Relative contribution of top-down and bottom-up controls on the regulation of the sponge Hymeniacidon perlevis (Montagu, 1814) in Patagonia: an experimental and observational approach.

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Abstract

Two main perspectives explain the structure of food webs: bottom-up and top-down controls, respectively driven by trophic resources and consumption pressure. There is evidence of the relative contribution of both controls over sponges in tropical environments, but it is still unknown how these controls mediate the regulation of sponge populations in temperate environments. To assess this, we performed *in situ* manipulative experiments and samplings on the worldwide-distributed sponge *Hymeniacidon perlevis* in two tidal channels from San Antonio Bay (Argentine Patagonia), with different anthropic nutrients loads. We first experimentally tested the relative contribution of the top-down and bottom-up controls on the individual sponge growth. Then, we identified the consumers of *H. perlevis*, assessing their consumption pressure. Finally, we assessed the abundance of *H. perlevis* and the concentration of particulate and dissolved trophic resources for the sponge at both tidal channels. We found that *H. perlevis* was more abundant and grew more in the channel with the highest concentration of trophic resources, despite the consumption pressure of several consumers (ophiuroids, polychaetes, crabs and fishes). Among the available trophic resources, nitrate, phosphate and total suspended solids best explained the abundance pattern of *H. perlevis* throughout a year. Our results show that the abundance and individual growth of *H. perlevis* is mostly bottom-up controlled, through particulate but mainly dissolved trophic resources. The role of a symbiotic pathway in the fulfillment of the nutritional requirements of *H. perlevis* is also discussed.

Introduction

Trophic dynamics is one energy transfer process that drives the abundance and distribution of organisms (Power 1992). Two main perspectives explain the structure of food webs: the bottom-up and top-down controls (Leroux and Loreau 2015). The bottom-up control perspective states that regulation of organisms is primarily mediated by the availability of resources (e.g., abundance of primary producers, concentration of limiting nutrients such as nitrogen and phosphorus) and, therefore, the regulation of higher trophic levels depends on the abundance of organisms from lower trophic levels (Valiela et al. 1997; Trussell et al. 2006). On the other hand, the top-down control perspective states that the abundance of lower trophic levels is regulated by trophic interactions at higher levels (e.g., predation, herbivory), spilling through the food web (Menge 1992; Nielsen and Navarrete 2004; Bracken and Stachowicz 2007). For decades, there has been a debate about the relative contribution of both the top-down and bottom-up controls on the structure and functioning of coastal-marine communities and populations (Hillebrand 2002; Masterson et al. 2008; Pawlik et al. 2018). Some authors point out that many marine benthic communities are regulated by consumers (top-down controls; see Duffy and Hay 2001; Steneck and Sala 2005). On the other hand, food availability and larval recruitment are bottom-up factors that affect the structure and functioning of aforementioned communities (Burkepile and Hay 2006) and are considered as the main forces determining the outcome of top-down controls (Lesser 2006). Despite the relevance of these controls in the becoming of marine communities and populations, the relative importance of both,

and their interaction, on natural systems has only been partially addressed (but see Moksnes et al. 2008; Martinetto et al. 2011; Wulff 2017).

Sponges (*Phylum Porifera*) are a key component of benthic systems, with a wide distribution from tropical to polar environments (Bell 2008b). Sponges are filter-feeders that graze on particulate and dissolved organic carbon (POC and DOC, respectively) (McMurray et al. 2016; Pawlik et al. 2018) and they also benefit from dissolved nutrients through their symbionts (Cheshire and Wilkinson 1991; Freeman and Thacker 2011; Bainbridge et al. 2012). Regarding POC, sponges actively remove and digest viruses, bacteria, yeasts, flagellates, diatoms, ciliates and detritus (Reiswig 1971; Hay 1996; Pile et al. 1996; Diaz and Ward 1997; Fu et al. 2006; Maldonado et al. 2010), while DOC constitutes the largest part of the diet of some tropical species (e.g *Xestospongia muta*, McMurray et al. 2016; Pawlik et al. 2018). Besides POC and DOC, dissolved nutrients such as ammonium, nitrates, nitrites and phosphates seem to be crucial in sponge growth, by promoting two feeding pathways. The first is the heterotrophic -indirect- pathway, where nutrients boost the phytoplanktonic productivity, leading to a greater availability of POC for the sponge (Bainbridge et al. 2012). The second involves an autotrophic -direct- pathway based on nutrient assimilation by the sponge photosynthetic symbionts and a subsequent translocation of complex compounds (photosynthates) to the sponge (Cheshire and Wilkinson 1991; Freeman and Thacker 2011). In this sense, among many photosynthetic symbionts on sponges (eukaryotic rhodophytes, diatoms, dinoflagellates and chlorophyte; Taylor et al. 2007), cyanobacteria are the most abundant in both tropical and temperate environments (Wulff 2006; Alex et al. 2012; Thacker and Freeman 2012).

Regarding consumers, sponges are consumed by several animal species (Wulff 2006). The main consumers in tropical waters are vertebrates, such as reef fishes and turtles (Wulff 2006). Records of sponge consumers in temperate systems are scarcer and more fragmentary than in tropical environments. In temperate environments consumers of sponges are mostly invertebrates like opisthobranchs, sea stars, urchins, chitons, limpets, crabs and endobiont polychaetes (Guida 1976; Wulff 2006; López-Acosta et al. 2023).

Some authors agree that sponge populations from tropical coral reefs are mainly bottom-up controlled (Lesser 2006; Lesser and Slattery 2013; Trussell et al. 2006), whereas others point out that they are only driven by a top-down control (Pawlik et al. 2013, 2015). The former found higher growth rates in the sponges *Callyspongia vaginalis*, *Agelas conifera* and *Aplysina fistularis* as the concentration of picoplankton increases in water column along a depth gradient (Lesser 2006; Trussell et al. 2006). However, the latter found higher growth rates in the sponges *C. vaginalis*, *C. armiguera*, *Iotrochota birotulata*, *Amphimedon compressa* and *Aplysina cauliformis* incubated under consumer exclusion, regardless of the concentration or availability of planktonic food in the depth gradient (Pawlik et al. 2013). Moreover, while in coastal systems nutrient loads have been steadily increasing (Reed and Harrison 2016), some studies showed a greater abundance of sponges in nutrient-rich systems (Bell 2008b; Wulff 2012). However, a recent aquarium assay revealed that the individual growth of the sponges *Carteriospongia foliascens*, *Cliona orientalis*, *Cymbastella coralliophila*, *Ircinia ramosa* and *Stylissa*

flabelliformis, seems unaffected by artificial enrichment of water with agricultural nutrients (Ramsby et al. 2020).

The effects of dissolved (DOC and nutrients) and particulate (POC) trophic resources and consumers on the regulation of the abundance and growth of sponge populations is still a topic of discussion, and few studies have addressed *in situ* their simultaneous effects (see Wulff 2017). Although there is evidence of the relative contribution of both top-down and bottom-up controls of sponge populations in tropical environments (Lesser 2006; Trussell et al. 2006; Lesser and Slattery 2013, 2018; Pawlik et al. 2013, 2015; Wulff 2017), it is still unknown how both controls mediate the regulation of sponge populations in temperate environments. To assess the relative contribution of top-down and bottom-up controls on the regulation of a temperate sponge population, we performed samplings and *in situ* manipulative experiments, focused on the widely distributed sponge *Hymeniacidon perlevis* (Montagu 1814) as a model organism. *Hymeniacidon perlevis*, inhabit diverse habitats from the Atlantic and Pacific oceans (*see* Alex et al. 2012; Longo et al. 2010; de Voogd et al. 2022) with its southernmost record in the Southwest Atlantic at San Antonio Bay, Argentina (SAB, 40°S, Gastaldi et al. 2018). This sponge is commonly found in closed and semi-closed basins and, particularly, in polluted waters such as harbor areas (Longo et al. 2010). *Hymeniacidon perlevis* feeds on microbes, such as, bacteria and yeasts (Maldonado et al. 2010), and has a high bioremediation potential given its high capacity to remove many human and marine fauna pathogens (Fu et al. 2006; Longo et al. 2010; Maldonado et al. 2010). Additionally, *H. perlevis* harbor a high diversity of photosymbiont cyanobacteria (Alex et al. 2012), although the nutritional contribution of cyanobacteria to the sponge is still unknown. On the other hand, there is no published data on which organisms prey on *H. perlevis* throughout its range of distribution (Bell 2008a). In SAB, *H. perlevis* is the most abundant sponge being found in the intertidal and shallow subtidal, with a seasonal pattern of abundance and its growth is strongly correlated with water temperature (Gastaldi et al. 2016, 2017). It is a fast-growing sponge ($9.3 \pm 6.1\%$ cover day^{-1} in summer) that can reach up to 30 cm diameter and 10 cm high (Gastaldi et al. 2018) being more abundant in autumn and less abundant in spring (Gastaldi et al. 2016, 2017).

