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Robert Arlinghaus*[1,2], Brett M. Johnson[3] and Christian Wolter[1]

[1]Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Department of Biology and Ecology of Fishes, Müggelseedamm 310, 12587 Berlin, Germany;
e-mail: arlinghaus@igb-berlin.de
[2]Humboldt-University of Berlin, Faculty of Agriculture and Horticulture, Institute of Animal Sciences, Inland Fisheries Management Research Group, Philippstraße 13, Haus 7, 10115 Berlin, Germany
[3]Department of Fish, Wildlife and Conservation Biology and Graduate Degree Program in Ecology, 1474 Campus Delivery, Colorado State University, Fort Collins, CO 80523-1474, USA

Review Paper

The Past, Present and Future Role of Limnology in Freshwater Fisheries Science

key words: angling, applied limnology, history, recreational fisheries, inland fisheries, social-ecological system

Abstract

Limnology has greatly influenced the field of freshwater fisheries science, particularly fisheries biology. However, both fields became increasingly disconnected during the 20th century, when major research traditions within limnology became more tightly focused and humans, even fish, were externalized. A paradigm shift occurring within freshwater fisheries science today is redefining research questions and approaches and is further challenging the role of limnology within fisheries science. Modern fisheries science has become a multidisciplinary, interdisciplinary and sometimes transdisciplinary endeavour that melds the social with the natural sciences to understand fisheries as social-ecological systems. Limnology remains important to capture some of the dynamics inherent in social-ecological fisheries systems, but becomes one of the many necessary scientific disciplines of fisheries science, rather than the primary supporting science that it used to be. To improve scholarly communication between limnologists and freshwater fisheries scientists, major shifts in perspective are needed.

It is hardly understandable why fish are only regarded as a component of the aquatic ecosystem or a means for biomanipulation in modern textbooks on limnology or limno-ecology, while the fisheries science as a natural component of theoretical and applied limnology in the spirit of Thienemann is not mentioned in the table of contents!
H.-J. Elster, 1993 (translated from German)

1. Introduction

Limnology as a scientific discipline studies the structure and function of inland waters. It has been called a subfield of ecology (Lampert and Sommer, 1999) that includes "everything that affects fresh water" (Naumann and Thienemann, 1922). This encompasses biological, physical, chemical, geological and hydrological aspects. Limnological thinking, from its early days in the late 19th century, has greatly influenced freshwater fisheries science, particularly freshwater fisheries biology (Elster, 1974, 1993). Limnology itself has traditionally been viewed as a "synthetic science for which purely zoological or botanical

* Corresponding author

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studies, though necessary, are no more than preliminaries" (NAUMANN and THIENEMANN, 1922). In modern terms, we would call this a holistic approach to understanding the structure and function of inland waters.

A major goal of freshwater fisheries biology has been to understand and predict fish population dynamics and fish production. This involved a different scientific paradigm compared to approaches commonly used in marine fisheries biology. For example, historically freshwater fisheries biology has explicitly considered the dependency of fish production on a variety of abiotic and biotic factors, including factors far from the narrow bounds of fish population dynamics, such as structure and size of the catchments, geological features and morphometry of the basins (BARTHELMES, 1981). This culminated in the development of various yield-prediction models based on morphometry of lakes and rivers or production related variables such as nutrient loading, primary productivity or biomass of invertebrates (RYDER, 1965; HRBÁČEK, 1969; OGLESBY, 1977; BARTHELMES, 1981). In contrast, marine fisheries science heavily relied on single-species models of stock dynamics to derive maximum sustainable harvest levels with limited feedback of fish to or from other features of the ecosystem or the food web (HJORT *et al.*, 1933; BEVERTON and HOLT, 1957; CUSHING, 1981). This was probably promoted by the vastly different scales at which fish production and fishing fleets operate in the oceans compared to inland waters, and the inability to understand complex ecological processes operating at such vast spatial and temporal scales. This is now changing as classical limnological processes such as top down control of food webs and trophic cascades (CARPENTER *et al.*, 1985) are being discovered in the marine environment (FRANK *et al.*, 2005), and an ecosystem approach to fishery modelling is promoted (WALTERS and MARTELL, 2004). This is unifying freshwater and marine fisheries science in recent years.

