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# François Alphonse FOREL

## and the oceanography of lakes

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### Abstract

In 1892, F.A. FOREL (FAF) created and defined the new science of Limnology as “the oceanography of lakes”. His aim was to establish an integrative discipline for the aquatic sciences in which diverse types of lake studies, from physics, chemistry and biology, to anthropology and economics, would complement and inform each other to produce a meaningful synthesis. FAF grew up in Morges, Switzerland, on the shores of Lake Geneva (lac Léman), and then left for 11 years to universities in France and Germany to study the natural sciences and medicine. Shortly after his return to Switzerland, he was appointed Professor of Anatomy and Physiology at the Academy of Lausanne. In the first years back at the lake, he made important discoveries about deep-living benthic animals and surface seiches that reinforced his early decision to adopt Lake Geneva as his “laboratory and aquarium” and to devote his career to limnological research. FAF’s remarkable breadth of interests and expertise culminated in 288 reports and publications, including the first text book in general limnology (published 1901), and the seminal, three-volume monograph on the Limnology of Lake Geneva (1892, 1895 and 1904). FAF’s success was the result of his passion for lakes and lake science, an ability to pose and critically evaluate insightful questions about the natural world, a flair for observation and for new observing technologies, a rigorous, encyclopedic ability to collect and synthesize all available information, and a natural talent for networking, collaboration and knowledge transfer. His view of lakes as coupled physical-chemical-biotic-human systems is particularly relevant to facing the challenges of global change, and the associated rapid shifts in ecosystem services at a planetary scale.

**Keywords:** Ecosystem services, Forel, Global change, History of Science, Lake Geneva, lac Léman, Limnology

### 1. Introduction

In the preface to his three volume treatise on Lake Geneva (known in Switzerland by its French name, Lac Léman), Prof. F.A. FOREL (Fig. 1) struggled with the question of what he should call his integrative approach to lake science. His research encompassed all aspects of the lake, from its morphometry, sediments, underwater light and mixing patterns, to its microbial, plant and animal ecology. He observed that the environmental characteristics of the lake were all closely interrelated, and he saw the lake as a system that was intimately tied to its surrounding catchment. As a doctor of medicine and the son of a local jurist and historian, he also identified the lake as a precious resource for the health and well being of the many people who lived around it in the past and present, and he quantified the lake fishing economy in a way that foreshadowed the modern concept of ‘ecosystem services’.

The broad sweep of F.A. FOREL’s research interests on the lake was simply too large to classify within any specialised subject area, and there were problems trying to insert it into any existing integrative discipline, as he explained in his preface (Forel 1892; p.VI; Fig. 2): *I wanted to achieve a generalisation, an overview of all the detailed facts, where each specialised study would be supported by the data from other studies. The theme of my description being partly terrestrial, this subject might be considered Geography. But the geography of waters is called Oceanography; I could therefore call the discipline Freshwater Oceanography. But a lake, no matter how large it might be, is not an ocean; the limited expanse gives each lake its own proper character that is very different from the unlimited expanse of the vast ocean.* F.A. FOREL went on to explain that this lack of fit to any existing discipline forced him to

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Fig. 1. Water color portrait of F.A. FOREL in the room he used as his study and laboratory, at his home in Morges on the shores of Lake Geneva (Lac Léman), Switzerland. In 1892, F.A. FOREL founded the new science of Limnology, defining it as “the oceanography of lakes”. (Undated painting by Ernest Bieler, reproduced by permission of the Forel family).

organic carbon cycles (acknowledged and praised by Raymond Lindeman some 40 years later), observations on the ecology of invasive species, notes on the intimate connection between human society and its freshwater resources, and the role of *Homo sapiens* as a powerful, biotic component of lake ecosystems. This F.A. FOREL perspective on Lake Geneva and its surroundings as a coupled physical-chemical-biotic-human system seems particularly relevant today as we face the enormous challenges of global change, and the associated rapid shifts in ecosystem services at a planetary scale (Williamson et al. 2009).

create a new word for a new discipline: ... *it is necessary to forge the word **limnology**. **Limnology** is thus **the oceanography of lakes**.*

With 100 years since the passing away of F.A. FOREL on 8 August 1912, it is an occasion to celebrate and take stock of his remarkable accomplishments. From the early 20<sup>th</sup> century onwards, F.A. FOREL has been recognized internationally as the founding authority of lake science. In what may be the first English language textbook on limnology, J.G. Needham (Professor of Limnology at Cornell University) and his co-author J.T. Lloyd (1916, p.76) noted *the profound influence of the Swiss Master, F.A. Forel, who is often called the ‘Father of Limnology’. He was the first to study lakes intensively after modern methods. He made the Swiss lakes the best known of any in the world. His greatest work “Le Léman”, a monograph on Lake Geneva, is a masterpiece of limnological literature. It was he who first developed a comprehensive plan for the study of the life of lakes and all its enviroing conditions.*

Needham and Lloyd’s tribute describes an impressive set of achievements, but F.A. FOREL’s life work and inspiration extend even beyond this list. His lesser known contributions include seminal insights into *lakes as microcosms*, hydrologic optics and lake water color, the nature of pelagic and littoral communities, the structure and function of aquatic food webs including microbial decomposition processes and