Previous studies showed a higher density of herbivores in a tidal channel of SAB enriched with anthropic nutrients (SAO channel), compared to a neighboring, non-enriched or control channel (CTL channel; Martinetto et al. 2010, 2011). In the SAO channel, these herbivores could likely support a higher density of consumers from upper trophic levels that also feed on sponges. However, *H. perlevis* is more abundant in the SAO channel than in the CTL channel (Gastaldi and Firstater pers comm). In this context, our main hypothesis is that, in relative terms, the population of *H. perlevis* is largely bottom-up controlled, both through dissolved and particulate trophic resources, with the consumer pressure being negligible. Thus, the main objective was to assess the relative importance of top-down and bottom-up controls on the regulation of the population of *H. perlevis*. For this, we experimentally evaluated changes on the growth of *H. perlevis* at contrasting levels of trophic resources available for the sponge (i.e. dissolved nutrients and POC proxies) and consumer presence. We investigated for the first time the consumption of *H. perlevis* by different *taxa* and developed an index to compare the consumption pressure on the sponge.

Finally, we investigated the relevance of the different trophic resources in the abundance pattern of *H. perlevis* in both channels. We specifically predict to find i., a higher individual growth of *H. perlevis* (in terms of surface area, volume and dry weight) in SAO channel than in CTL channel, regardless of the consumers presence; ii., a higher consumption pressure on *H. perlevis* in SAO than in CTL channel; iii., a higher concentration of trophic resources both dissolved nutrients (nitrate, nitrite and phosphate) and the proxies of POC (total suspended solids, organic matter and chlorophyll-*a* -as a surrogate of phytoplankton abundance-) in SAO than in CTL channel; iv., a higher sponge cover in the SAO channel, increasing along with the concentration of trophic resources.

Materials and methods

Study site

SAB, located in the northeast of the Argentine Patagonia (40° 46' S, 64° 54' W), is a hypersaline bay, given the low annual rainfall ($\sim$ 250 mm year $^{-1}$) making the salinity usually above mean values for sea water (see Pascual et al. 2001). It is a bay of 129 km^2 dominated by tidal currents with a semidiurnal and macrotidal regime (Perier 1994; Martinetto et al. 2011). The bay has a continuous input of anthropogenic nutrients from San Antonio Oeste city ($\sim$ 16000 habitants; https://www.indec.gob.ar/). Nitrogen-enriched groundwater filter directly from the house septic systems into the adjacent tidal channel (SAO channel; 88.6 µmol L^{-1} dissolved inorganic nitrogen; Teichberg et al. 2010), along with punctual industrial effluents from fish processing factories (Martinetto et al. 2011), directly affecting the flora and fauna living in the SAO channel (Martinetto et al. 2010; Teichberg et al. 2010).

Temporal samplings and *in situ* natural experiments were performed in two parallel tidal channels of SAB with similar geomorphological characteristics but contrasting anthropogenic influence. One is the aforementioned nutrient-enriched SAO channel (40°43'37" S, 64°56'54" W), and the other the control channel (CTL; 40°43'16" S, 64°56'49" W), isolated from the anthropogenic nutrient inputs by a sedimentary barrier that separate the channel from the city supply (Fig. 1). While both the concentration of dissolved oxygen and pH are higher in the SAO channel (Martinetto et al. 2011), other environmental variables of major interests for the ecology of sponges, such as water temperature, salinity, current speed and substratum composition, vary similarly throughout the year between channels (García et al. 2010; Martinetto et al. 2011; Fricke et al. 2016). Though unreplicated, natural experiments have provided valuable knowledge on ecological processes and patterns at the large and landscape scales (Davies and Gray 2015; Eger and Baum 2020). At SAB, the study of the tidal channels with contrasting anthropogenic nutrient inputs have contributed to the understanding of the eutrophication processes in coastal communities by studying benthic algal dynamics (Fricke et al. 2016), the complex interactions between nutrients, herbivores, and macroalgae (Martinetto et al. 2011) and the extent of the distribution of anthropogenic N into natural systems (Becherucci et al. 2019).

Individual growth of H. perlevis: an experimental study

To test whether the individual growth of *H. perlevis* varies with the consumers presence and different conditions of trophic resources availability, a field experiment manipulating the presence of consumers was deployed simultaneously at both channels. First, we collected sponges from the subtidal of the SAO channel and dissected them to obtain 130 fragments, hereafter called "*transplants*". Initial size of transplants was standardized using a two cm cutting mold in three directions because size can affect sponge growth during experimentation (see Duckworth et al. 1997; Gastaldi et al. 2017). Initial size was measured as the main surface area (cm^2), volume (cm^3) and dry weight (mg) obtained from 10 randomly selected transplants. We use a single cenital photo to obtain the surface area of each transplant by manually drawing the edge of the transplant with the free software ImageJ (http://rsb.info.nih.gov/ij/download.html). Using the software Autodesk Recap Photo 2018 Student Version we create 3D models with the photogrammetry technique (from at least 40 photographs from different angles) to estimate the volume of each transplant. Dry weights were obtained by drying the transplants (60°C for 72 hours). The remaining 120 transplants were placed in the subtidal of the SAO channel for two weeks for acclimatization and cut healing. Transplants were attached to PVC plates with plastic seals, plates were then fixed to the substrate with 6-inch steel nails (Fig. 2A). Then, the transplants were randomly assigned to one level of the following two factors: *Channel* (SAO channel, CTL channel; with high and low concentration of trophic resources, respectively), and *Consumers* (presence of consumers, exclusion of consumers, procedural control; Fig. 2). The level 'presence of consumers' consisted of the transplants attached to the PVC plates fixed to the substrate as explained above (Fig. 2A). The level 'exclusion of consumers' was obtained by placing the PVC plates with fixed transplants inside cylindrical cages of PVC (11 cm diameter, 32 cm length) covered with 2 mm pore plastic mesh along its surface and extremes (Fig. 2B). The level 'procedural control' consisted of the same cylindrical cage but with open extremes (Fig. 2C). Replicates of each treatment (*Channel* x *Consumers*) varied from 8 to 11 since some transplants were lost during the acclimatization. The experimental units were placed in the shallow subtidal (0.2-1 m depth during low tide since the sponge is found in the channels at around that depth) two meters apart from each other, at both channels. The experiment required weekly cleaning of the PVC structures, and lasted 72 days. At the end of the experiment, we retrieved 8 to 10 replicates per treatment, and obtained the final size of transplants in terms of surface area, volume and dry weights as mentioned above. We estimated individual growth of *H. perlevis* (%) in terms of each growth variable (i.e. surface area, volume, dry weight) as the difference between the final and initial value over the initial value per 100.

To span the potential variability in the abundance of consumers, the concentration of trophic resources and in the individual growth of the sponge along the year, the experiment was performed twice. The first was conducted from July to October 2018 (austral winter-spring transition) and the second, from March to June 2019 (autumn). Individual growth differences among treatments were evaluated with factorial two-way ANOVA tests, with *Channel* and *Consumers* as main fixed factors, and post-hoc Tukey tests. Homoscedasticity and normality were verified with Levene and Shapiro-Wilk tests, respectively.

Assessment of consumers: identification of consumers of *H. perlevis* and Consumption Pressure Index

Until this work there was -at least to the knowledge of these authors- no published information on consumers of *H. perlevis*, either in its global distribution or particularly at SAB. After the findings of the first experiment (winter-spring) we wanted to know: if there are no consumers of *H. perlevis* in the study site, or if there are consumers, but they do not significantly regulate the population of *H. perlevis*. Given that, we conducted some studies to first identify which organisms -if any- might be consuming the sponge and which of them might exert the greatest consumption on the sponge.

We first sampled in each channel the abundance of possible sponge consumers -guided by specific literature-, focusing on fishes and benthic organisms. Among the benthic organisms, we sampled crabs separately given their greater mobility. These organisms represent the most common coastal sponge consumers (see Randall and Hartman 1968; Guida 1976; Wullf 2006, 2012; Padilla Verdín et al. 2010; Pawlik et al. 2013; Belmonte et al. 2015) and were grouped solely for operational sampling reasons. Benthic organisms and crabs were sampled in June 2019 at low tide using cylindrical cores (10 cm in diameter; 10 replicates per channel) and quadrats (0.25 m^2; 10 replicates per channel), respectively. Fishes were sampled in May 2019 at low tide, by trawling with coastal nets (25 m long, 10 mm mesh size) for 10 m parallel to the coastline. All organisms were identified to the lowest taxonomic level (usually species) using local taxonomic guides and specific literature (de Buen 1953; Fauchald 1977; Rozbaczylo 1980; Boschi 1992; Cortés and Narosky 1997; Dyer 1997, 2006; Boschi and Cousseau 2004).

Among the collected specimens we identified which organisms would be consuming the sponge (hereafter 'potential' consumers) after searching for a certain incidence of *H. perlevis* styles (siliceous spicules) in their digestive tracts. Then, we designed an index to assess the relative consumption pressure exerted on the sponge among the potential consumers. To this, we first weighed 10 randomly selected individuals from each channel and taxon for sponge consumption analysis. All organisms were weighed when the abundance registered was lower than 10 individuals. Then, organisms were digested with nitric acid (15.7 N) to remove organic and calcareous material following Guida (1976). Small animals (< 1 cm) were completely digested, while only the soft parts (e.g., in limpets) or digestive tracts (e.g., in fish and crabs) were digested in larger animals. The clean inorganic remnant (digested sample) was obtained by successive washes (see Hajdu et al. 2011 for details). Digested samples were dried (60°C) until the residual liquid from the washes evaporated and then 1 mL of distilled water was added to each sample to achieve a constant volume. We observed by optical microscope an aliquot (0.2 mL) of each homogenized digested sample for the presence and counting of *H. perlevis* styles. The spicule was assigned to the species based on the size and general morphology of the styles (see Gastaldi et al. 2018 for spicules description and measures).

