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Community structure and trophic ecology of megabenthic fauna from the deep basins in the Interior Sea of Chiloé, Chile (41–43° S)

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ABSTRACT

Estuarine environments are complex ecological systems, which depend on multiple inputs of organic sources that could support their benthic communities. The deep-water megabenthic communities of the Interior Sea of Chiloé (ISCh, northern part of the fjord region of Chile) were studied to characterize their taxonomic composition and to trace the energy pathways supporting them by using stable isotope analysis (SIA). Megabenthic and demersal organisms as well as sunken macroalgal debris and terrestrial organic matter (TOM: wood, leaves, branches) were obtained by bottom trawling along an estuarine gradient covering 100–460 m water depth. Additionally, particulate organic matter (POM) and the sedimentary organic matter (SOM) were sampled and carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios were determined for all these organisms and potential food sources. A total of 140 taxa were obtained, including invertebrates (e.g. polychaetes, mollusks, crustaceans and echinoderms) bony fishes, rays and sharks. Based on the stable isotope values it was possible to infer a strong dependence on primary production derived from phytoplankton which is exported to the benthos. A potentially important contribution from sunken macroalgae to megabenthic consumers was established only for some invertebrates, such as the irregular echinoid *Tripylaster philippii* and the decapod *Eurypodius latreillii*. The trophic structure metrics suggest a similar isotopic niche width, trophic diversity and species packaging in the food webs among the major basins in the ISCh. It is thus concluded that the benthic food webs are supported principally by surface primary production, but macroalgal subsidies could be exploited by selected invertebrate taxa (e.g. detritivores) and terrestrial carbon pathways are important for certain specialized taxa (e.g. *Xylophaga dorsalis*).

1. Introduction

Food web structures are spatially heterogeneous and different among habitats and community composition (Polis et al., 1997). Estuarine environments are complex systems where the energy supply for benthic communities may depend on multiple inputs (e.g. terrestrial or riverine matter, marsh detritus, phytoplankton, seagrasses or benthic microalgae) and benthic decomposition processes (e.g. methane oxidizing, sulfate reducing and nitrification), which makes the understanding of the element fluxes (e.g. carbon and nitrogen) and food web structure difficult to achieve (Peterson, 1999). In general, it has been recognized that allochthonous inputs can significantly influence the energy, element and nutrient budgets of many habitats and via bottom-up effects drive the community dynamics at multiple trophic levels in marine, freshwater and terrestrial systems (Polis et al., 1997). Therefore the identification of the sources and composition of organic matter is of key importance for understanding the element cycles (e.g. carbon, nitrogen, oxygen) and also the contribution of allochthonous inputs as energy sources and nutrients supporting marine organisms (Vargas et al., 2011).

In general, fjord systems feature an estuarine gradient where terrestrial sources are more important in the shallower, inner parts of a fjord, whereas oceanic inputs dominate trophic fluxes in the deeper, outer parts of the fjords (Sepulveda et al., 2011). However, this

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general pattern might be confounded by water depth, as the shallow benthos of the inner fjord parts is also closer to the surface waters, which are generally dominated by freshwaters importing terrestrial organic matter. Deeper sediments, even if located in the inner parts of a fjord, might be dominated by oceanic carbon sources, because the inflowing deep waters bring in oceanic organic matter. Conversely, floating items of both oceanic and terrestrial origin may be transferred over long distances along the estuarine gradient, accumulating and mingling in frontal zones, which are often close to the outer stations (Hinojosa et al., 2010; Acha et al., 2015). If floating items persist and finally sink near these frontal zones, then they might become trophic subsidies for benthic organisms in these zones. Given that oceanic and terrestrial floating items accumulate and sink to the bottom at these fronts in the outer, deeper parts of a fjord or estuary, it can be hypothesized that at least some benthic organisms obtain energy from these oceanic and terrestrial sources.

The Interior Sea of Chiloé (ISCh) comprises a continuous series of deep basins formed by glacial erosion during the Quaternary and tectonic sinking of the central valley, which in combination with the subsequent rise in sea level and flooding of basins created a system of channels, fjords and interior gulfs (Silva and Prego, 2002, and references therein). The Reloncaví Sound (thereafter RS) and the Ancud Gulf (thereafter AG) are semi-enclosed deep basins (300–400 m), which act as sediment traps and also have a greater concentration of phytoplankton, primary production and zooplankton biomass than the adjacent and southernmost Corcovado Gulf (thereafter CG) (Silva and Prego, 2002; Lara et al., 2016). In general, circulation follows an estuarine pattern where water from the inner sea is exchanged with the Pacific Ocean mainly by the narrow, shallow Chacao Channel (4 km, 50 m depth) and the wider, deeper Boca del Guafo passage (66 km, 150 m depth; Silva et al., 2011). This complex topography controls the exchange of waters between coastal regions and the open ocean, creating micro-environments with oceanographic conditions that sustain unique ecosystems (Aracena et al., 2011), providing important ecosystem services, which have been scarcely measured or evaluated (Iriarte et al., 2010).

