



## Importance of mixotrophic nanoplankton in Aysén Fjord (Southern Chile) during austral winter

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### ABSTRACT

Mixotrophy, the combination of autotrophic and heterotrophic nutrition in the same organism, is widespread in planktonic algae. Several reports from temperate and high-latitude fjords in Scandinavia suggest the occurrence of a niche in late summer and autumn during post-bloom conditions in which mixotrophic algae can become important grazers in pelagic ecosystems, accessing the nutrients bound in their prey to overcome nutrient limitation. Here, we experimentally determined the trophic modes and bacterivory rates for the nanoplankton community (2–20  $\mu\text{m}$ ) in Aysén Fjord located in the Chilean Northern Patagonia during two contrasting seasons: winter and spring. While mixotrophic nanoplankton was virtually absent from the system in spring, in winter at occasions it even constituted the dominant trophic group of the nanoplankton with abundances of  $> 900 \text{ cells mL}^{-1}$ . This indicates a second niche for mixotrophs in winter, when mixotrophy allows overcoming light limitation.

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### 1. Introduction

Mixotrophy is defined as the ability of an organism to combine autotrophic and heterotrophic nutrition. The pervasive occurrence of mixotrophs in the plankton of both marine and freshwater ecosystems is now realized (Jones, 2000). Mixotrophy can be seen as a special form of omnivory allowing organisms to overcome nutrient, carbon, light, or energy limitation (Elser and Hessen, 2005). Surveys in Scandinavian fjords and coastal embayments have shown that mixotrophic nanoflagellates (nanoplankton size range 2–20  $\mu\text{m}$ ) can play an important role; mixotrophic flagellate algae dominate the protist community and constitute up to 86% of the total flagellate grazing (Havskum and Riemann, 1996). This phenomenon has been confirmed by less extreme but significant reports of mixotrophic nanoflagellates in such environments (Nygaard and Tobiesen, 1993; Havskum and Hansen, 1997). In the Chilean fjord region (43–56°S), the phytoplankton is typically dominated by large diatoms in spring and nanoflagellates in winter

(Pizarro et al., 2005). Small algae are more effective than their larger competitors at dissolved nutrient uptake and in their use of light for photosynthesis (Raven, 1998), which should favor them in periods of light or nutrient limitation, as well as in situations in which mixotrophy might also offer them an advantage. However, up to this point, the use of mixotrophy as a nutritional strategy has not been analyzed in the Chilean fjord region. Here, we experimentally investigate the winter and spring communities of nanoflagellate algae (2–20  $\mu\text{m}$ ), asking one simple question: Is mixotrophy a major strategy in small algae (to overcome light limitation) during winter in high-latitude oligotrophic fjord environments?

Although simple, this question has at least three major implications. First, mixotrophs complicate the flow of energy and nutrients in fjord food webs by functioning as both producers and consumers, rendering classical models of ecosystem functioning incomplete. Second, as a consequence, mixotrophy requires considering the nutrients bound in the prey of the mixotrophs, which might change the nutrients finally limiting photosynthesis (Jansson, 1998). Third, theoretical food-web models suggest that mixotrophy has considerable effects, e.g., changes in the overall primary production and carbon and nutrient channeling systems as well as new competitive pressures on phyto- and zooplankton (Jones, 2000; Tittel et al., 2003). Field studies contrasting the role and impact of mixotrophic

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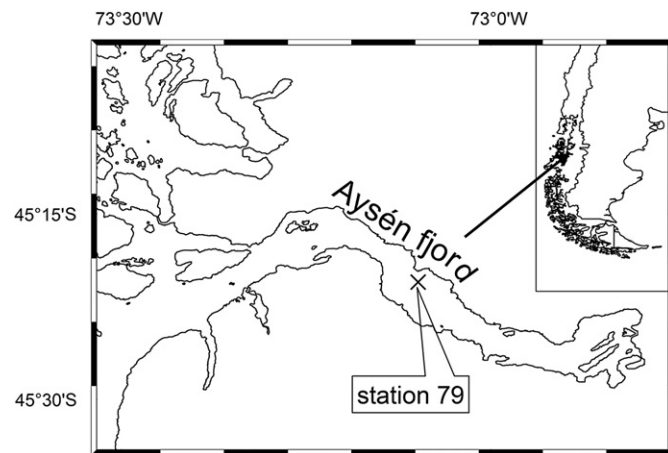
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nanoplankton between seasons are scarce for marine ecosystems and most were carried out at low-latitude environments (e.g., Christaki et al., 1999; Tsai et al., 2007). Although, mixotrophy describes many forms of nutritional strategies ranging from absolute autotrophy to absolute heterotrophy (Jones, 2000), herein our emphasis will be on algae that combine phototrophic autotrophy with phagotrophic heterotrophy. These algae were evaluated functionally by the possession of photo-pigments and their experimentally demonstrated ability to take up prey. We performed feeding experiments with fluorescently labeled bacteria (FLB) taken from a fjord in contrasting seasons and at different depths, relating our findings to various environmental variables. This work, therefore, bridges a remaining gap in our knowledge, suggesting a necessity to incorporate mixotrophy into the analyses of ecosystem functioning in the Chilean fjord region and in high-latitude fjord environments in general.