For the purposes of this paper, we argue that freshwater fisheries biology has been viewed by some as a branch of applied limnology (THIENEMANN, 1933) and fisheries scientists have historically considered it as an integrated scientific discipline that is neither hydrobiology nor biology of fishes, but something more holistic (WUNDSCH, 1931, 1932/1933; NIELSEN, 1999). Based on the tight ecological link between fish and the environment and the concern for the devastating pollution of many aquatic habitats in the early 1900s, one major research tradition within the freshwater fisheries discipline employed limnological methods (NIELSEN, 1999). However, modern limnology and what is today known as freshwater fisheries science diverged substantially during much of the twentieth century (RIGLER, 1982; BARTHELMES, 1988). In fact, we contend that limnology and freshwater fisheries science developed independent paths of scientific endeavour since limnology was narrowing its focus literally (*e.g.*, on microscopic planktonic organisms) and figuratively (*e.g.*, on water chemistry and hydrography) rather than on fish and fisheries (PERSSON *et al.*, 1988). Specifically, the importance of fish within the ecosystem, let alone fisheries thinking, has lost its once prominent position in limnology over time (NORTHCOTE, 1988; PERSSON *et al.*, 1988; MAGNUSON, 1991). For example, many early limnological textbooks devote 5% or less of their pages to fish (PERSSON *et al.*, 1988). Today, fisheries biology and fisheries sciences are completely missing in most limnological texts (ELSTER, 1993, quoted above). The reasons for the increasing alienation of limnology and fisheries science are related to societal changes in values, priorities and primary occupations (*e.g.*, loss of importance of the fisheries profession and other primary agricultural industries relative to service industries), altered modes of funding and organizing research (*e.g.*, changes in perspective among research funding organizations as to the value of applied research questions), differing research agendas in basic limnology and more application-oriented fisheries science, and finally, a rapid systemic transformation of inland fisheries from commercial to recreational fishing. A recent paradigm shift within fisheries science towards integration of social sciences is further challenging the historical linkage between limnology and freshwater fisheries biology/science today. To highlight these developments, we 1) briefly review the history of applied limnology using examples from

German research organizations; 2) outline major national and international societal and scientific trends within inland fisheries and freshwater fisheries science; and 3) reflect on the future role and importance of applied limnology for freshwater fisheries science.

2. History: Branching within the Field of Limnology in the 20th Century

Inland fishing is as old as human culture itself; subsistence fishing and hunting were paramount for the survival of early hunter-gatherer human communities and central elements of ancient human settlements around major rivers and lakes. The central role of fish and fisheries in the evolution of human society is indicated by the fact that there is no other aquatic organism with comparable presence in the historical archives dating back more than 2000 years (KOCH, 1925; HOFFMANN, 1994; WOLTER, 2007). Understanding fish diversity and abundance must certainly have captured the curiosity of early nature observers and led to several early writings about fish (*e.g.*, BALDNER, 1666; BLOCH, 1782) and fisheries (WALTON, 1853), particularly in times when industrial pollution and fishing intensity resulted in degradation of once abundant resources (ARLINGHAUS *et al.*, 2002). This applied perspective provided an impetus for limnology as a comprehensive scientific discipline (ELSTER, 1974), epitomized by the works of FORBES (1887) and FOREL (1901). In fact, fish were routinely studied by early limnologists as evidenced in the publications of the proceedings of the International Society of Limnology (formerly International Association of Theoretical and Applied Limnology; Societas Internationalis Limnologiae, SIL) (NORTHCOTE, 1988; MAGNUSON, 1991), which was founded in 1922 by THIENEMANN (Germany) and NAUMANN (Sweden). THIENEMANN himself was greatly inspired by applied fisheries questions in the early phases of his career (WUNDSCH, 1960). Given the importance of fish for humans and a relative ease to macroscopically examine and identify fish, it is not surprising that a basic limnological concept – the longitudinal zonation of rivers – was introduced for the first time by FRIČ (1872) and VON DEM BORNE (1877) using river fish assemblages in a fisheries context more than 100 years ago.

