and global warming, negative effects on the chemistry and ecology of aquatic environments can be greatly maximized (ROZEMEIJER et al., 2021; LI et al., 2021; RAULINO et al., 2021). Studies linking the increase in temperature due to climate change and water quality are still not widespread (STATHAM, 2011; PAERL et al., 2011). Mooij et al. (2005) and Statham (2011) suggest that climate change and its effects on temperature, hydrological cycles and nutrient cycling lead to a gradual increase in eutrophication phenomena in lakes and estuarine environments. To analyze the effects of climate change, especially temperature variations on ecological patterns such as phytoplankton stoichiometry, studies of latitudinal trends have proved to be a good approach (LEUNG et al., 2015; TRUBOVITZ et al., 2020; ZACAI et al., 2021). Optimal temperatures for the growth and development of phytoplanktonic communities are highly correlated with latitude (CHEN,

2015), so analyzing latitudinal effects together with environmental conditions, such as the trophic state, is a way to better understand the functioning and metabolism of microorganisms and their multiple regulators (ADDO-BEDIAKO et al., 2000; COLLOS et al., 2005; BISSINGER et al., 2008).

3. CHAPTER 2: LATITUDINAL PATTERNS AND TROPHIC STATUS INFLUENCE ON SESTON AND BACTERIAL C: N: P STOICHIOMETRY OF INLAND WATERS

3.1. INTRODUCTION

Several large-scale ecological patterns and processes are directly affected by landscape, climatic conditions, and latitude. In aquatic ecosystems, environmental variables that vary with the latitudinal gradient, such as solar radiation, temperature, and nutrient availability affect communities at the base of the food web such as phytoplankton (one of the main components of seston) and bacterioplankton (LEWIS JR., 1996; ANESIO et al., 2005; APPLE; DEL GIORGIO, 2006; EDWARDS et al., 2016). This has important repercussions for primary productivity, composition of planktonic communities (LEWIS, 1996), microbial metabolism (AMADO et al., 2013), and nutrient cycling (STERNER, 1998).

In order to better understand the cycling of global nutrients, such as carbon (C), nitrogen (N) and phosphorous (P), and their feedbacks to the biosphere, several studies have been adopting large-scales (e.g. worldwide, latitudinal, etc) observations of aquatic ecosystems (e.g. TRANVIK et al., 2009; KELLER et al., 2020; PARANAÍBA, 2021). Ecological Stoichiometry is the field of knowledge that relates environmental nutrients availability and proportions to organisms' chemical composition and metabolism and is an important driver of biological interaction in aquatic food webs (STERNER; ELSER, 2002; WELTI et al., 2017). C:N:P stoichiometric ratios have been widely studied since the 1930s, when Alfred Redfield demonstrated that in the oceans there was a remarkable constancy of this ratio at 106:16:1, for both the dissolved fraction and seston (particulate organic matter, including plankton). This pattern was attributed to the conditioning of the sea water chemistry by plankton organisms over the long water residence time (REDFIELD, 1934; 1958). In inland waters, however the C: N: P stoichiometric ratios differ on average from the Redfield ratios due to a number of fundamental differences: i) lower water residence time; ii) differences in the quantity and quality of autochthonous and allochthonous organic matter; iii) taxonomic differences; iv) intrinsic differences in metabolism, such as growth rates (e.g. COTNER et al., 2010; THEY et al., 2017).

The stoichiometry of both seston and bacteria, which are at the base of aquatic food webs, has been shown to be very variable in inland aquatic ecosystems and this variability could be the result of environmental conditions gradients across landscape and latitude that regulates

nutrients and light availability (COTNER et al., 2010; GODWIN; COTNER, 2015). Added to the factors already mentioned, the trophic state can be of paramount importance in determining the stoichiometric ratios in the inland aquatic ecosystems. For instance, bacteria growing in P-limited environments may have high C: P ratios in their biomass (GODWIN; COTNER, 2015), or even display high respiration rates to balance the amount of organic C through the release of CO₂ in order to keep P at adequate concentrations (CIMBLERIS; KALF, 1998, THEY et al., 2017). On the other hand, bacteria growing in P-rich environments show high growth rates and low C:P ratios in their biomass. High growth rates, determined by both higher concentrations of nutrients and higher temperatures, are related to a large allocation of P to ribosomal RNA for protein synthesis, as predicted by the Growth Rate Hypothesis (GRH – Elser et al. 1996). Thus, bacterial communities respond to these environmental stimuli through the variation in their elemental biomass composition, especially C, N and P. Moreover, bacterial metabolism and stoichiometry can be controlled by several physical and chemical factors in the environment (SCHIAFFINO et al., 2011). In marine ecosystems, for example, the seston C:P carbon ratio increases with latitude, as a function of global variations in temperature, nutrients, and biological diversity (MATINY et al., 2013).

The sunlight incidence and nutrients availability are the most important components in determining ecosystem structure and processes, including stoichiometry of organisms (SCHIAFFINO et al., 2011; MARTINY et al., 2013). Likewise, these environmental characteristics that vary with latitude, (i.e. solar radiation and water temperature, as well as nutrients such as N and P) are the most reported factors that regulate bacterial activity (COTNER; BIDDANDA, 2002; HALL. COTNER, 2007; BERGGREN et al., 2010). For example, bacteria from environments with higher temperatures and greater availability of nutrients have high metabolic rates, increased growth and high respiration rates (e.g. BERGGREN et al., 2010). In ecosystems with low availability of nutrients and variable resources, bacteria that have little capacity to regulate their homeostasis are dominant; this also increases the efficiency of assimilation of bioavailable nutrients (STERNER; ELSER, 2002; HESSEN et al., 2013). In eutrophic environments that are rich in nutrients fast-growing bacteria with low biomass C: P and N: P ratios are naturally selected and dominate (FUNK; VITOUSEK, 2007).

Inland aquatic ecosystems at different latitudes are subjected to different climate regulations, including levels of solar radiation, which are related to photosynthetic rates and temperature (LEWIS, 1996). In addition, there is a great deal of spatial variability in trophic

conditions (i.e. ecosystems varying from oligo to eutrophic mainly) due to human activities (SMITH; SCHINDLER, 2009). These environmental variations are vital for ecosystems functioning. For instance, limitation of bacterial growth by inorganic nutrients (N and P) has been observed in tropical and temperate ecosystems (FARJALLA et al., 2002; BREGGREN et al., 2010). Although it has been attributed the greater efficiency of bacterial growth in temperate regions to a lower limitation of N and P, and more pronounced in C (ie, low C: P ratios in seston), the opposite should be true for the tropics (AMADO et al., 2013). Therefore, nutrient remineralization rates are higher in tropical ecosystems, the nutritional competition with phytoplankton is fiercer, causing heterotrophic bacteria to be strongly limited by inorganic nutrients when it comes to tropical ecosystems (DOWNING et al., 1999; FLECKER et al., 2002). UV radiation releases labile P (COTNER; HEATH, 1990) and N (KIEBER, 2000) from refractory organic matter in aquatic environments, in addition to optimizing the release of dissolved organic carbon (DOC) (WETZEL et al., 1995). The rate of exposure to UV radiation can then redirect nutrient fluxes in the seston (mainly in phytoplankton organisms) and, consequently, influence the stoichiometry of bacterioplankton, which can derive a great part of its resource from this compartment (COTNER; BIDDANDA, 2002). As explained so far, we can assume that factors regulated by latitude in synergy with the trophic status of the ecosystems may have important effects on the stoichiometry of seston and bacterioplankton in inland waters from different regions, but we are not aware of any study addressing this question.

In this study, we aimed to evaluate the latitudinal variation of the C: N: P composition of seston and bacterial biomass together with the trophic status of 56 ecosystems from tropical and temperate regions of the Americas. We expect to find higher C: nutrient ratios in seston at low latitudes, where luminosity rates are higher, which allows for higher photosynthetic activity compared to temperate regions. Also, considering the light incidence in the tropics, we expect that the higher primary production and consequently the amount C results in higher C: P and C: N ratios for low latitude environments. Regarding the influence of the trophic state on the stoichiometry of seston and bacteria, we expect to find a greater tendency to be limited by nutrients and excess C, generating greater C: N: P, mainly for oligotrophs. However, eutrophics may have N contributions from fixative cyanobacterial blooms, which can lead to lower C: N and higher N: P.

The Americas extends along the northern and southern hemispheres, being the only one to occupy all the climatic ranges of the planet. The creation of the Collaborative Network in Aquatic Microbial Ecology in Latin America (μ SudAqua –

<https://sites.google.com/view/microsudaqua/home-english>) and the collaboration of data from the United States, allowed establishing this study with environments under different conditions in varied parts of the continent, and thus establishing a latitudinal range.

3.2. MATERIAL AND METHODS

3.2.1. Study area

The ecosystems studied in this work were analyzed under a spatial approach, which sought to establish a latitudinal as well as a trophic gradient across the Americas along the countries: Argentina, Brazil, Peru and the United States, ranging from latitudes 51° S to 47° N. All the 56 environments sampled in this work are listed in appendix (2 and 3).