## 2. F.A. FOREL’s early life

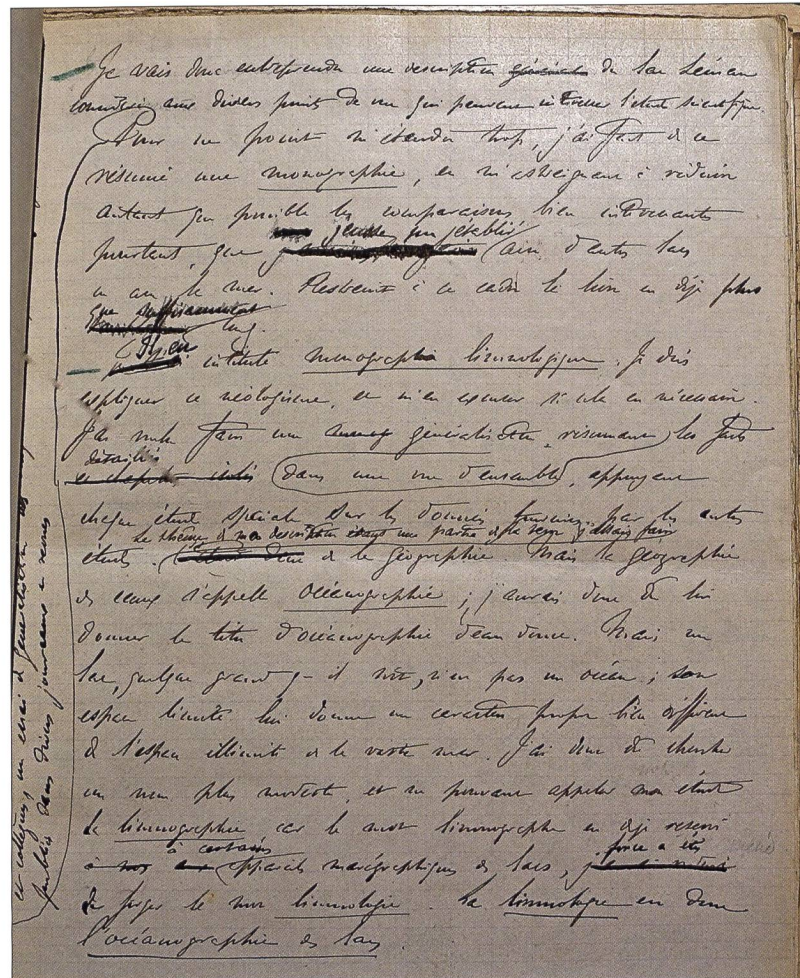
François Alphonse FOREL (FAF) was born on 2 February 1841 in the Swiss town of Morges, where the Forel family traces its ancestry back to Claude Forel, a parish officer and councillor who became established there in 1589. Morges lies 16 km from Lausanne and 50 km from the city of Geneva, but most importantly for the young FAF, the family home was on the shores of Lake Geneva that provided clean water, boat transport, productive fisheries, spectacular scenery, and many opportunities for exploration. His father, François Marie Etienne Forel (1765-1865) was a respected jurist-and historian, and FAF grew up surrounded by family members and friends who had diverse scholarly interests. His cousins included Alexis Forel (1852-1922), a chemist who became a well-known engraver, and Auguste Forel (1848-1931), who worked in the disparate fields of psychiatry and ant biology. FAF notes that one of his earliest recollections on the lake was at age 13, working with archaeological friends of his father to search for bronze-age artefacts in the submerged littoral zone. As in many European lakes, Lake Geneva contained the remnant pilings of ‘stilt villages’ that dated back several thousand years before the present. Using a modified grab from his canoe, FAF was able to snare three ancient bracelets from the lake floor, much to the surprise and perhaps

Fig. 2. The page of the original handwritten manuscript on which FAF defines 'Limnology' for the first time. This and other FAF manuscripts are archived in the Forel Documentation Center at the Musée du Léman (Lake Geneva Museum) in Nyon, Switzerland (www.museeduleman.ch by WF. Vincent).

chagrin of the professional archaeologists on board their adjacent boat. FAF's initial schooling was in his home town at Morges (Collège de Morges), and then later in Geneva at the western end of the lake, where he attended secondary school (Gymnase de Genève) followed by university studies at Geneva (Académie de Genève; Bachelor of Letters and Bachelor of Physical and Natural Sciences). At the age of 18, he left Switzerland for France to study medicine and natural history at the Académie de Montpellier for 2 years. He continued his medical studies in Paris, where his activities included training visits to hospitals as well as courses and seminars at the Museum of Natural History. He then moved to the University of Würzburg, one of the oldest and most traditional universities in Germany, to complete a final year of medical studies, graduating Doctor of Medicine at the age of 24, in July 1865. During this period, he developed a great interest in comparative animal anatomy (zootomy), and for the next three years he helped teach this subject at the university. Although he was encouraged to continue his career in Germany, he had been away from Morges for 11 years and now felt it time to return to look after his parents, whose two daughters had died at a young age. In 1867, he returned home and began to undertake studies on Lake Geneva. He was engaged as a lecturer in the Faculty of Sciences at the Academy of Lausanne in 1869, initially to teach microscopy and histology, and the next year was appointed to the position of Professor of physiology and anatomy in this faculty (Bertola 1999).

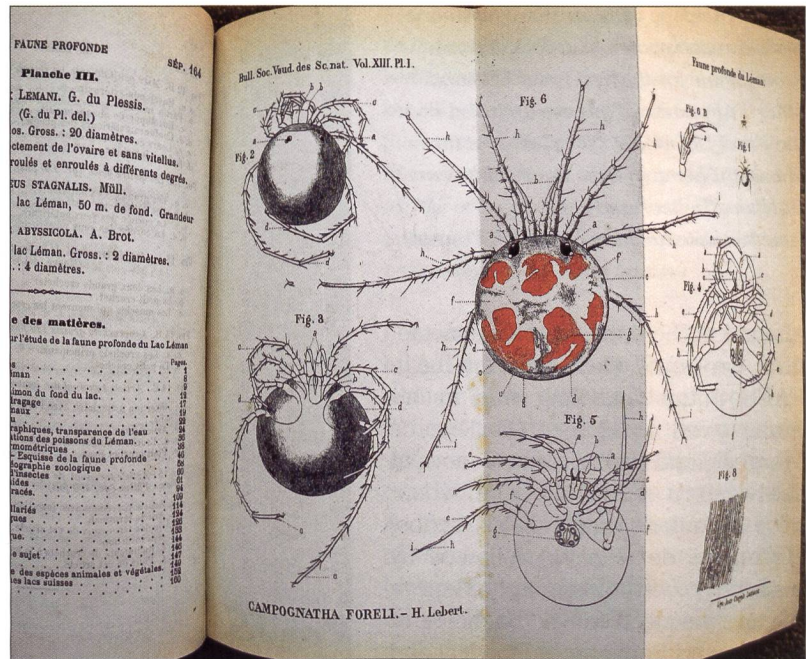
### 3. Early career discoveries and networking

Already a professor at the age of 29, FAF had a fairly light teaching load at the Academy, with 3 hours of lectures per week. Plenty of time was thus available for research, and he had the academic freedom to



choose his subject. FAF acknowledged that setting up a science program in anatomy, histology or physiology was the most logical set of options given his teaching duties in these subjects. But instead he made the decision that his laboratory would be Lake Geneva, and that the subject of his research would be all aspects of the physics and ecology of the lake. His former professor at Würzburg, Albert Kölliker, greeted this decision with some concern, and during his visit to Lausanne in 1871 he suggested that the young man focus on just one single, zoological topic. Fortunately, FAF was not to be dissuaded. His first years of research had already generated some very exciting results that likely reinforced his plans for a career in lake science. From the earliest days with his father onwards, he had a passion for working on the lake and unravelling its secrets, so much so that when later in life he was invited by an editor to write a textbook in limnology he initially refused, saying that he could not remain calm and impartial about this subject. He notes in the preface of the textbook that eventually emerged from this discussion: *My relation to limnology is much too personal and subjective for me to be able to give an objective presentation of the facts* (Forel 1901). The preface

Fig. 3. One of the deep-living invertebrates found in the sediments of Lake Geneva. FAF's zoobenthos project resulted in 49 scientific reports in collaboration with many taxonomic specialists from within and outside Switzerland, and stemmed from his discovery that lakes contain a distinct abyssal fauna adapted to the cold dark bottom environment. This water mite was described by the distinguished medical pathologist Hermann Lebert as the new species *Campognatha foreli*, now *Hygrobatas foreli*. From F.A. FOREL (1879). (Image by W.F. Vincent).



then goes on to explain the evident, that the editor was not persuaded by this objection, and the project went ahead.