Given that some organisms can uptake the spicules from the sediment or by feeding on sponge debris (Guida 1976), we considered that a taxon was a potential consumer of *H. perlevis* when at least half of the digested individuals had styles of *H. perlevis* in their tracts (incidence ≥ 50%). This criterion is conservative relative to other studies on diet analyses (see Dragovich 1970; Tayler 1972; Perier 1994).

To assess the relative consumption pressure over *H. perlevis* by potential consumers, a consumption pressure index (CPI) was designed. We include a variable quantifying consumers (A), multiplied by the per capita effect they exert (B) over the prey and divided by a variable that quantifies the availability of the prey (C). The resulting CPI (= A × B / C) is a dimensionless value that allows a quantitative ordering, of taxa or groups of consumers, from those that exert less to greater consumption pressure (lowest to highest CPI, respectively). However, the index does not determine whether the consumer significantly affects the abundance or growth of the sponge, or the degree of consumer preference for the sponge.

The abundance of consumers (A) was the density of each potential consumer *i-taxon* (D_i; number of individuals m^{-2}). The per capita effect of consumers (B) was calculated as the mean number of styles of *H. perlevis* in digestive samples (S_i) over the mean *i-taxon* body weight (W_i; mg), while the availability of the prey (C) was the cover of *H. perlevis* (*Cov*; m^2; see in two subsections below). Thus, the CPI by *taxon* was calculated as D_i × (S_i / Wi) / *Cov*. To assess the relative consumption pressure per channel, the CPI of the different *taxa* were pooled by channel and ordered for the lowest to the highest CPI and compared.

Assessment of trophic resources

To assess the differences in the availability of trophic resources for *H. perlevis* (for both the heterotrophic and autotrophic pathways) between channels, we measured chlorophyll-*a* (Chl-*a*), total suspended solids (TSS), organic matter (OM), nitrate (NO_3^-), nitrite (NO_2^-) and phosphate (PO_4^{-3}), at both channels. Water samples were taken monthly (4 L; n = 3 replicates per channel) during low tide, from July 2018 to June 2019. Chl-*a* concentration (μg L$^-$) was estimated after filtering 2 L of water with GF/F filters. Filters were then incubated overnight in ethanol (96%) at 4°C in darkness for Chl-*a* extraction (Marker et al. 1980). Absorbances were measured with a Persee T7 UV-Vis spectrophotometer and concentrations were calculated following the equations of Marker et al. (1980), after phaeopigments correction. Two additional liters of water were filtered (GF/F) to obtain the concentration of TSS (after drying the filters at 60° C for 72 h and weighing them again) and OM (after incinerating the dried filters at 500°C for 5 h and subtracting its weight to that of the TSS; mg L$^-$ for both). The resulting filtered water was used for the assessment of dissolved NO_3^-, NO_2^- and PO_4^{-3} concentrations (μmol L$^-$ for all) using colorimetric methods and UV-Vis spectrophotometer, following the methodology detailed in APHA (2012).

Differences in trophic resources concentration (Chl-*a*, TSS, OM, NO_3^-, NO_2^- and PO_4^{-3}) between channels and among months were evaluated with factorial two-way ANOVA tests, with *Channel* and *Month* as main fixed factors, after verifying homoscedasticity and normality assumptions with Levene and Shapiro-Wilk tests, respectively. Tukey tests were used for post hoc comparisons.

Abundance of H. perlevis: an observational approach

To assess the differences in the abundance of *H. perlevis* between channels, we sampled cover at both channels monthly from July 2018 to June 2019. Cover was estimated based on the photography of 10 quadrats (0.25 m^2) randomly placed on the shallow subtidal during low tide. Photos were processed with

the free software ImageJ. Differences in *H. perlevis* percent cover between channels and months were analyzed with the Scheirer Ray Hare Test (non-parametric equivalent to two-way ANOVA; Scheirer et al. 1976; Sokal and Rohlf 1995), with *Month* and *Channel* as main fixed factors.

To assess the effect of trophic resources on the abundance of *H. perlevis*, we used generalized linear models (GLMs; Crawley 2007), with a negative binomial error distribution and a log link function. We tested if the concentration of dissolved and particulate resources (Chl-*a*, TSS, OM, NO_3^-, NO_2^- and PO_4^{-3}), and their interaction with *Channel* and *Month* affected the percent cover of *H. perlevis*. Eighteen models, including those with additive and interaction effects between variables, were evaluated (Table 3). Three models were retained after comparing the Akaike Information Criterion (AIC) corrected for small samples ($\Delta AIC \leq 2$; Anderson and Burnham 2004; Zuur et al. 2009). Consumers were not included in the GLMs since our sampling did not consider the time variability in consumer abundance. Furthermore, because the effect of consumers on the sponge -experimentally assessed-, was not significant.

Table 2
Results of the analysis of (A) the concentration of trophic resources and (B) the abundance of *Hymeniacidon perlevis*. A- Results of the two-way ANOVA on the concentration of trophic resources for *H. perlevis* between *Month* and *Channel* as main fixed factors. B- Results of the Scheirer Ray Hare Test on the abundance of *H. perlevis* between *Month* and *Channel* as main fixed factors. '*' indicates p < 0.05.

A	Trophic resource	Source	df	F	p
	OM	*Month*	11	2.03	0.045 *
		Channel	1	0.16	0.683
		Month x Channel	11	0.95	0.495
		Residuals	48		
	TSS	*Month*	11	14.32	$1.11e^{-11}$ *
		Channel	1	7.21	0.009 *
		Month x Channel	11	2.72	0.008 *
		Residuals	48		
	Chl-*a*	*Month*	11	41.31	$< 2e^{-16}$ *
		Channel	1	22.77	$1.75e^{-5}$ *
		Month x Channel	11	15.41	$3.06e^{-12}$ *
		Residuals	48		
	NO_3^-	*Month*	11	78.33	$< 2e^{-16}$ *
		Channel	1	2480.8	$< 2e^{-16}$ *
		Month x Channel	11	74.64	$< 2e^{-16}$ *
		Residuals	48		
	PO_4^{-3}	*Month*	11	1152.8	$< 2e^{-16}$ *
		Channel	1	3785.3	$< 2e^{-16}$ *
		Month x Channel	11	339.3	$< 2e^{-16}$ *
		Residuals	48		
	NO_2^-	*Month*	11	209	$< 2e^{-16}$ *
		Channel	1	4970.4	$< 2e^{-16}$ *

A	Trophic resource	Source	df	F	p
		Month x Channel	11	208.9	$< 2e^{-16}$ *
		Residuals	48		
B	Abundance of *H. perlevis*	Source	df	H	p
		Month	11	17.12	0.104
		Channel	1	40.98	< 0.001 *
		Month x Channel	11	16.16	0.134
		Residuals	216		

Table 3
Results of GLMs analyses. The AICc and Delta AICc values are reported for each analyzed model, ordered from the lowest to the highest AICc value. Models that consider the additive and the interaction effect between variables are symbolized with '+' and 'x', respectively. Selected models (ΔAICc < 2) are indicated with '*'.

Model	AICc	ΔAICc
NO_3^- *	932.13	0.00
$NO_3^- + PO_4^{-3} + TSS$ *	932.5	0.38
$NO_3^- + PO_4^{-3}$ *	932.64	0.52
$NO_3^- + PO_4^{-3} + NO_2^- + TSS$	934.61	2.48
$NO_3^- + PO_4^{-3} + NO_2^- + Chl\text{-}a$	936.45	4.33
$NO_3^- + PO_4^{-3} + NO_2^- + Chl\text{-}a + TSS$	936.73	4.60
$NO_3^- + PO_4^{-3} + NO_2^- + TSS + OM + Chl\text{-}a$	936.78	4.65
$Channel + Month + NO_3^- + PO_4^{-3} + NO_2^- + TSS$	940.73	8.60
$Channel + Month + NO_3^- + PO_4^{-3} + NO_2^- + TSS + OM + Chl\text{-}a$	944.85	12.73
NO_2^-	947.46	15.33
$Channel \times Month \times NO_3^- \times PO_4^{-3} \times NO_2^- \times TSS \times OM \times Chl\text{-}a$	947.48	15.36
$Channel \times Month$	947.48	15.36
$PO_4^{-3} + NO_2^- + Chl\text{-}a$	951.46	19.34
$TSS + PO_4^{-3}$	975.36	43.23
PO_4^{-3}	975.58	43.45
TSS	984.54	52.41
OM	988.14	56.02
Chl-a	990.57	58.45

The analyses for the whole methodology were performed in R (R Core Team 2021). Used packages were: dplyr (Wickham et al. 2021) and readxl (Wickham and Bryan 2019) to obtain and manipulate data; car (Fox and Weisberg 2019), multcomp (Hothorn et al. 2008), emmeans (Lenth 2020), rcompanion (Mangiafico 2020), agricolae (de Mendiburu 2020), MASS (Venables and Ripley 2002) and MuMIn

(Barton 2020) for the several analyses and tests performed; ggplot2 (Wickham 2016), ggannotate (Cowgill 2020) and ggforce (Pedersen 2020) for creating and editing graphics.

