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Feeding of *Aulacomya atra* Under Different Organic Matter Sources (Autochthonous and Allochthonous) in a Chilean Patagonia Fjord Ecosystem

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Aulacomya atra is an active suspension feeder, spatially dominant in the shallow-water hard-bottom benthic communities of the Chilean Patagonia fjords. In this region, the vertical flux of autochthonous organic matter (OM) reaching the benthos is augmented by allochthonous OM both from a terrestrial origin and from intensive salmon farming. This mixed pool of OM represents a potential source of food for a variety of benthic consumers, but to date little is known about the degree of utilization of these materials by filter feeders organisms. In this context, feeding experiments on *A. atra* in Puyuhuapi Fjord, Chilean Patagonia, were conducted during summer and winter 2018–2019. These experiments were designed to determine ingestion rates (IR) of *A. atra* fed with autochthonous (bacterial and microplanktonic community) and allochthonous (salmon food pellet) OM. Additionally, samples of *A. atra* tissues and suspended particulate organic matter (SPOM) were taken from the study area for stable isotope analysis. Data from laboratory experiments indicated that *A. atra* can feed on both autochthonous and allochthonous OM, but higher IR were detected in individuals fed with salmon food pellets. Because the IR is sensitive to food particle density rather than specific type of food, diet preferences of *A. atra* in feeding experiments could not be determined. Stable isotope analyses indicate that *A. atra* in natural environment preferentially exploits food with an isotopic signal corresponding to autochthonous OM, highlighting the primary role of phytoplankton carbon in their diet. Extensive utilization of terrestrially derived OM is therefore unlikely, although utilization of OM derived from salmon farming is not precluded because of the overlap in isotopic signal between food pellets and marine plankton.

Keywords: *Aulacomya atra*, ingestion rate, stable isotopes, autochthonous and allochthonous food, Puyuhuapi Fjord

INTRODUCTION

In aquatic ecosystems, animals that feed on particles suspended in the water are collectively known as filter feeders (Jørgensen, 1990). Bivalves tend to be the dominant suspension feeders in benthic communities (Sebens et al., 2016; Filgueira et al., 2019), filtering large volumes of water whilst retaining a wide range of particle sizes (ca. 4–35 μm diameter) (Voudanta et al., 2016). By filtering water to satisfy their nutritional demands, these organisms remove substantial quantities of microscopic particles from seston, such as bacteria, phytoplankton, detritus, and suspended sediments (Wright et al., 1982; Langdon and Newell, 1996; Prins et al., 1998; Kreeger and Newell, 2000; Cranford et al., 2011). Therefore, these bottom dwelling organisms process large amounts of suspended organic matter (OM) and are often major agents of pelagic-benthic coupling and nutrient cycling (Norkko et al., 2001). The total amount of OM consumed by bivalves is largely determined by their ingestion rate (IR) (Riisgård, 1988) which is a parameter of great ecological importance, and critical to the understanding of their impact on particles fluxes in coastal environments (Winter, 1978). Filter feeding behavior in bivalves is known to be responsible for fluctuations in both the abundance and the composition of seston (Bayne, 1998; Prins et al., 1998). Several studies have suggested that bivalve grazing can control phytoplankton abundance (Cloern, 1982; Prins et al., 1998; Lonsdale et al., 2009; Lucas et al., 2016), favor small phytoplankton organisms (Greene et al., 2011; Jacobs et al., 2016; Cranford, 2019) and decrease phytoplankton production (Dolmer, 2000). Phytoplankton is clearly a major source of nutrition for these organisms (Vaughn and Hoellein, 2018), but bacteria and detritus from terrestrial origins have also been described as important food source for bivalves during periods of low phytoplankton abundance (Langdon and Newell, 1990; Kreeger and Newell, 1996). Mussels are also known to filter small particles of salmon feed (Reid et al., 2010; MacDonald et al., 2011) and fecal pellets from salmon farming areas (Reid et al., 2010), incorporating this waste material as a food source (Gao et al., 2006; Redmond et al., 2010; Handå et al., 2012a,b). Several studies have indicated that bivalves growing adjacent to salmon farming areas remove OM advected from cages by increasing their growth rates (Lander et al., 2004; Peharda et al., 2007; Sarà et al., 2009) and helping to reduce the negative ecological impacts of the salmon industry (Lefebvre et al., 2000; MacDonald et al., 2011) such as the increase in load of OM in the water column and seafloor (Quiñones et al., 2019).

In Chilean Patagonian fjords, salmon farming represents the principal aquaculture activity (Buschman et al., 2006). This industry releases large quantities of organic and inorganic wastes (uneaten feed, feces and excretory products) that modify the particulate and dissolved materials in the water column (Quiñones et al., 2019) and represent a permanent input of allochthonous OM into the local fjord ecosystem (Iriarte et al., 2014). This allochthonous OM, together with high levels of autochthonous OM produced by phytoplankton in Chilean fjords (Montero et al., 2011, 2017a,b), provides a heterogeneous pool of organic substrates available as food for benthic consumers.

Several studies have addressed trophic structure of benthic communities (Mayr et al., 2011; Zapata-Hernández et al., 2014; Andrade et al., 2016; Quiroga et al., 2016), but little information is available on the ecological role of bivalves species in the structure and functioning of Patagonian fjord ecosystems. One of the key suspension feeder in the Patagonian fjords is the ribbed mussel *Aulacomya atra* (Molina, 1782), which normally inhabits protected and semi-protected shallow rocky shores (Betti et al., 2017), and is often found in close vicinity to salmon farms. Despite its importance in bentho-pelagic carbon fluxes of the Patagonian fjords, little is known about the feeding behavior of *A. atra*, including its potential role in processing the uneaten salmon feed. The aim of the present study was to determine the capacity of *A. atra* to assimilate and ingest OM derived both from salmon feed (allochthonous), and from a phytoplankton and bacterial origin (autochthonous) by means of stable isotope analysis and experimental feeding studies conducted in Puyuhuapi Fjord, Chilean Patagonia, during summer and winter periods between 2018 and 2019.

