Ecological Processes and Nutrient Transfers from Land to Sea: A 25-Year Perspective on Research and Management of the Seine River System

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Introduction

Science is like a snowball, which grows by incorporating material extracted from the ground as it rolls. Research issues change over time, not only as a result of the internal dynamics of science itself, but also under the pressure of the changing expectations of an evolving society. This is what we wish to illustrate, following the thread of our nearly 30-year joint careers.

The starting point was in the early 1980s, the Golden Age of microbial ecology. At that time the progress of molecular biology made the direct measurement and observation of microbial life in aquatic environments possible. "And now, small is plentiful" was the title of a Nature Views and News article (Sherr 1989) highlighting the new position accorded to microorganisms (from protozoans to viruses) in our understanding of the ecological function of water environments. For the first time, these microorganisms were shown to be a quantitatively important compartment in the functioning of aquatic systems and the concept of the microbial loop was introduced, leading to an alternative to the linear trophic chain due to its role as a sink or a link for higher order consumers (Azam et al. 1983; Pace et al. 1984; Sherr and Sherr 1987, among the first). Microbial ecology of oceans and lakes thus developed rapidly, and together with the concept of bottom-up and top-down controls (Paine 1980) participated in the emergence of a comprehensive ecological theory including cascading effects and retroactive interactions (Carpenter et al. 2009).

River systems, however, long resisted such analysis, probably because of the complexity of these largely open systems: water quality and ecological function in a given river stretch are largely dependent on the upstream drainage network and

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watershed functioning. Dealing with these complex relationships remained a real scientific challenge, in spite of the development of the conceptual framework offered by the River Continuum Concept (RCC, Vannote et al. 1980), which proposed an interpretation of longitudinal functional changes along river systems from headwaters to river outlets.

This scientific challenge was also very much in line with a strong social demand, as in Europe this period was the beginning of water resource management at the watershed scale. This approach recognized that water quality in any stretch of river reflects the human activities in the upstream watershed. Agriculture, which feeds the watershed population, uses mineral fertilizers leaching to ground- and surface water. Drinking water comes from the river itself or from groundwater wells contaminated by agricultural pollution. Wastewater produced by domestic or industrial activities is returned to the river directly or after treatment. The resulting sludge is only partly used for fertilization of agricultural fields and the rest is landfilled. Nutrient pollution from point and diffuse sources accumulated in the river reaches the coastal sea where it triggers algal growth on which fish and shellfish production depends.

We have conducted environmental research on the Seine River system and adjacent marine areas since 1989 (Fig. 1). During this long period of time, the environmental issues and the corresponding management stakes have considerably changed,



Fig. 1 (a) Location of the Seine basin in France and (b) its hydrographic network in the north of France. (c) Paris agglomeration on the lower Seine River and its major wastewater treatment plants

as did the basic and applied research studies required to help decision making by the authorities in charge of this system. This chapter aims at summarizing the long-term alteration of the Seine River by human activity, the actions taken by managers to reduce this alteration, the success or failure of these actions, and the research questions that arose from all this.

1850–1990: Organic Pollution and Oxygen

As early as the end of the nineteenth century, increasing urban populations and generalization of wastewater collection systems discharging directly into the rivers caused severe organic pollution, often resulting in complete anoxia of long stretches of rivers downstream from large urban centers. At one time, aquatic systems and especially rivers were considered to be able to evacuate all the pollution generated by industrial and domestic activities. Several urban rivers were covered to hide their black color and putrid smell (Billen et al 1999; Garnier et al. 2013). The pollution of the Seine River, which was still directly used as a drinking water source, led to dramatic cholera epidemics causing the death of 30,000 people from 1832 to 1866. From 1850 on, with the development of Paris and its agglomeration, a long race against time started between the water needs of the population and equipping the river for water supply and sanitation (Mouchel et al. 1998). In 1964, the Seine-Normandy Water Agency was created (together with five other agencies for each of the largest water districts in France). Their main concern at the time was to solve the problem of oxygen depletion related to organic matter and ammonium contamination by urban effluent directly discharged into the surface waters or incompletely treated. All efforts were devoted to the implementation of urban wastewater treatment plants (WWTPs).