Results

Individual growth of H. perlevis: an experimental study

The individual growth of transplants varied only between *Channels*. These differences among the three growth variables were only observed during the winter-spring (Table 1, Fig. 3); while the growth during the autumn was similar between channels. No further differences due to *Consumers* or *Consumers* x *Channel* interaction were observed in either the winter-spring or autumn experiments for any of the three growth variables (Table 1, Fig. 3).

Table 1
Individual growth of *H. perlevis*. Two-way ANOVA results of the experiment replicated twice during winter-spring and autumn. Differences in surface area, volume and dry weight as sponge transplant growth variables assessed between *Channels* and *Consumers* as main fixed factors. '*' indicates p < 0.05.

Growth variable	Source	df	F	p	df	F	p
			Winter-spring			Autumn	
Surface area	*Channel*	1	21.06	$2.93e^{-5}$ *	1	0.36	0.548
	Consumers	2	0.43	0.652	2	1.77	0.18
	Channel x Consumers	2	0.38	0.685	2	2.12	0.13
	Residuals	51			49		
Volume	*Channel*	1	10.28	0.002 *	1	1.09	0.3
	Consumers	2	0.48	0.619	2	0.21	0.805
	Channel x Consumers	2	1.11	0.336	2	2.73	0.074
	Residuals	51			49		
Dry weight	*Channel*	1	9.54	0.003 *	1	0.8	0.374
	Consumers	2	0.28	0.755	2	0.14	0.862
	Channel x Consumers	2	0.63	0.533	2	1.36	0.264
	Residuals	51			49		

At the end of the experiment, transplants increased in surface area at both channels, being higher in the SAO (+ 89.5% in winter-spring, + 236.6% in autumn) than in the CTL channel (+ 13.9% in winter-spring, + 209.4% in autumn; Fig. 3A). Moreover, transplants increased in volume at the SAO channel (+ 39.6% in winter-spring, + 10.3% in autumn), but decreased in the CTL channel (-10% in winter-spring, -3.7% in

autumn; Fig. 3B). However, transplants decreased in dry weight at both channels, being steeper in the CTL (-46.2% in winter-spring, -19.9% in autumn) than in the SAO channel (-19.9% in winter-spring, -7.9% in autumn; Fig. 3C).

Assessment of consumers: identification of consumers of H. perlevis and Consumption Pressure Index

To assess the consumption of *H. perlevis*, we processed 159 individuals from all the sampled taxa (Table S1). Seven taxa from both channels did not show styles of *H. perlevis* in digestive samples, while eight taxa, four from each channel, had more than 50% incidence of styles (Table S1). In the SAO channel, an unidentified polychaete, the crab *Cyrtograpsus angulatus* and the Patagonian blennie *Eleginops maclovinus* had 50% of incidence while the crab *Cyrtograpsus affinis* had a 100% of incidence. In the CTL channel, the ophiuroid *Ophioplocus januarii* and the polychaete *Piromis sp.*, had 50% of incidence while the crab *Neohelice granulata* and the silverside *Odontesthes platensis* had an incidence of 100%.

Consumers from the CTL channel exerted a greater consumption pressure over *H. perlevis* than those from the SAO channel (CPI of 194.75 and 111.19 in CTL and SAO channels, respectively; Table S2). Moreover, benthic organisms like ophiuroids and polychaetes exerted the highest consumption pressure over the sponge (Fig. 4; Table S2).

Assessment of trophic resources

The SAO channel generally had greater and more variable concentrations of trophic resources than the CTL channel. The concentration of OM varied over time with no effect of the *Channel* (Table 2A), while the remaining resources were significantly affected by the *Month x Channel* interaction (Table 2A). The concentration of all particulate resources tended to increase towards the warmer months, in both channels. Higher values of TSS were recorded from October to April (Fig. 5-top), while OM peaked in November (Fig. 5-middle) and Chl-*a* peaked in November and January (Fig. 5-bottom). Regarding dissolved resources, only PO_4^{-3} increased towards the warmer months (January to March), being undetectable in the CTL channel in the colder months (Fig. 6-middle). Concentrations of NO_3^- and NO_2^- were higher and displayed great variations throughout the year in the SAO channel. In the CTL channel, the concentration of NO_3^- remained lower and constant (Fig. 6-top), while NO_2^- was mostly undetectable (Fig. 6-bottom). Summary statistics of annual concentrations of trophic resources are presented in Table S3.

Abundance of H. perlevis: an observational approach

The abundance of *H. perlevis* varied between channels while no differences were observed between *Months* or *Channel* x *Month* interaction (Table 2B). *Hymeneacidon perlevis* was more variable and abundant in the SAO than in the CTL channel (5.42 ± 7.4% and 1.29 ± 2.02%, respectively; Fig. 7). The period of greatest abundance was between February to June (Fig. 7). From the 18 evaluated models, the sponge cover was mainly explained by the variables NO_3^-, PO_4^{-3} and TSS (Table 3). The best model

only included the concentration of NO_3^- as the predictor variable (CI 95%: 0.008−0.01) and explained 23.3% of the total variance observed. The second included additive effects of NO_3^- (CI 95%: 0.007−0.01), PO_4^{-3} (CI 95%: -0.07−0.04) and TSS (CI 95%: -0.006−0.05) concentrations, explaining 24.7% of the total variance observed. The third best model considered the additive effects of NO_3^- (CI 95%: 0.006−0.01) and PO_4^{-3} (CI 95%: -0.01−0.05) concentrations and explained the 23.9% of the total variance observed.

Discussion

In this study, we found that the individual growth and abundance of *H. perlevis* was relatively higher in the SAO channel -where anthropic nutrient loads are higher- compared to the CTL channel. The bottom-up variables that better explained the abundance pattern of the sponge were the concentration of nitrate, phosphate and total suspended solids. We also found that some crabs, fishes, polychaetes and ophiuroids would be potential consumers of *H. perlevis.* However, the effects of consumers were negligible on the individual growth dynamics of the sponge, even though some benthic invertebrates (polychaetes and ophiuroids) of the CTL channel would be exerting the greatest consumption pressure over the sponge. These findings support our main hypothesis that the population of *H. perlevis* in San Antonio Bay is mainly bottom-up controlled, based on the concentration of trophic resources.

Previous studies addressing the "top-down and bottom-up" dichotomy in sponges have been conducted exclusively in tropical coral reefs, where changes in sponges density or biomass may affect the development and maintenance of corals (see Wulff 2012, 2017; Pawlik et al. 2018). Furthermore, in temperate environments the variability of their physical (e.g, solar radiation, temperature, duration and intensity of stratification of the water column) and biological conditions (e.g, changes in primary productivity) over wide spatial and temporal scales, hinders the generalization about the most influential factors in the regulation of populations (Schiel 2004; Lesser 2006). Through the prolific literature on the top-down and bottom-up regulation and their interaction in filter feeders on temperate coasts, (see Menge 1992, 2000; Menge et al. 1997), this is the first study to assess the relative contribution of top-down and bottom-up controls on the regulation of a sponge population, in a temperate environment.

Here, we found that changes on the individual growth of *H. perlevis* transplants during the experiment are consistent with seasonal growth dynamics observed at temperate environments (Cao et al. 2007; Gastaldi et al. 2020). However, while transplants increased in surface area and volume, they decreased in dry weight. Such inconsistencies between variables may be related to specific growth mechanisms that sponges develop after a disturbance on its somatic structure (Ayling 1983) and have already been observed in *H. perlevis* in the SAO channel (see Gastaldi et al. 2017). In general, during the first two−four weeks after tissue cuts, sponges show morphological and structural changes involving instances of cellular disorganization and transformation, differentiation and cell rearrangement, where transplants may lose weight (de Caralt et al. 2008) although this is not necessarily reflected in a decrease in its volume or surface area given the three-dimensional rearrangement of its structure (Ayling 1983).

During the experimentation, we found that channels with contrasting trophic resource concentration affect the growth of *H. perlevis* only during winter-spring. This suggests that the availability of trophic resources has a differential effect on individual sponge growth, probably related to its physiological state and annual growth cycle. Channels with different concentrations of resources had significant effects during the season with lower growth rates of the sponge, since after winter dormancy, the sponge begins to grow in spring (Cao et al. 2007; Gastaldi et al. 2020). In this sense, a greater subsidy of trophic resources in the SAO channel at the beginning of the growth season could favorably stimulate its growth. On the other hand, this does not happen during the autumn, when the sponge grows more than in winter-spring. Although autumn is not the season when *H. perlevis* reaches its greatest individual growth (see Cao et al. 2007; Gastaldi et al. 2016, 2020), it seems that trophic resources are not the determining factor for the sponge growth. It is likely then, that other variables than trophic resources would best explain sponge growth dynamics, while low levels of resources are sufficient for its growth and maintenance. During the autumn, other abiotic factors could become more relevant. For instance, in SAB, the population abundance of the sponge seems to be strongly related with seawater temperature (Gastaldi et al. 2016, 2017).