One of FAF's early successes was the accidental discovery of a deep-living nematode in the lake. In April 1869, two years after his return from Germany, he was making observations on the deposition and rippling of sediments on the lake floor, and with a metal sampling plate he brought up some sediment, from a depth of 40 m offshore from Morges. Placing a subsample under the microscope to examine the nature of this silty material, he was startled to see a nematode swimming about, a species identified as *Mermis aquatilis*. He was immediately overcome by an exciting revelation: that the lake floor of Lake Geneva was not a sterile desert as previously thought, but in fact could be the habitat for a specialized community of deep-living benthic animals. The very next day he constructed a dredge and returned to the lake to sample it at many depths, confirming that diverse species of animals occurred in the sediments, even to 300 m, the deepest abyssal region of the lake. This was the start of a long term project that achieved enormous success, in part because of FAF's early decision to work collaboratively with specialists on different animal phyla rather than keeping the samples and discoveries to himself. From 1874 to 1879, this project produced a series of 49 published reports with 19 collaborators (Fig. 3) and later culminated in FAF's 1885 publication *La faune profonde des lacs suisses* (The Deep Fauna of Swiss Lakes). This volume in fact is broader than suggested by the title, with sections on physical and chemical limnology, and descriptions of several large lakes of the world. The ecological historian Frank Egerton comments: *The Société Helvétique des Sciences Naturelles [Swiss Society for the Natural Sciences] had requested the work and awarded a prize for it. It must have been the best general work on freshwater biology available at the time* (Egerton 1962).

In those first years back at Lake Geneva, FAF made another discovery that also defined his career over the subsequent decades. The boat harbor at Morges had two exits to the lake, one for the boats and a second much smaller one only 2 m across to allow water exchange. From 7 May 1869 to 11 May 1870 he took a series of careful measurements of the flow of water through this smaller aperture, discovering that the currents continuously oscillated in direction, sometimes flowing into the harbor and then a few minutes later reversing to flow back out into the lake. Two insightful revelations came to him as he observed this curious pattern of oscillating flow. Firstly he surmised that it was somehow connected to the periodic rise and fall of lake level that had been noted around the lake and especially at the city of Geneva for hundreds of years, and that was referred to in the local Swiss French dialect as a 'seiche', meaning rocking backwards and forwards. Secondly and most importantly, he concluded that these phenomena were the result of standing waves propagating throughout the lake. His first paper on this subject was published shortly thereafter (Forel 1873), and he continued to amass data from his own observations and from other sources around the lake. This interest in physical limnology was likely stimulated and encouraged by his former professor of mathematics and physics, and later research and teaching colleague, Dr. Charles Dufour, whose broad research interests included meteorology, glaciology and geology (Egerton 1962). In 1876, FAF constructed the first of a series of *limnographs*, an automated instrument that could obtain a continuous record of lake level. This device followed the design of tide gauges used by oceanographers, but unlike the marine versions at the time, it

could resolve mm-level fluctuations in water level, and even picked up the vibrations of steam ships passing many km away.

Over the subsequent 20 years, FAF worked with many colleagues at Lake Geneva, Lake Constance and elsewhere to define the properties of surface seiches, and he corresponded on this subject with scientists around the world, including specialists in France, Germany, England, Australia, Japan and the USA. He was frustrated by his lack of formal training in differential calculus, but through his network of colleagues he found the expertise that he needed to develop a quantitative theory of seiches. One of his contacts at the University of Leipzig passed on to him a treatise published in 1828 by a family member, a mathematician by the name of J-R Merian who had applied Lagrangian analysis to the problem of water movement in a rectangular tank. FAF transformed and applied this equation to lake basins, and found that he could estimate the average depth of the lake based on the period ( $t$ ) of the seiche. However, he was still unsatisfied with the complexity of the equation, and continued to discuss this in his meetings and correspondence with other researchers.

It was finally a distinguished physicist at the University of Glasgow who provided the aid that FAF was seeking. In a letter to FAF dated 6 October 1876, Professor William Thomson, better known as Lord Kelvin, took the Merian-Forel formula, simplified it for the condition that lake depth ( $h$ ) is very small relative to lake length ( $L$ ), and deleted the minor terms to produce the elegant approximation:

$$t = L\sqrt{gh}$$

In a detailed discussion and application of this equation, Forel (1892) noted that this was appropriate only to basins of simple morphometry, and that for more complex basins, other formulations were required, such as that developed by the French engineer Paul du Boys, another colleague whom FAF had recruited into his seiche discussions.

Over the period 1871-2, FAF participated in two meetings at Nyon to define a broad spectrum of research on Lake Geneva. These meetings had been formally commissioned by two scientific societies, and brought together distinguished scholars from Geneva and Lausanne. Their work culminated in a report prepared and signed by FAF as secretary of the commission, on 3 June 1872, that outlined 14 research topics that needed to be addressed, including geomorphology, bathymetry, sedimentology, lake transparency, currents, water chemistry, aquatic flora and fauna, and the archeological features of the lake. The document was published that year in No. 401 of the Bulletin of the Vaud Society of Natural Sciences (Vaud is the canton or governing district along the northern shore of Lake Geneva), and it described the limnological methods that would be applied, as well as a proposed

budget that totalled 15000 Swiss francs. Perhaps for this latter reason, the plan was not implemented, however it stands as the first comprehensive environmental research proposal for a lake, and its formulation and signing 140 years ago might be considered the birth of limnology (Bertola, 1999). At the very least, it set the research agenda for FAF over the next few decades, which ultimately resulted in his three volume treatise on the limnology of Lake Geneva, covering all of the topics described in this 1872 report.