Since its publication in 1925, the Streeter and Phelps model was used by sanitation engineers to connect river dissolved oxygen concentration and point discharge of organic matter (expressed in biochemical oxygen demand, BOD). The representation of the organic matter degradation process by a simple first-order kinetic equation could not, however, account for the (micro)-biological nature of the processes involved. Indeed, together with organic matter and ammonium, WWTPs also released microorganisms that play a direct role in the metabolism of these substances once released in surface waters (Garnier et al. 1991). Particularly striking is the dynamics of nitrifying organisms which, in the Seine River, develop only slowly after the release of ammonium by Paris WWTPs, so that their effect is only apparent 200 km downstream, in a second, delayed oxygen depletion area at the entrance of the estuarine sector of the river, whereas the river has completely recovered from the first zone of anoxia, immediately downstream of Paris (Fig. 2) (Garnier et al. 2007).

Such phenomena could only be accurately simulated by a second-generation model, explicitly taking into account the dynamics of microorganisms, such as the RIVE model that we developed for that purpose (Billen et al. 1994; Garnier et al. 2002). This model consisted of a detailed description of the processes related to substrate uptake, growth, and mortality of autotrophic and heterotrophic microorganisms



Fig. 2 The long-term evolution of urban organic pollution of the Seine River downstream from Paris. (**a**) Organic and ammonium loading from the Paris agglomeration from the mid-nineteenth century and existing treatment capacity. The wastewater treatment capacity could not be implemented with the increase of pollution loading until the very recent years. (**b**) Simulation, with the model of in-stream microbial processes, of oxygen and ammonium concentration profiles along the Seine River from Paris to the sea, from the mid-nineteenth century to recent years. The improvement of organic matter elimination from wastewater through conventional activated sludge processes finally solved the oxygen depletion problem immediately downstream from the Paris agglomeration in the early 1990s. However, until the recent implementation of nitrification and denitrification treatment of wastewater (2007), a second oxygen depletion zone occurred 200 km downstream, due to nitrification of ammonium

present in aquatic systems in a limited sector of the river. Most parameters involved in the corresponding kinetic equations were directly measured either in the field or in the laboratory using the methods developed in aquatic microbial ecology, so that the model offers a generic representation of microbial metabolism in aquatic systems and does not require any calibration steps.

1990-2000: Eutrophication and Algal Blooms

The problem of eutrophication, i.e., excessive development of algae due to excess nutrients, was noticed in stagnant aquatic systems as early as the 1960s (Vollenweider 1968), and the peak of disturbance was reached in the 1980s, before efficient programs of nutrient abatement measures were implemented. Awareness of eutrophication problems came only later for rivers (Descy 1992; Garnier et al. 1995) and coastal waters (Cugier et al. 2005; Lancelot et al. 2011; Passy et al. 2013; Turner and Rabalais 1994).

In the case of the Seine River system, heavy blooms of diatoms occurred regularly in spring, reaching a biomass above $100 \mu g/l$ chlorophyll *a*, severely hindering drinking water production, by clogging sand filters, increasing water pH above 8, which precluded the use of aluminum salts as flocculating agents, and increasing the level of dissolved organic matter in distributed treated water. These blooms generally collapsed after 2 or 3 weeks, resulting in oxygen depletion in the river.

Since these blooms are not generated in the main branch of the Seine River crossing Paris, but in the upstream drainage network (Fig. 3a), a new modeling approach had to be developed to understand their dynamics and predict their response to phosphorus (P) abatement programs. The Riverstrahler model, developed for that purpose, encapsulated the RIVE model of ecological processes, describing the dynamics of nutrients and microorganisms including several types of bacteria and organic matter, three taxonomic classes of phytoplankton (diatoms, Chlorophyceae, and Cyanobacteria), and two groups of zooplankton, into a description of the hydrology of the upstream part of the basin, where the complex network of tributaries is replaced by a regular river confluence scheme of increasing stream order (Strahler 1957) with mean morphological characteristics.