MATERIALS AND METHODS

Study Area and Sampling of *Aulacomya atra*

The study was conducted in Puyuhuapi Fjord which extends for about 90 km between 44°19′ S and 44°57′ S in northern Chilean Patagonia (**Figure 1**), and runs in a N–NE direction, connecting directly to the open sea via the Moraleda Channel at its mouth, and through the Jacaf Channel near the head (Schneider et al., 2014). The hydrography of this area is characterized by an estuarine type of circulation with a vertical two layer structure, comprised of a highly variable 5–10 m deep freshwater layer overlying a more uniform, saltier sub-pycnocline layer (Schneider et al., 2014 and references therein). The deeper saline water originates from Sub-Antarctic Surface Water (SAAW) characteristic of open ocean environments in these latitudes (Chaigneau and Pizarro, 2005). The freshwater upper layer is mainly supplied by the Cisnes River and by rain runoff (Schneider et al., 2014). The surface outflow of buoyant freshwater in the fjord carries high concentrations of silicic acid derived from rivers, while SAAW waters are typically enriched with nitrate and orthophosphate (Silva, 2008). Surface salinity is higher in the north than in the south, suggesting an intrusion of oceanic surface waters into the north of Puyuhuapi Fjord through the Jacaf Channel, forced by westerly winds (Schneider et al., 2014).

Aulacomya atra was collected in the Puyuhuapi Fjord during summer (February) and winter (July) in 2 years, 2018 and 2019 (**Supplementary Table 1**). Samples of *A. atra* for both feeding experiments and stable isotopes analysis were collected by scuba diving at depths ranging from 5 to 10 m at several sampling stations (**Figure 1**). After collection, mussels for the feeding experiment were transferred to the field laboratory, cleaned of epibionts and debris, and maintained in a 200-liters seawater tank with constant aeration and at ambient temperature prior to the experimental protocols (approximately 24 h after collection).

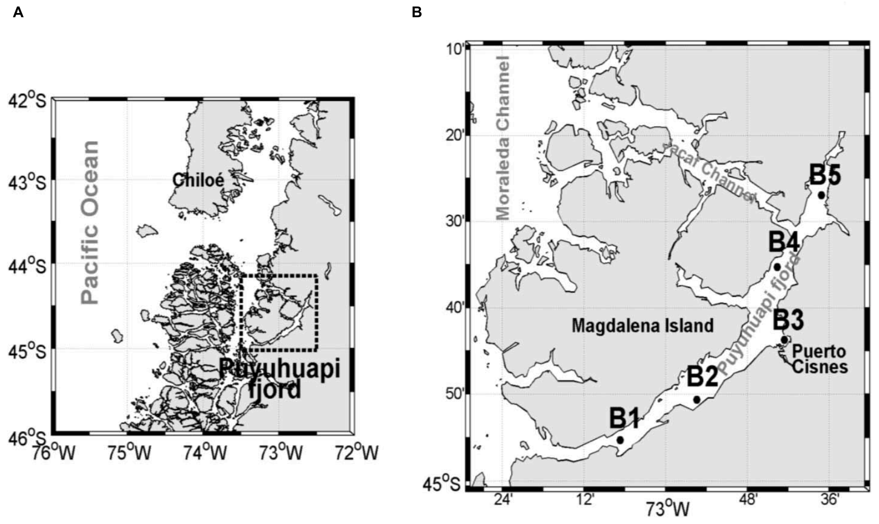

FIGURE 1 | (A) Location of the study area in Chilean Patagonia, **(B)** close-up of the study area with the position of the sampling stations along the Puyuhuapi Fjord.

Mussels for the stable isotopes analysis were treated as described in detail in section "Stable Isotopes."

Feeding Experiments

The feeding experiments were performed using plastic aquaria, each of 6-liters capacity and provided with a pumped air supply (3 L/min). Three different type of food (treatments) were tested: bacterial community, planktonic community, and allochthonous OM derived from salmon food pellets.

The first treatment – referred here as the bacterial community treatment (BC_T) – was prepared by gravity filtering seawater onto 22-μm mesh to remove large zooplankton and microphytoplankton. A peristaltic pump was then used to gently filter this water through 0.8-μm pore size sterile membrane filters (Millipore) in order to separate bacteria from the rest of the planktonic community (including potential predators). The second treatment – referred here as planktonic community treatment (PC_T) – was prepared by gravity filtering seawater onto 150-μm mesh to remove larger plankton. The third treatment consisted of 0.2-μm filtered seawater amended with salmon food pellets (SFP_T). This treatment was prepared by gravity filtering seawater onto 22-μm mesh. Then, a peristaltic pump was used to gently filter this water through 0.2-μm sterile membrane filters (Millipore), in order to remove bacteria and other microorganisms. Finally, 1 g of salmon food pellet was finely ground into particles <1 mm using a mortar; this powder was then added to the filtered water. For each treatment, an experimental and a control aquaria were used. At the beginning of each experiment, both aquaria were filled with the filtered water (BC_T, PC_T, SFP_T water, depending on the treatment) and one specimen of *A. atra* was placed in each experimental aquarium, whilst the control ones remained without individuals. The experiments began as soon as *A. atra* valves opened. Triplicate water samples of 500 mL were taken from experimental and control aquaria at the initial time ($t1$), and again 1 h later ($t2$). Samples from $t1$ and $t2$ were processed for particulate organic carbon (POC) analyses. Total POC was measured by filtering 500 mL water samples on pre-combusted GF/F glass microfiber filters (4 h at 450°C) which were then frozen at –20°C until analysis. Prior to the analysis, filters were defrosted and acidified with HCL. After acidification, the HCL was removed and the filters were dried at 50°C for 24 h. Filters were analyzed at the Laboratory of Biogeochemistry and Applied Stable Isotopes (LABASI, PUC), Chile.