#### 4. Correspondence and monographs

Throughout his 25 years of tenure at the Academy of Lausanne, FAF maintained in addition to his teaching duties, a continuous output of scientific publications, frequent presentations at scientific meetings, and prolific correspondence with colleagues in Switzerland and abroad. He thrived on collaborations, for example with the renowned French limnologist André Delebecque (author of the classic monograph on French lakes; Delebecque 1898) to produce the first bathymetric maps of Lake Geneva. The dozens of letters archived at the Center for Documentation (Fig. 2) include an exchange with John Le Conte, Professor of physics and former president of the University of California at Berkeley, and the first limnologist to work on Lake Tahoe, California-Nevada. Among his remarkable diversity of research topics, FAF had been fascinated by the interplay between sunlight and lakes, both at the lake surface and in the propagation of light through the water column. He established a standard protocol for the use of the Secchi disk, a white circular plate that had been invented by Priest Angelo Secchi to measure the transparency of the Mediterranean Sea. It was extensively tested by FAF in Lake Geneva as early as 1874 (Forel 1895; p. 410), only a few years after its publication (Secchi 1866). FAF then applied his standardized Secchi disk method to describe the seasonal dynamics of lake water transparency, showing the variations from around 15 m in winter to around 5 m in summer. He also developed a number of novel approaches in hydrologic optics, including an in situ method based on photographic plates to measure photochemically active radiation, and a color scale based on mixtures of colored reagents to quantify lake color (Fig. 4). In a letter dated April 9<sup>th</sup> 1884, Le Conte responds to FAF's query as to why Tahoe was apparently more transparent than Lake Geneva, and suggests that it is the result of an absence of active glaciers in the Tahoe basin. Le Conte also expresses his interest in installing one of FAF's high-tech limnographs in Lake Tahoe to measure seiches, but he mentions the difficulty of finding people who are attracted to science rather than profit: ... *it is difficult to find an investigator. Surrounded as you are by all the adjuncts of an*

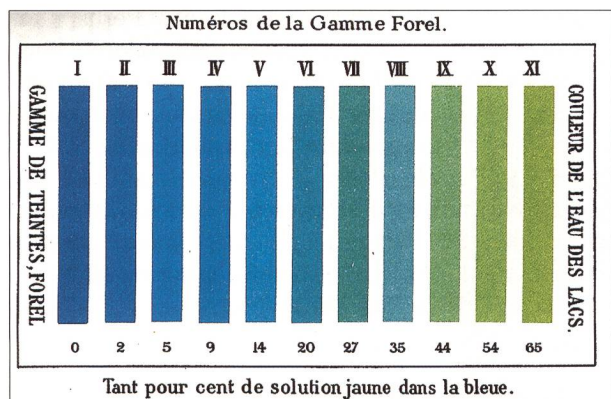


Fig. 4. The F.A. FOREL scale for lake color. From Forel (1895). (Image by W.F. Vincent).

old civilization, it is difficult for you to appreciate the conditions of our new and undeveloped civilization. The overwhelming influence of the commercial spirit almost paralyzes the genuine seeker of truth. The worship of gold inspires all classes of society; and the true scientific spirit is correspondingly stifled... Reciprocating your desire to have closer scientific relations, I remain with sentiments of the highest regard and esteem, Yours Most Sincerely, John Le Conte.

FAF's work over the next two decades resulted in dozens of reports, notes and scientific articles, but throughout this time he was working towards the bigger synthesis. His many articles on benthic fauna in Lake Geneva and other lakes were brought together in a collected volume in 1885, and a year later he revised and published a little guidebook to Lake Geneva that briefly touched on many of its limnological features (Forel 1886). All of this work combined with his encyclopedic collection of facts about the lake was to feed into the ambitious overview that he had embarked on two decades earlier. On 2 February 1891, perhaps to mark his 50<sup>th</sup> birthday that day, FAF submitted the complete manuscript of the first volume of *Le Léman – Monographie Limnologique* to the printer. After more than 18 months of proofs and painstaking corrections by himself and his colleagues, Volume I was finally published, in August 1892.

Forel (1892) is a remarkable work in many ways. It begins by defining Limnology as a new branch of science, and articulates the vision that he had formulated as a young scientist: to describe Lake Geneva from diverse yet connected points of view. He dedicates the book to his father, to whom he pays homage for introducing him at the age of 13 to scientific study and to the art of observing and interrogating Nature; I have continued under the eyes of my dear [father] to work on the numerous and diverse problems that a lake, a true microcosm, poses to human curiosity; encouraged and guided by his counsel I have devoted the best of my activities as a naturalist to this research (p. V). The Preface also

explains the intended audience, actually many audiences: fellow scientists, other readers interested in an explanation of natural features that they are intrigued by or admire, the people who live around the lake for whom the vast water mass of Lake Geneva is an ocean that intervenes in so many aspects of their individual lives and society, and the boatmen and fishermen who live on the lake, who live from the lake, and who hold the precise knowledge and methods for their professional activities (p. XI). In this defining moment for limnology, FAF thus captures the broad spectrum of end-users of lake science, from fundamental to applied limnology. In so doing, he also shows how human beings are an integral part of the lake ecosystem, a theme that he comes back to in great detail in the third volume.

Volume I presents a rich compendium of information, from a summary of field apparatus for limnological studies, to detailed descriptions of the geographic setting, hydrographic features, geology, climatology and hydrology. Throughout there is a meticulous attention to earlier work, the history of development of knowledge on each subject and full acknowledgement of previous authors and investigators, including many unpublished data sets. The volume finishes with his bathymetric map of Lake Geneva, with the 25 m isobaths based on 11 955 soundings. FAF notes that 4338 of the soundings came from the distinguished French scientist André Delebecque, his respected limnological counterpart who was based at Thonon, on the opposite side of the lake.

FAF submitted Volume II of his treatise two years after the first, and it was published in December 1895. In terms of limnological theory, this has turned out to be the most important of the three volumes, with sections on lake hydraulics (including seiches), thermal characteristics of the lake and hydrologic optics. These were followed by a short section on lake acoustics (focusing on the speed of sound in water and air), and a 70 page section on water chemistry. In a chapter in the latter section entitled *Dissolved materials in the water of the lake* he clearly links lake chemistry to catchment properties, for example: *The sulfate concentration of 64 mg [L<sup>-1</sup>], chalk sulfate in particular, is considerable. It is due to the presence of gypsum in many valleys of the watershed, in particular in the large valley of the Rhone...* (Forel 1895; p.608). He noted that the dissolved organic carbon concentrations were low but variable, perhaps associated with variations in rainfall and runoff, and asked the question, still non-trivial today *What is the nature of these organic materials in the lake water? This question has not been sufficiently studied* (Forel 1895; p. 616). On the sampling date of 30 November 1880, the lake was still stratified, but well oxygenated even at the bottom, with 7.08 cm<sup>3</sup> O<sub>2</sub> L<sup>-1</sup> at 300 m depth (Forel 1895; p. 622). FAF thereby established an

important baseline value for gauging the magnitude of change in Lake Geneva during its period of rapid eutrophication in the 20<sup>th</sup> century.

Forel (1895) presented a huge amount of thermal data for the Lake Geneva water column based on dozens of profiles from his own work (much of which was with a high resolution reversing thermometer), as well as data from many colleagues including André Delebecque. He made heat budget calculations for the lake, and identified the importance of density currents and convection. His thermal profiling allowed him to define the annual pattern of stratification and mixing, as well as interannual fluctuations in hypolimnetic temperatures. FAF developed a logical way to classify lakes based on their stratification regimes: 'polar lakes' defined as those in which ice and cold water overly warmer water during winter stratification, followed by mixing in summer; 'tropical lakes' in which warm water overlies cold during the stratified period followed by mixing in winter; and 'temperate lakes' in which there is an alternation between the 'polar' and 'tropical' modes of stratification, separated by periods of mixing. Hutchinson (1957) later acknowledged and adopted FAF's approach, but replaced the confusing terminology in which Lake Geneva is classified as a 'tropical lake' despite its temperate location by terms based on mixing each year (cold monomictic, warm monomictic, dimictic, etc).

