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A tribute to Winfried Lampert: how he injected an integrative vision of evolutionary ecology into the aquatic sciences

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With 2 figures

Prof. Dr. Winfried Lampert passed away on March 6, 2021. A detailed obituary about Winfried can be found in Stibor et al. (2021). This current special issue has been composed to honor Winfried for his scientific legacy and for his many years of service as Editor-in-Chief of the *Archiv für Hydrobiologie* (renamed *Fundamental and Applied Limnology* – FAL in 2007). Here we want to highlight his scientific impact and heritage that are reflected and noted in the scientific contributions included in this special issue. Short direct quotes from the contributing authors to this special issue, are noted (Fig. 1), which indicate how each publication is related to or inspired by Winfried Lampert's work. Papers in this special issue have been organized around broad themes, which reflect the impact that Winfried's work has had on the field.

Background – setting the stage

After his doctoral dissertation, Winfried Lampert started his scientific career in the field of ecophysiology, a well-established research field at this time. However, he transformed it from a zoological-oriented autecology of individuals, towards a concept-based and experiment-driven research of much wider focus, including evolutionary thinking. His primary model organism was *Daphnia.* He was fascinated by this key player in freshwater systems together with its special applicability to be used as a model system, including its relatively easy cultivation and the rapid production of large numbers of "standardized clones" by parthenogenesis. His sense for accuracy in experiments brought controlled experimental systems to a new level, still unsurpassed today. His flow-through systems to culture and feed *Daphnia* under highly controlled conditions are still state-of-the-art. His ideas and the available experimental facilities such as his flow-through systems or the famous, 11.5 m tall, twin indoor Plankton Towers (Lampert & Loose 1992) attracted foreign researchers from all over the world (De Meester et al. 1995; Dodson et al. 1997; Sterner et al. 1998; Gliwicz et al. 2001; Havel & Lampert 2006; Spaak & Boersma 2006; Larsson & Lampert 2011). Soon, the Max-Planck Institute for Limnology (MPIL) in Plön (FRG) became a hotspot for the scientific exchange of new ideas in the study of aquatic systems. The combination of state-of-the-art equipment often not found elsewhere, along with the presence of "big shots "in limnology & ecology, enthusiastic early ca-

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“Winfried Lampert started his career working with the single currency approach, mainly focusing on carbon (C), and later included multiple currencies of food quality…… it is of utmost importance that we understand what we do when we deal with nutrient ratios” (A. Balkoni et al.)

“Winfried’s vision of a multi-disciplinary approach to incorporate modern evolutionary and ecological principles to the study of aquatic systems inspired generations of aquatic scientists, including ourselves” (E. Kiehnau & L. Weider)

“Winfried regretfully mentioned that the towers would be great for studying plankton migration at the population scale, but we would still learn little or nothing about the behavior of individual Daphnia……research focused on the chemical inducibility of DVM in *Daphnia*, which was a very hot topic at the time, rather than on the … behavioral patterns of individuals (P. Dawidowicz et al.)

“..efforts to better understand biodiversity in aquatic communities and how predator-prey induction (cyclomorphosis) fits into schemes of multiple species interactions……. how to explore long-term issues of predator-prey interactions and evolution using resting eggs from sediment cores” (C. Kerfoot & H. Boriss)

“..the role of adaptive maternal effect in plastic reaction of individuals to selection forces corresponds well with the credo displayed in the central place of the Max Planck Institute: “Natural selection is ecology in action”. (A. Mikulski & J. Pijanowska)

“Winfried mechanistically broke down the well-known negative effects of cyanobacteria on Daphnia abundance into several types of interference. …we have tried to independently test for the effects of a toxic strain and of its microcystin-free mutant in order to indirectly test for the importance of microcystin (‘the toxin’) for negative effects of Daphnia. ” (E. von Elert)

“…empirical data can confirm and inform theoretical concepts and, most importantly, stimulate their improvement - or ultimately lead to the development of new theories. We choose a series of case studies ….. to document the strength of linking theory with observational data for abiotic and biotic system level assessments” (R. Adrian et al.)

“Experiments and observations investigating ecological concepts can be only as good as the technical possibilities to measure the necessary parameters to test hypotheses” (M. Ilić et al.)

“..investigate the consequences of Daphnia diel vertical migration for the distribution of phosphorus within a stratified water column” (K.F. Schachtl et al.)

„… also sharpened our understanding of how Daphnia physiology and behavior influence and are influences by other community members of lake and ponds”(C. Cáceres et al.)