Regarding consumers, we found some *taxa* might be potential consumers of *H. perlevis*. However, consumers were not relevant controlling the individual growth of the sponge, in any of the experimental instances. Therefore, temporal variations in the abundance of predators -if any- or in their consumption rate would potentially result in a negligible effect on the sponge growth. It is also possible that the mesh used to exclude consumers in the consumer exclusion cage was not effective enough to avoid small organisms. However, we did not observe bite marks on the surface of the sponge nor the presence of organisms inside the consumer exclusion cages during the weekly cleaning of the experimental units. We found that except for the occurrence of the unidentified polychaete in both channels, the rest of the potential consumers of *H. perlevis* when they were collected in one of the channels did not appear in the other, and vice versa (see Table S1). This could be due to the fact that the communities in both channels differ, maybe related to the anthropogenic nutrients input (see Martinetto et al. 2010). The methodology we used to identify the potential consumers of *H. perlevis* is limited. The mere presence of spicules inside an organism is not absolute evidence of their consumption, because spicules are often found in sediment and debris (Guida 1976). However, the setting of the conservative threshold of 50% of incidence strengthens the identification criterion. Furthermore, we found that only in some of the potential consumers identified here there were also spicules of other sponge species from the bay, although in lower abundances than *H. perlevis* (Gastaldi 2016). These findings allow us to assume that the identified potential consumers are eating sponges. According to this, we found spicules of the sponges *Pachychalina tenera*, *Halichondria elenae*, and *Cliona celata* in the fish *Odontesthes platensis* and the crabs *Cyrtograpsus affinis*, *C. angulatus* and *Neohelice granulata*.

Contrasting conclusions have been reported from top-down and bottom-up studies on tropical coral reef sponges. Some studies conclude that there is no evidence of a bottom-up control, and that individual sponge growth is only top-down controlled (Pawlik et al. 2013, 2015). These studies highlight that in tropical coral reefs there is no food limitation for sponges (either POC or DOC) that could lead to a

bottom-up control (Pawlik et al. 2015, 2018). On the other hand, other studies agree on the relevance of bottom-up control on sponges (Lesser 2006; Trussell et al. 2006; Lesser and Slattery 2013, 2018; Wulff 2017). For instance, a recent study showed that several sponge species from coral reefs -when consumers are excluded- reach higher growth when transplanted to sites with higher concentrations of picoplankton and dissolved nutrients, while their growth is not affected by predation when they are incubated in their original site (Wulff 2017). Our study, the first carried out in a temperate system, reveals that *H. perlevis* growth is mostly bottom-up controlled. At the end of the experimental study, transplants were bigger when incubated in the channel with higher concentration of trophic resources, at least during the winter-spring. Despite the presence in both channels of several consumers of *H. perlevis*, these did not have a significant effect on the growth of the sponge. Therefore, in SAB, the top-down control over *H. perlevis* growth would be negligible compared to the bottom-up control.

A greater abundance of *H. perlevis* was also recorded in the channel with the highest concentration of trophic resources and, among the bottom-up variables considered, those best explaining the variability of the sponge cover were the concentration of nitrate, and to a lesser extent, phosphate and total suspended solids. Some authors have already found a positive correlation between the abundance of sponges and the concentration of trophic resources (Bell 2008b; Wulff 2012). These relationships are associated with the concentration of both DOC and POC (Reiswig 1971; see Lesser and Slattery 2013; Wulff 2017; Pawlik et al. 2018; Pawlik and McMurray 2020). DOC accounts for a large part of the sponge diet (Pawlik et al. 2018; Pawlik and McMurray 2020), for example, ~ 70% of the diet of the giant barrel sponge *Xestospongia muta* is based on DOC (McMurray et al. 2016). Unfortunately, here we neither measured DOC concentration nor its relationship with the abundance of *H. perlevis* in SAB. Future studies should consider the analysis of DOC concentration and its contribution to the growth and abundance of the sponge. On the other hand, sponges can actively filter up to 75–99% of particulate suspended solids (~ POC, Ribes et al. 1999). For example, the abundance of *Cliona delitrix* on coral reefs increases with the concentration of suspended organic matter along a gradient of a sewage discharge (Chaves-Fonnegra et al. 2007). Likewise, at the Caribbean coral reefs, an increase in density of *Callyspongia vaginalis* along a depth gradient is driven by a higher concentration of picoplankton in deeper waters, mostly phytoplankton, prochlorophytes and heterotrophic bacteria (Lesser and Slattery 2013). According to this, in this study we found that in SAB, the variability in the cover of *H. perlevis* could be related to the availability of total suspended solids as a proxy of POC concentration.

A positive correlation between the abundance or biomass of sponges and the concentration of nutrients (dissolved inorganic nitrogen and phosphorus) at enriched environments is mainly attributed to the rapid intake of nutrients by bacterioplankton or phytoplankton, leading to a greater availability of particulate trophic resources for sponges (Reiswig 1971, 1974; see Holmes 2005; see Ramsby et al. 2020) or POC. In SAB, the concentrations of nutrients were significantly higher in the SAO channel than in the CTL channel (by two orders of magnitude higher for nitrate). Here, the difference in the concentration of nutrients is due to an anthropogenic supply through both point sources (fish processing factories) and diffuse sources (septic system) of sewage (Teichberg et al. 2010; Martinetto et al. 2011; Fricke et al. 2016). Since sponges harbor photosymbionts that fix nutrients into complex carbon compounds (photosynthates) that

are then transferred to the sponge (see Cheshire and Wilkinson 1991; Weisz et al. 2010; see Freeman and Thacker 2011), a higher nutrient concentration would affect the abundance and growth of sponges via the autotrophic pathway (Reiswig 1981; de Goeij et al. 2008; Wulff 2012). The variation in the abundance pattern of *H. perlevis* in relation to the concentration of nitrate, phosphate and total suspended solids suggests that the sponge could be supporting its nutritional requirements, not only by a heterotrophic pathway but also by an autotrophic pathway, through its photosymbionts. For example, *Aplysina cauliformis*, a Caribbean sponge, obtains up to 75% of its energy reserves from photosymbionts (Freeman and Thacker 2011). However, the role that *H. perlevis* symbionts (e.g., cyanobacteria; see Alex et al. 2012) may have on the nutritional requirements of the specie is still unknown.

In summary, a higher concentration of trophic resources was recorded in the channel next to the city. There, both the abundance and individual growth of *H. perlevis* were greater, increasing its cover along with the concentration of trophic resources. Contrary to our prediction, the greatest consumption pressure was exerted by the potential consumers of the channel isolated from the city, where the concentration of trophic resources is lower, while in both channels, the effect of predation -if any- on the individual sponge growth was masked by the bottom-up control.

Declarations

by MMB and all authors commented on previous versions of the manuscript. MMB, MG and FF read and approved the final manuscript.

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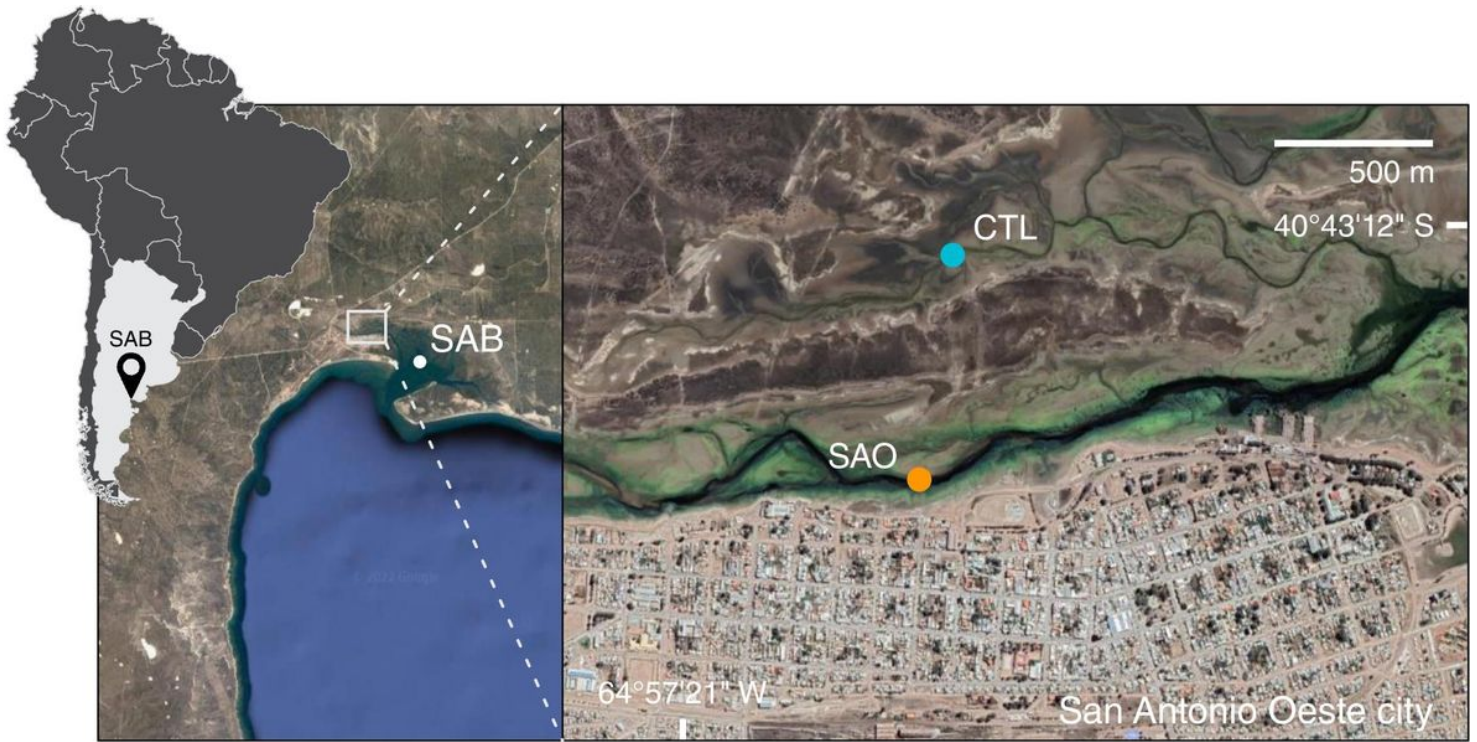
Figures