3.2.2. Sample collection and filtration

Water samples for the determination of physical and biological parameters, as well as for filtration to determine the amount of C, N and P of bacteria and seston were collected from the sub-surface of each ecosystem. The water samples were placed in previously sanitized polypropylene bottles and kept under refrigeration, not exceeding 12 hours until the filtration process. All samples were sequentially filtered through pre-combusted (for 4 h at 550 °C) and weighed glass-fiber filters of 1.6 µm (for seston analysis; Whatman GF/A) and 0.7µm (for bacterial community analysis; Whatman GF/F) pore size, respectively according to the filtration scheme shown in figure 1 (see THEY et al., 2017). After filtration, the filters were dried in an oven at 60 °C, weighed until constant mass, stored in individual aluminum foil envelopes, and refrigerated at -20 ° C until analysis.

3.2.3. Environmental variables and chlorophyll a

Turbidity, pH, dissolved oxygen, water depth and temperature were estimated using multiparameter probes (U50 – Horiba). The transparency of the water was measured using a Secchi disk. Chlorophyll a (Chl-a) was extracted from GF/F filters with 90% ethanol and measured by spectrophotometry (JESPERSEN; CHRISTOFFERSEN, 1987).

3.2.4. C, N, and P

In all fractions (seston and bacteria), the total concentrations of C, N and P were analyzed. Total organic carbon, dissolved organic carbon, total nitrogen and dissolved nitrogen were obtained through analysis in a Total Organic Carbon Analyzer (TOC-V Shimadzu). The particulate organic carbon content retained in the 1.6 µm and 0.7 µm filters were analyzed in

the solid module of the TOC Analyzer (SSM-5000). The particulate content of P and N retained in the filters and the total phosphorus of the liquid samples was obtained by digestion with potassium persulfate (CARMOUZE, 1994). After digestion, TN was measured by chemoluminescence in a TOC-V (Shimadzu), and TP was obtained by spectrophotometry (Lambda 365 UV/vis Perkin Elmer) by the ascorbic acid method (MACKETETH et al., 1978). The stoichiometric ratios between elements were expressed as atomic ratios of C, N and P for each fraction.

3.2.5. Statistical Analysis

In order to test the pair-wise association between the absolute concentrations of chemical elements (C, N and P) by latitudinal bands (temperate vs. tropical) and trophic state (eutrophic vs oligotrophic), simple linear regressions were performed for seston and bacteria. Differences in slopes of the relationships according to levels of latitude and trophic state were tested with Analysis of Covariance (ANCOVA) by inspecting the significance of the interaction term.

The association between elemental ratios (C:N, C:P and N:P) and the module of the latitude were tested by non-parametric linear correlation (Spearman test). This test was also performed by latitudinal bands (temperate vs. tropical) and trophic status (eutrophic vs. oligotrophic). Differences in stoichiometric ratios C:N, N:P and C:P (μM) of seston and bacteria between latitudinal bands (temperate vs. tropical) and trophic state (eutrophic vs oligotrophic) were also tested through Wilcoxon–Mann–Whitney test. Statistical tests were performed in R 4.0.2 (R Core Team, 2021). For all analyses we adopted an alpha = 0.05.

3.3. RESULTS

Absolute C concentrations ranged from 0.05 to 949.44 for seston, and 0.02 to 970.31 for bacteria. N concentrations varied from 0.002 to 160 in seston and from 0.001 to 162.86 in bacterial fraction. P concentrations ranged from 0.001 to 6.349 in seston and from 0.0003 to 6.52 in bacteria. In all situations, the bacterial fraction showed greater variation compared to seston. The C:N ratios varied between 4.1 and 46.9 in the seston and from 2.8 to 51.0 in the bacterial fractions. N:P ratios varied between 0.29 and 157.00 in the seston and from 0.07 to 82.00 in the bacterial fractions. The C:P ratio varied between 9.7 and 2,134.0 in the seston and from 1.8 to 1,675.0 in bacterial fraction.

When nutrient concentrations were tested for association using simple linear regressions (C vs. N, C vs P and N vs P), it was observed that all relationships were positive meaning the increase of one element in relation to the other. Seston C vs. N were positively correlated in both temperate and tropical environments with $R^2 = 0.95$ and p-value <0.0001 (temperate environments) and $R^2 = 0.95$ and p-value <0.0001 (tropical environments) (figure 2 A). Bacterial C vs. N from temperate environments presented $R^2 = 0.95$ and p-value <0.0001 and those from tropical environments presented $R^2 = 0.65$ and p-value <0.0001 (figure 2 B). Seston C vs. P, temperate environments present $R^2 = 0.91$ and p-value <0.0001 , while for tropical environments $R^2 = 0.31$ and p-value = 0.02 (figure 2 C). For bacteria C vs. P, temperate environments had $R^2 = 0.92$ and p-value <0.0001 , and tropical environments have $R^2 = 0.63$ and p-value = 0.0002 (figure 2 D). Seston N vs. P from temperate environments had $R^2 = 0.97$ and p-value <0.0001 (figure 2 E). Bacteria N vs. P from temperate environments have $R^2 = 0.97$ and p-value <0.0001 and from tropical environments have $R^2 = 0.82$ and p-value <0.0001 (figure 2 F).

When grouped by trophic state (eutrophic vs. oligotrophic), all relationships between nutrients were positive and significant. Seston C vs. N in eutrophic environments presented $R^2 = 0.94$, and p-value <0.0001 . In oligotrophic environments $R^2 = 0.89$ and p-value <0.0001 (figure 3 A). For bacteria from eutrophic environments, C vs. N had $R^2 = 0.95$ and p-value <0.0001 , for oligotrophic environments, the values were $R^2 = 0.97$ and p-value <0.0001 (figure 3 B). For seston C vs. P of eutrophic environments, the values were $R^2 = 0.92$ and p-value <0.0001 , in oligotrophic environments: $R^2 = 0.25$ and p-value = 0.007 (figure 3 C). C vs. P for bacteria from eutrophic environments showed $R^2 = 0.94$ and p-value <0.0001 , whereas in oligotrophic environments, the values were $R^2 = 0.82$ and p-value <0.0001 (figure 3 D). N vs. P of seston in eutrophic environments had values of $R^2 = 0.98$ and p-value <0.0001 , in oligotrophic environments $R^2 = 0.51$ and p-value <0.0001 (figure 3 F). N vs. P of bacteria in eutrophic environments showed $R^2 = 0.92$ and p-value <0.0001 , in oligotrophic environments, $R^2 = 0.86$ and p-value <0.0001 (figure 3 E).

The seston C: N, N: P and C: P ratios were significantly and negatively correlated with latitude, but bacteria nutrient ratios were not correlated with latitude. ($\rho = 0.2$; $P = 0.001$), in addition, seston C: N, C: P and N: P decrease with latitude, which means a more nutrient-rich biomass. In general, while seston ratios present significant variation with latitude, bacterial ratios do not (figure 4). Considering only the oligotrophic ecosystems, seston N: P and C: P were negatively correlated with latitude (figure 5 C and E), whereas considering only the

eutrophic ecosystems, C: N from seston and bacteria were negatively correlated with latitude. Both seston C: N and bacteria C: N ratio decrease with latitude in eutrophic environments, which does not occur in oligotrophic environments (figure 5). The C: P ratio did not show any change either with latitude or trophic status for the two groups. The seston N: P ratio decreases with latitude in oligotrophic environments and increases in eutrophic environments.

3.4. DISCUSSION

In this study, we can highlight as main results: the stoichiometric ratios C: N, C: P and N: P of seston decrease with increasing latitudes, which does not occur for bacteria. The C: N ratio of seston and bacteria decreased with latitude in eutrophic environments, which did not occur for oligotrophic environments. In the former where there is greater nutritional limitation, primary production is favored, which explains the greater amount of C in the seston, pattern followed by bacteria. On the other hand, C: P ratios did not follow variation patterns consistent with the trophic state or latitude. Both spatial and environmental factors must be considered when determining the distribution and chemical compositions of communities such as seston and bacteria, and furthermore the anthropic influences on their most varied activities must be considered. Due to the high luminosity rates, associated with temperature, the seston C:P ratio was higher in low latitude environments.

The greatest stoichiometric variations were recorded in bacterial fractions from oligotrophic environments. According to Godwin e Cotner (2014) and Godwin et al. (2017), in ecosystems where P concentrations are lower and C: P ratios tend to be higher, it is expected to find organisms with more flexible stoichiometric behavior. In addition, bacteria in P-deficient environments can act as consumers or regenerators of inorganic nutrients, this will depend on how they relate to their sources of nutrients, seston is one of these sources (COTNER et al., 2010). Conversely, bacteria from more productive lakes tend to be closer to their maximum growth rates and present less flexible N: P biomass than those from less productive environments (GODWIN; COTNER, 2015). For instance, in figure 6 B we can observe the different behavior of the bacterial N: P ratio under different trophic conditions. The trophic state of the system directly affects the chemical composition of bacterial biomass (COTNER; BIDDANDA, 2002), which in turn interferes with stoichiometry (GODWIN; COTNER, 2015).