“Life table analyses were central to a large number of experiments taking place in Winfried Lampert’s Department at the MPI Plön” (J. Pijanowska et al.)

“.. it became obvious that inducible defenses are more the rule than the exception when organisms adapt to cyclically changing predator conditions” (M. Horstmann et al.)

Fig. 1. Quotes from the authors or coauthors of the contributions for the Winfried Lampert Honorary Issue.

reer postdocs and motivated doctoral students resulted in what was sometimes called “the golden years of Limnoecology”. Hence, a large number of Winfried’s students and early career co-workers continued successful careers in science.

Winfried started his work on *Daphnia* by investigating its feeding dynamics, deeply rooted in autecology and ecophysiology, but coming to a new level by his developments of highly controlled experimental systems that examined evolutionary ecological questions. From there he started to explore the interactions of *Daphnia*, both with its food and with its predators, including more and more ultimate questions of how these interactions evolved. His work was important for limnology but has far reaching consequences, as his study systems also served to test general ecological concepts. His belief that limnological experiments can be also useful and fruitful test systems for general ecological concepts resulted in the famous textbook “Limnoecology” (written together with Ulrich Sommer – Lampert & Sommer 1997; Lampert & Sommer 2007), which has been translated into several languages.

Winfried Lampert’s main contributions

Winfried Lampert has influenced a wide variety of fields and researchers, and it is a challenge to describe these in a structured way. Here, we accept this challenge, and using a pelagic foodweb as a model (Fig. 2), we identified four major research areas where

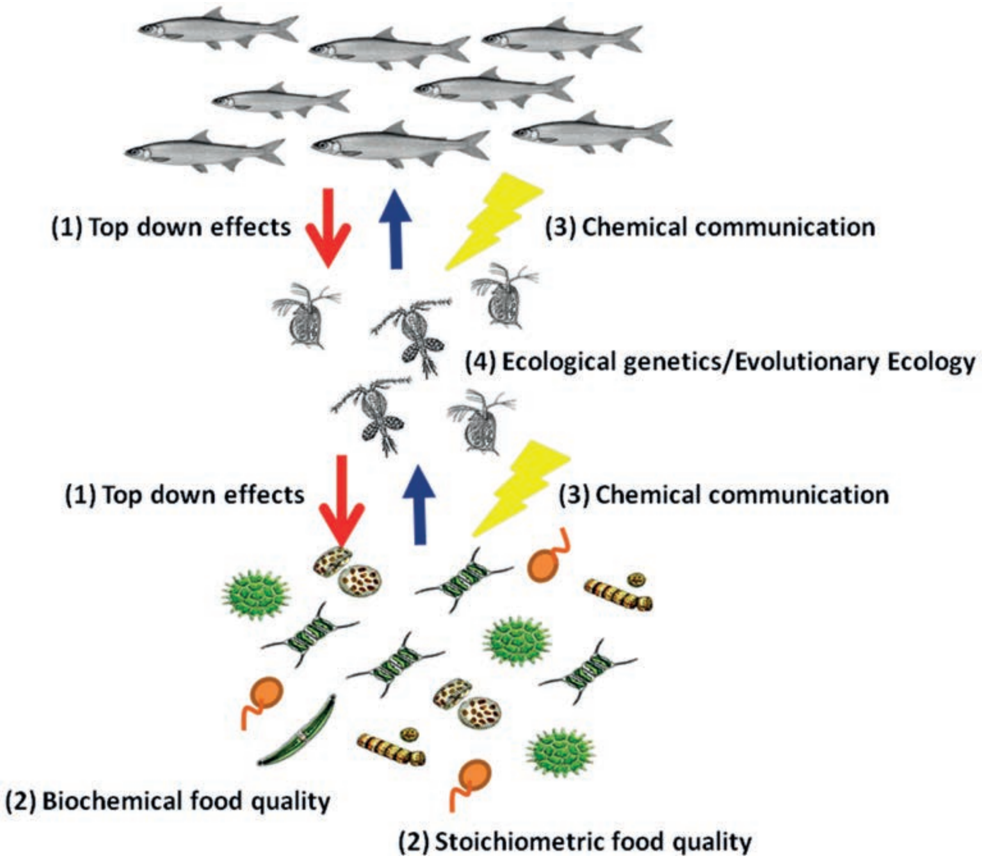

Fig. 2. Simplified pelagic freshwater food web showing major research areas of Winfried Lampert and his group.

his legacy is longstanding. Interestingly, even though Winfried never worked in marine systems himself, many of the concepts that he worked on crossed the "salty barrier", as exemplified by the fact that three of us (i.e., M. Boersma, U. Sommer, H. Stibor) are or were at marine institutions, while a fourth (B. Santer) serves as Managing Editor for *Marine Biology*. Thus, it is clear that Winfried Lampert's work has been cited widely and crosses over many scientific borders.