FAF's approach was always to formulate questions and to test ideas, often by way of competing hypotheses and an encyclopedic synthesis of observations from all sources including his own original work. This led to rapid insights and rejection of alternatives, for example in his work on surface seiches in which he readily eliminated hypotheses for causal mechanisms such as electrical storm effects and periodic injection of melt waters from glaciers. Not all of his conclusions have survived the test of time, and he himself fully acknowledged that science is a continuously evolving process. Glacial erosion, for example, is now thought to have played a much greater role in carving out the Lake Geneva basin than FAF surmised (Wildi et al., 1999). FAF was reluctant to accept the presence of internal waves in the lake, despite evidence in his own data of thermocline tilting, which he erroneously attributed to the mixing of more dense water from the Rhone at the western end of the lake (Forel 1895, p.354). In fact the evidence and theory from Scotland of internal waves came late in his career, and at an unfortunate time when he had a medical problem with his hands that curtailed his fieldwork on the lake.

## 5. Human and biological limnology

At the age of 54, and after 25 years of academic service as a professor, FAF retired from the Académie de Lausanne, and was then able to devote even more

time to his limnological studies. His massive collection and synthesis of information continued, as did his prolific output of publications. He produced his limnological textbook in 1901 (*Handbuch der Seenkunde: Allgemeine Limnologie*), and published Volume III of the monograph in May 1904. The latter included the biological limnology of the lake, its history of human occupation going back to neolithic times, the navigation history of the lake up to the present, and the fishery.

From his childhood onwards, FAF was intensely aware of the significance of Lake Geneva to the people who lived around it, including for the many generations of his own family who lived at Morges. In his development of the new science of limnology, FAF made it quite clear that human activities, past and present, were part of the structure and functioning of lacustrine systems. In Volume III of the monograph, FF details the aquatic and semi-aquatic biota of the lake, and the first species he defines as follows:

### VERTEBRATES;

### MAMMALS, PRIMATES:

*Man, Homo sapiens L., is not an essentially aquatic species, but has become so by way of his activities; the calling of fishermen, sailors, ... etc results in many such people living a semi-lacustrine life, making mankind almost an erratic species of the lake fauna.* (Forel 1904, p. 26). Forel goes on to note that humankind also has negative impacts on the lake waters: *he builds ports and quays, he channels the inflows, he dams the outflow, he discharges into the lake the products of his factories, the sewers of his villages, the ashes of his steam boats etc. All of these actions modify the lake environment, and directly or indirectly impact on the biological functions of its inhabitants. Mankind exerts a more powerful effect than any other animal on Nature and its inhabitants* (Forel, 1904; p. 26). On this same theme, FAF also documented the arrival of invasive plant and animal species in the lake through human means. For example, he describes how the North American macrophyte *Elodea canadensis* was imported to Geneva in 1869 and was planted in ponds and streams to favor fish production. By 1880 it had escaped into the lake, and three years later invaded the boat harbor near FAF's residence at Morges. After the first few years of spectacular growth and displacement of other aquatic plant species, by 1900 its population size had begun to stabilise and contract, and *all worries about the unstoppable invasion by this American weed disappeared. After its phase of exuberant and frightening expansion over several years, Elodea settled down as a calmer vegetation type. It became of no greater concern than the Potamogeton and Myriophyllum that grew beside it.* (Forel 1904; p.



162; Fig. 5). He also describes the introduction and proliferation of mute swans on the lake and reports his detailed observations on their phenotypic variation and behavioural ecology, noting for example: *Although of very little intelligence, swans can have strong passions and even show signs of corruption that are truly deplorable.* (Forel 1904; p. 38).

FAF's Volume III provides a detailed overview of the plant and animal communities of Lake Geneva, separated according to the semi-aquatic edge of the lake, the littoral and pelagic zones, and the abyssal region with its deep-living benthic communities. From his discoveries in 1869 onwards, the latter communities were of special interest to FAF and he devotes many pages to describing the communities, including the deep living moss *Thamnium lemani*; microbial mats, in part composed of oscillatorian cyanobacteria (especially abundant during the period of higher water column transparency in winter and spring); and 79 species of animals ranging from protists to fish. He describes the monotonously cold, dark *climate* in the deep region of the lake and asks the question, do the organisms of this zone show any general characteristics? He identifies several common features and then goes on to consider the origins and evolution of the Lake Geneva biota. He was also greatly interested in the deep-living populations of crustacean zooplankton and their nocturnal migration habits: *These animals, capable of extensive active movement, come to the surface during the night – perhaps only the nights when the lake is calm, perhaps also only those nights when the moon does not shine too brightly – and they descend during the day to depths that are less illuminated or in obscurity* (Forel 1904; p. 222). FAF also



Fig. 5. F.A. FOREL and associates collecting aquatic macrophytes from Lake Geneva. F.A. FOREL observed *Elodea canadensis* with great concern when it entered the lake as an invasive species. (Image courtesy of the Musée du Léman and the Forel family).

gives credit to Auguste Weismann (1877) for independently coming to the same conclusion in Lake Constance.

## 6. Microbial limnology

FAF's Volume III also provides an introduction to aquatic microbial ecology, and he makes some insightful observations that are still highly relevant today. The methods in microbiology available at the time were of course extremely limited relative to those now currently available, but the microscope shown in the painting of his laboratory (Fig. 1) would have provided him with the first indications of Lake Geneva's microbial world. He collected together all the available bacterial count data from water hygiene records, and noted (despite estimates many orders of magnitude below those obtained with modern methods) their great abundance everywhere: *No serious analysis, to my knowledge, has indicated any lake water completely free of microbes* (Forel 1904; p. 360). He pointed out from this synthesis that the bacterial population size is especially high in the surficial sediments, in rivers, in waste water, and parts of the lake near sewage outfalls, with lowest concentrations in the offshore pelagic zone. He separated the bacteria into functional groups, and underscored the essential role that they play in the carbon cycle of lake ecosystems through the degradation of organic materials.