Figure 1

Satellite image from San Antonio Bay (SAB; left panel), located in the northeast of Argentine Patagonia. The two sampled channels and the city nearby are shown in the right panel. SAO indicates the channel enriched with anthropic nutrients from San Antonio Oeste city, and CTL indicates the channel isolated from nutrients supply. Images extracted from Google Earth.
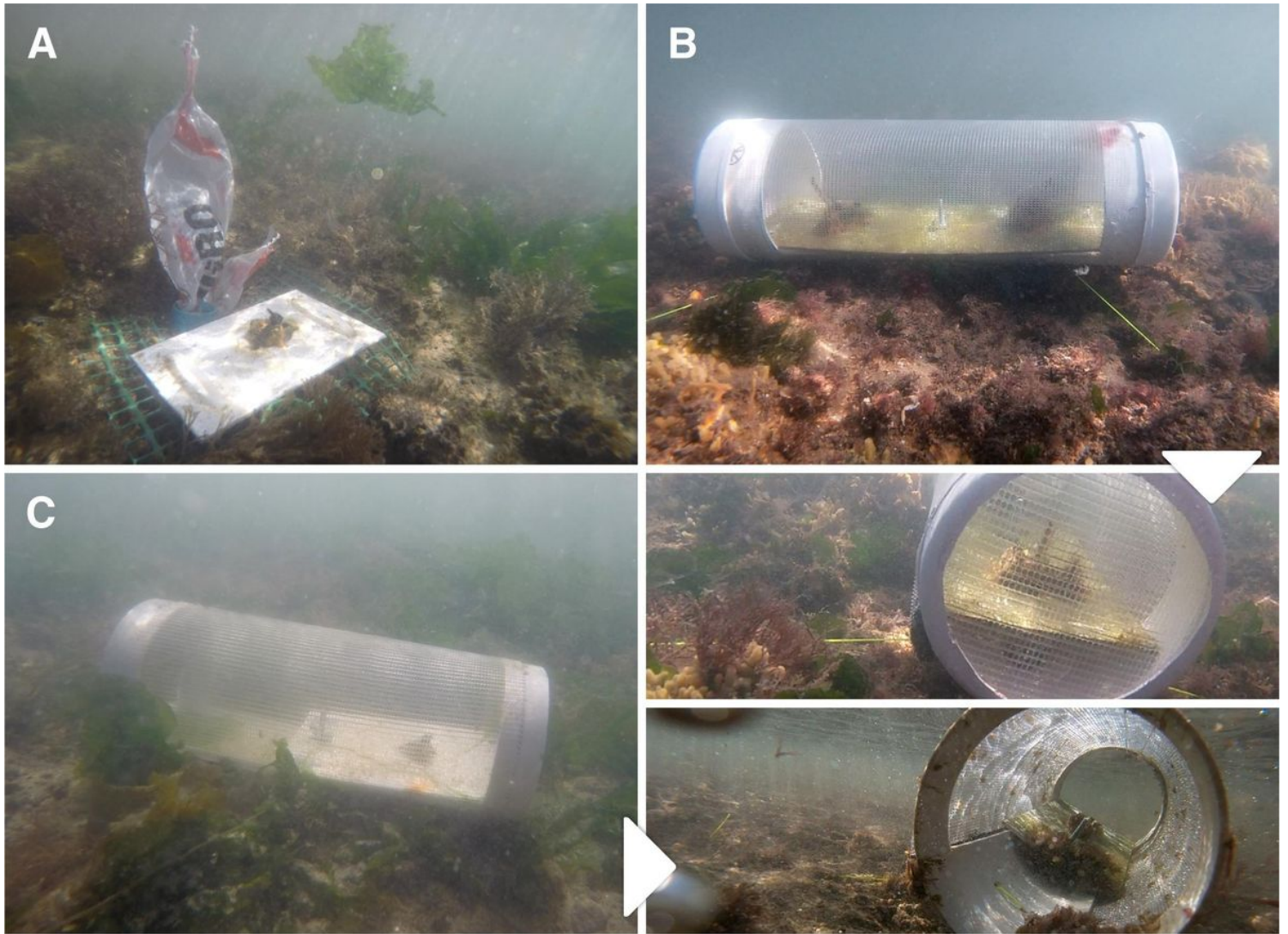
Figure 2

Detail of the experimental units corresponding to the levels of the *Consumers* factor: Presence of consumers (A), exclusion of consumers (B - below: detail of closed ends with mesh), procedural control (C - right: detail of open ends).
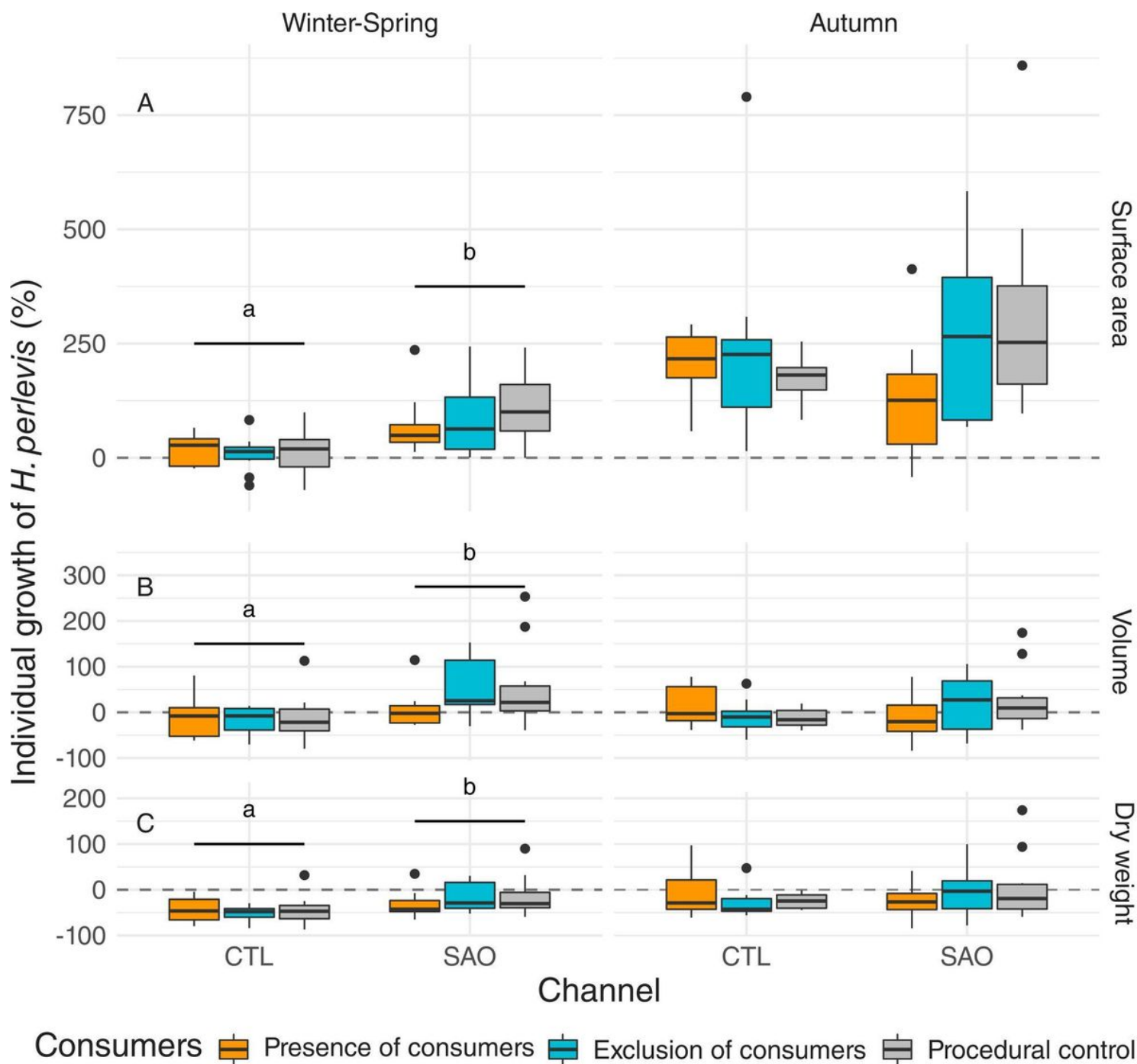
Figure 3