(1) Top-down view of plankton dynamics

The explanation of the clear-water phase by zooplankton grazing (Lampert & Schober 1978) became a cornerstone in the development of the concept of top-down control in limnology (Carpenter et al. 1985). A pronounced minimum of phytoplankton biomass in meso- and eutrophic lakes during late spring/early summer, just following the spring bloom, had already been known for some time but remained unexplained. Winfried's explanation was based on the coincidence of phytoplankton decline with maximal abundances of the herbivorous zooplankton *Daphnia* and of highly favorable growth conditions for phytoplankton, documented by light, nutrient concentrations, and high primary production:biomass ratios. In a later study in mesotrophic Lake Schöhsee, direct measurements of grazing rates confirmed the crucial role of grazing (Lampert et al. 1986). An inter-lake comparison showed grazing rates of 1.0 to 2.5 d^{-1} during the clear-water phase.

The studies on the clear-water phase focused on the numerical top-down effect on prey populations. In contrast, Winfried's studies on the ultimate cause of zooplankton diel vertical migration focused on the evolutionary effect, i.e. the selection for avoidance of being eaten (Stich & Lampert 1981).

When Winfried started his career, two schools of thought competed in providing a convincing explanation for the adaptive value of vertical migration for zooplankton. Why should zooplankton spend parts of the daily light phase in deeper, darker, colder and usually less food rich waters? The bottom-up school favored explanations which touted a metabolic advantage, e.g. saving respiratory losses in colder water (Mclaren 1963). The other school of thought suggested, that spending daytime at greater depths would protect zooplankton from predation by optically-oriented fish (Kerfoot 1985). In a sequence of studies, Winfried provided increasingly convincing evidence for the predator-avoidance hypothesis. The most important milestones were: a seasonal study in Lake Constance showed differential migration behaviors of the very closely-related congeners, *Daphnia hyalina* and *D. galeata* (Stich & Lampert 1981). *D. galeata* does not migrate, has higher birth rates, but also higher death rates. *D. hyalina* migrates during summer, has lower birth rates as a consequence of less food and lower temperature in deeper waters, but it also has lower death rates. It does not migrate during spring, when fish predation is unimportant. Calculations based on a number of metabolic studies have shown that any metabolic advantage suggested for part-time residence in colder water is far less than the disadvantage of slower somatic growth production and development under cooler and food-deprived conditions (Lampert 1993). In a final step, Winfried used the opportunities and funding at the MPIL to build the aforementioned twin indoor plankton towers in which vertical stratification of the temperature, chemical conditions and of food availability could be manipulated and precisely controlled. Here, vertical migration of *Daphnia* could be initiated by fish "smell", i.e., by adding water from aquaria with fish, containing substances (kairomones) taken as signal of fish presence by *Daphnia* (Lampert & Loose 1992; Loose et al. 1993).

What have we learned?

The idea of top-down control in aquatic ecosystems dates back to the size-efficiency-hypothesis (Brooks & Dodson 1965) and the keystone predator concept (Paine 1966). While Paine's work related to marine benthos, Brooks & Dodson's work belonged to the field of limnetic plankton ecology, which demonstrated the impact of fish predation on the size-structure of zooplankton communities. However, the world view of the limnological community was dominated by eutrophication research at that time and questions of the conversion of increased nutrient richness into increased phytoplankton biomass and production and adverse side effects of this increase, exemplified a classic bottom-up perspective. In this scientific environment, the work of Lampert and his colleagues coalesced into the international Plankton Ecology Group (PEG), which represented a "scientific revolution" in the sense of a paradigm shift (Kuhn 1962).

When one of us (U. Sommer) joined the Limnological Institute at Constance in 1979, Winfried Lampert had already left Constance for his further career steps, but the clear-water phase was one of the flagships of our understanding of the functioning of the pelagic ecosystem of Lake Constance and other meso- and eutrophic lakes. Accordingly, grazing effects of zooplankton on phytoplankton played a key role in a synthesis paper written on behalf of the PEG (Sommer et al. 1986). This paper was U. Sommer's first experience of scientific cooperation with Winfried and subsequently U. Sommer was hired to join Winfried's department at the MPIL. Half a decade later, U. Sommer moved from limnology to marine ecology and the analysis of top-down effects of zooplankton on phytoplankton became one of his core topics.

