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Allochthonous subsidies of organic matter across a lake–river–fjord landscape in the Chilean Patagonia: Implications for marine zooplankton in inner fjord areas

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ABSTRACT

Ecosystems can act as both sources and sinks of allochthonous nutrients and organic matter. In this sense, fjord ecosystems are a typical interface and buffer zone between freshwater systems, glaciated continents, and the coastal ocean. In order to evaluate the potential sources and composition of organic matter across fjord ecosystems, we characterized particulate organic matter along a lake–river–fjord corridor in the Chilean Patagonia using stable isotope ($\delta^{13}C$) and lipid (fatty acid composition) biomarker analyses. Furthermore, estimates of zooplankton carbon ingestion rates and measurements of $\delta^{13}C$ and $\delta^{15}N$ in zooplankton (copepods) were used to evaluate the implications of allochthonous subsidies for copepods inhabiting inner fjord areas. Our results showed that riverine freshwater flows contributed an important amount of dissolved silicon but, scarce nitrate and phosphate to the brackish surface layer of the fjord ecosystem. Isotopic signatures of particulate organic matter from lakes and rivers were distinct from their counterparts in oceanic influenced stations. Terrestrial allochthonous sources could support around 68–86% of the particulate organic carbon in the river plume and glacier melting areas, whereas fatty acid concentrations were maximal in the surface waters of the Pascua and Baker river plumes. Estimates of carbon ingestion rates and $\delta^{13}C$ in copepods from the river plume areas indicated that terrestrial carbon could account for a significant percentage of the copepod body carbon (20–50%) during periods of food limitation. Particulate organic matter from the Pascua River showed a greater allochthonous contribution of terrigenous/vascular plant sources. Rivers may provide fjord ecosystems with allochthonous contributions from different sources because of the distinct vegetation coverage and land use along each river's watershed. These observations have significant implications for the management of local riverine areas in the context of any human project that may modify terrestrial habitats as well as the productivity, food webs, and community structure of rivers, lakes, fjords, and the coastal ocean in the Chilean Patagonia.

1. Introduction

For decades, ecologists working in food web analysis have focused their studies on interactions among elements of well-defined ecosystems, putting little emphasis on the interactions and transitions among the ecosystems themselves. Recently, it has become increasingly apparent that fluxes of energy and biogeochemical elements across operationally defined systems represent an important and usually neglected component of ecosystem dynamics (e.g., Polis et al., 1997; Carpenter et al., 2005). The fact that ecosystems might act as both sources and sinks of allochthonous nutrients and detritus is essential for understanding primary productivity and food web dynamics at a landscape level (Jefferies, 2000).

Fjords constitute a typical case requiring a landscape-wide approach to ensure a thorough understanding of ecosystem functioning and vulnerability under natural or anthropogenic stressors. These areas represent an interface and a buffer between freshwater systems (i.e., lakes and rivers), glaciated continents,

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and the coastal ocean, where fjord marine communities are also simultaneously influenced by the open sea, the surrounding coastal terrain, and freshwater runoff (Gorsky et al., 2000). Carbon and nutrient dynamics occur at the land–sea interface in fjords, where large quantities of nutrients are transported and incorporated into the organic matter (OM) (Burrell, 1988).

The coastal area off the Chilean Patagonia, which extends from Reloncaví Fjord (41° 20′S) to Cape Horn (56°S), is characterized by about 84,000 km of broken coastline, considering all the contours of its multiple islands and peninsulas, with hundreds of channels and fjords (Silva and Prego, 2002). The inland seas comprised in this area include a variety of channel and fjord systems that have a typical estuarine circulation pattern determined by an offshore surface flow of freshwater over an onshore flow of oceanic water (Silva, 2008). Rivers in the Chilean Patagonia are born in the oriental slopes of the Andes Mountain; these rivers are relatively short and their flow into fjord waters is usually regulated by several lakes, configuring a continuous lake–river–fjord corridor (Niemeyer and Cereceda, 1984). For most fjord ecosystems, the high turbidity of river plumes and interactions between autochthonous organic particles and allochthonous particulate organic carbon from rivers or glaciers (e.g., Syvitski and Murray, 1981; Eisma, 1993) lead to the enhancement of a complex OM particle pool available for different marine plankton consumers.

Defining the sources and composition of OM across ecosystems is essential for understanding the carbon cycle and, in particular, the importance of terrestrial or estuarine derived carbon as a source of energy and nutrients supporting marine organisms in Patagonian fjords. Stable isotopes constitute a useful tool for inferring sources of OM cycling in aquatic ecosystems (Canuel et al., 1995; Sobczak et al. 2005; Martineau et al., 2004; McCallister et al., 2006). Similarly, fatty acids have been used extensively as lipid biomarkers for terrigenous and planktonic OM in many aquatic and sedimentary environments (Wakeham and Beier, 1991; Mannino and Harvey, 1999). Here, our primary objective was to assess the relative contributions of allochthonous (i.e., terrigenous) and autochthonous (i.e., both from freshwater and marine plankton) sources to the POM pool throughout a relatively pristine, natural lake–river–fjord corridor by employing nutrient stoichiometry (N, P, Si:N ratios), isotopic analyses (δ^{13}C), lipid biomarkers (fatty acid composition), and standard measurements of bacterial, protozoan, and phytoplankton carbon. In addition, by using estimations of prey-specific carbon ingestion rates and measurements of δ^{13}C and δ^{15}N in small copepods, we aimed to explore the potential utilization of autochthonous vs. riverine allochthonous OM by omnivorous copepods inhabiting the oligotrophic waters of river plumes in an inner fjord ecosystem.