The model correctly simulates the timing of algal development and its geographical distribution in the river network (Garnier et al. 1995; Passy et al. 2013), allowing one to predict the distribution of autotrophic and heterotrophic metabolisms along the river continuum from the description of river network morphology and hydrology as well as the distribution of point and diffuse sources of nutrients (Billen et al. 1994; Garnier and Billen 2007) (Fig. 3a).

Banning polyphosphates from laundry powders in European countries (Billen et al. 1999; Van Drecht et al. 2009), followed by systematically implementing P treatment of urban wastewater, reduced point sources of P tenfold in the Seine watershed. Even though diffuse sources of P, originating from arable soil erosion,



Fig. 3 (a) Modeling the development pattern of phytoplankton (chlorophyll concentration) along the river continuum from headwater to estuary in different seasons (redrawn from Garnier et al. 1995) and (b) the autotrophic/heterotrophic activities (trajectories in the classical P/R diagram (redrawn from Billen et al. 1994)). (c) Long-term reduction of P contamination of the drainage network (variations of total P concentration at the entrance of the Seine estuarine zone (Poses) over the last 25 years, and the resulting decrease in the frequency and intensity of algal blooms)

continue to provide P to sustain algal growth, the general reduction of P loading clearly decreased both the frequency of occurrence and the general level of algal blooms in the downstream sectors of the Seine River system (Fig. 3b).

In the coastal zone of the Seine Bight, algal development is also highly dependent on nutrient fluxes discharged by the Seine River. However, the situation is quite different. In rivers, nitrogen (N), mainly originating from diffuse agricultural sources, is present in large excess with respect to the requirements of algal growth, and P is the most limiting factor of algal growth. Silica (Si), stemming from rock weathering, is most often in excess but can become limiting for diatoms at a high P load (Billen et al. 2007). In marine coastal areas, after mixing with nutrient-poor seawater, all three nutrients, N, P, and Si, are able to limit algal development at some stage of the seasonal cycle and to determine the taxonomic composition of algal communities. We showed that the amount of N or P discharged by rivers in excess over Si with respect to the stoichiometry of diatoms is a good indicator of coastal eutrophication potential (ICEP, Billen and Garnier 2007), characterizing the risk of development of undesirable, often harmful, non-diatom blooms. Since the strong reduction of P fluxes by the Seine was not accompanied by a similar reduction of N. coastal eutrophication remained and is manifested by summer blooms of toxic dinoflagellates following the spring diatom bloom. The occasional occurrence of toxic Pseudo-nitzschia blooms, preventing the commercialization of shellfish, is also likely to be a consequence of unbalanced river inputs of nutrients; there is indeed evidence that their domoic acid toxin production is controlled by N (Trainer et al. 2012). Due to the excess in N over P and Si at the coast of most developed countries with intensive agriculture, a substantial reduction of nitrate concentration in river water could decrease eutrophication problems (Passy et al. 2015).

2000–2015: Agricultural Pollution and Nitrate Contamination

The concern about nitrate concentrations in freshwater is not motivated only by the need to reduce coastal eutrophication. It also arose from preoccupations about the drinking water supply. More than 300 dwellings were closed in the Seine basin during the last 10 years because of nitrate levels above the drinking water standard (11 mgN/l). More generally, the environmental losses of N along the whole N cascade from agricultural soils through the atmosphere and hydrosphere cause a large number of problems, such as atmospheric pollution (namely fine particles of NH_4NO_3), greenhouse gas emissions (N₂O, mainly emitted by agricultural soils and the third-ranking cause of atmospheric warming), and loss of terrestrial and aquatic biodiversity (Sutton et al. 2011).