In our study, the seston fraction of tropical environments showed a greater range of variation in the stoichiometric ratios C: N, C: P and N: P, compared to temperate environments, the same applies to bacteria in their C: N and N: P ratios. On the other hand, the C: P ratio of

bacteria from both temperate and tropical environments did not show great differences in their average variation compared to each other (figure 6 A). Beisner et al. (2006) concluded that communities such as phytoplankton (the main component of seston) and bacteria have their dispersion and composition better explained by environmental factors than by spatial factors. On the other hand, testing both factors separately are of great importance, as spatial factors can present false correlations with environmental factors that affect the chemical composition of bacteria (SOMMARUGA; CASAMAYOR, 2009). In this sense, Schiaffino et al. (2011) concluded that both geographic location and environmental conditions were influential on the chemical composition of bacterioplankton in a study that evaluated 45 environments in a transect from Argentinean Patagonia to Maritime Antarctica.

In general, seston had higher C:P ratios in low latitude environments (figure 7 C). This pattern was expected considering that higher sunlight incidence and temperatures have a direct effect on the photosynthetic rates under nutrient saturation conditions (BAUMERT; UHLMANN, 1983). Higher radiation may drive ecosystems to N and P limitation and thus, phytoplankton tends to become nutritionally impoverished by getting richer in C, which results in higher C: nutrients in their biomass (STERNER et al., 1998; ELSER; GOLDMAN, 1991; LEWIS, 1996). Despite the strong regulation of light in photosynthesis, this effect can be modulated by temperature and nutrient availability. When several factors regulate a biological process, there is a dynamic use of other limiting resources, as in the case of the regulation of phytoplankton biomass by temperature, light and nutrients, in addition to the latitudinal regulation only (LEWIS, 1974; STERNER et al., 1998).

The distribution of the stoichiometric ratios of seston and bacteria are very heterogeneous along the latitudinal gradient in the current work. In tropical inland waters, due to high temperatures, the metabolism of organisms increases considerably compared to temperate ecosystems (AMADO et al., 2013). Bioavailable P is then rapidly assimilated and incorporated into the biomass, causing levels of this nutrient to be often below detection limits compared to C and N (ESTEVEZ, 1998). Nonetheless, higher growth rates due to higher temperature demands higher P content to support biomass growth (Growth rate hypothesis).

The ability of bacteria to regulate their stoichiometry will depend on which nutritional resource is limiting to bacterial growth (SCOTT et al., 2012). Bacteria have multiple strategies to regulate their homeostasis, and the high availability of P can select for more homeostatic strains (GODWIN; COTNER, 2014). Stoichiometric flexibility is closely linked to the absolute content of P in bacteria, anthropogenic inputs of this nutrient can lead to the prevalence of more

homeostatic bacteria, reducing the ability of natural communities to buffer changes in the availability of organic P and C (GODWIN; COTNER, 2018). In this way, it is necessary to consider, in addition to spatial and environmental factors, the influence and human activities such as land use and their impacts on ecosystems and organisms, since the excess of N and P found in aquatic ecosystems, above all, is directly linked to agricultural activities and urbanization (STUTTER et al., 2018; LIU et al., 2019; CHEN et al., 2021).

3.5. CONCLUSION

This study highlights the interplay between latitude and trophic state in regulating seston and bacterial stoichiometry. We can see that latitude has a greater influence on the composition of the seston, which performs greater relative fixation of C at low latitudes, due to the high rates of luminosity. This pattern is not followed by bacteria, which maintain their stoichiometry independent of the resource. Godwin E Cotner (2014) found great variation in the C: P ratios in bacteria grown in the laboratory, showing the high flexibility of these organisms. However, the C: P variation was not found in communities in ecosystems, since metabolic flexibility does not confer any advantage in the environment. Therefore, even though bacteria are potentially flexible when isolated in the laboratory, communities in the nature remain with more stable stoichiometric ratios. Climate, input of allochthonous organic matter, and the land use in the watershed are also other factors that may mask the effect of latitude on the stoichiometry of bacteria and seston. More studies are needed to better investigate the influence that each factor can exert on the stoichiometry of bacterial biomass and seston.

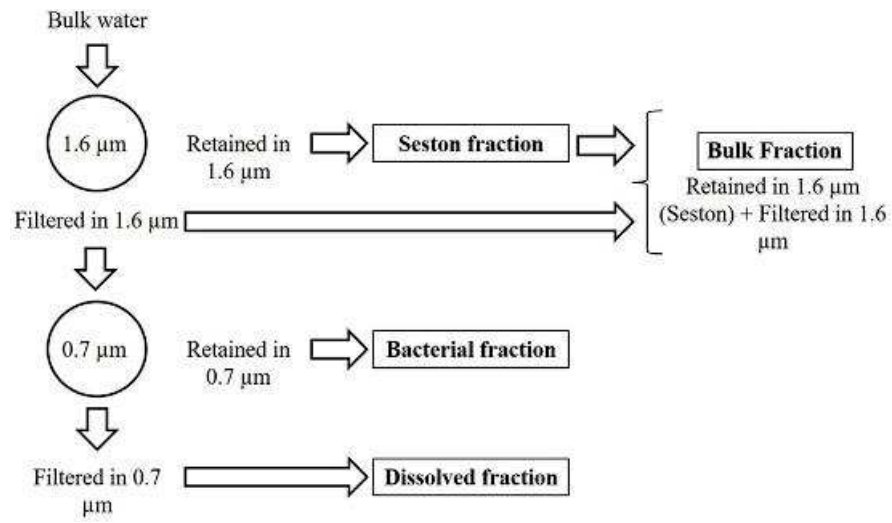
4. GENERAL CONCLUSIONS

Increasingly, human action has a harmful effect on nature. Toxic residues from their activities have a great capacity to change the functioning, often irreversibly, of ecosystems. An example of this is the eutrophication of water bodies that are so important for their various ecological and social functions. The discharge of effluents from domestic and industrial sewage and residues from unsustainable agriculture unbalance the functioning of aquatic ecosystems, being extra sources of nutrients in unnecessary and sometimes harmful quantities. The chemistry of ecosystems and their organisms is closely linked, and ecological stoichiometry helps us to understand these relationships.

To better understand the stoichiometric functioning of aquatic environments and their organisms, spatial gradients, such as latitude, help us understanding the regulation of chemical patterns in aquatic ecosystems. Latitude regulates temperatures and luminosity levels, which are important variables in the functioning of ecosystems and in the metabolism of aquatic organisms. The trophic state of an aquatic ecosystem is also an important factor to be considered in stoichiometric studies; the amount of inorganic nutrients influences several regulatory factors in the metabolism of aquatic organisms and, consequently, in ecosystem functioning. All these characteristics are also related to spatial conditions according to different land uses across the landscape.

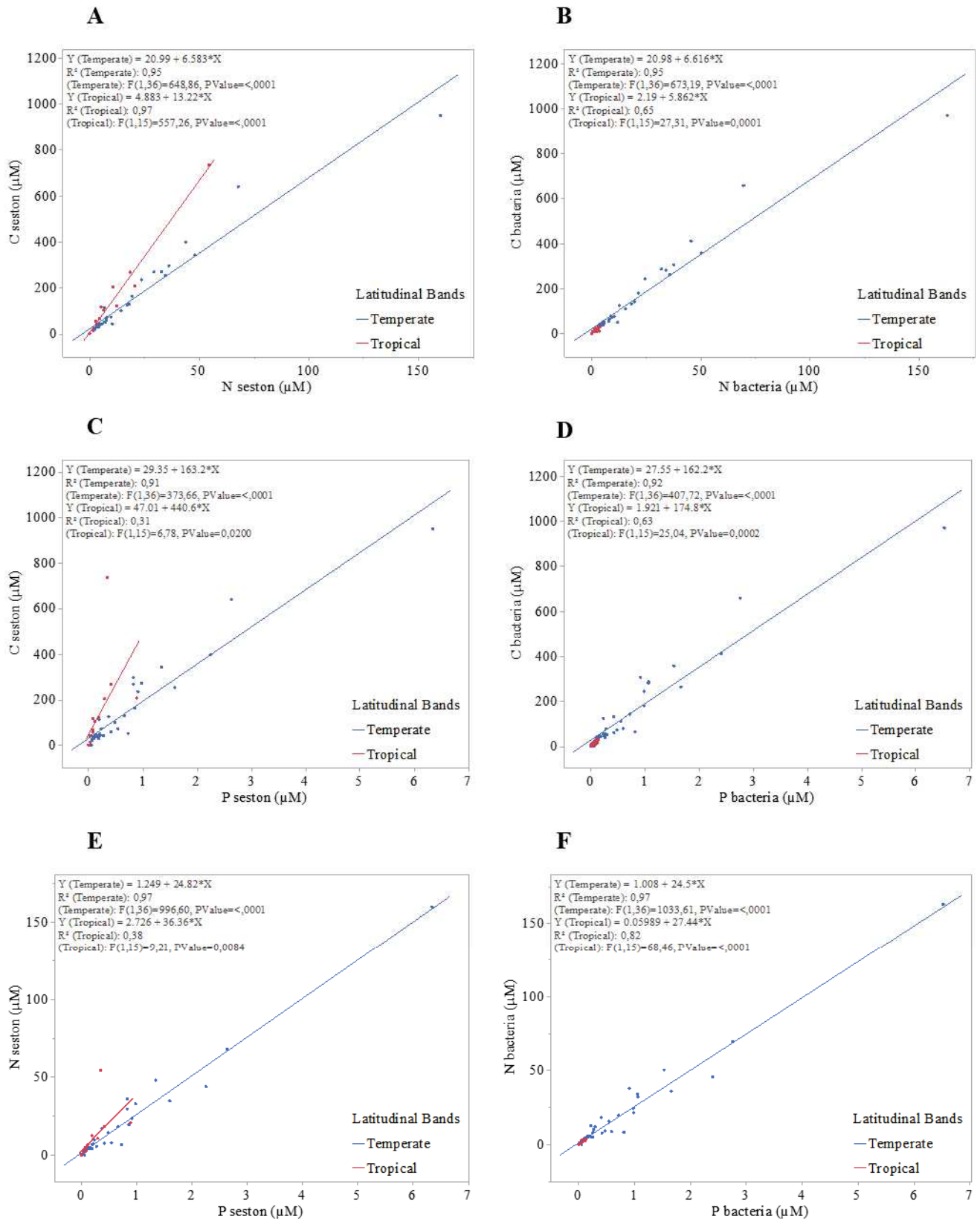
In general, we can conclude that the stoichiometry of organisms such as seston and bacteria is influenced by spatial and environmental factors. Such factors may be of natural origin, anthropic origin, or a combination of them. In an increasingly impacted world, it becomes very difficult to assess the chemical composition of organisms and ecosystems without considering human actions and their consequences. This study concluded that, first, the intensification of unrestrained human activities such as the increase in land use and occupation in an unsustainable manner and the discharge of not-properly treated effluents (from industrial, agricultural, and urban areas) can lead to environmental imbalances at elementary levels, changing natural biogeochemical processes. This may have consequences not only to global climate but also impacts aquatic ecosystem functioning locally. We can also conclude that, the geographic location of the environments (latitude), together with the trophic state of the environments, play a role of stoichiometric regulators of seston and bacteria. Therefore, stoichiometric studies that approach spatial and environmental factors and that consider the ecological imbalance caused by human actions reveal patterns that are more consistent with the real and current situations of aquatic ecosystems.