In Volume II, FAF had observed that even clean natural waters contain microbes, and he cautioned the reader not to be alarmed about this: *Secondly, and this is a very important point, all microbes are not necessarily unhealthy. Much to the contrary, the immense majority of these minute beings are completely innocent* (Forel 1894; p. 637). In Volume III he goes further in a chapter entitled *The Circulation of organic material* to explain how mineral materials entering the lake are converted to organic materials that are distributed among three forms: A. *Dissolved organic matter forms the general reserve that is stored in the waters of the lake....B. Organic material in the bodies of dead organisms and detritus (débris morts)....C. Organic matter in the state of living plants and animals*, and that these compartments are connected, ultimately forming substrates for microbial decomposition and remineralisation: *How many successive incarnations is this organic material subjected to as it passes from plants to the animals that feed on it! An alga, for example a diatom, is eaten by a rotifer; which is eaten by a copepod, which is eaten by a cladoceran, which is eaten by a whitefish, which is eaten by a pike, which is eaten by an otter or by a human. The small and the weak are the prey for the large and the strong, and they in turn are eaten by the larger*

and stronger; or if they escape, they will not avoid the microbes responsible for decomposition, which all organisms are directly or indirectly subject to. After this incarnation in the plant or animal, the organic material passes from an organized state to a state of solution. (Forel 1904; p. 368) Decades later, the celebrated ecologist Raymond Lindeman praised FAF for providing a brilliant exposition of the general nature of food cycles that will serve even today as an introductory account of trophic relationships (Lindeman 1941; cited in: Sterner, 2012).

Although FAF was unaware of the enormity of the total bacterial biomass and respiration in Lake Geneva, his rough calculations of the allochthonous input of organic matter led him to conclude that a large part of the organic material that enters the lake from its inflows is emitted into the atmosphere as a result of the gases that are products of decomposition and putrefaction over organic material living and dead, escaping without stop into the atmosphere (Forel 1904; p. 369). Perhaps this is the first recognition of lakes as heterotrophic ecosystems.

## 7. Lake ecosystem services

The historical importance of a lake to its people was a theme that FAF had been introduced to as a child. His father was very interested in the *palafittes*, the bronze-age villages built on stilts within the littoral zone of Lake Geneva, and other lakes in the region (Fig. 6). FAF participated in his father's archeological exploration of the extensive site at Morges, where several thousand remnant pilings could be found in the lake, and this stimulated his lifelong interest in these ancient *cités lacustres*. In Volume III of his

treatise he devotes 78 pages to this subject, documenting the artifacts that had been collected (some dating back to the stone age) and formulating hypotheses about the mode of life of these prehistoric peoples, their origins, the plants and animals that they depended upon, and the value of the lake to them for its multiple ecosystem services: *Add to this notion of security against any kind of attacks, the undeniable allure that such constructions over the lake would offer... Having the lake in front, around, below; having only to jump down to take a bath or travel by canoe; to simply throw a net to harvest abundant fish; to be warmed in winter by the tepid atmosphere of the lake and to be refreshed in summer by comforting lake breezes; to have clean sanitation for disposal to the lake of household waste; to enjoy the constant changes in the mood of the lake, sometimes calm, other times whipped up by storms, bathed in light, sometimes in the sad grey hues of mist... We the residents of the lake, we know the powerful charm, always renewed and rejuvenated, that these waters provide...* (Forel 1904; p. 448). More recent studies have indicated that many of these houses may have been outside the lake, and that the stilts may have also offered protection against changing lake levels.

In the final sections of Volume III, Forel (1904) addresses two aspects of Lake Geneva's geo/ecosystem services in quantitative economic terms: ship transport and commercial fishing. He describes the long history of navigation on the lake, from the canoes of the stilt villagers to naval vessels, merchant barques, fishing boats and the arrival of steam ships. FAF quantifies the commercial steamship tonnage at the time and its passenger capacity, and to illustrate the commercial value of these activities he presents the financial report of the steamship company CGN based out of Lausanne. This company, even more



Fig. 6. A reconstruction of a bronze age stilt village on Lake Constance, Germany, similar to the type surmised from the archaeological remains at Lake Geneva. The archaeology of this "cité lacustre" and the close relationship of its people to the lake were of great interest to F.A. FOREL and his father. (Image by D. Straile, Limnological Institute, University of Konstanz).

active on Lake Geneva today, reported that its receipts for passenger and freight services in 1901 totaled 1.24 million Swiss Francs. He concludes the navigation section with chapters on the laws and customs for vessels on the lake, the evolution over hundreds of years of the distinctive merchant barque design and the history of ports on the lake.

In considering the fishery, Forel (1904) was aware that several fish species (notably lake trout, Arctic char, whitefish, carp, pike and perch) had been part of the diet of lake residents from prehistoric times onwards. He traces the laws governing the management of the lake fishery back to 1043, when King Henry III granted Archbishop Hugo de Besançon the right to fish in Lake Geneva. FAF then details the harvest data, the tax imposed on catches, and the >300-fold rise in fish prices per pound over 5 centuries. He begins a chapter entitled *Statistics* by stating *Statistics on the Lake Geneva fishery are almost non-existent. The State, which is uniquely competent and capable of obtaining such information, has consistently retreated from the difficulties of these tasks.* He also notes the natural suspicion of fishermen towards the collection of such statistics, and their legitimate fear that this would translate into yet more regulations and taxes. Not to be deterred, FAF combed the regions for all available numbers on the French as well as Swiss sides of the lake, noting the particular lack of data from the latter. He presents the annual exports from France to Switzerland of fish caught in the lake (49 to 122 tonnes per year), and provides the annual receipts for a wholesale fish merchant at Geneva. All of these statistics allow him to make the first order estimates that 1200 fisherman worked at that time on the lake, and that the fishery generated retail sales of around 1.5 million Swiss Francs per year. Concerning the latter estimate, he cautions that it is *Not necessary to emphasize the uncertainty and imprecision of this number* (Forel 1904; p. 650).

## 8. Contributions outside limnology

The name Forel is well known to most limnologists, but several other branches of science have also greatly benefited from his observations and insight, including glaciology, seismology and archaeology. His contributions were so numerous (a publication list of 288 titles was published with his obituary; Blanc, 1912) and diverse that at the commemoration ceremony for FAF and the unveiling of a special medallion, two years after his death in 1914, Paul-Louis Mercanton noted: *François A. Forel was a great naturalist, his name was known everywhere and for such diverse reasons that many a scholar outside Switzerland thought that there must exist several François Forels* (p. 39).

Throughout his life, FAF enjoyed trips to the Swiss Alps and explored many glaciers of the region. His father had taken him at the age of 14 to the Sea of Ice Glacier (Mer de Glace) on the northern slope of Mt Blanc, and had stimulated his scientific interests by pouring a little red wine on the ice, showing how it flowed into the fissures to reveal the crystalline structure of the glacier. FAF published many glaciological studies and over the 30 year period, published an annual report on the state of Swiss glaciers. He was instrumental in setting up the International Glaciological Commission, and was its first president, later honored by the naming of the Forel Glacier (lat. 67.48 °S, long. 66.50 °W) in Graham Land, Antarctica. He was also active in the local alpine club, and among other activities encouraged a Swiss expedition to Greenland, which in his honor gave the name Mount Forel to the highest peak that they encountered, one of the highest in all of Greenland (lat. 66.93 °N, long. 36.79 °W; 3383 m asl).