The field of limnology developed rapidly at the end of the 19th century and in the beginning of the 20th century (ELSTER, 1974; FREY, 1963). In Europe, a milestone of institutionalized limnological research was the founding of the Zoological Station in Naples (Italy) in 1872 (DOHRN, 1879). This station largely influenced the foundation of various limnological and fisheries biological research organizations throughout Europe (HEMPEL, 2003). For example, in Germany the scientific field of limnology was profoundly influenced by the founding of the Hydrobiological Station in Plön in 1891 by ZACHARIAS, later world-renowned as the Max-Planck-Institute for Limnology (ELSTER, 1974; LAMPERT, 2007). Only two years later, the Biological and Fisheries Experimental Station in Berlin, now part of the Leibniz-Institute of Freshwater Ecology and Inland Fisheries, was formed (KOWALCZUK, 1989; STEFFENS and SCHÄPERCLAUS, 1993). Both of these organizations were situated in the lowlands of northern Germany and did not study the ecology and the fisheries in pre-alpine or alpine lakes. To fill this gap, the Institute for Lake Fisheries and Lake Research in Langenargen at Lake Constance was founded by DEMOLL in 1920 (PROSKE, 2005). Historically, it is interesting that these founder stations of fundamental limnological (Plön) and applied limnological and fisheries biological (Berlin, Constance) research in Germany were established years after the collapse of several high profile fisheries such as sturgeon (*Acipenser sturio*) and Atlantic salmon (*Salmo salar*), and at least a decade after the first large scale fish stocking and introduction programs were launched by the German Fisheries Association (VON DEM BORNE, 1882; SCHIEMENZ, 1919). Thus, it appears that limnological and fisheries-oriented research organizations were primarily founded to understand or provide support for management of already heavily altered aquatic ecosystems and impoverished fisheries (although fish introductions and stocking were probably not seen negatively in those times).

As the field developed, during the 20th century, limnology began to organize into several more or less distinct research traditions. Differentiating these groups is subjective and oversimplifies reality; however, we contend that three major branches are distinguishable within limnology. The first branch, fundamental or basic limnology, studied ecological and hydrological processes and mechanisms within aquatic ecosystems (LAMPERT, 2007). Scholars devoted to this tradition often developed an experimental approach, controlling as many confounding factors as possible, manipulating entire aquatic ecosystems or mimicking nature in laboratory environments (RINGELBERG, 1997). The aim was an improved understanding of ecological processes in freshwater systems, with no immediate practical applications intended (RINGELBERG, 1997; LAMPERT, 2007). Humans and tangible products provided by aquatic systems were largely outside the purview and consequently, heavily manipulated (exploited) fish stocks, and their ecology were typically not the focus of fundamental limnological studies.

A second branch was concerned with solving or contributing to issues of societal importance such as understanding the impacts of euthrophication on structure and function of aquatic ecosystems (VOLLENWEIDER, 1976). Such limnologists often took a whole system perspective and a comparative approach to study anthropogenic change in aquatic systems. Informing water managers for the benefit of society was an explicit goal. However, fish and fisheries were often treated as vectors and not objects of studies (ELSTER, 1993), and humans were commonly considered as non-natural external disturbances only, whose largely undesirable impacts were the driving force of the inquiry (*e.g.*, pollution, nutrient input). This research tradition produced much research that culminated in the development of ecotechnologies to enhance socially desirable states of ecosystem metrics such as high water quality (DITTRICH and KOSCHEL, 2002; MEHNER *et al.*, 2002).

A third branch of limnology was focused on understanding the underlying processes leading to products and services that aquatic ecosystems provide for humans, traditionally mainly fish, and how to use scientific knowledge to use natural resources more sustainably. These scientists for example studied the mechanisms and processes controlling fish production and called themselves fisheries biologists, or more generally, fisheries scientists (WUNDSCH, 1932/1933, 1960). As already mentioned, when working in freshwaters, they were often applied limnologists with a fisheries focus approaching fish production from the "bottom-up". These scientists viewed themselves as knowledge providers for better management of fisheries resources (SCHIEMENZ, 1919). As soon as fishers and fisheries professionals concerned themselves not only with the mere physical act of capture but also with ecological relationships leading to fish production, fish were seen as the end product of a continuous exchange of organic matter through predator-prey interactions, physico-chemically induced nutrient dynamics and energy fluxes. It was quickly realised that in order to understand fisheries and fish production the entire aquatic environment had to be studied by a variety of methodological approaches, many of which were used in limnology (WUNDSCH, 1931, 1963; ELSTER, 1974; BARTHELMES, 1981, 1988). Producing solid fundamental understanding about the way inland waters function was seen as prerequisite to solve pressing issues of societal concern, but the ultimate aim of fisheries scientists was (and continues to be) applying scientific knowledge to management and thereby improving fisheries for the benefits of those that depend on (commercial fishers) or simply enjoy catching fish (recreational fishers) (WUNDSCH, 1960; RIGLER, 1982; MAGNUSON, 1991; NIELSEN, 1999; ARLINGHAUS, 2006).

