

## Stoichiometric constraints in plankton communities of Patagonian lakes: Implications for *Parabroteas sarsi* distribution and conservation

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**ABSTRACT.** The Patagonian region, from the Andes to the steppe, includes a profuse hydrographic network with deep and shallow lakes. Here, we analyze the stoichiometric constraints for the large predaceous copepod *Parabroteas sarsi* in fish and fishless lakes. For this purpose, we examined previous literature data on the composition of the zooplankton community in different Patagonian lakes with and without fish (mainly introduced in the XX century) and own laboratory and field experiments. The ecological stoichiometry theory predicts that consumers need to attain specific elemental ratios to achieve maximum growth, and the geometric framework of nutrition proposes that consumers may need to combine food items to fulfill nutrient requirements. We show that the predaceous copepod does not necessarily encounter prey that fulfills their stoichiometric requirements, thus growth is impaired. However, through the combination of different prey, this predator can fulfill its requirements. In the presence of fishes, food webs change towards smaller-sized zooplankton species with the loss of low C:nutrient ratio species. In this sense, we demonstrate the direct and indirect impact of fish introduction on the stoichiometric balances and the disappearance of this invertebrate predator in lacustrine food webs.

[**Keywords:** ecological stoichiometry, predation, food webs, copepods, cladocerans]

**RESUMEN. Restricciones estequiométricas en las comunidades planctónicas de lagos patagónicos: Implicancias para la distribución y la conservación de *Parabroteas sarsi*.** La Región Patagónica, que incluye desde los Andes hasta la estepa, posee una red hidrográfica profusa, con lagos profundos y someros. En este trabajo analizamos las restricciones estequiométricas en redes tróficas con la presencia del copépodo depredador *Parabroteas sarsi*. Para ello, examinamos datos previos sobre la composición de la comunidad del zooplancton en lagos patagónicos con y sin peces (introducidos principalmente en el siglo XX) y experimentos propios de laboratorio y de campo. La estequiometría ecológica predice que los consumidores necesitan obtener relaciones elementales específicas para alcanzar máximas tasas de crecimiento. Por su parte, el marco geométrico de la nutrición propone que los consumidores pueden necesitar incluir diferentes ítems alimentarios para cumplir con sus requerimientos nutricionales. En este sentido, demostramos que el copépodo depredador no necesariamente encuentra presas que cumplan con sus requisitos estequiométricos, por lo que su crecimiento poblacional se ve limitado. Sin embargo, la combinación de diferentes presas le permite a este copépodo alcanzar sus requerimientos elementales. En presencia de peces, las redes alimentarias cambian hacia especies del zooplancton de menor tamaño y se pierden especies con menor relación carbono:nutrientes. En tal sentido, señalamos el impacto directo e indirecto de la introducción de peces en los balances estequiométricos y en la desaparición de este depredador invertebrado en las redes tróficas lacustres.

[**Palabras clave:** estequiometría ecológica, depredación, tramas tróficas, copépodos, cladóceros]

### INTRODUCTION

Ecological stoichiometry examines, through the study of elemental imbalances, the trophic relationships linking the elemental composition of organisms with their food web interactions and ecosystem functioning (Sterner and Elser 2002). The transfer of different elements (C, N and P) may be limited by the specific metabolic needs of each organism, which will, in turn, affect the quality of available resources for higher trophic levels (Elser et al. 2003). Primary

producers reflect the nutrient status and light availability of their surrounding environment (weak stoichiometric homeostasis) and can achieve divergent C:N:P when limited by nutrients (Sterner et al. 1997; Sterner and Elser 2002) because they obtain energy (mostly sunlight) and nutrients from different, uncoupled, sources within their environment. In contrast, consumers exhibit a greater degree of regulation of their elemental body composition (stoichiometric homeostasis)

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because elements are bonded together in the biochemical constituents of their food (Frost et al. 2005). This condition implies that primary consumers may face elemental imbalances with their food (Elser et al. 2003; Acharya et al. 2004). However, feeding on different algae species may provide multiple elements in different ratios than those provided by a single species; thus, herbivores can optimize their dietary stoichiometry when feeding on a diverse natural prey assemblage (Herstoff et al. 2021). Although studies on these imbalances in consumer-resource interactions have mainly focused on autotroph/herbivore dynamics (Acharya et al. 2004; Andersen et al. 2004), stoichiometric constraints may also affect interactions between species regardless of their trophic level (Moe et al. 2005). In this sense, invertebrate planktonic predators are also highly vulnerable to stoichiometric imbalances, whether excess or deficit of nutrients in different prey is involved (Laspoumaderes et al. 2015).