The rate of change in POC concentration from control (kc) and experimental (kg) aquaria was calculated according to Frost (1972) equation:

$$C_2 = C_1 e^{k(t2-t1)}$$

where C_1 and C_2 are POC concentrations (mg C L^{-1}) at initial ($t1$) and final time ($t2$), respectively, and k (h^{-1}) corresponds to the rate of change in POC concentration during the experiments. The grazing coefficient is g (h^{-1}) and was calculated according to Ribes et al. (1998) equation:

$$g = kc - kg$$

where kc and kg are the rates of change in POC concentration from control and experimental aquaria, respectively.

The clearance rate, CR (volume swept clear per individual per time) was calculated according to Ribes et al. (1998) equation:

$$CR = V\left(\frac{g}{n}\right)$$

where V is the volume of the aquaria (L), n is the number of *A. atra* in the experimental aquaria and g is the grazing coefficient (h^{-1}). For comparative purposes, clearance rates were also standardized (CR_s) to constant biomass of 1 g *A. atra* dry flesh weight (Cranford et al., 2011). Finally, the ingestion rate, I (particles ingested per individual per time) was calculated as the product of CR (L individual^{-1} h^{-1}) and the concentration of POC (mg L^{-1}) using Ribes et al. (1998) formula:

$$I = CR \times C$$

where C is the initial POC concentration (C_1) in the experimental aquaria, calculated according to the following equation (Frost, 1972; Saiz, 1993):

$$C = \frac{C_1[e\{(kc - kg)\ (t2 - t1)\} - 1]}{(t2 - t1)\ (kc - kg)}$$

When the rate of change in POC concentrations was higher in experimental (kg) than in control (kc) aquaria, negative grazing coefficients (g) were obtained. Negative g are reported in **Table 1**; according to previous studies, negative values were set up to zero (Strom and Fredrickson, 2008; Stoecker et al., 2014, 2015; Anderson et al., 2018; Menden-Deuer et al., 2018; Anderson and Harvey, 2019), in order to calculate the mean and standard error of grazing in each treatment, and subsequently to estimate means and standard deviations in CR and IR. The significance of grazing (g values > 0) for each food type (treatments) was tested by comparing the rate of change in POC concentration from control (kc) and experimental (kg) aquaria using a two-tailed Wilcoxon test. Individual values of kc and kg for each experiment (**Table 1**) correspond to the average of three replicates obtained from control (**Supplementary Table 1**) and experimental (**Supplementary Table 2**) aquaria, respectively. Wilcoxon test was applied to seven experiments conducted under PC_T (autochthonous source), nine under BC_T (autochthonous source), and five under SFP_T (allochthonous source). In this last case, Wilcoxon test considered an alpha = 0.1 due the low number of sampling points.

To examine the relationship between CR and size/weight of the individuals under study, after each experiment, shell lengths and dry (24 h at 60°C) flesh weights were determined for each individual.

The non-parametric Kruskal–Wallis test (H) was used to examine differences in g, CR and IR between the different food sources (treatments). Kolmogorov-Smirnov test (K-S) was used to examine seasonal differences in CR and CRs.

Stable Isotopes

Three specimens of *A. atra* were collected from each sampling station for stable isotopes analysis in the study area (**Figure 1**). After collection, mussels were maintained in filtered seawater (0.2 μm) in a plastic container for 24 h and were then rinsed with distilled water and frozen at –20°C. Frozen samples were thawed and dissected. *A. atra* tissues were lyophilized and grounded prior to analysis.

In order to measure the stable isotope composition in suspended particulate organic matter (SPOM), samples were monthly collected from three depths (2, 10, and 20 m) from March to May 2018 and from July 2018 to February 2019 at sampling station B4. In addition, samples from 2 and 20 m depth were obtained from station B3 between March and May 2018 and in July 2018. Water samples (5 L) were filtered under gentle vacuum through GF/F filters (pre combusted for 4 h at 450°C) and refrigerated prior to analysis. The isotopic signal from salmon food pellets used in the feeding experiments of February/July 2018 and February 2019 was also measured. Tissues, filters and salmon food pellets samples were analyzed at the Laboratory of Biogeochemistry and Applied Stable Isotopes (LABASI, PUC, Chile) with an Isotope Ratio Mass Spectrometer (Thermo Fisher Scientific, Delta V Advantage IRMS) coupled with and Elemental Analyzer (Flash, EA 2000). Data are expressed in the standard ∂ unit notation:

$$\partial^{13}C \ or \ \partial^{15}N = \left(\left(\frac{Rsample}{Rstandard}\right) - 1\right) \times 1000‰$$

where R represents the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio for carbon and nitrogen, respectively, reported relative to VPDB for carbon and to atmospheric N_2 for nitrogen.

The non-parametric Kruskal–Wallis test (H) was used to examine seasonal differences in carbon ($\partial^{13}C$) and nitrogen ($\partial^{15}N$) signals from *A. atra* tissue and SPOM samples. In addition, isotopic signals ($\partial^{13}C$ and $\partial^{15}N$) from different sampling stations were also examined using test H.