Unfortunately, over time the importance of fish and fisheries as a part of limnology declined (RIGLER, 1982; PERSSON *et al.*, 1988; MAGNUSON, 1991), and thus, the "fish(eries)" and "non-fish(eries)" branches of applied limnology became increasingly distinct. In addition, many limnologists became isolated from applied issues and were instead driven by a desire for fundamental scientific, particularly ecological inquiry. Over time, limnologists and fisheries scientists studied different problems, in different systems, at highly different spatial and temporal scales, published in different journals, attended different conferences, and within certain research organizations, took their coffee break in different rooms and at different times. Consequently, RIGLER (1982) noted that fisheries biologists and limnologists rarely interacted because they could not effectively communicate with each other. He went on to say that they could not communicate because they did not share the same paradigm about the functioning of aquatic ecosystems. Indeed, limnologists were mainly interested in fine-scale mechanisms and processes, while "piscicentric" fisheries biologists were intrigued by the ultimate outcome of ecological processes for fish and fisheries (RIGLER, 1982). Therefore, academic ecologists (including limnologists) often became aloof from the "real world" sometimes ignoring prior work of fisheries biologists (KERR, 1980), while fisheries biologists often "forgot" potential contributions of their studies to limnology and ecology in general (LARKIN, 1978). For many limnologists focusing on the chemical and hydrological aspects of lakes and rivers, fish, let alone fishers, were barely part of the ecosystem that was studied. Major work of such pure limnologists focused on chemical and physical aspects of lakes, phytoplankton and zooplankton dynamics, possibly facilitated by less complicated sampling methods and faster generation of results compared to studying slow growing and late maturing fish that can also be more difficult to sample. Beside fish, we would add that also anglers and fishers, and their social and economic environment as well as all activities associated with fisheries management, were not regarded by many limnologists as part of their research agenda. This hampered progress in freshwater fisheries science as it impoverished communication among limnological and fisheries researchers and research organizations.

3. Paradigm Shifts in Fisheries Science and the Future Role of Limnology

Fisheries science has often been too narrowly viewed as fisheries biology, and even today some definitions of fisheries science focus mainly on the biology of the exploited species (i.e. fisheries biology, HART and REYNOLDS, 2002). Fisheries biology traditionally has placed strong emphasis on population dynamics of exploited stocks and, because of the motivation to continuously harvest fish, a very strong emphasis on how to sustain a maximum yield. This was particularly pronounced in fisheries dominated by commercial interests (LARKIN, 1978) and has also for a long time driven freshwater fisheries science (WUNDSCH, 1963; BARTHELMES, 1981; NIELSEN, 1999). Today, in nearly all industrialized societies, the importance of commercial fishing is decreasing in favour of recreational uses of fish stocks (WELCOMME, 2001; ARLINGHAUS *et al.*, 2002). Associated with this transition, societal values and perspectives of what constitutes "good" fisheries practice and sustainable fisheries management is also changing (NIELSEN, 1999). For example, fish translocation and introduction of non-native species of fisheries value were commonly accepted and ubiquitously used to enhance fisheries until only recently. This was seen as an effective way to exploit "underutilized" food resources, *e.g.*, the direct use of primary production by introducing herbivorous and phytoplanktivorous Asian carp species in German lakes in 1965–1968 (STEFFENS, 1986). Nowadays, commercial fisheries are under heavy economic pressure to survive and most freshwater fisheries are solely exploited by anglers (ARLINGHAUS, 2004, 2006). Intensive stocking and introduction programs are increasingly criticized by a conservation-oriented public, and today introductions of non-natives are banned by fisheries and nature conservation legislation all over Germany. Fisheries management must cater for changing and more diverse demands from anglers as well. Therefore, the objective of maximum biological yield that traditionally has been associated with fisheries biology (LARKIN, 1977, 1978) and inland fisheries management (NIELSEN, 1999; ARLINGHAUS *et al.*, 2002) has been supplanted by alternative, more diverse management objectives in recreational fisheries, but the underlying fisheries research to provide scientific background on how to achieve more diverse objectives is largely lacking (ARLINGHAUS, 2006). Indeed, the traditional limnology-driven freshwater fisheries biology, at least in the form it was taught and understood in the commercial inland fisheries context (BARTHELMES, 1981), has not academically prepared the (German) fisheries manager to account for these changes. Traditional fisheries research is for example neither tailored towards recreational fisheries nor does it account for the dynamic interplay between humans (anglers) and the natural systems in an overly meaningful way.