Stoichiometric homeostasis (i.e., the degree to which organisms regulate their elemental composition when facing imbalanced resources) is important for understanding the nature of trophic interactions in food webs (Sterner and Elser 2002). However, this concept is also a key indicator of species dominance and ecosystem structure (Yu et al. 2010). Herbivore recycling will have larger effects on producer biomass, and predator-prey feeding relationships are key determinants of the strength of cascading trophic interactions (Leroux and Michel 2010). Thus, the stoichiometric theory can lead to understand the effect of multiple anthropogenic and natural perturbations on populations and species interactions (Andersen et al. 2004). Therefore, to conserve key ecosystem services is important not only to pay attention to overall biodiversity but also to species having different stoichiometric homeostasis, as strongly homeostatic species are especially important in maintaining high production and ecological resistance to disturbances (Yu et al. 2010).

Elemental mismatches at the base of the food web (primary producers) can have different effects on higher trophic levels (predators) depending on the capacity of the species in the primary consumer assemblage (prey) to deal with imbalanced resources. Elemental imbalances could be sufficiently large to change the elemental composition of the prey assemblage (Hall et al. 2004; Laspoumaderes

et al. 2013) and hence food quality for predators. As a consequence, predators can suffer nutritional imbalances as a result of weak stoichiometric homeostasis in their prey (Malzahn et al. 2007; Boersma et al. 2009; Schoo et al. 2010) or due to changes in the relative availability of stoichiometrically contrasting prey.

The planktonic food web of Patagonian lakes has four main trophic levels: producers, herbivores, planktivores (both invertebrate and vertebrate predators) and piscivores; although, vertebrate planktivores and piscivores are facultative. Nutrient limitation is a common feature for many Patagonian aquatic environments resulting in high C:nutrient ratios in algae in response to such resource limitation (Balseiro et al. 2004; 2007), that impose low food quality for upper trophic levels (Balseiro et al. 2008; Laspoumaderes et al. 2013). It is remarkable the presence of a large calanoid copepod *Parabroteas sarsi* that preys on a vast variety of organisms including large algae, rotifers, cladocerans and copepods (Balseiro and Vega 1994; Vega 1995). This copepod is extremely sensitive to fish introduction, a common practice in Patagonia. It disappeared in shallow lakes that were stocked with fishes (Modenutti and Balseiro 1994; Reissig et al. 2006; Lancelotti et al. 2017) but it remained in some deep lakes due to the presence of an effective depth refuge (Reissig et al. 2004). In previous studies analyzing natural and experimental populations of *P. sarsi*, we found variable homeostatic responses (regarding carbon:phosphorus —C:P— ratios) as a result of different feeding strategies throughout ontogeny (Laspoumaderes et al. 2010) and a high sensitivity to prey quality (C:P) in later instars (Laspoumaderes et al. 2015). Here, we will analyze the structuring of pelagic food webs through stoichiometric limitation in different lakes of Patagonia with the presence of the predator *P. sarsi*. The different analyses are based on literature data including the distribution and field and experimental data on this large predator. We suggest that fish stocking in naturally fishless lakes has the potential to produce substantial stoichiometric imbalances in the food web. We will discuss the direct and indirect effect of fish introduction on population limitation of *P. sarsi* due to direct fish predation but also due to the alteration in the zooplanktonic community structure that leads to stoichiometric imbalances generated by the loss of certain prey. These concepts are important for the conservation practices of this

endangered top predator of the Patagonian indigenous food web.

## MATERIALS AND METHODS

Data on *P. sarsi* was obtained from published literature (Scopus®) including their distribution (Heywood 1967; Heywood 1970; Hansson and Tranvik 1996; Reissig et al. 2006; De los Ríos and Rivera 2008; Diaz et al. 2019 and data therein) and ecological data (Table 1). In addition, we re-analyzed our

own ecological data on the stoichiometric constraint of the species (Laspoumaderes et al. 2010; 2015) to explain their prevalence in the different systems and fish impacts that affect this particular species. The C:P ratios were calculated from direct measurements of particulate C and P. Carbon was measured in a Thermo Finnigan EA1112 CN analyzer and P with the ascorbate-molybdenum method (APHA 2005). Body sizes were obtained by measuring individuals under stereomicroscope.

**Table 1.** Summary of the scientific publication concerning field studies and experiments on *Parabroteas sarsi* trophic relationship and population control.

**Tabla 1.** Resumen de las contribuciones científicas sobre estudios a campo y experimentales en las relaciones tróficas y control poblacional de *Parabroteas sarsi*.