To assess the potential contribution of the different carbon sources (allochthonous and autochthonous) in the diet of *A. atra,* and in the SPOM samples, an isotopic mixing model was used (Dauby, 1989; Fry, 2006). Allochthonous terrestrial OM (TOM) is isotopically lighter than its marine counterpart (Bianchi, 2007). In Chilean fjords TOM has an average $\delta^{13}C$ isotopic signals of −29‰ while autochthonous marine OM (MOM) has an average $\delta^{13}C$ isotopic signal of −1‰ (Vargas et al., 2011; Lafon et al., 2014; González et al., 2019). The isotopic mixing model considered three end members recorded in this study: (i) autochthonous OM from a marine source with a $\partial^{13}C$ of −18.3 (measured at station B4, 2 m depth), (ii) allochthonous OM from a terrestrial source with a $\partial^{13}C$ of −29.9 (measured at station B4, 20 m depth), and (iii) allochthonous OM from salmon food pellets used in feeding experiments with a $\partial^{13}C$ of −21.94.

RESULTS AND DISCUSSION

Differences in rates of change of POC concentrations in control (**Supplementary Table 2**) and experimental (**Supplementary Table 3**) aquaria were used to calculate grazing by *A. atra* (**Table 1**). The highest average grazing values were recorded on bacterial community (0.20 h^{-1} ± SE 0.08) and salmon food pellet treatment (0.26 h^{-1} ± SE 0.12), while planktonic community treatment showed the lowest (0.05 h^{-1} ± SE 0.02). Grazing values greater than zero; obtained when the rate of change of POC concentration was significantly higher under control conditions than in experimental aquaria (**Figure 2A**), indicated that *A. atra* was able to feed on both of the autochthonous sources of OM (bacterial and total microplanktonic community; Wilcoxon test, $p < 0.05$) and on the allochthonous source (ground salmon food pellet; Wilcoxon test, $p < 0.1$). The present study therefore confirms observations that ribbed mussels are omnivores, feeding on a wide array of organic particles (Kreeger et al., 2018), and highlights the ability of

TABLE 1 | Variables calculated during the feeding experiments.

Date	(h^{-1}) *Kc*	(h^{-1}) *Kg*	(h^{-1}) *g*	Treatment	L ind^{-1} h^{-1} C rate	mg C ind^{-1} h^{-1} I rate	g D Weight	mm Length	L g^{-1} h^{-1} C rate (s)
22-February-18	−0.44	−0.06	**−0.38**	PC_T	0	0	6	132	0
25-February-18	0.06	0.16	**−0.11**	PC_T	0	0	7	120	0
22-February-19	0.49	1.17	**−0.68**	PC_T	0	0	7	115	0
22-February-19	0.33	0.82	**−0.49**	PC_T	0	0	5	100	0
16-July-18	−0.12	0.05	**−0.17**	PC_T	0	0	6	112	0
22-February-18	0.34	0.33	0.01	PC_T	0.08	0.04	8	126	0.01
25-February-18	0.06	−0.06	0.11	PC_T	0.68	0.17	2	106	0.34
16-July-18	−0.34	−0.39	0.06	PC_T	0.34	0.12	6	111	0.06
25-February-19	0.10	−0.12	0.22	PC_T	1.30	0.31	8	106	0.16
09-July-19	−0.03	−0.21	0.18	PC_T	1.06	0.19	6	98	0.18
09-July-19	−0.03	−0.04	0.01	PC_T	0.08	0.01	4	97	0.02
10-July-19	−0.05	−0.10	0.05	PC_T	0.30	0.04	6	101	0.05
21-February-18	0.18	0.25	**−0.07**	BC_T	0	0	13	128	0
25-February-18	0.10	0.19	**−0.10**	BC_T	0	0	6	119	0
26-February-18	0.07	0.16	**−0.08**	BC_T	0	0	11	115	0
21-February-18	0.23	0.20	0.03	BC_T	0.16	0.03	7	137	0.02
17-July-18	0.17	−0.002	0.17	BC_T	1.03	0.28	7	109	0.15
23-February-19	1.06	0.07	1.00	BC_T	5.98	1.31	12	118	0.50
23-February-19	1.33	1.15	0.19	BC_T	1.11	0.10	3	112	0.37
25-February-19	0.67	0.27	0.40	BC_T	2.39	0.41	4	95	0.60
25-February-19	0.60	0.29	0.31	BC_T	1.88	0.33	4	110	0.47
08-July-19	0.02	−0.10	0.13	BC_T	0.76	0.10	5	92	0.15
08-July-19	−0.14	−0.17	0.04	BC_T	0.24	0.03	6	110	0.04
09-July-19	0.02	−0.11	0.12	BC_T	0.73	0.10	4	111	0.18
21-February-18	−0.54	0.40	**−0.94**	SFP_T	0	0	6	125	0
26-February-18	−0.68	0.29	**−0.97**	SFP_T	0	0	5	103	0
23-February-19	−0.83	−0.47	**−0.37**	SFP_T	0	0	7	101	0
21-February-18	0.29	0.27	0.02	SFP_T	0.13	0.25	6	111	0.02
26-February-18	0.18	−0.07	0.24	SFP_T	1.40	2.19	4	109	0.36
17-July-18	1.69	0.85	0.85	SFP_T	5.07	11.38	7	124	0.72
23-February-19	1.23	0.59	0.64	SFP_T	3.82	20.89	7	106	0.55
26-February-19	0.32	−0.01	0.33	SFP_T	1.98	10.41	5	105	0.40

Kc, rate of change in POC concentration in control aquaria; Kg, rate of change in POC concentration in experimental aquaria; g, grazing coefficient; C rate, clearance rate by individual; C rate (s), clearance rate standardized by weight; I rate, ingestion rate by individual; D weight and length, dry weight and length of Aulacomya atra in feeding experiments. Negative values in bold were substituted by zero to calculate C rate and I rate.