Figure 1 - Filtration scheme carried out with the liquid samples



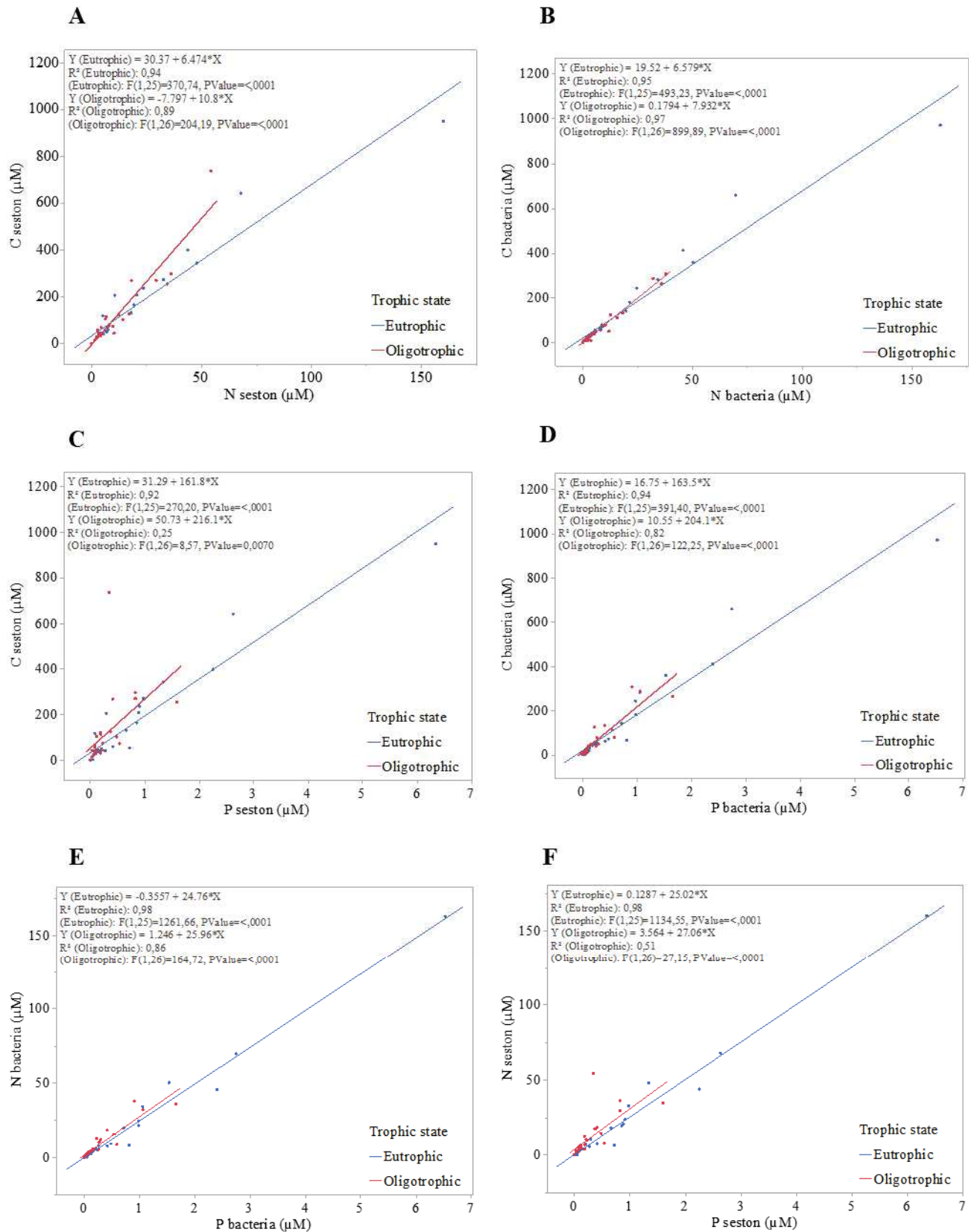
Fonte: They et al. 2017

Figure 2 - Simple linear regressions between the concentration of nutrients Carbon, Nitrogen and Phosphorus of seston and bacteria separated by latitudinal bands



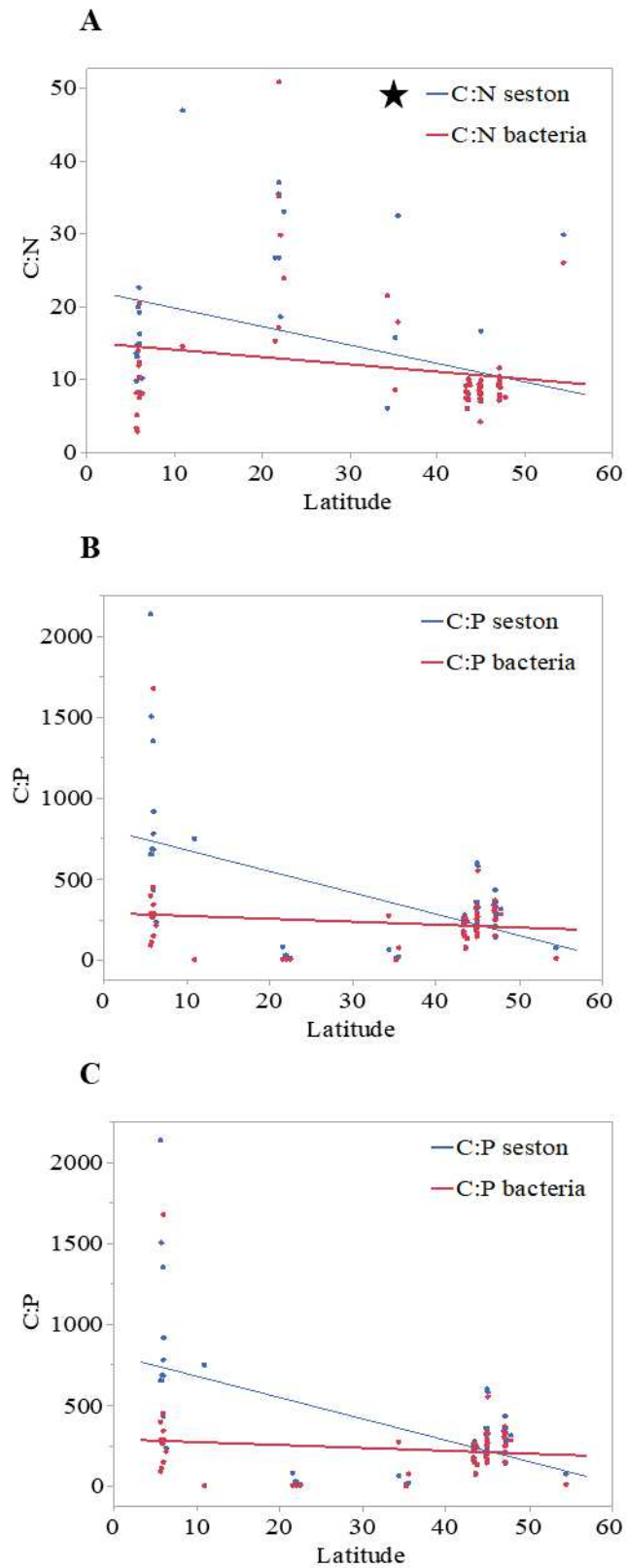
Fonte: Elaborado pela autora (2021).