FAF was also fascinated by earthquakes, and in collaboration with the Italian geophysicist Michele de Rossi he developed the Rossi-Forel scale, a precursor to the now familiar Richter scale for earthquake intensity. At the International Geophysical Conference in Zurich there was a resolution to set up an International Earthquake Commission, to which he was appointed vice-chair in 1907. Each year he continued to amass data in the region including via appeals to the public for information, so much so that he was even known locally as the *Director of Earthquakes*.

From his earliest days as a teenage amateur scientist with his father, FAF was also interested in the people who lived in the past around the lake, and he made a number of important contributions in archaeology, and in the final two years of his life, he catalogued his father's collection of bronze age artifacts. On top of all this, FAF was also active in local government affairs and held various positions on the Morges Council and in the canton. He was the father of four children: Cécile, Marie, Hilda and François. Mme Porret-Forel tells us that her grandfather particularly enjoyed having his daughter Marie come out on the boat with him during sampling expeditions. By all accounts FAF was an affable and generous man who greatly enjoyed the company of others and thrived on working and discussing his work with colleagues in Switzerland and around the world. Even Auguste Forel, who severely commented on many people he came in contact with, had nothing but praise for his cousin: *He was a keen scientific worker and observer, and in later years he became famous for his important investigations of the Lake of Geneva. He always signed his work 'F.A. Forel', so that at Morges he was known as 'FAF'. Kindness and benevolence, together with a happy optimism accompanied him throughout his life* (Forel 1937; p. 83).

## 9. The F.A. FOREL legacy

François Alphonse FOREL (Fig. 7) was such a prolific scientist, author and scholar that it is difficult to summarize the full scope of his enduring contributions. In the aquatic sciences, however, his name is clearly associated with the birth of limnology. FAF concludes at the end his third volume (*Conclusions and Final Reflexions*; Forel 1904) that he is *happy to pay homage to the geographic method* that he has employed in his new science of limnology, an integrative approach that *allows us to generalize, to abandon specializations after having harnessed their discoveries, and to contemplate the overview made up of the facts garnered from diverse disciplines of science.* (p. 669). However in these closing pages he also stresses the individuality of lakes, and warns against simply extrapolating from his own ensemble of data at Lake Geneva, or uncritically applying his approach: *I have been led to theoretical dissertation, discussion and development far in excess of a simple statement of things. I do not regret having so often succumbed to going beyond the pure objectivity of the facts to try to find the necessary theoretical explanations; but I cannot present my book as a model for the description of other lakes* (p. 668). He also notes how the quest to get closer to scientific truths is an ongoing process that progresses rapidly from generation to generation, and he describes at length the joy of doing science: *a simple fact well studied, a little hypothesis well supported, can provide us with as much immediate pleasure as the grandest theories have given to a Newton, Darwin, Helmholtz or Pasteur* (p. 673).

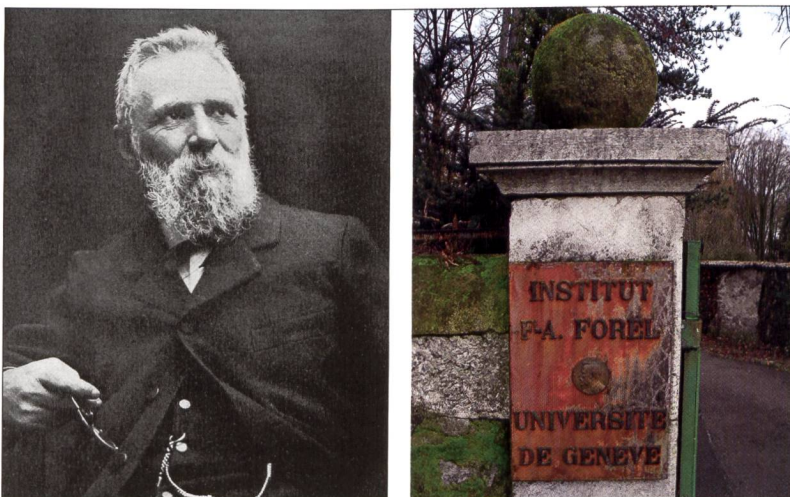


Fig. 7. François Alphonse FOREL (left) has been honored in many ways, including by the founding of the Institute F.-A. FOREL (right) in his name at the University of Geneva in 1980. This limnological institute is renowned for its multidisciplinary studies on lakes (website: [www.unige.ch/forel](http://www.unige.ch/forel)). (Left: image courtesy of the Musée du Léman and the Forel family; Right: image by W.F. Vincent).

FAF logically combined the Greek word *limne* for lake (and also pond, swamp) with *logos* to create the new word *limnology*, but was it the best choice? Today, limnology certainly extends from lakes into pools, ponds, swamps, mires, bogs and other wetlands. In 1922, August Thienemann and Einar Naumann founded the International Association of Theoretical and Applied Limnology (Societas Internationalis Limnologiae, SIL) and more broadly defined Limnology as the study of inland waters, which now includes rivers and streams (e.g., Wetzel 2001) and even estuaries (e.g., Horne and Goldman 1994). Despite this increasing breadth, however, Limnology is still not widely known among the general public. The limnologist Jonathon Cole, former president of the Association of the Sciences of Limnology and Oceanography (ASLO), laments *In some ways it is unfortunate that François Alphonse FOREL (1841-1912), the first to use the term limnology, was both conversant with ancient Greek, and unwilling to compromise linguistic purism by combining perhaps a more widely recognized Latin word for inland water with the Greek -logos* (Cole 2009). But what exactly would that word be? The obvious alternatives are unattractive hybrids, and seem limited in meaning. At any rate, limnology remains well established in the names of many of our professional journals and societies, including ASLO and its publications.

Most modern textbooks of limnology refer to FAF in passing as the founder of limnology, and usually cite the three volume monograph on Lake Geneva (Lac Léman). Few, however, acknowledge FAF's publication of the first textbook in limnology, entitled *Handbuch der Seenkunde: Allgemeine Limnologie (Textbook of Lake Science: General Limnology)*. Forel wrote this in French at the request of a German publisher, and then asked his friend and colleague Dr. Wilcez at the University of Lausanne to translate it into German for publication (Forel 1901). It was reviewed for the Royal Geographical Society by H.R. Mills who read the German text soon after publication and noted that the appearance of this *handbook of Limnology may be looked upon as the formal admission of the science of lakes to its independent position somewhere on the borderlands of geography, very near the place occupied by oceanography. Prof. Forel is the one man capable of writing such a book...* (Mills 1901). The book was also well received in the United States, where a review signed by