These ecosystems are characterized by complex marine-terrestrial-atmospheric interactions that result in high biological production (Aracena et al., 2011). In the interior parts of the system, the principal sources of particulate material are the biological productivity in the surface waters, fluvial runoff and coastal erosion (Silva and Prego, 2002, and references therein). However, strong seasonality imposes an external influence on the phytoplankton which displays seasonal variation in biomass, primary production, and species composition (González et al., 2010; Lara et al., 2016). Values of Chlorophyll-a and primary productivity in the ISCh and the head of fjords range from 1 to 25 mg Chl-a m^{-3} and 1 to 23 mg C m^{-3}, respectively (Iriarte et al., 2007), with 25–50% of the surface primary productivity arriving at the bottom after sinking through the water column (Silva and Prego, 2002, and references therein). In addition, the interaction between the diluted waters provided from the fjords and the subantarctic water masses generate estuarine conditions (Rosenberg and Palma, 2003), creating saline fronts throughout the fjord region between 42° S and 56° S (Davila et al., 2002; Acha et al., 2004). These frontal zones constitute important retention areas where the biological productivity is enhanced (Sobarzo, 2009), possibly also by floating biotic items.

A high proportion of floating wood has been observed in the fjord region, fueled by an abundant wood supply along the densely forested coast and river banks, and facilitated by the generally short distance from the forest to the sea (Hinojosa et al., 2011, and references therein). This wood material can be transported long distances from its origin before sinking, eventually constituting important organic matter pulses to the seafloor (Wolff, 1979; Smith, 1983; Vetter and Dayton, 1998). In the Patagonian region, forests are recognized as an important terrestrial carbon source (Sepulveda et al., 2011), explaining a great proportion of the organic component in the sediments and representing trophic subsidies to the benthic communities, potentially controlling their biomass, diversity and functional group composition, as suggested from other fjord systems (McLeod and Wing, 2009; Bernardino et al., 2010; McLeod et al., 2010; Fleury and Drazen, 2013). A similar process has been inferred for floating patches of the large kelps *Macrocystis pyrifera* and *Durvillaea antarctica*, which are transported by the continuous tidal in- and outflow to the oceanic openings north and south of Chiloé, where they are retained by strong western winds (Hinojosa et al., 2010), reaching high biomasses in these retention zones (>1000 kg km^{-2}). When sinking, these kelps potentially fuel dense detritivore populations in different coastal and deep water benthic habitats (e.g. Vetter, 1994). These kelp accumulations reaching the bottom contain much more labile organic matter than wood, being consumed by scavenging invertebrates and decomposed by microbes at higher rates than wood falls of similar mass (Bernardino et al., 2012, and references therein), constituting thus an important fraction of the diet of their consumers ($>50\%$; Bernardino et al., 2010) and potentially playing an important role in the organic matter cycles in the Patagonian fjords (Hinojosa et al., 2011).

The study of nutritional pathways and trophic structure is a fundamental requirement to understand the energy flow from the base to higher trophic levels in food webs (Nilsen et al., 2008). The analysis of natural biological tracers, such as stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) constitute a robust approach often used to trace energy flow pathways throughout food webs (Michener and Schell, 1994). While $\delta^{13}C$ is generally used to identify carbon fixation pathways in primary producers and the food sources of heterotrophic consumers (DeNiro and Epstein, 1978), enrichment of $\delta^{15}N$ between two adjacent trophic levels (~3.4‰; Minagawa and Wada, 1984; Post, 2002) allows the estimation of relative trophic positions of different constituents of the food web (Cabana and Rasmussen, 1996; Carlier et al., 2007) if basal values are known. Furthermore, stable isotope analyses allow the study of isotopic niches, providing for time- and space-integrated representations of the trophic ecology of organisms, populations and communities and also providing powerful tools for studying ecological responses to anthropogenic impacts (Layman et al., 2007a; Jackson et al., 2011).

The ISCh represents a complex estuarine system where several deep basins are on the one hand connected to fjords, receiving multiple inputs of organic matter from fluvial runoff, coastal erosion and adjacent evergreen forest, and on the other hand influenced by the organic matter associated to water masses and kelp accumulations sunken at the outer, estuarine fronts. This offers an ideal opportunity to examine the functioning of deep-water benthic communities in large estuarine systems and the food sources fueling them.

Based on the carbon and nitrogen stable isotope analysis of a large variety of organisms from the ISCh, the aims of this study are: (i) characterize the megabenthic communities in the area, (ii) trace the origin of carbon sources that support the benthic fauna (e.g. terrestrial origin), (iii) determine the trophic structure of benthic consumers present in the different parts of the system (i.e. RS, AG and CG), and (iv) compare possible differences in the isotopic niche width among communities. Thus, this study may also be considered as a base-line of the benthic food web, which in addition to the identification of the sources of heterogeneity in their trophic structure might also be useful for environmental management in the basins of the ISCh. This kind of primary information is crucial for such a fragile ecosystem facing a scenario of changes in the availability of food sources associated to anthropogenic alterations (e.g. salmon farming, hydroelectric projects and global climate change, among others) to the benthic ecosystem.

2. Materials and methods

2.1. Study site and sample collection

Samples of megabenthic fauna and terrestrial sources were col-