Individual growth (%) of *H. perlevis*. Transplants growth in surface area (A), volume (B) and dry weight (C), incubated in both channels, at presence of consumers, exclusion of consumers and procedural control conditions (midline, box, and whiskers show median and quartiles). Growth is shown for winter-spring (left) and autumn (right) experimental instances. Different letters indicate differences in growth between channels (Tukey test; $p < 0.05$). Note scale differences on the y- axis among growth variables. SAO indicates the channel enriched with anthropic nutrients from San Antonio Oeste city, and CTL indicates the channel isolated from nutrients supply.
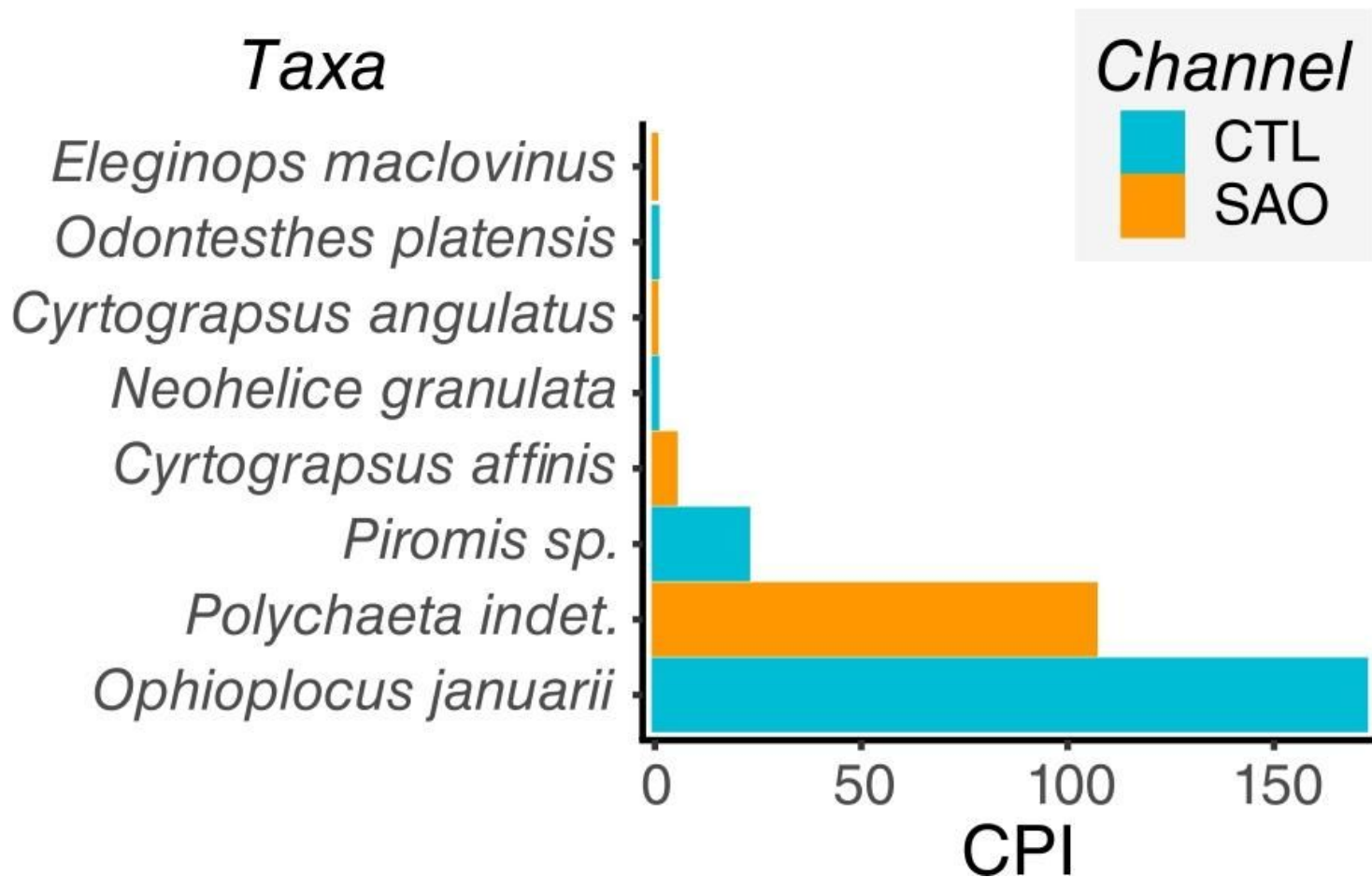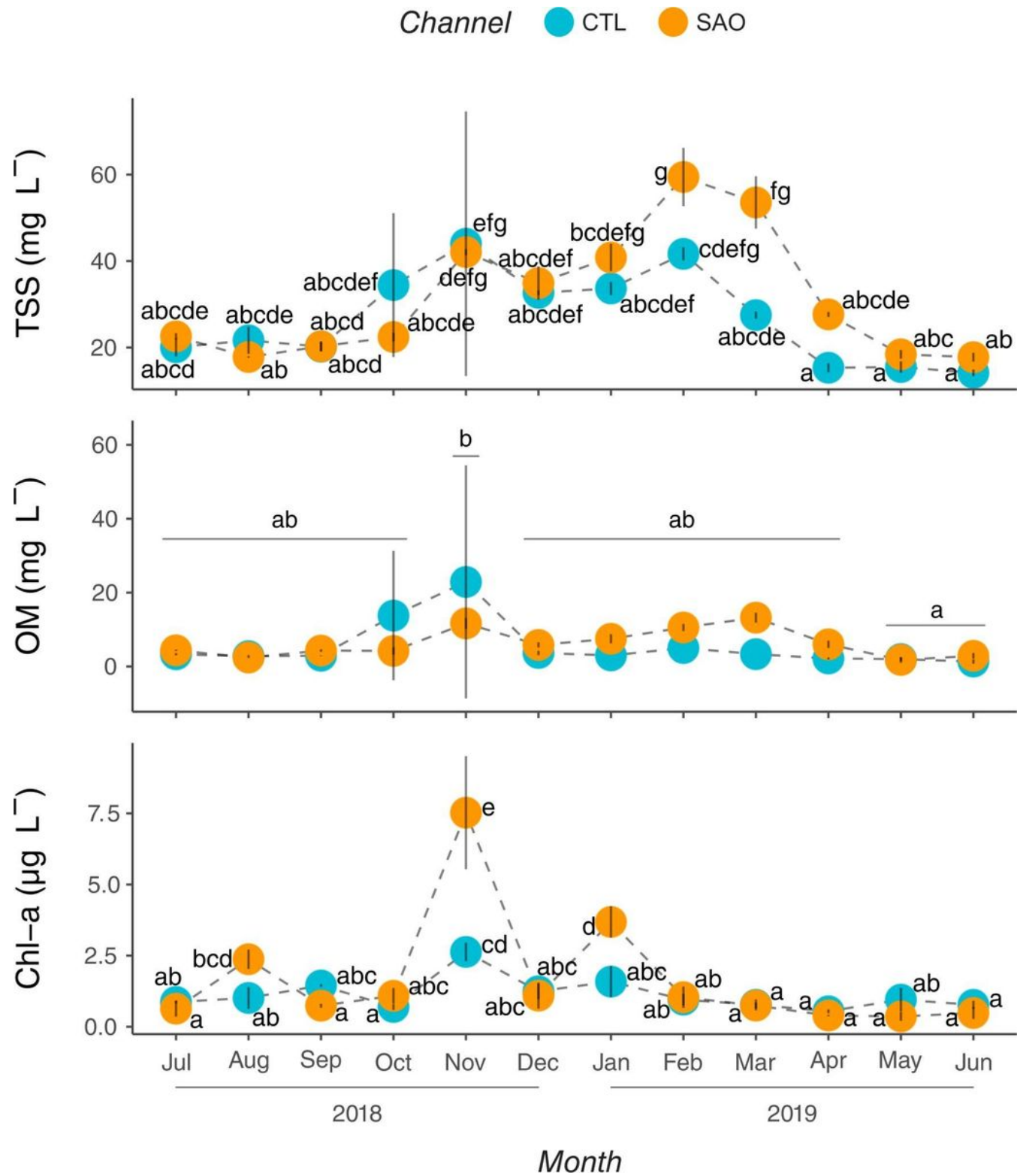
Figure 4

Consumption pressure index (CPI) of the *taxa* identified as consumers of *H. perlevis* from both channels. SAO indicates the channel enriched with anthropic nutrients from San Antonio Oeste city, and CTL indicates the channel isolated from nutrients supply.

