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20th century human pressures drive reductions in deepwater oxygen leading to losses of benthic methane-based food webs

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A B S T R A C T

Freshwater lakes play a key role in the global carbon cycle as sinks (organic carbon sequestration) and sources (greenhouse gas emissions). Understanding the carbon cycle response to environmental changes is becoming a crucial challenge in the context of global warming and the preponderance of human pressures. We reconstructed the long-term (1500 years) evolution of trophic functioning of the benthic food web, based on methanotrophic ancient DNA and chironomid isotope analyses). In addition, human land use is also reconstructed in three different lakes (eastern France, Jura Mountains). Our findings confirm that the benthic food web can be highly dependent on methane-derived carbon (up to 50% of the chironomid biomass) and reveal that the activation of this process can correspond to a natural functioning or be a consequence of anthropic perturbation. The studied lakes also showed a similar temporal evolution over the last century with the disappearance of the profundal aquatic insects (Chironomidae, Diptera), considered as keystone for the whole lake food web (e.g., coupling benthic-pelagic), inducing a potential collapse in the transfer of methane to top consumers. This functional state, also called the dead zone expansion, was caused by the change in human land-use occurring at the beginning of the 20th century. The strong modification of agro-pastoral practices (e.g., fertilization practices, intensive grazing, and sewage effluent) modified the influx of nutrients (by diffuse and/or point-source inputs) and induced a significant increase in the trophic status and organic matter sedimentation to reach unprecedented values. Further studies should be planned to assess dead zone expansion and, according to the regime shift theory, to provide environmental tipping points for sustainable resource management.

1. Introduction

Lake ecosystems have undergone environmental changes across a multi-millennial time scale, and their functionings have adapted to these evolutions. Over the last two centuries, human pressures have become the main driver of ecosystem evolutions and have induced dramatic changes including biodiversity and ecological services losses (Dodds et al., 2013) and perturbations of biogeochemical cycles (Anderson et al., 2014). Freshwater lakes play a key role in the regulation of the global carbon cycle (Tranvik et al., 2009), and an understanding of the responses of the lake carbon budget facing environmental changes is a crucial challenge to predict future trend in lacustrine ecological trajectories.

Photoautotrophic production, including aquatic and terrestrial plant organic matter, is the main basal source of carbon and energy for the benthic food web (Meili, 1992). It is generally assumed that the transfer of this organic matter to higher trophic levels occurs through direct incorporation into consumers' biomass (Grey et al., 2000) or is mediated by microorganisms (Goedkoop and Johnson, 1992). Recent studies have revealed that bacterial methane (CH_4) production can complete this pathway (e.g., Ravinet et al., 2010). Biogenic CH_4 is the end product of the degradation of organic matter under anaerobic conditions (Rudd and Hamilton, 1978). A portion of this CH_4 production is released into the atmosphere, but up to 75% of this gas is used as a source of energy and carbon by

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methane-oxidizing bacteria (MOB; Schubert et al., 2010). MOB can then become a food source for consumers and significantly contribute to the entire lake food web (Sanseverino et al., 2012), particularly to the benthic food web (Jones et al., 2008; Belle et al., 2015a; Belle et al., 2016). As the benthic food web plays a key role in the whole lake functioning (i.e., benthic-pelagic coupling Wagner et al., 2012), the recognition of the trophic reliance on CH_4 in the last few decades has provided a new perspective on lake trophic functioning. In this context, the assessment of the biogenic CH_4 contribution to the benthic food web is a key step to understand it transfer in the whole lake food web.

Warm temperatures and high lacustrine productivity enhance CH_4 production in aquatic ecosystems (Juutinen et al., 2009; Yvon-Durocher et al., 2014; Gonzalez-Valencia et al., 2014). However, global warming and changes in nutrient availability are also the most important forcing factors affecting the current lake evolution (Leavitt et al., 2009; Taranu et al., 2015). As consequences of an increasing thermal stability and/or heterotrophic activities of organic matter degradation, these changes in limnological conditions can lead to a switch from hypoxia to anoxia (Chapra and Canale, 1991; Jankowski et al., 2006; Frossard et al., 2013b; Ito and Momii, 2014). This dramatic decrease in dissolved oxygen concentrations leads to the appearance of "dead zones" where benthic metazoan organisms disappeared completely (Conroy et al., 2010; Belle et al., 2016). This situation could affect the whole lake functioning because macrobenthic fauna is often an important prey component for the pelagic food chain (Sanseverino et al., 2012; Wagner et al., 2012). The understanding of the environmental factors that drive the abrupt transition needs the use of long-term time series of past CH_4 dynamics in aquatic ecosystems.