## 2. Material and methods

### 2.1. Study area

The study was carried out in the inner sound of Aysén Fjord in Southern Chile (45°22'S, 73°04'W, see Fig. 1 for map) during austral



**Fig. 1.** Location of the study area in the context of the Patagonian fjord system as indicated by the arrow (right); location of station 79 in Aysén Fjord (cross).

winter (2–6 August 2007) and austral spring (8–11 November 2007) on board the R/V *AGOR Vidal Gormaz*. Aysén Fjord is a typical, silled, high-latitude fjord with a freshwater inflow (Cáceres et al., 2002). Salinity, temperature, and density were measured with a Seabird 19 CTD. Salinity and density measurements were visualized using the software Ocean Data View (Schlitzer, 2008). Seawater samples were gathered with a Teflon-coated Niskin bottle rosette system. Nutrient analyses comprising orthophosphate ( $\text{PO}_4^{3-}$ ), nitrate ( $\text{NO}_3^-$ ), and silicic acid ( $\text{Si}(\text{OH})_4$ ) were performed for standard depths (0, 2, 5, 10, 25, 50, 75, 100 m) every 3 h from 2 to 3 August and from 7 to 8 November 2007. Samples were stored at  $-25^\circ\text{C}$  in aseptically polyethylene-bottles (50 mL) until their analysis using an automatic nutrient analyzer according to Atlas et al. (1971). Three qualitative depths were defined and used to determine the size-fractionated chlorophyll-*a* (Chl-*a*) concentrations and primary production (PP), bacterial abundance (BA), and bacterial production (BP); these were designated surface (0 m in winter, 5 m in spring), chlorophyll maximum (chlor. max.), and dark (25 m). The chlor. max. depth was designated daily following the CTD profile analysis in the halocline between the freshwater influenced upper layer and the underlying saltier water masses (see Table 1 for overview). Measurements of PP by size classes ( $<2$ ,  $2$ – $20$ ,  $>20$   $\mu\text{m}$ ) were performed for the three depths in analysis using the  $^{14}\text{C}$ -isotope incorporation method described by Steemann-Nielsen (1952). Chl-*a* concentrations were measured for the same depths and size classes using a digital Turner PS 700 fluorometer after Chl-*a* extraction in 90% v/v acetone. For a detailed description of both methods refer to Iriarte et al. (2007, and citations therein). Samples for BA were preserved in glutaraldehyde (6.0% W/V in 0.2  $\mu\text{m}$  prefiltered seawater), stained with DAPI (4',6-diamidino-2-phenylindole; final conc. of  $1 \mu\text{g mL}^{-1}$ ), and subsequently collected on 0.2- $\mu\text{m}$  black Nucleopore<sup>®</sup> filters (Porter and Feig, 1980).

Water for BP estimations was incubated in parallels using water samples from the same oceanographic bottle as for PP experiments. BP was estimated by the incorporation of  $l$ -[ $^{14}\text{C}(\text{U})$ ]-leucine into proteins at a final concentration of 10 nM (Simon and Azam, 1989). Triplicate samples of 10 mL and a formalin-killed control were incubated at the in situ temperature and darkness for 1 h. After incubation, samples were filtered over 0.22  $\mu\text{m}$  membrane filters and extracted with cold 5% trichloroacetic acid. Samples were frozen on board and counted in a liquid scintillation counter in the laboratory. Leucine incorporation was converted into biomass production using the carbon fraction of proteins of 0.86 (Simon and Azam, 1989). The bacterial volume was calculated from length and width measurements of at least 20 cells per sample by using

**Table 1**

Overview over the experiments: sample date, sample depth, and in situ temperature, salinity and bacterial abundance.

| Experiment | Date (mm/dd/yyyy) | Depth (m) | Temperature ( $^\circ\text{C}$ ) | Salinity (PSU) | Bacterial abundance ( $10^6$ cells $\text{mL}^{-1}$ ) |
|------------|-------------------|-----------|----------------------------------|----------------|---|
| 1          | 08/02/2007        | 1         | 7.2                              | 18.7           | 4.9   |
| 2          | 08/02/2007        | 10        | 9.5                              | 29.0           | 3.6   |
| 3          | 08/02/2007        | 25        | 9.9                              | 30.2           | 2   |
| 4          | 08/04/2007        | 1         | 8.7                              | 8.7            | 5.9   |
| 5          | 08/04/2007        | 5         | 9.4                              | 29.1           | 3   |
| 6          | 08/04/2007        | 25        | 9.9                              | 30.3           | 2.2   |
| 7          | 08/06/2007        | 1         | 9.4                              | 29.2           | 3.5   |
| 8          | 08/06/2007        | 5         | 9.4                              | 29.3           | 1.3   |
| 9          | 08/06/2007        | 25        | 10.3                             | 30.4           | 2.2   |
| 10         | 11/08/2007        | 5         | 9.2                              | 8.5            | 9.7   |
| 11         | 11/08/2007        | 10        | 9.5                              | 27.7           | 3.9   |
| 12         | 11/08/2007        | 25        | 9.5                              | 29.6           | 1.7   |
| 13         | 11/09/2007        | 5         | 9.7                              | 27.6           | 5   |
| 14         | 11/09/2007        | 10        | 9.5                              | 28.6           | 2.8   |
| 15         | 11/09/2007        | 25        | 9.5                              | 29.4           | 2.6   |
| 16         | 11/11/2007        | 5         | 9.8                              | 27.1           | 8.8   |
| 17         | 11/11/2007        | 10        | 9.6                              | 28.3           | 3.5   |
| 18         | 11/11/2007        | 25        | 9.5                              | 29.5           | 2.3   |

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