Waterbody	Main findings	Study Type	References
Lakes Carrillaufquen, NF1 and Ne Luan	Absence in the presence of fish	Field Study	Modenutti and Balseiro 1994
Laguna Fantasma	Antipredator defenses. Predation evasion	Laboratory experiments	Balseiro and Vega 1994
Laguna Fantasma	Sexual dimorphism, Predation rates	Laboratory experiments	Vega 1995
South Georgia	Predation impact	Field study experiments	Hansson and Tranvik 1996
Laguna Fantasma	Functional responses of predation	Experimental study	Vega 1997
Laguna Fantasma	Predation impact on zooplankton	Field study	Vega 1998
Laguna Fantasma	Antipredator defenses	Field study and laboratory experiments	Diéguez and Balseiro 1998
Laguna Fantasma	Diet and developmental stages. Sexual dimorphism	Field study	Vega 1999
Antarctic lakes	Food webs	Field study/isotopes	Hansson and Tranvik 2003
Lake Rivadavia	Cascading effect on microbial food web	Field incubation experiments	Modenutti et al. 2003
Lake Puesto, Toro and Flamingo	Mycosporine-like amino-acids (MAAs) content	Field study	Tartarotti et al. 2004
Lake Rivadavia	Vertical distribution. Predation rates	Field study and laboratory experiments	Reissig et al. 2004
Different lakes in Patagonia	Absence in the presence of fish	Field study	Reissig et al.2006
Laguna Los Juncos	UVR exposition	Experimental study	De Los Ríos 2007
Lagunas Mallín, Ñirihuau, Fantasma and Chancho	Predation on <i>P. sarsi</i> by <i>Mesostoma</i>	Field study and laboratory experiments	Trochine et al. 2008
Laguna Fantasma	MAAs accumulation by radiation exposure	Laboratory experiments	García et al. 2010
Laguna Fantasma	Rotifer predation	Laboratory experiments	Gilbert and Diéguez 2010
Laguna Fantasma	Oxidative stress, carotenoids and other defense mechanisms	Laboratory experiments	Souza et al. 2010
Laguna Fantasma	Diet, stoichiometry and developmental stages.	Field study	Laspoumaderes et al. 2010
Laguna Fantasma	Predation on <i>P. sarsi</i> by <i>Notonecta</i>	Experimental study	Jara et al. 2012
Laguna Fantasma	Sexual dimorphism	Field study	García et al. 2013
Laguna Fantasma	Stoichiometric constraint, knife edge hypothesis	Experimental study	Laspoumaderes et al. 2015
Santa Cruz pond	Absence in the presence of fish	Field study	Lancelotti et al. 2017
Laguna Fantasma	Oomycetes diseases effect on survival	Field study	García et al. 2018
Laguna Los Juncos	Antipredator induced defenses	Experimental study	Wolinski et al. 2020

## RESULTS AND DISCUSSION

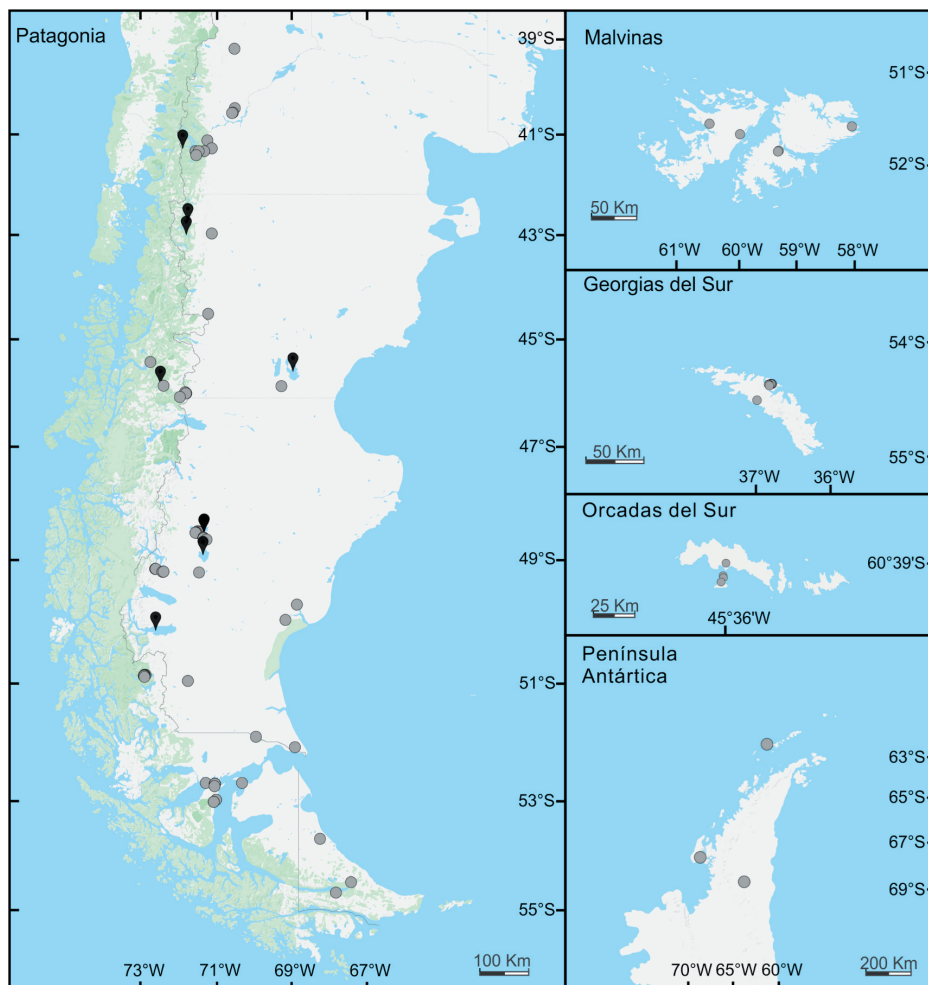
### *Parabroteas sarsi* distribution and differences in morphology