Figure 5

Concentration of particulate trophic resources. Concentration of total suspended solids (TSS, top, mg L⁻), organic matter (OM, middle, mg L⁻) and chlorophyll-*a* (Chl-*a*, bottom, µg L⁻) (mean ± standard deviation) in water of both channels (n = 3 per month and channel by each trophic resource; N = 72 by each trophic resource) throughout the study period. Different letters indicate different concentrations between treatments (Tukey test; p < 0.05). Note scale differences on the y- axis among trophic resources. SAO

indicates the channel enriched with anthropic nutrients from San Antonio Oeste city, and CTL indicates the channel isolated from nutrients supply.
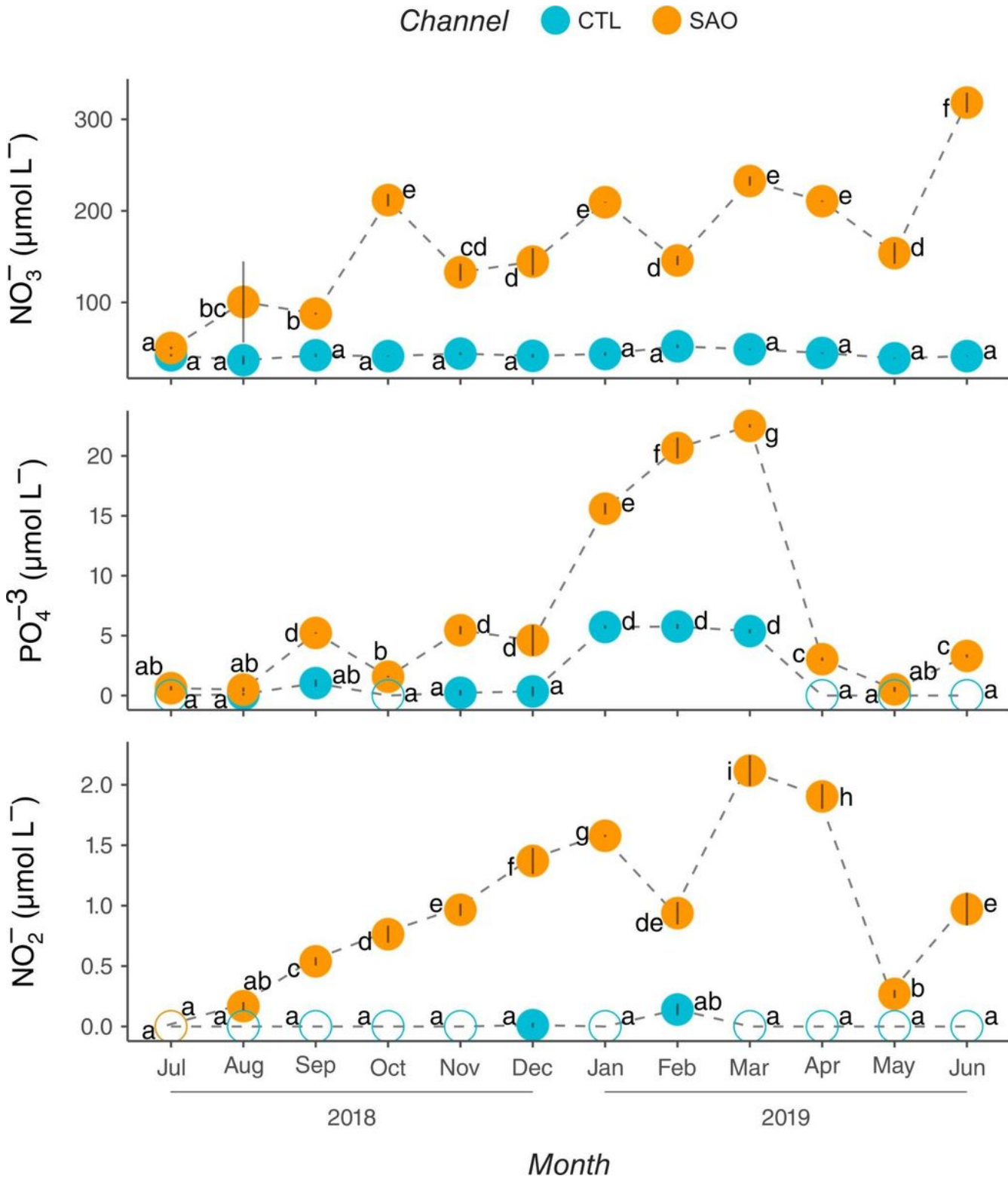

Figure 6

Concentration of dissolved trophic resources. Concentration of nitrate (NO_3^-, top, µmol L$^-$), phosphate (PO_4^{-3}, middle, µmol L$^-$) and nitrite (NO_2^-, bottom, µg L$^-$) (mean ± standard deviation) in water of both

channels (n = 3 per month and channel by each trophic resource; N = 72 by each trophic resource) throughout the study period. Different letters indicate different concentrations between treatments (Tukey test; p < 0.05). Note scale differences on the y- axis among trophic resources. Empty circles indicate undetectable values of the dissolved nutrient. SAO indicates the channel enriched with anthropic nutrients from San Antonio Oeste city, and CTL indicates the channel isolated from nutrients supply.
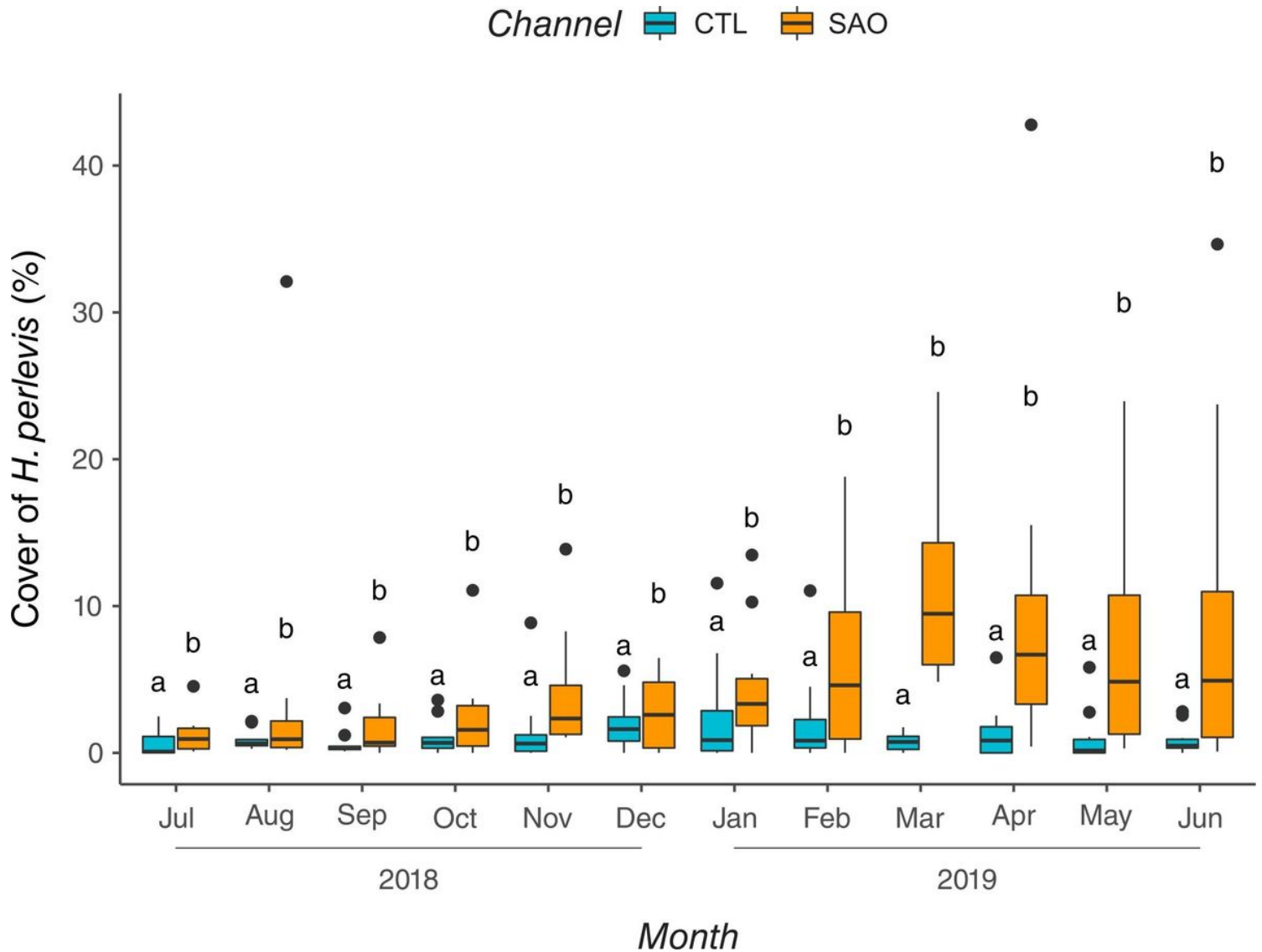

Figure 7

Hymeniacidon perlevis percent cover in both channels throughout the study period (midline, box, and whiskers show median and quartiles). N = 240. Different letters indicate differences in cover between channels. SAO indicates the channel enriched with anthropic nutrients from San Antonio Oeste city, and CTL indicates the channel isolated from nutrients supply.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementarymaterialMarelloetal2023.docx
- floatimage1.jpeg