A. atra to filter both small (bacterial community <0.8 μm) and large (ground salmon food pellet <1 mm) food particles. Bacteria are generally too small to be efficiently retained by the gills of most bivalves, however, the particular morphology of gills of ribbed mussels – such as *A. atra* and *Geukensia demissa* (Dillwyn, 1817) – makes these species very effective grazers of bacteria (Wright et al., 1982; Stuart and Klumpp, 1984; Langdon and Newell, 1990). The bacterial community therefore makes an appreciable contribution to the diet of these species (Stuart et al., 1982; Kreeger and Newell, 1996). Bacterial ingestion by *A. atra* may also represent an important step in the vertical transfer of food and energy in Patagonian fjord ecosystems, and could be a particularly important route for allochthonous OM (from terrestrial origin or from salmon farming waste) entering indirectly into the benthic food web as material assimilated by bacterial community (Zapata-Hernández et al., 2014).

Consumption of salmon waste particles (uneaten food and feces) by blue mussels (*Mytilus edulis*; Linnaeus, 1758) under laboratory conditions has been described in the literature (Reid et al., 2010; MacDonald et al., 2011; Handå et al., 2012b). These studies have shown that mussels not only have the ability to efficiently capture and ingest particulate organic material (POM) from salmon feed and feces, but in some cases, mussels can in fact select fish feed particles and utilize them more efficiently than feces particles (Handå et al., 2012b). POM derived from salmon cages has previously been shown to be a food source as important as microalgae for mussels (Reid et al., 2010). In feeding experiments, clearance rates (CR) measured in bacterial (0–5.98 L ind^{-1} h^{-1}) and salmon food pellet (0–5.07 L ind^{-1} h^{-1}) treatments were quite similar and showed a range of values greater than those measured in planktonic community treatment (0–1.30 L ind^{-1} h^{-1}) (**Figure 2B**). However, no significant differences were observed between the different food sources

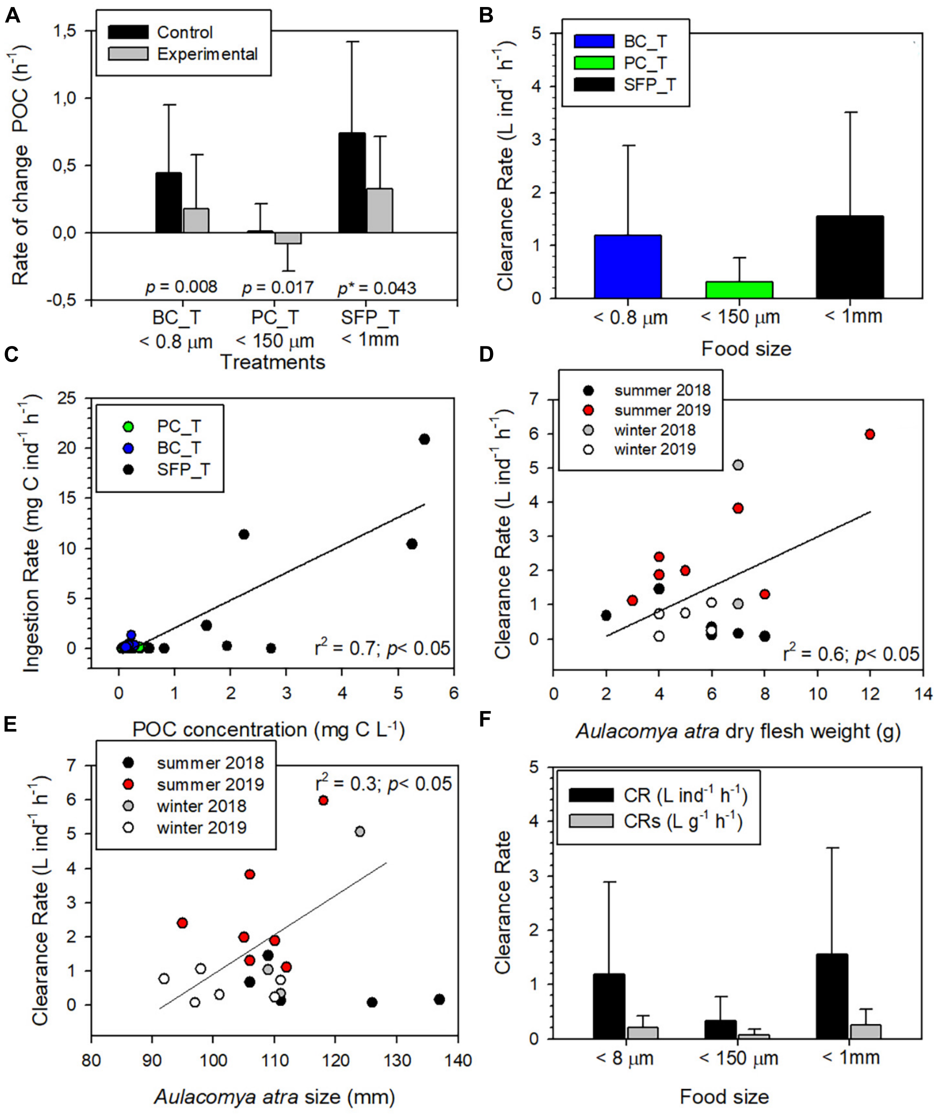

FIGURE 2 | (A) Rate of change in POC concentrations (average ± SD) from feeding experiments in control and experimental aquaria under bacterial community (BC_T), planktonic community (PC_T) and salmon food pellet (SFP_T) treatments. The mean value in both control and experimental aquaria correspond to all experiments carried out under the same treatment with a grazing coefficient > 0 (**Table 1**), *p*: *p*-value with alpha = 0.05, *p**: *p*-value with alpha = 0.1. **(B)** *Aulacomya atra* clearance rate (average ± SD) in each type of treatment. The mean value correspond to all experiments carried out under the same treatment. **(C)** Relation between POC concentration and ingestion rate (IR) of *A. atra* during feeding experiments. **(D)** Clearance rate as a function of dry flesh weight in *A. atra* during sampling campaigns. **(E)** Clearance rate as a function of *A. atra* size during sampling campaigns. **(F)** Comparison between clearance rates by individual (CR) and those standardized by weight (CRs) in each treatment.