Environmental N losses from agriculture can be estimated from the soil N balance of arable soils integrated over the entire crop rotation cycle. The N balance is calculated as the difference between total fertilization (N inputs to the soil as synthetic or organic fertilizer, manure, symbiotic N_2 fixation, and atmospheric deposition) and export of N with harvested crops (Anglade et al. 2015). For arable

soils, in the absence of systematic winter cover by catch crops, more than 70% of the N balance is leached during the winter drainage period, so that the average nitrate concentration of infiltrating water can be easily predicted from the values of the N balance based on experimental measurement of N leaching (Benoit et al. 2014, 2015). Organic cash crop farms in the Seine watershed, practicing long and diversified rotation where cereals alternate with legume feed crops such as alfalfa, are often thought to be an alternative. We have instrumented a number of the few existing commercial organic farms in the Seine watershed and demonstrated that they produce significantly lower N losses than conventional farms, with, however, very similar yields in terms of total protein content (Benoit et al. 2014; Anglade et al 2015).

The historical reconstruction of the N balance at the scale of the Seine watershed showed a period of rapid increase in the second half of the twentieth century, corresponding to the transition from traditional agriculture, based on a close connection between crop farming and animal husbandry, to industrial cash crop farming dependent on synthetic fertilizers. This increase was followed, with a few decades' delay due to the inertia of the vadose and aquifer reservoirs, by a considerable increase of nitrate contamination of ground- and river water (Fig. 4a). After the 1980s, improvement of farming practices, namely under the incentive of European environmental regulations and efforts to calculate the required N fertilization based on the needs of crop development, resulted in a decrease in the N balance, which stabilized nitrate contamination of ground- and surface waters. The N surplus remains too high, however, to meet the drinking water standard in infiltrating water, suggesting that good agricultural practices, based on equilibrated fertilization at the very high yield expected, now have reached their limits. Further improvement of water quality will therefore require more radical change not only in farming practices, but also in the general organization of the whole agro-food system at a global scale (Billen et al. 2015).

The current agro-food system of the Seine basin is today characterized by a strong disconnection of crop farming and livestock farming. While the basin exports 90% of its crop production, it has to import most of its animal protein requirements for human consumption from the Brittany and Pays de la Loire regions, where most of the livestock is now concentrated and fed to a large extent with South America-imported soybeans and cakes. In both regions, the environmental N losses are considerable (Fig. 4b). A conversion of agricultural systems to organic farming would lead, however, to a large part of the production consisting of forage legumes instead of cereals. Consequently, the generalization of this type of crop farming would require a reconnection with livestock, as a local outlet for forage production as well as a way to recycle P as a finite resource (Garnier et al. 2015). This reconnection, which implies redistributing livestock at the scale of French regions, should also be accompanied by a reduction of the proportion of animal proteins in the human diet, both for ethical and public health reasons. Thus, a group of scientists published the Barsac declaration (http://www.nine-esf.org/



Fig. 4 (a) (*Left*) Long-term reconstruction of the N yield vs. N fertilizer inputs of cropland in the Seine watershed. (a) (*Right*) The current average N balance (i.e. N fertilizer inputs minus N yield) of conventional and organic crop rotations is also indicated, as well as the maximum value compatible with nitrate concentration standards for drinking water. (b) Schematic representation of nitrogen transfers through the agro-food chain of the Seine watershed in the current situation and in a hypothetical organic-local and Demitarian scenario

barsac-declaration), advocating a "Demitarian diet," i.e., a reduction by a factor two of the portion of meat and milk in the Western human diet. Based on these considerations, we constructed an "organic-local and Demitarian" scenario for the Seine watershed (Billen et al. 2012) and extended it to the whole of France. We thus demonstrated its ability to feed the population and still export part of its production while producing much less environmental contamination (Fig. 4b).

The scenario is constructed in such a way as to be easily translated into the input files required to run the Riverstrahler model. It was therefore possible to compare the water quality resulting from this radical scenario with the current scenario and that of a scenario of improved sustainable agriculture based on the generalization of catch crop implementation during winter. The results show that the margins of improvement by sustainable agriculture, although significant, are much more limited than what could result from the organic-local and Demitarian scenario, in terms of groundwater contamination, river water quality, and N fluxes to the coastal zone (Fig. 4c).