This copepod inhabits shallow ponds and large and deep lakes from Southern South America and Antarctic and Subantarctic lakes (45–68° S) (Bayly 1992; Diaz et al. 2019) (Figure 1). The species is one of the largest planktonic copepods in the world since the body is up to 7.5 mm in length and has a marked sexual dimorphism with females larger than males (Heywood 1967; 1970). Larger individuals (5–7 mm) are generally present in shallow lakes (Balseiro and Vega 1994; Hansson and Tranvik 2003). In these environments, the species is red-pigmented due to the presence of carotenoids (Souza et al. 2010) presenting also a high concentration of UV-protecting

compounds as Mycosporin like Amino Acids (MAAs) (Tartarotti et al. 2004; García et al. 2010). However, individuals from deep lakes are colorless and smaller in size (3–3.2 mm) (Reissig et al. 2004). Interestingly, in the genetic study of copepods from Patagonia Adamowicz et al. (2007) detected for *P. sarsi* a great intraspecific genetic diversity, with two lineages showing 5.5% divergence. However, further genetic, morphological, or breeding evidence should be investigated to arrive at conclusive results about the nature of these lineages (Adamowicz et al. 2007).

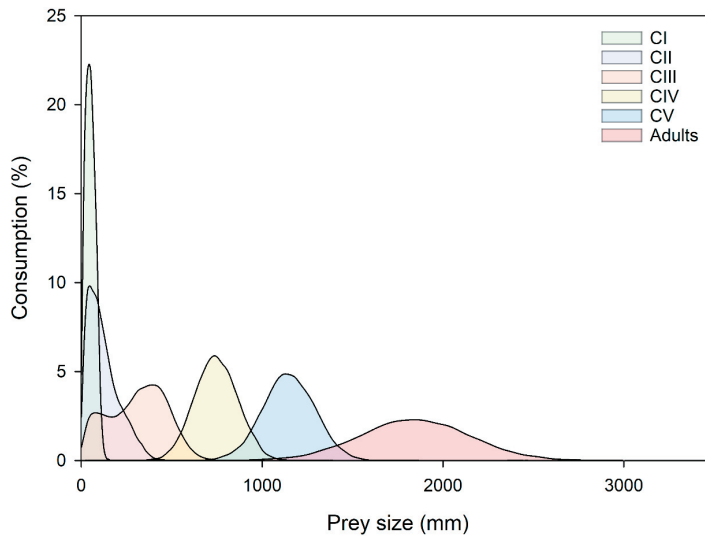
### *Diet and stoichiometric constraints*

*Parabroteas sarsi* switches from microphagy (20–100 µm) in nauplii and copepodites I to macrophagy (100 µm up to 3 mm) as it molts to later instars (Figure 2). The second and the third



**Figure 1.** Map of the distribution of the predaceous copepod *Parabroteas sarsi*. Black symbols indicate lakes with fish; grey circles, fishless lakes.

**Figura 1.** Mapa con la distribución de *Parabroteas sarsi*. Símbolos negros indican lagos con peces; símbolos grises, lagos sin peces.



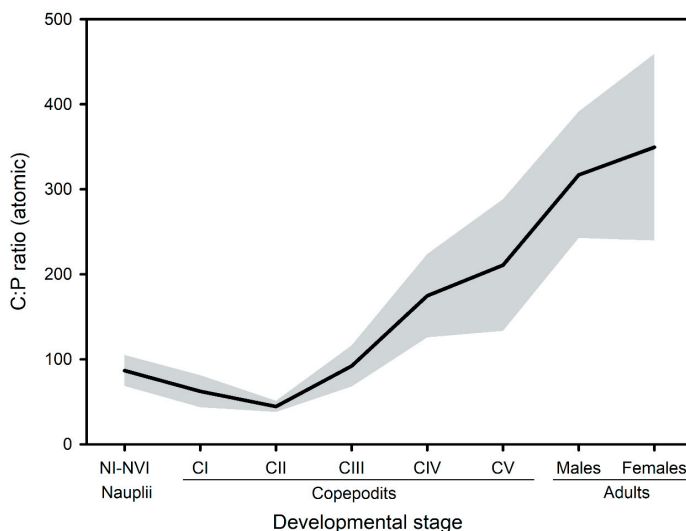
**Figure 2.** Size spectrum of food items eaten by each developmental copepodite and adult instar of *Parabroteas sarsi*.