(Kruskal–Wallis test, $p > 0.05$). The highest ingestion rates (IR) (2.19 to 20.9 mg C ind^{-1} h^{-1}) were obtained for salmon food pellet treatment (allochthonous OM) (**Figure 2C**) indicating that *A. atra* was able to capture and ingest salmon feed more efficiently than bacteria and microplanktonic organisms (Kruskal–Wallis test, $p < 0.05$). In contrast, highest IR values of between 0.17 and 0.31 mg C ind^{-1} h^{-1} recorded under autochthonous feeding conditions were significantly lower (Kruskal–Wallis test, $p < 0.05$) for the planktonic community treatment than the range of 0.28–1.31 mg C ind^{-1} h^{-1} recorded in bacterial treatment (**Figure 2C** and **Table 1**). These results do not necessarily represent a selection or preference of *A. atra* for a given food type since the diets provided in this study were not mixed. Highest IR values were associated with higher POC concentration (IR and POC concentration were positively correlated, **Figure 2C**, $r^2 = 0.73$, $p < 0.05$). Overall, salmon food pellet treatment with POC concentration >2 mg C L^{-1} had a greater IR (>10 mg C ind^{-1} h^{-1}) than those treatments with a lower POC concentration (**Figure 2C**).

Clearance rates (values > 0) was positively correlated to dry flesh weight of *A. atra* (more clearly observed during the 2019 summer campaign; $r^2 = 0.64$, $p < 0.05$) and with *A. atra* size (more clearly observed during winter campaigns and summer 2019; $r^2 = 0.3$, $p < 0.05$), suggesting that in most cases, an increase in weight and/or size of *A. atra* results in a higher CR (**Figures 2D,E**). The weight-standardized clearance rate (CRs) showed the same pattern as CR, although the values observed were lower (**Figure 2F**). Seasonally, CR and CRs were both significantly higher in summer than in winter (Kolmogorov-Smirnov test, $p < 0.05$), probably associated with the influence of water temperature on bivalve metabolic rates. Indeed, greater CR values are generally associated with high temperature (Haure et al., 1998; Sylvester et al., 2005; Kang et al., 2016). During summer, experiments were conducted within the 15–18°C temperature range whereas in the winter period the temperature range was lower (8–10°C). CR and IR values measured in this study for *A. atra* well agree with those reported in previous laboratory studies, both with *A. atra* (Griffiths and King, 1979) and with other species of mussels such as *M. edulis* (MacDonald et al., 2011; Handå et al., 2012b).

Stable isotopes show long-term nutrition, yielding accurate information about the characteristics of the assimilated food (Valiela, 1995), being among the most suitable tools to describe trophic relationships in coastal ecosystems (Wada et al., 1991). In this study carbon (∂^{13}C) and nitrogen (∂^{15}N) signatures from samples of *A. atra* tissue and SPOM from the Puyuhuapi Fjord were plotted together (**Figure 3A**). ∂^{13}C and ∂^{15}N values of *A. atra* tissues did not differ significantly (Kruskal–Wallis test, $p > 0.05$) among sampling station throughout the study period (B1: ∂^{13}C −18.5 ± 0.9‰, ∂^{15}N 9.5 ± 0.7‰; B2: ∂^{13}C −19.5 ± 1.7‰, ∂^{15}N 9.3 ± 0.7‰; ‰; B3: ∂^{13}C −20.1 ± 2.2‰, ∂^{15}N 9.1 ± 0.2‰; B4: ∂^{13}C −19.9 ± 1.2‰, ∂^{15}N 8.4 ± 0.4‰;