Figure 3 - Simple linear regressions between the concentration of nutrients Carbon, Nitrogen and Phosphorus of seston and bacteria separated by trophic status



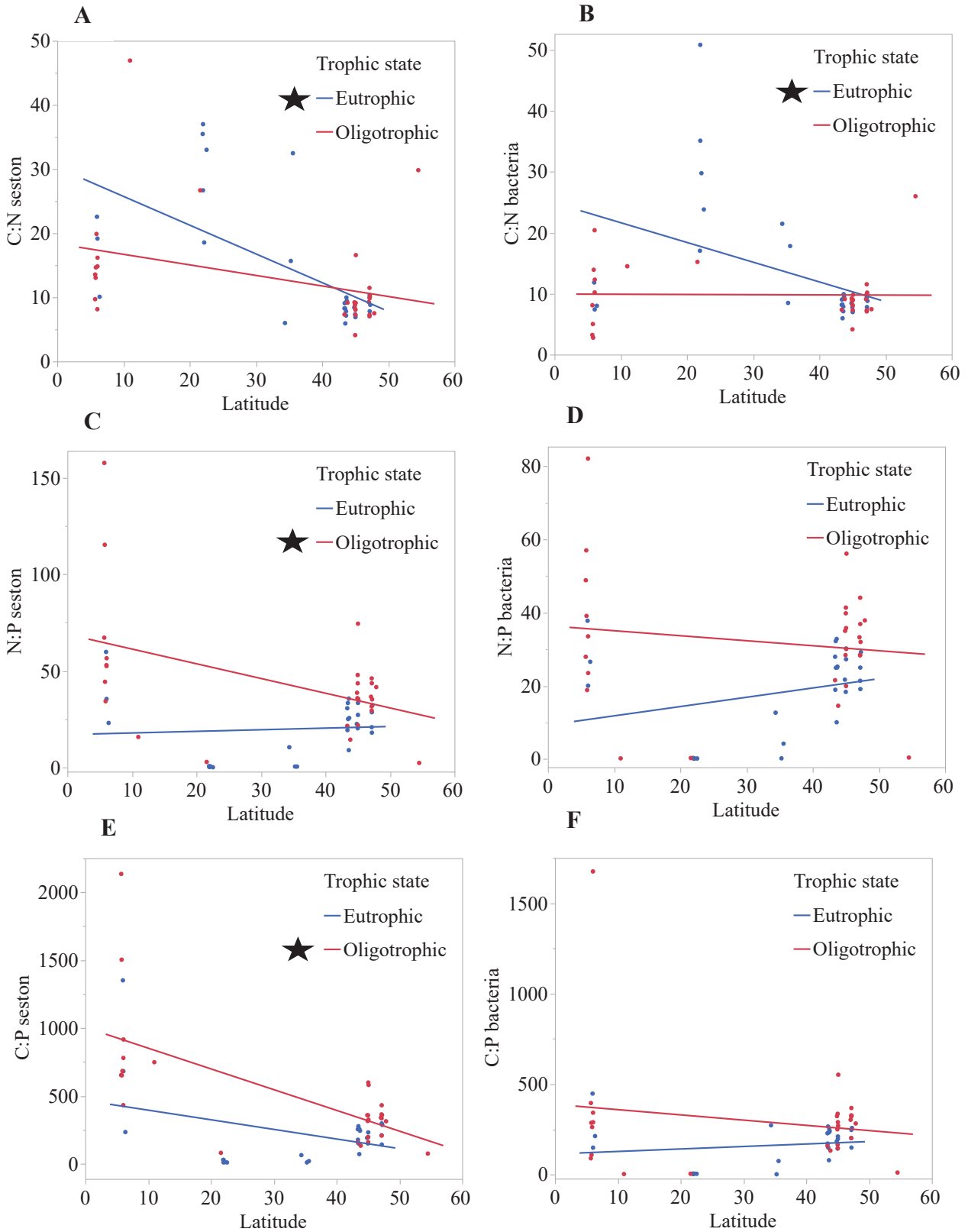
Fonte: Elaborado pela autora (2021).

Figure 4 - Simple linear regression between the stoichiometric ratios of seston and bacteria by latitude (module)



Fonte: Elaborado pela autora (2021).

Figure 5 - Simple linear regression between the stoichiometric ratios of seston and bacteria by latitude (module), separated by trophic status



Fonte: Elaborado pela autora (2021).

Figure 6 - Boxplots comparing means of stoichiometric ratios between seston and bacteria separated by trophic state and by latitudinal bands