**Figura 2.** Espectro de tamaños de los ítems alimentarios de cada estadio de desarrollo de copepoditos y adultos de *Parabroteas sarsi*.

copepodite developmental stage (CII and CIII) begins to ingest some animal items (rotifers) in addition to algae. Copepodite stages CIV and CV and adults feed predominately on animal food items (cladocerans and copepods). During development, there is an exponential increase in the size of the mouthparts of the predator, in particular the grasping maxillipeds (Diéguez and Balseiro 1998). In addition, the morphology of the mandibles changes from molar shape to teeth pointed shaped mandibles (Balseiro personal observation). These morphological changes allow the predator to access larger prey. However, larger prey implies an increase in the handling time decreasing the predation rate (Vega 1997). Thus, an increase in prey size (i.e., *Daphnia* and *Conochilus*) with the concomitant development of the predator results in an effective antipredator strategy

(Balseiro and Vega 1994; Diéguez and Balseiro 1998; Wolinski et al. 2020). This is of particular importance in temporary ponds where *P. sarsi* populations develop univoltine and synchronous generations (Diéguez and Balseiro 1998; Vega 1999).

The changes in food items can be related to stoichiometric imbalances during the developmental stages of the copepod. Interestingly, during the transition from microphagy (mostly algae) to macrophagy (mostly crustaceans), there is a reduction in the elemental imbalance between *P. sarsi* and its food (Laspoumaderes et al. 2010). Noticeably, there is a weakening in the stoichiometric homeostasis during ontogeny as revealed by the increase in the variability of C:P (Figure 3). A high imbalance and a low somatic C:P variability imply a great investment in



**Figure 3.** Changes in the C:P ratio of *Parabroteas sarsi* throughout its development. Grey area denotes the standard deviation of the elemental ratio.

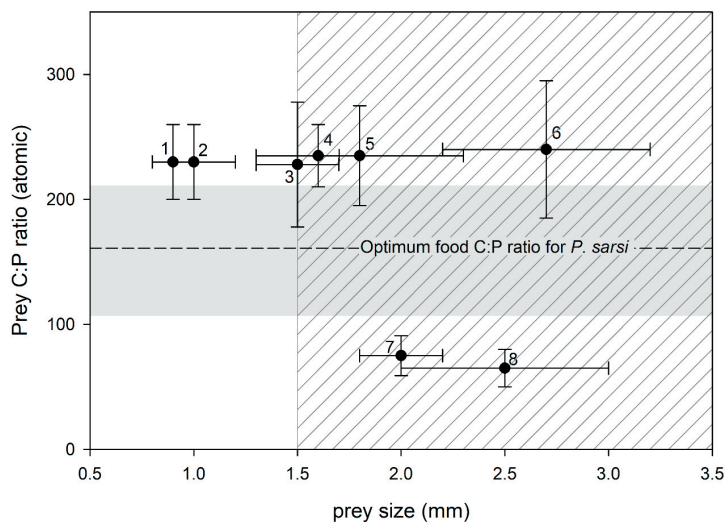
**Figura 3.** Cambios en las relaciones C:P de *Parabroteas sarsi* a lo largo del desarrollo. El área gris indica una desviación estándar.

maintaining the internal body elemental ratio (strong stoichiometric homeostasis) (Wang et al. 2012). As *P. sarsi* shifts diet during development, the difference between the elemental ratios (C:P ratio) of the food and that of the copepod decreases, reducing the elemental imbalance faced by the copepod (Laspoumaderes et al. 2010). Thus, the early stages of copepodites (CI and CII) have a great imbalance, but with a rather low and very stable somatic elemental ratio (Figure 3). However, when *P. sarsi* shifts diet towards animal prey faces a lower imbalance (animal prey have much similar elemental ratios) but shows a higher variability in its somatic C:P ratio (Figure 3). This increase in variability with low elemental imbalance implies an extremely low investment in maintaining the elemental somatic ratio (weak stoichiometric homeostasis). As shown in an experiment where adults of *P. sarsi* were fed only one of its main prey (*Boeckella gracilis* vs. *Daphnia commutata*), the prey C:P ratio greatly affected their elemental composition (Laspoumaderes et al. 2015). This implies that secondary production of *P. sarsi* would depend greatly on the selected prey or combination of prey that ensures the required body C:P ratio.

The later instar of copepodites (CIV and CV) and adults access to a variety of prey, that

include not only different sizes but a wide range in somatic C:P ratios. Prey sizes range from 1 mm (*Boeckella gracilipes* and *Boeckella michaelsoni*) to 3 mm (*Boeckella poppei* and *D. commutata*) with intermediate sizes (around 2 mm) in other *Boeckella* species and *Daphnia dadayana* (Figure 4). In addition, prey exhibit differences in C:P ratio having the cladocerans the lowest C:P (around 60) while copepods show higher values (200-300) (Figure 4). Thus, the ingestion of a variety of prey with different elemental compositions, as it was observed in natural environments (Laspoumaderes et al. 2010), would balance the predator somatic C:P ratio. In this sense, the coexistence with alternative prey (cladocerans and copepods or different copepod species) will favor the persistence and growth of this giant predator copepod.