Societal changes demand a radical change in the focus of fisheries science from the traditional emphasis on fish and their natural environment, to a purview that includes the complex of social, economic and political factors driving the behaviour of fishers and anglers as individuals and fisheries as systems (LARKIN, 1978; CARPENTER and BROCK, 2004). Although the idea of the necessity to account for the complex nature of the human dimensions of fishers and anglers in fisheries science and management is not new (*e.g.*, LARKIN, 1978), it has been just recently that freshwater fisheries science coupled human dynamics with fish dynamics in a meaningful way (*e.g.*, CARPENTER and BROCK, 2004). It should be an important signal that a luminary contemporary limnologist such as STEVEN R. CARPENTER, well known in the field for milestone publications inspiring decades of fundamental *and* applied limnological research (*e.g.*, CARPENTER *et al.*, 1985), is pursuing the integration of the social and ecological sciences within limnology and fisheries science (CARPENTER and BROCK, 2004; CARPENTER and FOLKE, 2006). Before this very recent development, fishers and anglers and their dynamics were viewed "essentially as gremlins in an otherwise orderly statistical machine" (LARKIN, 1978). But, particularly in fisheries systems dominated by regionally mobile, highly diverse predators called anglers, human dynamics contribute to the properties of fisheries as systems (CARPENTER and BROCK, 2004). In this context, the diversity of angler behaviour (ARLINGHAUS, 2004) is just beginning to be appreciated. A new fisheries science deals with the fish stocks, interactions of fish and other ecosystem components, aquatic-terrestrial coupling, heterogeneous users of fish stocks and inland waters, and the type and nature of decision makers at all levels, all together forming a coupled social-ecological system known as a freshwater fishery (ARLINGHAUS *et al.*, 2007). Limnology remains important to capture some of the dynamics inherent in social-ecological fisheries systems, but becomes one of the many necessary scientific disciplines of fisheries science, rather than the primary supporting science that it used to be. In the new fisheries science, humans are part of the system to be studied and are not further regarded as an external, non-natural disturbance to be avoided. It is time to know more about the human user of fish stocks and their behavioural dynamics to advance freshwater fisheries science, but methods on how to achieve this must be found outside traditional limnology.

However, studying solely humans separately from the ecosystem and the fish stocks would be unsatisfactory, because human predation on fish stocks and fisheries management measures such as stocking drive limnological processes and potentially influence the structure and function of entire ecosystems (ROTH *et al.*, 2007). Moreover, understanding the dynamics of the behaviour of anglers in part depends on the type of feedback signals originating from the aquatic ecosystem and therefore one cannot separate the study of anglers from the study of aquatic ecosystems. What is indeed needed is a perspective that truly lives interdisciplinary and provides substance to it rather than lip service, a perspective, in which social and natural scientists work together on a common system called a fishery. This requires limnologists and fisheries biologists that were exclusively concerned with fish production dynamics to broaden their perspective and start studying the dynamics of humans exploiting or depending on aquatic ecosystems on the same footing as they ascribe to zooplankton and phytoplankton or "fish food". In the same vein, traditional fisheries scientists must broaden their perspective to study the coupled social-ecological system instead of focusing on the dynamics of a particular, valuable fish species exclusively. To establish large interdisciplinary groups that study (and solve) fisheries problems of contemporary interest, convergence of traditional limnology and modern fisheries science is needed, but social sciences as well as biological sciences must be equally represented to truly advance the field.

4. Conclusions

Most problems in contemporary freshwater fisheries are not biological, but social ones (ARLINGHAUS, 2004, 2006). They will be properly resolved only by promoting interdisciplinary and transdisciplinary research and the integration of social and limnological/fisheries biological research. If fisheries science does not include a focus on the user of fish resources (fisher and angler), the science can be called fisheries biology, limnology, ichthyology, ecology, hydrology, or whatever else fits (ROYCE, 1983). If we call it fisheries science, we should remember that fishing is a human activity (ROYCE, 1983). We should also be reminded that fisheries science is more than fish and fisheries biology; it involves an interdisciplinary approach to understand the human and biological dynamics of social-ecological *fisheries systems* by crossing and melding the boundaries between the natural and the social sciences. What is crucially needed to advance this science is that 1) fundamental limnologists (branch 1) start (re)appreciating the value of applied questions to generate fundamental insights (or at least do not disregard them as inferior science); 2) applied limnologists (branch 2) begin to view humans as a part of nature with a legitimate role within aquatic ecosystems and culturally shaped landscapes/catchments; and 3) fisheries scientists start appreciating the limitations of their historic heavy focus on the fish ("fish biologists"), separate from the fisher, separate from the decision maker. Only then will limnologists and fisheries scientists be able to move closer together again and start re-establishing what has been lost – fruitful scientific cooperation that advances both fields. This call does not constitute a paradigm shift for limnology *per se*, but illuminates a new role for applied limnology within the complex field of fisheries science.

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