2. Material and methods

2.1. Study area

The study area (Fig. 1) comprises a large region of the Chilean Patagonia (from ~36.5° to ~50°S), including the Baker River watershed and its adjacent fjords and channels. Two main glacial fields encase the adjacent mountains of this area: the Northern Patagonian Ice Field between 46° and 47°S and the Southern Patagonian Ice Field between 48° and 52°S. Presently, several glaciers that descend towards the coastline (e.g., Steffen Glacier, Fig. 1) are beginning to break up at the fjord heads, creating icebergs that dilute salty waters upon melting (Silva and Calvete, 2002). However, discharges from several local rivers constitute the major source of freshwater and allochthonous OM to these marine ecosystems.

The Baker River is Chile's largest river in terms of water volume (1133 $m^3\,s^{-1}$) and is fed by different lakes, glaciers, and ice fields. The Baker River flows out of Bertrand Lake, which is fed by General Carrera Lake (Fig. 1), runs along the east side of the Northern Patagonia Ice Field, and empties into the Baker Channel, near the village of Caleta Tortel. The river forms a delta, dividing into two major arms, of which only the northernmost is navigable. The delta acts as a sieve, filtering freshwater and sediment from the continent before it reaches the salty water in the Baker Channel. The freshwater discharge of Pascua River constitutes another important freshwater and OM source to the fjord ecosystem (753 $m^3\,s^{-1}$). Pascua River originates in Lake O'Higgins (48°20′S, 73°00′W) and, after travelling 67 km, flows into Mitchell Fjord (48°13′S, 73°18′W). Vegetation in this area is dominated by evergreen forests, deciduous forests, and peatlands; the dominant species of the landscape are representatives of the family Nothofagaceae (Rodriguez et al., 2008). In this area, precipitation ranges from 1000 to 7000 mm yr^{-1} on the western side of the Andes (National Water Directorate, http://www.dga.cl). Most of the terrestrial subsidies to the channels and fjords originate in the surrounding native forests covering major watersheds and in particles from ice melting. The nearshore region, associated with the Baker and Pascua river plumes, is supposed to exhibit efficient recycling of riverine nutrients between the phytoplankton and microflagellate grazer communities and under spring–summer conditions, when the quantity and quality of light is available for photosynthesis and the microphytoplankton community is dominated by diatoms (Pizarro et al., 2005). The freshwater ecosystems of the Baker and Pascua river basin are economically important because this basin is considered to contain Chile's major remaining hydroelectric potential.

2.2. Sample collection

The oceanographic field work in the southern Chilean fjords and channels was performed in austral spring (2–15 November 2009) onboard the RV *AGOR Vidal Gormaz* (CIMAR 14 Fiordos cruise). Of the 54 oceanographic stations performed during CIMAR 14 Fiordos, we selected eight oceanographic stations for the present study. Simultaneous freshwater sampling was conducted at Carrera Lake, Bertrand Lake, and Baker River during a field campaign across the lake–river–estuary corridor. Surface freshwater samples (3–10 L) from the Baker watershed were collected between 13 and 15 November 2008 at four sites (Fig. 1): (1) Carrera Lake, where its waters enter the Baker River; (2) Bertrand Lake; (3) an intermediate site in the Baker River; and (4) the lower portion of the Baker River near its delta area at Caleta Tortel village. The eight oceanographic stations sampled onboard the RV *AGOR Vidal Gormaz* were comprised of: (1) two stations located in the Baker (St. 12) and Pascua (St. 10) river plumes; (2) two stations in the vicinity of the Steffen Glacier (St. 13, 14); (3) one station near the Tempanos Glacier (St. 21, only for nutrients and δ^{13}C analyses) in the Southern Patagonia Ice Field; (4) and three stations evenly distributed along a transect from Messier Channel (St. 17), to Wide Channel (St. 31), to the more oceanic-influenced Concepción Channel (St. 40) (Fig. 1). During the oceanographic cruise, two additional freshwater samples for nutrient analyses were also taken: one at the Baker River mouth and the other at the Pascua River mouth (Fig. 1).

2.3. Fjord hydrography, nutrients, and plankton carbon biomass

During the research cruise, temperature and conductivity profiles were recorded with a CTD Seabird 19. Seawater samples (50 mL) for dissolved oxygen and nutrient analyses were collected