Conclusion: From Microbial Ecology to Territorial Biogeochemistry

The temperate Seine watershed that we are living in has been our favored and main case study for experimental microbial ecological studies, but the approaches we have developed have been deployed to other watersheds, to other water-agrofood systems in the world. In France, it was applied to the Loire basin, one of the few large European rivers which has not undergone channelization, as well as to the adjacent Scheldt River systems, one of the most populated river systems in the world. The Danube was the object of several EU projects where the changes induced by the collapse of the Eastern economies could be evidenced (Garnier et al. 2002). Near-pristine conditions were found in the Nordic Kalix and Lule rivers in the far north of Sweden (Sferratore et al. 2008). Under subtropical monsoon conditions, the Red River Basin in Vietnam was also studied along the same lines (Lee et al. 2014). We introduced the concept of the unicity of microbial processes, showing that from upstream to downstream and within a large gradient of climate and human impacts, these processes obey the same kinetics, with quite similar parameters, even though their manifestations in terms of ecological functioning may strongly differ depending on the constraints set by morphology, hydrology, climate, land use and anthropogenic pressures. Even though the description of the biogeochemical processes is far from being complete, the concept of their unicity in the large range of environmental conditions met in aquatic systems from headwater streams to the ocean is particularly fruitful, helping to generalize local field studies.

In addition, challenging the application of concepts and methods developed in marine and lacustrine environments to river systems, we finally developed an original modeling approach (Riverstrahler) for studying not only the river system, but also the terrestrial watershed it drains, with its agricultural and urban systems impacting the coastal marine zone into which it flows. We recently coined the term "water-agro-food systems" to designate this complex mosaic of aquatic and terrestrial ecosystems, deeply modified, exploited, and managed by a society. As such, water-agro-food systems can be viewed as territories, and we have named "territorial biogeochemistry," the branch of science that describes and tries to understand the functioning of such complex systems, their internal and external exchanges of material, and the (physical, chemical, biological, or social-economic) mechanisms controlling these exchanges. Here we open the way to a comprehensive and, why not, citizen-oriented way of practicing science, helping to clarify the societal choices to which we are confronted to address the threat of global change.

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Josette Garnier and Gilles Billen

Connecting lakes and coastal seas with rivers and their watersheds is one of our most fulfilling accomplishments. In the mid-1980s, Josette, with a position at the CNRS in Paris, was studying the ecological functioning of lakes (especially urban sand-pit lakes) while Gilles was involved in marine research at the University of Brussels (Belgium). In 1989, when a new interdisciplinary program (the PIREN-Seine Program) was launched by the CNRS on the Seine River, we both jumped on board: Josette, keen to escape her 42-ha lake, Gilles, prone to seasickness, delighted to step onto solid ground. In June 1989, finding themselves alone together, at midnight, in a small boat in the middle of the Seine River for a 24-h sampling cycle, they already hoped that the PIREN-Seine Program would be long lasting.

We married in 1992 in Brussels, then Gilles left Belgium for a position at the French CNRS. For more than 25 years, we have been co-constructing the now triedand-true biogeochemical/ecological Riverstrahler model, which we continue to improve and have implemented beyond the Seine to a wide variety of watersheds, from Nordic to subtropical systems. Field work has remained a major occupation, to which we rapidly associated our young daughter, even before she could walk. Thanks to faithful and friendly collaborations, we linked Riverstrahler to coastal zone models, making it possible to assess the measures required in the terrestrial watershed and the river network to mitigate marine eutrophication problems: and thus the loop was closed. Today, most of our energy is devoted to collaborative research projects, focusing on nutrient losses from agriculture and promoting alternative and sustainable water-agro-food-systems management.

We have jointly supervised a large number of graduate students. Many of them have been awarded academic positions, and just as they feel a member of a family during their Ph.D., we still take an interest in their career and keep close contact with them all.

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