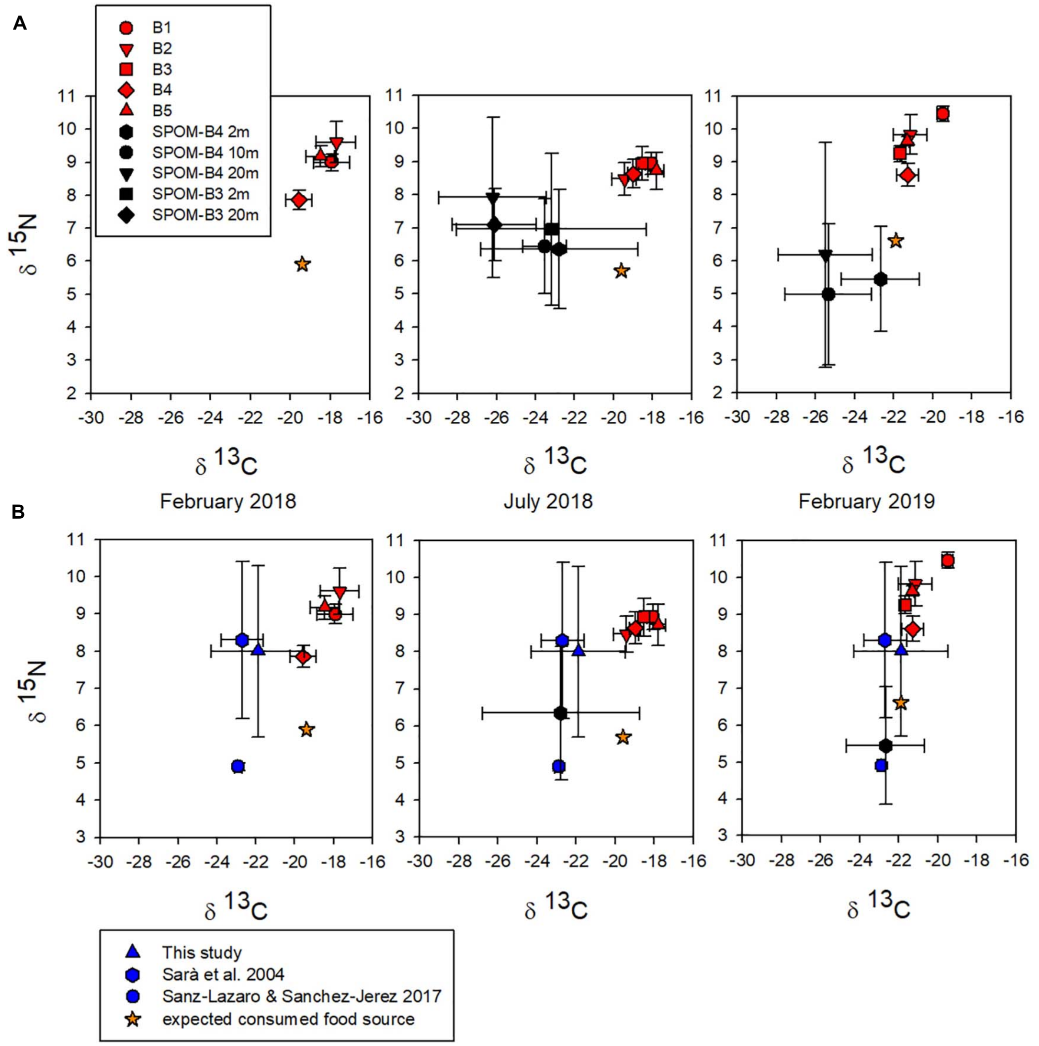

FIGURE 3 | (A) ∂^{13}C and ∂^{15}N biplot showing stable isotopic composition of *Aulacomya atra* tissues (red shapes) and of suspended particulate organic matter (SPOM) (black shapes). Samples of *A. atra* were obtained from different sampling stations across the Puyuhuapi Fjord (from B1 to B5). Samples of SPOM were obtained from different sampling depths (2, 10, and 20 m) in B4 and B3 stations. The orange star indicates the expected isotopic signature of the preferred food source. **(B)** ∂^{13}C and ∂^{15}N biplot showing stable isotopic composition in *A. atra* tissues and in pellet salmon food from this study and others.

B5: ∂^{13}C −19.2 ± 1.9‰, ∂^{15}N 9.2 ± 0.5‰) (**Figure 3A** and **Supplementary Table 4**). Likewise, the ∂^{15}N of *A. atra* tissues was quite similar seasonally (February 2018: 8.9 ± 0.8‰, July 2018: 8.7 ± 0.2‰ and February 2019: 9.6 ± 0.7‰) and showed no significant differences (Kruskal–Wallis test, $p > 0.05$) (**Figure 3A** and **Supplementary Table 4**). On the contrary, ∂^{13}C values of *A. atra* tissues were significantly different (Kruskal–Wallis test, $p < 0.05$) between February 2018 (−18.4 ± 0.8‰), July 2018 (−18.6 ± 0.7‰) and February 2019 (−20.9 ± 0.9‰) (**Figure 3A** and **Supplementary Table 4**). These seasonal differences observed in ∂^{13}C values might be related to the different food source (i.e., autochthonous vs. allochthonous) that was available in the water column for consumption of *A. atra*. In fact, ∂^{13}C values in SPOM samples – that include a wide range of potential food source for filter feeder organisms – between March and July 2018 at surface layer (2–10 m) ranged from −18.3 to −27.1‰, while between August 2018 and February 2019 ranged from −21.5 to −29.7‰ (**Figure 3A**). Different seasonal ranges observed in the isotopic signal of SPOM were possibly determined by the contribution of oceanic surface water and the increase in freshwater discharge, that usually occur in the Puyuhuapi Fjord during winter and spring months, respectively (Schneider et al., 2014). Oceanic waters are indicative of a strong marine component (∂^{13}C average = −19‰), while freshwater discharge has a high terrestrial signature (∂^{13}C average = −29‰) (Vargas et al., 2011; Lafon et al., 2014; González et al., 2019). In addition, depleted values of ∂^{15}N with values low 4‰ (as those observed between August 2018 and February 2019 in the study area) are indicative of a high terrestrial signal (Sepúlveda et al., 2011). ∂^{13}C and ∂^{15}N values of SPOM from 2 and 20 m did not show significant differences between sampling station B3 and B4 (Kruskal–Wallis test, $p < 0.05$; **Figure 3**).

Average ∂^{13}C values of SPOM (2–20 m) among March 2018 and July 2018 (−24.4 ± 1.7‰) and between August 2018 and February 2019 (−25.2 ± 0.4‰) were significantly more depleted (Kruskal–Wallis test, $p > 0.05$) than those measured in *A. atra* tissues in July 2018 (−18.6 ± 0.7‰) and February 2019 (−20.9 ± 0.9‰) (**Figure 3A** and **Supplementary Table 4**). Likewise, average ∂^{15}N values of SPOM between March 2018 and July 2018 (6.9 ± 0.6‰) and between August 2018 and February 2019 (5.5 ± 0.6‰) were significantly lower (Kruskal–Wallis test, $p > 0.05$) than those measured in *A. atra* tissues in July 2018 (8.7 ± 0.2‰) and February 2019 (9.6 ± 0.7‰) (**Figure 3A** and **Supplementary Table 4**). These ∂^{13}C and ∂^{15}N signatures of *A. atra* tissues and SPOM samples well agree with previous reports in Chilean fjords (Mayr et al., 2011; Andrade et al., 2016) and with studies on bivalves in fish farming areas (Mazzola and Sarà, 2001; Gao et al., 2006; Redmond et al., 2010).