The growth rate hypothesis states that differences in C:P ratios imply differential allocation of P to rRNA for the synthesis necessary for acquiring rapid growth rates (Elser et al. 2003). Thus, a reduction in P availability will reduce growth rates (Hessen et al. 2002). However, the relationship between C:P ratio of the food and the achieved growth rates does not vary monotonically but shows a humped-shaped curve with an optimum food elemental ratio (Boersma and Elser 2006). This



**Figure 4.** Size and C:P ratio of the potential prey of *Parabroteas sarsi*. The solid horizontal line indicates the optimum C:P ratio of the food and the grey area indicates the C:P ratio of the food that allows positive growth of the predator. The striped area indicates the sizes of zooplankton that are removed by fish introduction. 1: *Boeckella gracilipes*; 2: *B. michaelsoni*; 3: *B. gracilis*; 4: *B. gibbosa*; 5: *B. brevicaudata*; 6: *B. poppei*; 7: *Daphnia dadayana*; 8: *D. commutata* (1-6: calanoid copepods; 7-8: cladocerans).

**Figura 4.** Tamaños y relaciones C:P de presas potenciales de *Parabroteas sarsi*. La línea horizontal indica la relación C:P óptima del alimento y el área gris indica la relación C:P del alimento que permite crecimiento positivo del depredador. El área rayada indica los tamaños del zooplancton que son removidos por la introducción de peces. 1: *Boeckella gracilipes*; 2: *B. michaelsoni*; 3: *B. gracilis*; 4: *B. gibbosa*; 5: *B. brevicaudata*; 6: *B. poppei*; 7: *Daphnia dadayana*; 8: *D. commutata* (1-6: copépodos calanoideos; 7-8: cladóceros).

curve is known as the knife-edge hypothesis and means that too low C:P food would be as bad as too high C:P, regardless of the P content (Bullejos et al. 2014; Elser et al. 2016).

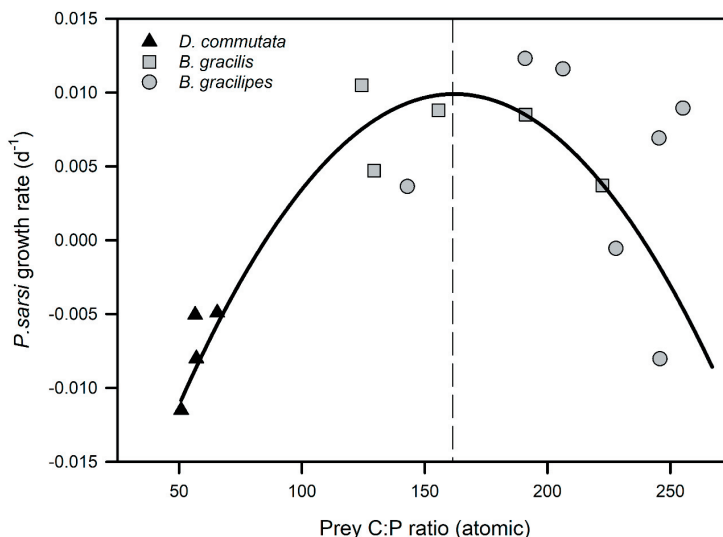
When consumers have food items that do not match the consumer's requirement (i.e., excess of an element and deficit of other), they can display a compensatory feeding (Suzuki-Ohno et al. 2012) to acquire enough of the element in deficit. However, this behavior implies overconsumption of the element in excess and the need to get rid of it (Darchambeau et al. 2003). Alternatively, it has been proposed that consumers may combine food items of different quality to obtain food that fulfills the consumer's requirements. This food compensation has been conceptualized in the Geometric Framework of Nutrition (Raubenheimer and Simpson 2004; Simpson and Raubenheimer 2011; Sperfeld et al. 2017). In the case of the predator copepod *P. sarsi*, the C:P ratio of most prey differ from the optimum one for the predator (Figure 4). This implies that one prey alone cannot adequately feed the predator, that has such low homeostatic capability. In addition, the growth rates of this predator are very sensitive to the elemental ratios of its food (Figure 5). However, the combination of prey (mainly copepods and *Daphnia*) would provide a balanced diet to ensure an adequate C:P ratio for maximum growth.