The use of lake sediments as ecological archives allows the reconstruction of the CH_4 cycle response to environmental changes. Biogenic CH_4 exhibits a very low carbon isotope composition (currently ranging from −70‰ to −50‰ and as low as −80‰ in lakes across Europe; Whiticar, 1999; Rinta et al., 2015). Based on the principle "I am what I eat" (DeNiro and Epstein, 1978), analysis of the carbon isotopic composition of consumers allows estimation of the relative contribution of biogenic CH_4 to their biomass. Chironomid larvae (Diptera) are excellent indicators of CH_4 availability in lakes (van Hardenbroek et al., 2009) because they can colonize profundal sediments under low O_2 concentrations (Brodersen et al., 2004); moreover, their biomass can be derived from a significant portion of MOB assimilation (up to 80%; Jones et al., 2008), and they have a negligible trophic fractionation (Frossard et al., 2013a). Due to high chitin content, the chemical signature of the most sclerotized portion of their exoskeleton (the head capsule, HC) is stable at millennial timescales (Verbruggen et al., 2010). Stable isotope analysis of carbon performed on this material provides reliable information about the temporal evolution of MOB contribution to the chironomid biomass (Wooller et al., 2012). In addition, deep sediment from stratified lakes provides excellent conditions for aDNA preservation (Coolen and Gibson, 2009). The past temporal evolution of MOB communities can be reconstructed by quantitative polymerase chain reaction (qPCR) quantification using specific primers of aDNA extracted from sediments (Belle et al., 2014, 2015b).

To understand the responsible factors for the temporal changes in the CH_4 cycle, human activities must be studied. Anthropogenic pressures (mainly agro-pastoral practices) in the lake catchment area or in the vicinity of the lake can be reconstructed using analysis of pollen and coprophilous fungi ascospores (van Geel et al., 2003). Several sedimentary proxies can be studied to reconstruct the environmental lakes conditions. The accumulation rate of sedimentary organic carbon can be studied to summarize all of the organic input sources (Meyers and Ishiwatari, 1993). Moreover, the temporal evolution of the trophic status can be evaluated using models based on subfossil diatoms (Bigler et al., 2007) and sedimentary pigment analyses (especially carotenoids; Guilizzoni et al., 2011).

This study aimed to identify the factors responsible for the switch from benthic trophic reliance on CH_4 to "dead zones" in three different lakes from the Alps and Jura Mountains (eastern France). First, the long-term (approximately 1500 years) temporal evolution of the CH_4 cycle was assessed using combined analyses of carbon stable isotopes and MOB aDNA. Second, land-use history was reconstructed using coprophilous fungi spores and pollen analysis. Third, the temporal dynamics of CH_4 influx through the benthic food web was estimated by the estimation of the mass of CH_4-derived carbon stocked into chironomid biomass. Finally, an analysis of environmental conditions was applied to illustrate the dramatic development of the "dead zone".

2. Methods

2.1. Site description

The three lakes (Fig. 1) were chosen because they have different morphological characteristics (Table 1). Lake Narlay and Lake Remoray have already been identified as lakes with a high transfer of biogenic CH_4 trough benthic food web (Belle et al., 2014, 2015b). Lake Narlay and Lake Remoray (Fig. 1) are located in the Jura Mountains (eastern France). At the present day, the catchment area of Lake Narlay is 61% forest (including 32% mixed forest, 16% hardwood forest and 13% coniferous forest), 34% agricultural parcels, and 5% urban area (CORINE Land Cover 2006; Büttner and Kosztra, 2007). The lake has a surface area of 41 ha, and the water depth reaches a maximum of 40 m. The watershed basin of Lake Remoray consists of 46.7% forest (mainly coniferous forest), 42.5% agricultural parcels, 5.5% peat bog, 2.6% water area, and 2.7% urban area (CLC 2006; Büttner and Kosztra, 2007). The water depth of this moderately sized lake (95 ha) reaches 27 m. Lake Brevent is located in the Alps Mountains (Aiguilles Rouges massif) at 2125 m a.s.l. The lake has a surface area of 2.9 ha, and the water depth reaches a maximum of 20 m. Its catchment area is only composed of sparse vegetation (CLC 2006; Büttner and Kosztra, 2007).

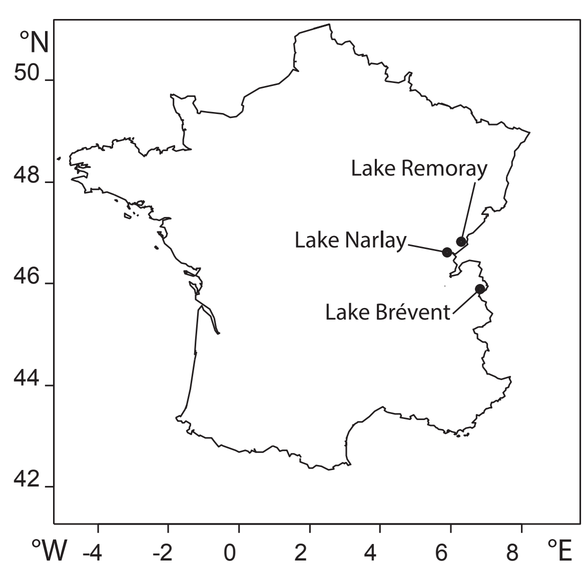

Fig. 1. Localization map of the studied sites.