Since the potential food sources ingested by *A. atra* are those which are depleted by 1‰ in ∂^{13}C and by ~ 3‰ in ∂^{15}N compared to the tissues of this consumer (Minagawa and Wada, 1984; Rau et al., 1990; Post, 2002), we might expect that the preferentially exploited food source shows values of −19.4‰ ∂^{13}C and 5.9‰ ∂^{15}N in February 2018, −19.6‰ ∂^{13}C and 5.7‰ ∂^{15}N in July 2018 and −21.9‰ ∂^{13}C and 6.6‰ ∂^{15}N in February 2019 (**Figure 3**). These isotopic ratios were close to the more enriched range of SPOM isotopic signal from 2m deep in the water column (**Figure 3**) that mainly correspond to autochthonous organic production by marine phytoplankton, with ranges of ∂^{13}C between −18 and −22‰ (Goericke and Fry, 1994) and ∂^{15}N between 6 and 7‰ (Wada et al., 1987). In this context, the results indicate that *A. atra* preferentially exploits food resources with signals consistent with autochthonous marine OM in Puyuhuapi Fjord. However, the average isotopic composition of the salmon food pellets used in feeding experiments from this study (∂^{13}C −21.9 ± 2.4‰, ∂^{15}N 8.0 ± 2.3‰) and in other studies (∂^{13}C −22.7 ± 1.1‰, ∂^{15}N 8.3 ± 2.1‰ from Sarà et al., 2004 and ∂^{13}C −22.9 ± 0.2‰, ∂^{15}N 4.9 ± 0.1‰ from Sanz-Lazaro and Sanchez-Jerez, 2017; **Figure 3B**) overlaps with marine phytoplankton signal in SPOM samples, mainly in February 2019 (**Figure 3B**). Estimating the contribution of this allochthonous salmon feed material to the diet of *A. atra* is therefore not so clear cut. The mixing equations clarify this point and indicate that both allochthonous material derived from uneaten salmon feed and autochthonous materials highly contribute to its diet (**Supplementary Table 5**). In February and July 2018, the greatest relative contributions (92–99%) came from autochthonous OM, while the terrestrial contribution to the diet of *A. atra* was minimal (1–23%) throughout the study (**Supplementary Table 5**). Regarding SPOM samples, the highest relative contributions were from autochthonous OM (40–60%) and allochthonous material from salmon pellet food (58–87%) in surface waters (2–10 m). In subsurface waters (20 m) the highest contributions (40–70%) were mainly from allochthonous terrestrial material (**Supplementary Table 5**).

The influence of allochthonous carbon sources on hard-bottom benthic communities in Chilean fjords has been poorly studied to date. Some authors have suggested that allochthonous material from a terrestrial origin plays a minor role as a food for suspension feeders (Mayr et al., 2011; Zapata-Hernández et al., 2014) and that autochthonous OM from phytoplankton production provides one of the principal food sources to these populations (Andrade et al., 2016). Our data confirm that phytoplankton carbon plays a primary role in the diet of *A. atra* and apparently excluding extensive utilization of terrestrially derived OM. However, the present study cannot preclude significant utilization of OM derived from salmon farming.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

PM: study design, data collection, analysis of data, interpretation of results, and manuscript leader. MC: study design, data collection, analysis of data, and manuscript revision. FB: data collection and manuscript revision. GB: manuscript revision. GD: study design, critical revision, and edition of final version of the manuscript. All authors contributed to the writing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.612406/full#supplementary-material

Supplementary Table 1 | Date, season, and geographical coordinates of *Aulacomya atra* sampling sites in the Puyuhuapi Fjord.

Supplementary Table 2 | Initial (C1) and final (C2) POC concentration [mean ± standard deviation (SD)] in control aquaria from different treatments during feeding experiments. Kc corresponds to rate of change in POC concentration estimated in control aquaria during feeding experiments. PC_T, planktonic community treatment; BC_T, bacterial community treatment; and SFP_T, salmon food pellet treatment.

Supplementary Table 3 | Initial (C1) and final (C2) POC concentration [mean ± standard deviation (SD)] in experimental aquaria from different treatments during feeding experiments. Kg corresponds to rate of change in POC concentration estimated in experimental aquaria during feeding experiments. PC_T, planktonic community treatment; BC_T, bacterial community treatment; and SFP_T, salmon food pellet treatment.

Supplementary Table 4 | ∂^{13}C and ∂^{15}N values [mean ± standard deviation (SD)] measured in *Aulacomya atra* tissues and in suspended particulate organic matter (SPOM) in the Puyuhuapi Fjord during the study period. For the location of the sampling station in the Puyuhuapi Fjord, refer to **Figure 1**.

Supplementary Table 5 | Possible contributions (%) of the three main carbon sources to the carbon isotopic signal of *Aulacomya atra* and suspended particulate organic matter (SPOM) estimated using the mixing model (Dauby, 1989; Fry, 2006). Three δ^{13}C end-member obtained in this study were used in the mixing model: autochthonous marine end-member δ^{13}C (−18.3), allochthonous terrestrial end-member δ^{13}C (−29.9) and allochthonous pellet end-member δ^{13}C (−21.9).

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