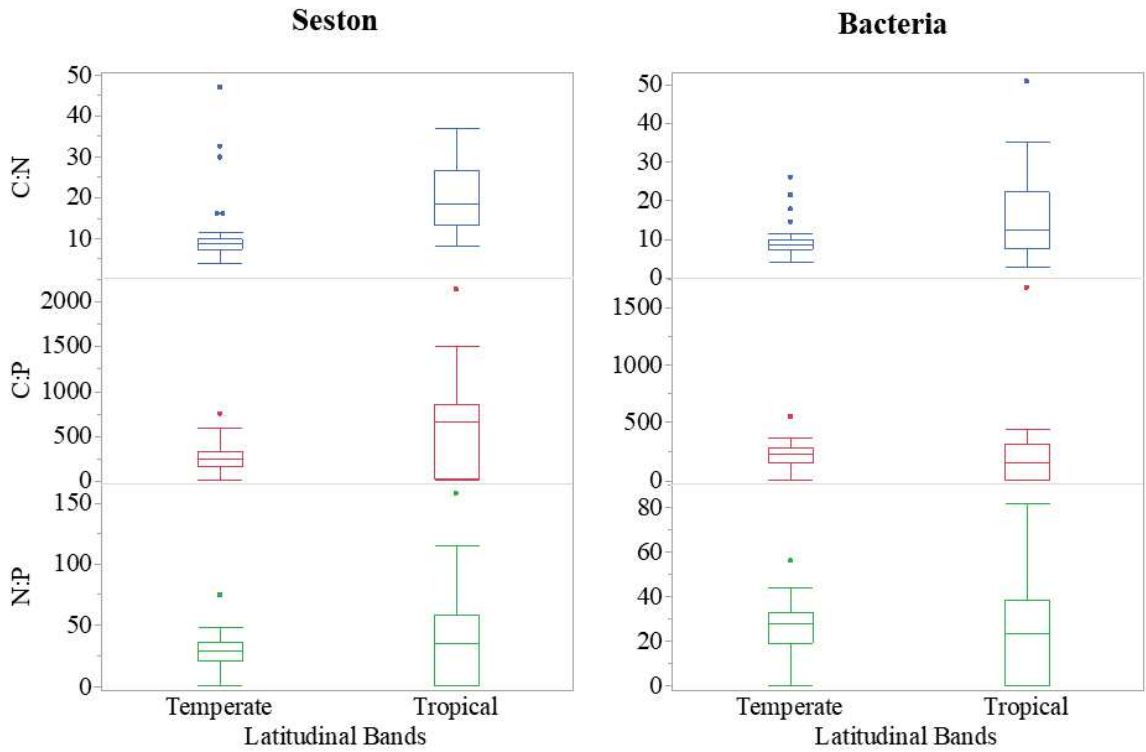
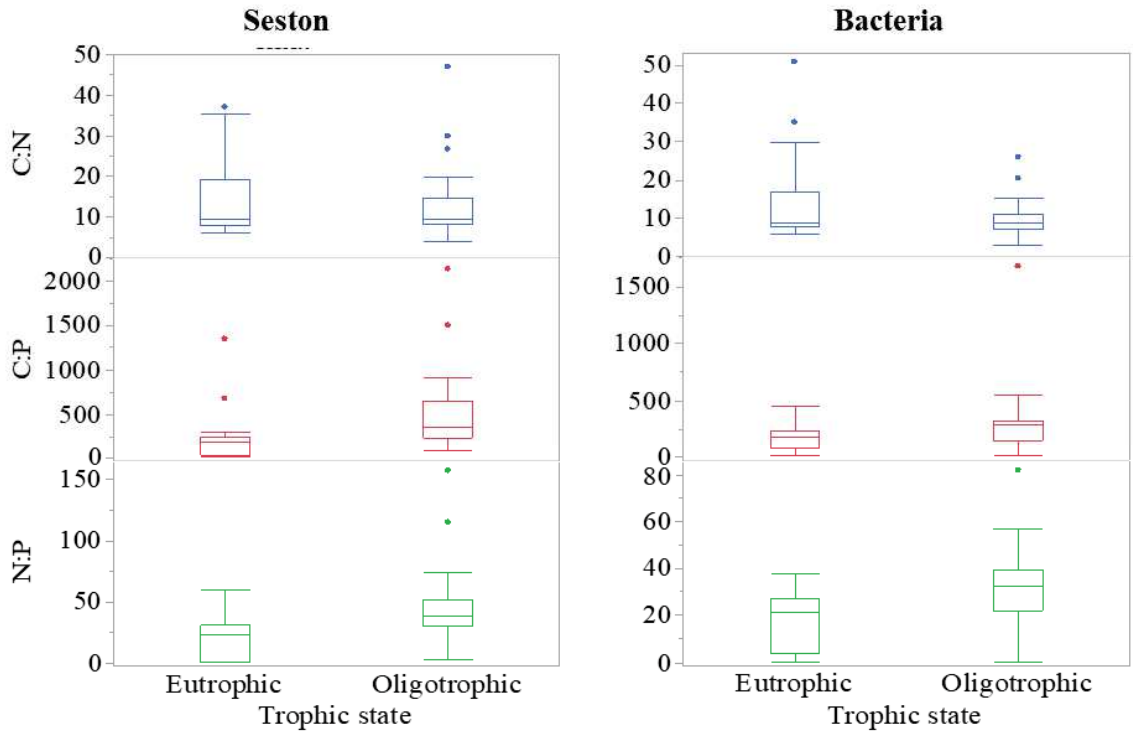
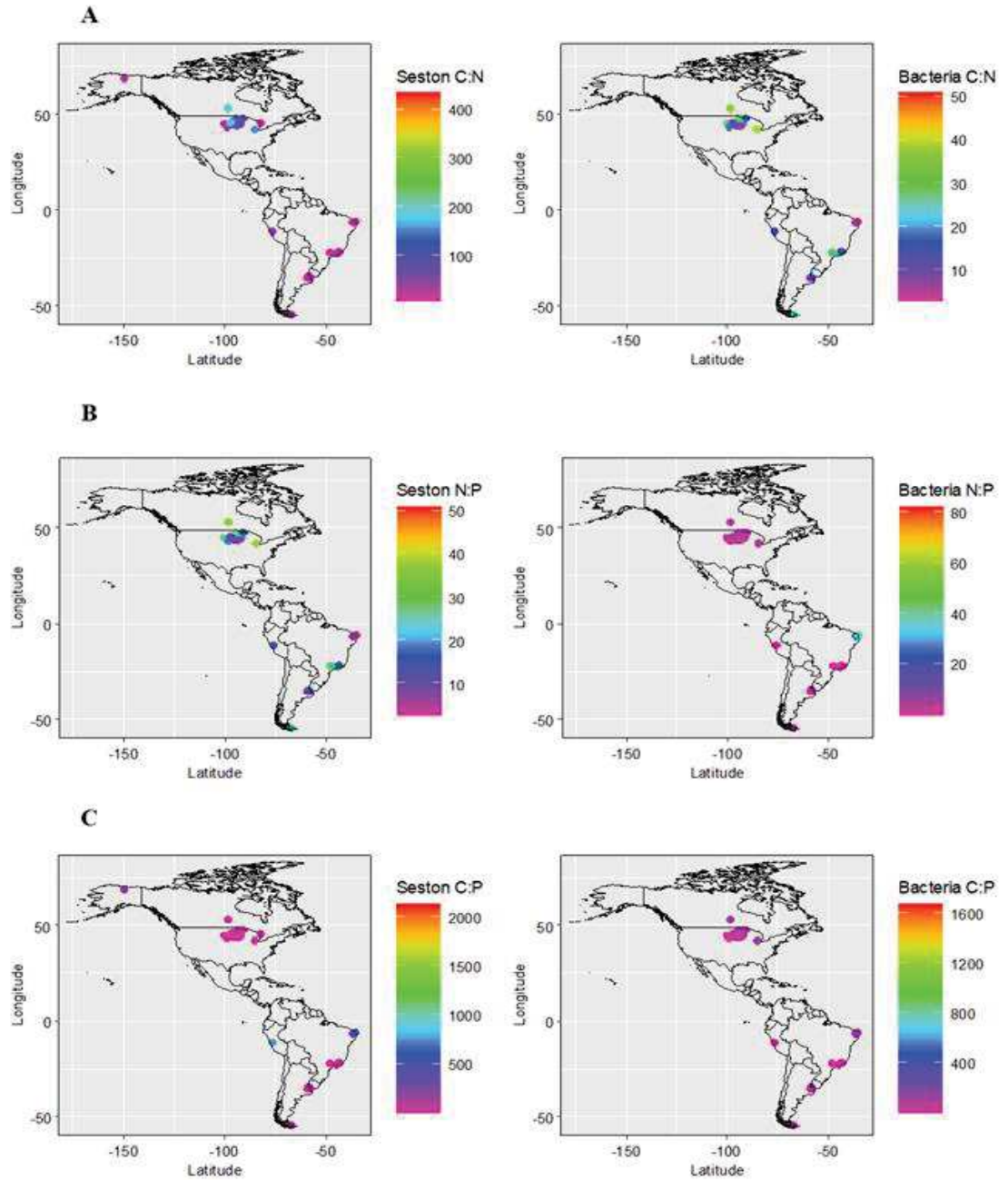


Figure 6 b:



Fonte: Elaborado pela autora (2021).

Figure 7 - Maps showing the stoichiometric ratios of seston and bacteria across the American continent at the points sampled.



Fonte: Elaborado pela autora (2021)

Table 1 - Sampled points

System name	Geographic coordinates	Type	Trophic State	Country
Extremoz	05°42'45.1"S / 35°17'06.3"W	Coastal lake	Oligotrophic	BR
Lagoa Azul	05°42'48.2"S / 35°15'56.6"W	Reservoir	Oligotrophic	BR
E. A. Jundiá	05°53'23.3"S / 35°21'32.6"W	Coastal lake	Oligotrophic	BR
Jambeiro	05°52'06.3"S / 35°20'25.2"W	Coastal lake	Oligotrophic	BR
Jiqui	05°55'08.3"S / 35°11'14.0"W	Coastal lake	Oligotrophic	BR
Ilhota	05°59'22.6"S / 35°07'32.1"W	Coastal lake	Eutrophic	BR
Bonfim	06°03'00.2"S / 35°12'05.8"W	Coastal lake	Oligotrophic	BR
Carcará	06°03'54.6"S / 35°09'45.3"W	Reservoir	Oligotrophic	BR
Calimã	06°04'00.1"S / 35°05'59.4"W	Reservoir	Eutrophic	BR
Arituba	06°04'46.6"S / 35°06'14.4"W	Reservoir	Oligotrophic	BR
Cruzeta	06°23'23.9"S / 36°47'35.6"W	Reservoir	Eutrophic	BR
Junin	10°59'56.3"S / 76°06'32.7"W	Lake	Oligotrophic	PERU
Chapeu D'uvas	21°35'11.1"S / 43°31'49.8"W	Reservoir	Oligotrophic	BR
Santa Fé	21°57'51.8"S / 43°18'32.8"W	Reservoir	Eutrophic	BR
Bonfante	22°00'37.0"S / 43°16'08.9"W	Reservoir	Eutrophic	BR
Monte Serrat	22°01'07.0"S / 43°18'02.6"W	Reservoir	Eutrophic	BR
Broa	22°11'32.2"S / 47°53'01.0"W	Reservoir	Eutrophic	BR
Funil	22°33'07.7"S / 44°34'55.5"W	Reservoir	Eutrophic	BR
Río Luján	34°23'42.0"S / 58°36'20.7"W	River	Eutrophic	ARG
Lobos	35°16'47.9"S / 59°07'06.5"W	Lagoon	Eutrophic	ARG
Chascomús	35°35'35.5"S / 58°01'30.6"W	Lagoon	Eutrophic	USA
E. Okoboji	43°22'58.5"N / 95°06'35.8"W	Lake	Oligotrophic	USA
W. Okoboji	43°23'00.2"N / 95°09'32.2"W	Lake	Eutrophic	USA
Center	43°24'38.4"N / 95°08'14.1"W	Lake	Eutrophic	USA
Spirit	43°28'40.4"N / 95°05'57.8"W	Lake	Eutrophic	USA
Bella	43°30'39.8"N / 95°37'12.6"W	Lake	Eutrophic	USA
Okabena	43°37'06.6"N / 95°37'05.3"W	Lake	Eutrophic	USA
Hall	43°37'14.1"N / 94°27'56.2"W	Lake	Eutrophic	USA
Fox	43°40'31.0"N / 94°42'30.0"W	Lake	Eutrophic	USA
Big Twin	43°43'49.1"N / 94°44'51.2"W	Lake	Eutrophic	USA
Fish	43°50'47.5"N / 95°02'42.3"W	Lake	Oligotrophic	USA
Mitchell	44°51'32.3"N / 93°29'54.0"W	Lake	Eutrophic	USA
Christmas	44°53'44.7"N / 93°32'35.2"W	Lake	Oligotrophic	USA
Minnetonka	44°57'16.3"N / 93°32'36.3"W	Lake	Oligotrophic	USA
Round	44°59'38.6"N / 93°03'45.7"W	Lake	Eutrophic	USA
McCarrons	44°59'54.0"N / 93°06'48.7"W	Lake	Oligotrophic	USA
Medicine	45°00'28.6"N / 93°25'13.2"W	Lake	Oligotrophic	USA
Josephine	45°02'09.6"N / 93°09'12.3"W	Lake	Oligotrophic	USA
Owasso	45°02'18.5"N / 93°06'44.7"W	Lake	Eutrophic	USA
Johanna	45°02'36.9"N / 93°10'16.9"W	Lake	Oligotrophic	USA
Eagle	45°04'32.1"N / 93°24'45.3"W	Lake	Oligotrophic	USA
Turtle	45°06'02.5"N / 93°08'14.0"W	Lake	Oligotrophic	USA
Boot	47°03'45.8"N / 95°16'06.1"W	Lake	Oligotrophic	USA
Arco	47°09'56.4"N / 95°10'05.0"W	Lake	Oligotrophic	USA
Deming	47°10'13.6"N / 95°10'05.6"W	Lake	Oligotrophic	USA
E. Twin	47°10'27.4"N / 95°09'53.2"W	Lake	Eutrophic	USA
Mary	47°11'06.2"N / 95°10'00.7"W	Lake	Oligotrophic	USA
Elk	47°11'21.5"N / 95°13'00.5"W	Lake	Eutrophic	USA
Itasca	47°11'56.6"N / 95°10'34.1"W	Lake	Eutrophic	USA
Ozawandib	47°13'50.1"N / 95°16'19.0"W	Lake	Oligotrophic	USA
Long	47°16'34.5"N / 95°17'57.1"W	Lake	Eutrophic	USA
Vermilion	47°52'40.9"N / 92°28'34.4"W	Lake	Oligotrophic	USA
Escondido	54°31'48.9"S / 67°12'01.7"W	Lake	Oligotrophic	ARG

