Long-term trajectories of aquatic communities of the Middle Loire River: functional responses to climate warming and water quality improvement

Trajectoires à long terme des communautés aquatiques de la Loire moyenne: réponses fonctionnelles au réchauffement climatique et à l’amélioration de la qualité de l’eau

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RÉSUMÉ
Il est difficile de distinguer la part des changements climatiques des modifications tendancielles de qualité d’eau pour expliquer les évolutions temporelles des communautés aquatiques observées. Les jeux de données relevant respectivement des sciences biogéochimiques et des sciences écologiques sont souvent analysés séparément. Nous en proposons ici une analyse intégrée sur la Loire moyenne pour une période de plus de 30 ans (1980-2013). Sur cette période, la température moyenne de l’eau a augmenté, alors que les débits ont diminué. Le phosphore a été réduit, mais pas les nitrates. Les changements hydroclimatiques ont entraîné un remplacement graduel des taxons rhéophiles par des taxons plus limnophiles et plus thermo-tolérants, incluant certaines espèces invasives comme la corbicule (Corbicula sp.). Mais globalement la communauté d’invertébrés s’est aussi enrichie de taxons pollu-o-sensibles, en réponse à l’amélioration de la qualité de l’eau et à la réduction du phosphore. Il semble en effet qu’une transformation de la production primaire ait été à l’œuvre, évoluant du phytoplancton vers des biofilms épilithiques et des macrophytes. L’exemple de la Loire moyenne montre ainsi (i) qu’il existe des trajectoires subtiles des communautés aquatiques difficilement prévisibles et (ii) que les premières traductions d’un réchauffement thermique de l’eau n’ont pas forcément été dans le sens d’une érosion taxonomique, grâce aux efforts simultanés de meilleure maîtrise de la pollution phosphorée.

ABSTRACT
Disentangling the relative effects of global climate changes and water quality trends on long-term trajectories of freshwater communities can be a complex task. Corresponding datasets are also often studied separately by hydrogeochemists and hydrobiologists. Here, we present an integrative analysis of the Middle Loire River over more than three decades (1980-2013). Over this 30-year period, the Loire River has experienced a significant rise in water temperature, along with a significant discharge reduction. Phosphorus has been reduced, but not nitrogen. Hydroclimatic changes have given rise to a gradual replacement of pollution-sensitive and rheophilic taxa by pollution- and/or thermo-tolerant and limnophilic taxa, including invasive species like the Asian clam (Corbicula sp.). Nonetheless, this shift towards assemblages more tolerant and resistant has been partially confounded by the local water quality improvement, enabling the settlement of new pollution-sensitive taxa during the last years. In particular, a likely transfer of the primary production from phytoplanktonic organisms to epilithic biofilms and macrophytes seemed to be involved. Consequently, the example of the Middle Loire River illustrates (i) how long-term trajectories of freshwater communities can be subtle and difficult to predict and (ii) how improved water quality management can significantly help to reduce the biodiversity loss expected in response to climate change.

KEYWORDS
Climate change, Invertebrates, Long-term trends, Middle Loire River, Phytoplankton, Water Quality
Streams and rivers are among the most vulnerable ecosystems to climate change. As a result, aquatic species living in running waters are strongly exposed to climate-induced, thermal and hydrological fluctuations and associated water quality variations. Moreover, global hydroclimatic changes can interact with other environmental factors to shape structural and functional attributes of biological communities. Here, we investigate the relative effects of hydroclimatic and water quality factors on aquatic communities of the Middle Loire River (France) over more than three decades.

1 WATER QUALITY AND HYDROCLIMATIC TRENDS

The Middle Loire River has exhibited a significant decline in phosphate concentrations over the period 1980-2013, especially from the beginning of the 1990s, while no reduction in nitrate concentrations was highlighted (Fig. 1b,c; Minaudo et al. 2015). In the same time, the mean annual water temperature increased from 12°C to 14°C and the mean annual discharge declined from 400 m³.s⁻¹ to 200 m³.s⁻¹ over the three decades (Fig. 1f; Minaudo et al. 2015), mainly driven by global warming (Floury et al. 2012).

Furthermore, these trends were accompanied by a strong decrease in phytoplankton biomass, estimated here by chlorophyll-a concentrations, with values always lower than 100 µg.L⁻¹ after 2002, and even lower than 50 µg.L⁻¹ after 2006 (Fig. 1a; Floury et al. 2012, Minaudo et al. 2015). Consistently, a decrease in amplitudes of variation for oxygen concentrations and pH was observed in parallel to this marked decline of phytoplanktonic activity (Fig. 1d,e).

**Figure 1.** Long-term trends and seasonal components of chlorophyll-a (a), phosphate (b) and nitrate (c) concentrations over the period 1980-2013. Corresponding time series of monthly medians of both daily minimum and maximum of oxygen concentrations (d) and pH (e) and their amplitude dynamics. Long-term trends in water temperature and discharge (f). After Minaudo et al. 2015.
2 LONG-TERM RESPONSES OF BIOLOGICAL COMMUNITIES

2.1 Changes in composition of invertebrate communities

Results from previous analyses performed on the period 1980-2008 (Floury et al. 2013; Floury et al. 2017) were strongly supported by the new analysis performed on the 5-year extended period 1980-2013. In particular, the taxonomic richness of invertebrate communities has been continuously increasing, with a number of taxa rising in average from 20 to 40 over the three decades (Fig. 2; Floury et al. 2013).

Functionally speaking (i.e. with respect to life-history traits), this significant rise in diversity was the double consequence of (i) a growing proportion of taxa exhibiting biological features adapted to hydroclimatic changes (e.g. limnophilic taxa, Fig. 3; Floury et al. 2017) and (ii) a colonization by taxa following a likely transfer of the primary production from phytoplanktonic organisms to epilithic biofilms and macrophytes (e.g. biofilm scrapers, Fig. 3; Floury et al. 2017).
2.2 Potential consequences on other communities

The functional changes described as regards to invertebrate communities can have broader consequences at the ecosystem scale. For example, we highlighted a significant increase in the relative abundances of benthic fish species (Fig. 4), which has probably responded in cascade to the phosphorus decrease, the diversification of the primary production and, finally, the increase in benthic invertebrate prey.

Other biotic interactions, like the role of invasive mollusk filterers on the decline of phytoplankton communities, should also be investigated in the future.

![Figure 4. Long-term trends in the relative abundances (within the entire community) of benthic fish species (i.e. \textit{Barbatula barbatula}, \textit{Barbus barbus}, \textit{Gobio gobio} and \textit{Rhodeus sericeus}). Data from EDF, Dampierre CNPE. Original results.](image)

DISCUSSION

A significant increase in diversity of invertebrate communities of the Middle Loire River has been highlighted over the period 1980-2013. Community responses to hydroclimatic changes were quite predictable over the three decades. Conversely, the trophic shift observed was more unexpected a priori because of the complex interplay between climatic and biochemistry drivers. Nevertheless, life-history traits of invertebrates enabled to disentangle such trends a posteriori. As a consequence, the exceptional long-term series on the Middle Loire River have demonstrated that improved water quality management can significantly help to reduce some adverse effects of climate change, with wider implications for the whole ecosystems.

LIST OF REFERENCES