Food items selection by copepods, based on their elemental ratio was demonstrated for the marine copepod *Acartia tonsa* (Meunier et al. 2016; Herstoff et al. 2021). In this case, the copepods were able to effectively select

diatoms that better match the required elemental ratio. Similarly, *P. sarsi* does not encounter prey that matches its optimum C:P for growth. However, the predator combines different food items and, in this way, can achieve the required nutrition (Figure 4). The humped growth-food quality relationship observed for this copepod (Figure 5) shows that this predator has a very narrow C:P range that allows positive growth (shaded area in Figure 4). Strikingly, no prey matches such elemental ratio within the range of C:P where *P. sarsi* females have positive growth, regardless of the lake. Consequently, this predator needs to combine prey including cladocerans to attain positive growth.

#### Food webs

Early studies in the Antarctic region described this copepod in lakes lacking fish, mollusks, macrophytes and often insect larvae (Heywood 1970). Thus, studies have considered this predator interacting with two functionally important trophic levels (i.e., primary producers and grazers) (Hansson and Tranvik 1996, 2003). However, more recent studies in Patagonia revealed that *P. sarsi* is present in both, deep and shallow lakes interacting in different levels of complexity in food webs (Modenutti et al. 2010). From a total of 101 Patagonian aquatic environments (deep and shallow lakes and wetlands) from Chile and Argentina in which the presence of *P. sarsi* was observed (Figure 1), 92 of them were fishless, while in lakes with fishes, 7 correspond to deep lakes (presence of a vertical refuge) and only 2 to shallow vegetated lakes.



**Figure 5.** The growth rate - C:P ratio of food relationship of *Parabroteas sarsi*. Note the humped-shaped curve that fits the knife-edge hypothesis.

**Figura 5.** Relación tasa de crecimiento - C:P del alimento en *Parabroteas sarsi*. Nótese la relación parabólica que se ajusta a la hipótesis del filo de la navaja.

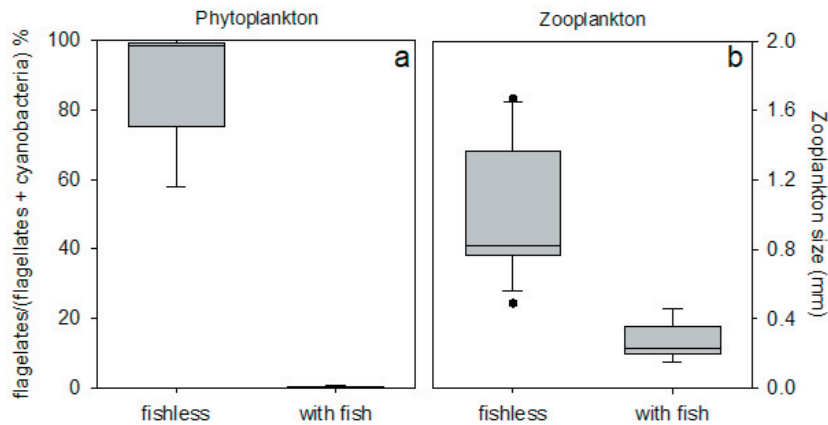
In some of the deep glacial lakes of the Patagonian Andes, *P. sarsi* is present in low abundances (Menu Marque and Marinone 1986; Pizzolon et al. 1995; Reissig et al. 2004). Individuals in these deep lakes are remarkably smaller, feeding on different prey items such as the copepod *B. michaelsoni*, cladocerans such as *D. commutata* neonates and juveniles and rotifers as *Conochilus hippocrepis* (Modenutti et al. 2003, Modenutti personal observation). *P. sarsi* presented an uneven vertical distribution inhabiting the deeper layer of the euphotic zone (approximately 30-40 m depth) (Reissig et al. 2004). These deep layers constitute an effective refuge against fish predation (Balseiro et al. 2007) since day-light strongly affects the coexistence of planktivorous fish and large zooplankton (Wright and Shapiro 1990; Tessier and Welser 1991) and dim light at deep lake layers prevents visual detection by fish (Lampert 1993; DeRobertis 2002). Patagonian deep lakes are inhabited by a mix of indigenous and exotic fish assemblage that may coexist with the predaceous copepod. Zooplankton diel vertical migration was observed in many Andean lakes and is a common behavior to avoid fish predation (Balseiro et al. 2007; Modenutti et al. 2018). Interestingly, *P. sarsi* did not display vertical migration patterns remaining in their deep refuge during day and night time (Reissig et al. 2004), where it can access their main rotifer, cladoceran, and copepod prey (Modenutti et al. 2003).