Fonte: Elaborado pela autora (2021).

Table 2 - Statistical information

Stoichiometric ratios vs. Latitude

		<i>Seston</i>	<i>Bacteria</i>
<i>C: N</i>	R ²	0.2	0.04
	p-value	0.0006	0.1412
<i>N: P</i>	R ²	0.1	0.001
	p-value	0.016	0.7711
<i>C: P</i>	R ²	0.31	0.02
	p-value	0.001	0.3598

Fonte: Elaborado pela autora (2021).

Table 3 - Statistical information

Stoichiometric ratios vs. Latitude (environments divided by trophic status)

		<i>Eutrophic</i>		<i>Oligotrophic</i>	
		<i>Seston</i>	<i>Bacteria</i>	<i>Seston</i>	<i>Bacteria</i>
<i>C: N</i>	R ²	0.38	0.18	0.12	0
	p-value	0.0006	0.0282	0.0659	0.9486
<i>N: P</i>	R ²	0.01	0.08	0.21	0.02
	p-value	0.7026	0.143	0.0136	0.4526
<i>C: P</i>	R ²	0.13	0.03	0.44	0.03
	p-value	0.0627	0.3959	0.0001	0.3484

Fonte: Elaborado pela autora (2021).

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**APPENDIX 1 – STOICHIOMETRIC RATIOS OF SESTON AND BACTERIA –
LATITUDINAL BANDS (FIGURE 6)**

N: P seston

Residuals				
Min	1Q	Median	3Q	Max
-41.22	-11.236	0.439	9.476	116.041

Coefficients:

	Std.		t value	Pr(> t)
	Estimate	Error		
(Intercept)	28.277	4.364	6.48	3.09e-08 ***
Fator1Tropical	13.236	7.849	1.686	0.0976

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 26.9 on 53 degrees of freedom

Multiple R-squared: 0.05092, Adjusted R-squared: 0.03301

F-statistic: 2.844 on 1 and 53 DF, p-value: 0.09761

C: P seston

Residuals				
Min	1Q	Median	3Q	Max
-589.64	-121.38	-4.06	83.23	1535.09

Coefficients:

	Std.		t value	Pr(> t)
	Estimate	Error		
(Intercept)	258.89	58.48	4.427	4.81e-05 ***
Fator1Tropical	340.45	105.19	3.236	0.00209 **

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 360.5 on 53 degrees of freedom

Multiple R-squared: 0.165, Adjusted R-squared: 0.1493

F-statistic: 10.47 on 1 and 53 DF, p-value: 0.002088

C: N seston

Residuals				
Min	1Q	Median	3Q	Max
-11.811	-3.716	-2.147	-0.64	36.013

Coefficients:				
	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	10.893	1.369	7.955	1.32e-10 ***
Fator1Tropical	9.055	2.463	3.677	0.000552 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
 Residual standard error: 8.441 on 53 degrees of freedom
 Multiple R-squared: 0.2032, Adjusted R-squared: 0.1882
 F-statistic: 13.52 on 1 and 53 DF, p-value: 0.0005524

N: P bacteria

Residuals				
Min	1Q	Median	3Q	Max
-25.355	-6.902	1.728	8.385	57.592

Coefficients:				
	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	25.556	2.698	9.471	5.44e-13 ***
Fator1Tropical	-1.052	4.854	-0.217	0.829

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
 Residual standard error: 16.63 on 53 degrees of freedom
 Multiple R-squared: 0.0008853, Adjusted R-squared: -0.01797
 F-statistic: 0.04696 on 1 and 53 DF, p-value: 0.8293

C: P bacteria

Residuals				
Min	1Q	Median	3Q	Max
-249.56	-94.75	-8.05	58.47	1423.12

Coefficients:				
	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	218.89	38.32	5.712	5.18e-07 ***
Fator1Tropical	33.28	68.92	0.483	0.631

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
 Residual standard error: 236.2 on 53 degrees of freedom
 Multiple R-squared: 0.00438, Adjusted R-squared: -0.01441
 F-statistic: 0.2332 on 1 and 53 DF, p-value: 0.6312

C: N bacteria

Residuals				
Min	1Q	Median	3Q	Max
-13.396	-2.407	-1.151	0.321	34.658

Coefficients:				
	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	9.577	1.259	7.604	4.82e-10 ***
Fator1Tropical	6.597	2.265	2.912	0.00524 **

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
 Residual standard error: 7.764 on 53 degrees of freedom
 Multiple R-squared: 0.138, Adjusted R-squared: 0.1217
 F-statistic: 8.481 on 1 and 53 DF, p-value: 0.00524

N: P seston

Residuals				
Min	1Q	Median	3Q	Max
-41.669	-13.592	-0.535	8.489	113.365

Coefficients:				
	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	20.11	4.761	4.224	9.49e-05 ***
Fator1Oligotrophic	24.08	6.673	3.608	0.000683 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
 Residual standard error: 24.74 on 53 degrees of freedom
 Multiple R-squared: 0.1972, Adjusted R-squared: 0.1821
 F-statistic: 13.02 on 1 and 53 DF, p-value: 0.0006827

C: P seston

Residuals				
Min	1Q	Median	3Q	Max
-431.53	-189.86	-74.45	65.28	1627.72

Coefficients:				
	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	216.24	70.39	3.072	0.00335 **
Fator1Oligotrophic	290.46	98.65	2.944	0.00480 **

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
 Residual standard error: 365.7 on 53 degrees of freedom
 Multiple R-squared: 0.1406, Adjusted R-squared: 0.1244
 F-statistic: 8.669 on 1 and 53 DF, p-value: 0.004796

C: N seston

Residuals

Min	1Q	Median	3Q	Max
-8.886	-5.728	-4.076	2.511	33.919

Coefficients:

	Std.		t value	Pr(> t)
	Estimate	Error		
(Intercept)	14.422	1.814	7.949	1.35e-10 ***
Fator1Oligotrophic	-1.435	2.543	-0.564	0.575

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 9.428 on 53 degrees of freedom

Multiple R-squared: 0.005972, Adjusted R-squared: -0.01278

F-statistic: 0.3184 on 1 and 53 DF, p-value: 0.5749

N: P bacteria

Residuals

Min	1Q	Median	3Q	Max
-31.788	-9.451	1.547	8.105	50.108

Coefficients:

	Std.		t value	Pr(> t)
	Estimate	Error		
(Intercept)	18.223	2.905	6.274	6.62e-08 ***
Fator1Oligotrophic	13.765	4.071	3.381	0.00136 **

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 15.09 on 53 degrees of freedom

Multiple R-squared: 0.1774, Adjusted R-squared: 0.1619

F-statistic: 11.43 on 1 and 53 DF, p-value: 0.001362

C: P bacteria

Residuals				
Min	1Q	Median	3Q	Max
-290.62	-131.58	-4.42	49.44	1381.76

Coefficients:				
	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	162.44	43.71	3.716	0.000488 ***
Fator1Oligotrophic	131.09	61.26	2.14	0.036989 *

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 227.1 on 53 degrees of freedom