R.D.S. in the *Journal of Geology*, a prestigious scientific journal published by the University of Chicago Press, appeared the same year and stated: *It brings together in concise, comprehensive and readable form the general principles of limnology...In an appendix is given an outline for the prosecution of lacustrine studies, and also a bibliography. The volume is the best compendium on the subject...* In surveying the current limnological literature, FAF's third volume (Forel 1904) seems largely unknown. Yet the concepts and approaches made in that volume are vitally relevant to the application of limnological principles toward managing the world's freshwaters. As described above, FAF saw human beings as a key component of limnology, from two perspectives. Firstly, humans are part of the coupled lake-catchment ecosystem biota (his species list of lacustrine fauna began with *Homo sapiens*) and we depend upon lakes for reasons as diverse as safe drinking water, waste disposal, reliable food supplies and the aesthetic and psychological pleasure of being on and near water. FAF would be pleased that in the *Encyclopedia of Inland Waters*, the article on the origins and nature of limnology (Cole 2009) is followed by one on the aesthetic values of lakes and rivers, and then by another on aquatic ecosystem services. More than 100 years ago, FAF not only identified the many ecosystem services provided by Lake Geneva, he even quantified one of them, the fishery, in precise economic units of Swiss Francs (Forel 1904). Secondly, FAF considered *Homo sapiens* to be the most powerful of all aquatic species, with a capacity to not only to benefit from lakes, but also to cause them great harm. His examples included the pollution by cities and their sewage discharges, the waste

streams from industries, the pressure of overfishing, the release of coal ashes from boats and the introduction of non-native plant and animal species (Forel 1904). Once again his work underscored the interrelatedness of each component of the ecosystem, and how the perturbation of one would ripple throughout the entire physical-chemical-biological-human system. Here now, in the 21st century at a time of increasing perturbation of the world's freshwaters by climate change, long range contaminants, species invasions and multiple other stressors, it would seem to be a good moment to rediscover FAF's greatest legacy: his advocacy for an integrative approach in which each discipline informs the other, toward an overall synthesis that includes humankind in the past, present and future, and that informs policy decisions and environmental stewardship. If F.A. FOREL were here today to write a *limnology of global change*, he would likely encourage us to pay close attention to the role of humans in the biosphere, and to understand the human presence as a component part of all aquatic ecosystems.

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## Bibliographie

- **BERTOLA C.** 1999. François-Alphonse Forel (1841-1912), p. 3-17. *In*: Bertola, C., Goumand C., and Rubin J.F. (eds.), *Découvrir le Léman: 100 ans après François-Alphonse Forel. Actes du colloque pluridisciplinaire, Nyon 16-18 septembre 1998.* Editions Slatkine, Geneva.
- **BLANC H.** 1912. Le professeur Dr. François-Alphonse Forel, 1841-1912. *Actes de la Société helvétique des sciences naturelles*, 95: 110-148.
- **COLE JJ.** 2009. Limnology as a discipline, p. 6-13. *In*: Likens GE (ed.), *Encyclopedia of Inland Waters*, Elsevier, Oxford, U.K.
- **DELEBECQUE A.** 1898. *Les lacs français.* Chamerot et Renouard, Paris. 436 p.
- **EGERTON FN.** 1962. The scientific contributions of François-Alphonse Forel, the founder of limnology. *Schweizerische Zeitschrift für Hydrologie*, 24: 181-199.
- **FOREL A.** 1937. *Out of My Life and Work.* W.W. Norton & Co., Inc. New York (First English Edition). 352 p.
- **FOREL F-A.** 1873. Première étude sur les seiches. *Bulletin de la Société Vaudoise des Sciences Naturelles*, 12: 213.
- **FOREL F-A.** (ed.) 1879. *Matériaux pour servir à l'étude de la faune profonde du Lac Léman.* Collection du Bulletin de la Société Vaudoise des Sciences Naturelles, 459 p.
- **FOREL F-A.** 1885. *La faune profonde des lacs suisses.* Mémoire de la Société helvétique des sciences naturelles, H. Georg, Basel, 234 p.
- **FOREL F-A.** 1886. *Le Lac Léman: précis scientifique.* H. Georg, Basel, 76 p.
- **FOREL F-A.** 1892. *Le Léman - Monographie Limnologique.* E. Rouge, Lausanne, Tome I, 543p.
- **FOREL F-A.** 1895. *Le Léman - Monographie Limnologique.* E. Rouge, Lausanne, Tome II, 651 p.
- **FOREL F-A.** 1901. *Handbuch der Seenkunde: Allgemeine Limnologie.* Bibliothek geographisches Handbücher herausgegeben von Prof. Dr. Friedrich Ratzel. J. Englehorn, Stuttgart, 249 p.
- **FOREL F-A.** 1904. *Le Léman - Monographie Limnologique.* E. Rouge, Lausanne, Tome III, 715 p.
- **HORNE AJ, GOLDMAN CR.** 1994. *Limnology.* McGraw-Hill, New-York, 576 p.
- **HUTCHINSON GE.** 1957. *A Treatise on Limnology: Vol. 1. Geography and Physics of Lakes.* Wiley, New-York, 1016 p.
- **MERCANTON P-L.** 1914. François-Alphonse Forel: Son œuvre en géophysique, p. 26-39. *In*: Discours prononcés à la cérémonie commémorative à l'inauguration du monument de F.-A. Forel à l'aula du Palais de Rumine, à Lausanne le 29 novembre 1913. Société Vaudoise des Sciences Naturelles (SVSN), Lausanne.
- **MILLS HR.** 1901. Prof. Forel on limnology. *The Geographical Journal*, 17: 296-298.
- **NEEDHAM JG, LLOYD JT.** 1916. *The Life of Inland Waters.* The Comstock Publishing Company, Ithaca, N.Y. 438 p.
- **SECCHI A.** 1866. Relazione dell' esperienze fatte a bordo della pontificia pirocorvetta l'Immacolata Concezione per determinare la trasparenza del mare. *In*: Cialdi A. *Sul moto ondoso del mare*, p.258, Roma.
- **STERNER RW.** 2012. Raymond Lindeman and the trophic dynamic viewpoint. *ASLO Bulletin*, 21: 37-51.
- **VINCENT WF, BERTOLA C.** 2012. Forel's limnology: From lake physics to ecosystem services. *ASLO Bulletin*, 21: 69-77.
- **WEISMANN A.** 1877. *Das Thierleben im Bodensee.* Lindau.
- **WETZEL RG.** 2001. *Limnology. Lake and River Ecosystems.* 3<sup>rd</sup> Edition, Academic Press, New York. 1006 p.
- **WILDI W, MOSCARIELLO A, PUGIN A.** 1999. Histoire glaciaire du Léman, p. 399-414. *In*: Bertola, C, Goumand C, and Rubin JF (eds.). *Découvrir le Léman: 100 ans après François-Alphonse Forel. Actes du colloque pluridisciplinaire, Nyon 16-18 septembre 1998.* Editions Slatkine, Geneva.
- **WILLIAMSON CE, SAROS JE, VINCENT WF, SMOL JP.** 2009. Lakes and reservoirs as sentinels, integrators, and regulators of climate change. *Limnology and Oceanography*, 54: 2273-2282.