The wide diversity of Patagonian freshwater ecosystems includes a series of shallow lakes that are mainly fishless (Modenutti et al. 1998). The food webs of these shallow lakes seemed to be simple: producers, consumers and invertebrate predators (*P. sarsi*) and other facultative invertebrate predators (*Mesostoma ehrenbergi* and insects) (Trochine et al. 2008; Jara et al. 2012). In these environments, predators show uniform horizontal distribution patterns (Trochine et al. 2009) and coexist with different prey (*Boeckella* and *Daphnia* species). The role of *P. sarsi* in these environments is of a top invertebrate predator, preying upon the mentioned main grazers. However, many Patagonian fishless lakes have been stocked with fish for recreational purposes (Macchi et al. 1999). The rainbow trout (*Oncorhynchus mykiss*) is the most widely distributed salmonid species (Pascual et al. 2002) and native fishes (*Percichthys trucha* and *Odonthestes bonariensis*) were also introduced to fishless lakes (Quirós and Baigún 1985; Quirós 1990). These

introductions resulted in a strong effect on zooplankton body size, driving to a smaller and narrower size spectrum (less than 1.5 mm) (Modenutti and Balseiro 1994). In addition, loss of biodiversity and changes in biomass in both, phytoplankton and zooplankton, was observed in lakes all along Patagonia (Reissig et al. 2006) and in the Strobel and Buenos Aires plateau area (Lancelotti et al. 2017; Izaguirre et al. 2018). The disappearance of *P. sarsi* was a rule in all the shallow lakes in which fishes were introduced (Modenutti and Balseiro 1994; Reissig et al. 2006; Lancelotti et al. 2017). However, fish introduction not only implies modification in zooplankton size and biomass. Here we showed that it also has stoichiometric implications. This change in the zooplankton assemblage implies a loss of species with a low C:P ratio in particular large cladocerans such as *Daphnia*. Consequently, the predator will encounter prey with a narrow and high C:P ratio that does not fulfil its stoichiometric requirements (Figure 4). The final result would be that the copepod not only is reduced by visual predation by fish but also in their populations growth because prey assemblage does not accomplish with predator C:P stoichiometric necessities.

Anthropogenic impact by introducing species in different environments is changing the habitat in which species interactions occur. In this sense, the alteration of food webs by stocked fish produces not only a substantial change in the prey susceptible to fish predation (large zooplankton species, including *P. sarsi*) but also in lower trophic levels (algae) (Figure 6). Most of the lakes inhabited by *P. sarsi* have a mixture of potential prey for the predaceous copepod, mostly *Daphnia* spp. and different-sized species of *Boeckella*. Small *Boeckella* species (*B. gracilipes* and *B. michaelsoni*) feed mainly on nanoflagellates (Hansson and Tranvik 1996; Balseiro et al. 2001) while large species (*B. poppei*) have access to larger algae (Weller 1977). Experiments carried out in mesocosms with *P. sarsi* interacting with cladocerans and boeckellids revealed that the high predation rates on *B. michaelsoni* cascade down to nanoflagellates and picoplankton (Modenutti et al. 2003). Based on this study, it can be suggested that, in turn, the disappearance of *P. sarsi* due to fish introduction may have potential cascading effects on the food web (Figure 6). Fish introduction causes not only the disappearance of the predator but also their prey. Interestingly in an early study, Hansson and Tranvik (1996) calculated that





**Figure 6.** a) Comparison of phytoplankton between fishless shallow lakes and shallow lakes where fish has been stocked, showing the increase in the cyanobacteria (note that in fish stocked lakes, flagellates drop to almost 0 and cyanobacteria increases to more than 98%). b) Comparison of total zooplankton size between shallow fishless lakes and lakes stocked with fish.

**Figura 6.** a) Comparación del fitoplancton entre lagos someros sin peces y lagos someros a los que se les introdujeron peces, mostrando el incremento en cianobacterias (nótese que en los lagos donde se introdujeron peces, la proporción de flagelados cae casi hasta 0 y las cianobacterias aumentan a más del 98%). b) Comparación del tamaño del zooplancton (considerando todos los componentes) entre lagos someros sin peces y lagos con introducción de peces.

fish would theoretically remove up to 17% per day of the *Boeckella* population. Further evidence on Patagonian shallow lakes after fish introduction indicates a substantial reduction in zooplankton in particular of prey with stoichiometric importance (low C:P ratio) as *Daphnia*. This also caused an increase in the biomass of phytoplankton, especially with the dominance of cyanobacteria (Reissig et al. 2006; Izaguirre et al. 2018).

*Parabroteas sarsi* has a restricted distribution in South America (45–68° S); however, its presence provides important information on the quality of the environment. Shallow lakes with *P. sarsi* imply that the food web remains the original one (i.e., without or before fish introduction). This condition is important for conservation-related decisions. In particular, fish introduction in Patagonia has been related to the decline in populations of amphibians and birds (Ortubay et al. 2006; Lancelotti

et al. 2010; Lancelotti et al. 2017). Here, we showed that the maintenance of the integrity of the food web have also stoichiometric implications since the top predator attained only positive growth when a mixture of different C:P and size prey are provided (Figure 4). This condition allows the predator to maintain its elemental homeostasis. At the community level, stoichiometric homeostasis was also positively correlated with ecosystem function and stability (Yu et al. 2010). Thus, the stoichiometric homeostasis of the food web can be also a powerful bioindicator of ecosystem structure, function and stability that can be applied for conservation practices in these environments.

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