Multiple R-squared: 0.07953, Adjusted R-squared: 0.06216

F-statistic: 4.579 on 1 and 53 DF, p-value: 0.03699

C: N bacteria

Residuals				
Min	1Q	Median	3Q	Max
-7.513	-5.138	-2.374	1.041	37.361

Coefficients:				
	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	13.471	1.569	8.585	1.32e-11 ***
Fator1Oligotrophic	-3.644	2.199	-1.657	0.103

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 8.153 on 53 degrees of freedom

Multiple R-squared: 0.04925, Adjusted R-squared: 0.03131

F-statistic: 2.745 on 1 and 53 DF, p-value: 0.1035

APPENDIX 2 – ECOSYSTEMS AND NUTRIENT DATA

<i>System name</i>	<i>C seston</i>	<i>C bacteria</i>	<i>N seston</i>	<i>N bacteria</i>	<i>P seston</i>	<i>P bacteria</i>
Extremoz	120.696	7.202	12.427	2.238	0.185	0.080
Lagoa Azul	736.222	23.390	54.345	2.889	0.345	0.059
E. A. Jundiaí	41.650	7.052	3.194	1.405	0.028	0.025
Jambeiro	267.917	10.040	18.274	3.614	0.411	0.092
Jiqui	55.561	9.701	2.795	0.697	0.081	0.037
Ilhota	116.481	16.540	5.163	1.397	0.086	0.037
Bonfim	13.563	8.845	1.667	0.433	0.031	0.005
Carcará	66.250	11.235	4.468	1.102	0.085	0.033
Calimã	204.083	18.056	10.653	2.435	0.299	0.121
Arituba	103.095	23.506	6.376	1.912	0.113	0.081
Cruzeta	207.315	28.844	20.558	3.603	0.887	0.136
Junin	1.214	0.033	0.026	0.002	0.002	0.012
Chapeu Duvas	0.068	0.024	0.003	0.002	0.001	0.005
Santa Fé	0.067	0.032	0.002	0.002	0.002	0.006
Bonfante	0.047	0.042	0.002	0.001	0.005	0.007
Monte Serrat	0.065	0.028	0.002	0.001	0.002	0.011
Broa	0.080	0.060	0.004	0.002	0.006	0.012
Funil	0.068	0.034	0.002	0.001	0.007	0.008
Río Luján	0.170	0.075	0.028	0.00349	0.003	0.0003
Lobos	0.539	0.092	0.034	0.011	0.054	0.052
Chascomús	0.196	0.047	0.006	0.003	0.010	0.001
E. Okoboji	253.140	263.010	34.600	35.790	1.596	1.660
W. Okoboji	35.930	41.330	4.340	5.060	0.141	0.181
Center	398.120	411.170	43.820	45.500	2.251	2.402
Spirit	271.140	280.820	32.810	34.080	0.979	1.057
Bella	949.440	970.310	160.070	162.860	6.349	6.526
Okabena	51.680	64.390	6.620	8.170	0.725	0.812
Hall	343.260	357.510	48.040	50.290	1.343	1.532
Fox	234.820	243.100	23.520	24.510	0.914	0.980
Big Twin	640.860	658.270	67.820	69.560	2.635	2.753
Fish	72.070	78.520	7.870	8.610	0.541	0.591
Mitchell	163.430	180.160	19.420	21.380	0.857	0.985
Christmas	38.270	41.680	4.150	4.520	0.107	0.129
Minnetonka	40.320	44.020	4.610	5.000	0.128	0.176
Round	41.060	60.570	5.590	7.750	0.274	0.422
McCarrons	42.490	49.310	10.360	11.870	0.216	0.298
Medicine	296.030	306.170	36.190	37.700	0.829	0.911
Josephine	30.060	37.830	4.140	5.190	0.188	0.260
Owasso	130.180	141.650	18.060	19.590	0.661	0.718
Owasso	48.640	55.240	7.040	7.910	0.210	0.262
Johanna	40.100	46.930	4.990	5.800	0.067	0.162
Eagle	268.620	286.810	29.460	31.960	0.828	1.062
Turtle	112.710	124.170	6.800	12.630	0.194	0.225

Boot	20.720	25.730	2.240	2.830	0.061	0.085
Josephine	25.810	33.000	2.250	2.860	0.071	0.101
Arco	100.810	110.270	14.310	15.560	0.485	0.546
Deming	124.770	132.320	17.190	18.210	0.372	0.413
E. Twin	40.230	47.400	4.030	5.030	0.192	0.235
Mary	34.920	40.460	3.540	4.060	0.081	0.110
Elk	43.970	53.830	4.250	5.450	0.148	0.218
Itasca	58.560	71.170	7.490	9.130	0.413	0.477
Ozawandib	34.140	40.710	3.360	4.000	0.095	0.125
Long	28.610	34.260	3.240	3.890	0.100	0.133
Vermilion	72.660	76.550	9.680	10.270	0.232	0.271
Escondido	0.080	0.072	0.003	0.003	0.001	0.006

APPENDIX 3 – ECOSYSTEMS AND STOICHIOMETRIC RATIOS

<i>System name</i>	<i>C: N seston</i>	<i>C: N bacteria</i>	<i>N: P seston</i>	<i>N: P bacteria</i>	<i>C: P seston</i>	<i>C: P bacteria</i>
Extremoz	9.71	3.22	67.25	27.95	653.18	89.94
Lagoa Azul	13.55	8.10	157.55	48.86	2134.43	395.57
E. A. Jundiaí	13.04	5.02	115.25	57.02	1502.67	286.24
Jambeiro	14.66	2.78	44.45	39.12	651.64	108.67
Jiqui	19.88	13.92	34.38	18.86	683.37	262.50
Ilhota	22.56	11.84	59.87	37.80	1350.79	447.55
Bonfim	8.14	20.41	53.06	82.10	431.75	1675.29
Carcará	14.83	10.20	52.56	33.54	779.41	341.99
Calimã	19.16	7.41	35.59	20.06	681.76	148.69
Arituba	16.17	12.30	56.61	23.51	915.35	289.11
Cruzeta	10.08	8.01	23.18	26.59	233.74	212.86
Junin	46.91	14.50	15.95	0.20	748.04	2.91
Chapeu Duvas	26.68	15.21	3.02	0.30	80.61	4.59
Santa Fé	35.46	17.04	0.82	0.32	29.03	5.51
Bonfante	26.68	50.83	0.38	0.13	10.21	6.39
Monte Serrat	36.99	35.10	0.76	0.07	28.23	2.61
Broa	18.55	29.77	0.69	0.17	12.85	5.14
Funil	32.99	23.82	0.29	0.18	9.70	4.26
Río Luján	5.99	21.47	10.63	12.68	63.74	272.26
Lobos	15.67	8.48	0.64	0.21	9.98	1.78
Chascomús	32.46	17.82	0.61	4.22	19.74	75.14
E. Okoboji	7.32	7.35	21.68	21.56	158.61	158.44
W. Okoboji	8.28	8.17	30.78	27.96	254.82	228.34
Center	9.09	9.04	19.47	18.94	176.86	171.18
Spirit	8.26	8.24	33.51	32.24	276.96	265.68
Bella	5.93	5.96	25.21	24.96	149.54	148.68
Okabena	7.81	7.88	9.13	10.06	71.28	79.30
Hall	7.15	7.11	35.77	32.83	255.59	233.36
Fox	9.98	9.92	25.73	25.01	256.91	248.06

Big Twin	9.45	9.46	25.74	25.27	243.21	239.11
Fish	9.16	9.12	14.55	14.57	133.22	132.86
Mitchell	8.42	8.43	22.66	21.71	190.70	182.90
Christmas	9.22	9.22	38.79	35.04	357.66	323.10
Minnetonka	8.75	8.80	36.02	28.41	315.00	250.11
Round	7.35	7.82	20.40	18.36	149.85	143.53
McCarrons	4.10	4.15	47.96	39.83	196.71	165.47
Medicine	8.18	8.12	43.66	41.38	357.09	336.08
Josephine	7.26	7.29	22.02	19.96	159.89	145.50
Owasso	7.21	7.23	27.32	27.28	196.94	197.28
Owasso	6.91	6.98	33.52	30.19	231.62	210.84
Johanna	8.04	8.09	74.48	35.80	598.51	289.69
Eagle	9.12	8.97	35.58	30.09	324.42	270.07
Turtle	16.58	9.83	35.05	56.13	580.98	551.87
Boot	9.25	9.09	36.72	33.29	339.67	302.71
Josephine	11.47	11.54	31.69	28.32	363.52	326.73
Arco	7.04	7.09	29.51	28.50	207.86	201.96
Deming	7.26	7.27	46.21	44.09	335.40	320.39
E. Twin	9.98	9.42	20.99	21.40	209.53	201.70
Mary	9.86	9.97	43.70	36.91	431.11	367.82
Elk	10.35	9.88	28.72	25.00	297.09	246.93
Itasca	7.82	7.80	18.14	19.14	141.79	149.20
Ozawandib	10.16	10.18	35.37	32.00	359.37	325.68
Long	8.83	8.81	32.40	29.25	286.10	257.59
Vermilion	7.51	7.45	41.72	37.90	313.19	282.47
Escondido	29.82	25.99	2.52	0.43	75.18	11.10