During the 1980's the study of top-down effects in pelagic food webs developed from a relatively minor program to a mainstream activity in limnology, giving birth to rather broad concepts such as the trophic cascade (Carpenter et al. 1985). This concept posited that fewer planktivorous fish would lead to increased zooplankton abundances, which in turn would lower phytoplankton abundances, when observed annually. An applied sidetrack was the idea of biomanipulation as a restoration tool for eutrophied lakes (Shapiro & Wright 1984). Either direct removal of planktivorous fish or their reduction by stocking with (piscivorous) predators should lead to higher herbivorous zooplankton biomass, thus stronger grazing pressure on phytoplankton, and lower phytoplankton biomass, and clearer water even at elevated nutrient concentrations.

Lasting heritage and where to go

Winfried Lampert's contributions to top-down effects in pelagic food webs appeared in a period when this topic was highly controversial. He was one of the leading protagonists in this "battle". Now the issue is more-or-less settled, and most agree that the prevalence of top-down vs. bottom-up effects is a question of scale (see Lampert & Sommer 1997; Lampert & Sommer 2007). Large-scale comparisons between ecosystems of widely different nutrient levels have to be interpreted from a bottom-up perspective, while seasonal events or differences between lakes of similar nutrient richness, but different fish stocks, call for a top-down explanation. The clear-water phase and predator avoidance as ultimate drivers of vertical migration have become standard textbook knowledge.

(2) The effect of food quality on plankton dynamics

Even though it has been long clear that prey characteristics influence the quality of algae as food for zooplankton, the study of the exact factors that determine food quality of algae within and between prey species is relatively new. Early studies on grazing and the consumption of phytoplankton by zooplankton (e.g. Lampert 1977a; Lampert 1977b; Lampert 1977c; Lampert 1977d) focused on carbon as a single currency. As a result, many of the extant models describing planktonic interactions in oceans and lakes still essentially consider carbon as the main currency. So, what are the factors that determine food quality for zooplankton? And how has Winfried Lampert contributed to advance our understanding of the importance of those factors? As indicated above, Winfried's early work was focused on carbon as the determining factor, but as early as 1987, in a paper on feeding and nutrition in *Daphnia* (Lampert 1987), he acknowledged that *"salad is not always just salad"* (see also Wiltshire & Boersma 2016), and that different algal species represent different qualities of food for *Daphnia* (Ilić et al. 2023).

In his 1987 paper, he also briefly described the potential effects of biochemical limitations, but finishes this paragraph with *"Under natural conditions, however, Daphnia will rarely have a uniform diet, so that the problem of missing essential food components may not be so serious"*. This view changed in the mid-1990s, when Winfried realized and then fully embraced and championed the concept that there are three main aspects of food quality of algae as food for zooplankton: (macro) nutrient stoichiometry, morphology, and biochemical composition. First, it was discovered that the green algae *Scenedesmus obliquus* can either change its cell wall thickness as a result of the presence of zooplankton predators, with resulting lower feeding success of these same predators (Hessen & Van Donk 1993; Van Donk & Hessen 1993), or can start growing in colonies (Lampert et al. 1994), with the same result (see also the chemical communication section below).

More-or-less at the same time, together with his Ph.D. student Dörthe Müller-Navarra, Winfried carried out studies on the effects of essential fatty acids on *Daphnia* growth and reproduction (Müller-Navarra 1995a; Müller-Navarra 1995b; Müller-Navarra & Lampert 1996). Together, these authors showed that in correlational studies, the content of highly unsaturated fatty acids, especially eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), is related to zooplankton performance. This work was closely followed by a study in the Plön plankton towers, led by Robert Sterner, which investigated the light-nutrient hypothesis, i.e. the impact of changing light conditions on the carbon to phosphorus ratios in algae, and the resulting changes in food quality for zooplankton (Sterner et al. 1998).

One of Winfried's rules of engagement in science was that he did not want to be an author on papers where he had the feeling he did not contribute enough. As a result, his impact on the field from later work is a bit more difficult to decipher, but very much there, as exemplified by the large body of work that originated from his MPIL department in later years or from colleagues who continued to study the subject after they had moved to other places, often with their own students (Lürling & Van Donk 1997; Boersma 2000; Boersma & Stelzer 2000; Wacker & Von Elert 2001; Boersma & Kreutzer 2002; Von Elert 2002; Martin-Creuzburg & Von Elert 2004; Müller-Navarra et al. 2004; Von Elert 2004; Martin-Creuzburg et al. 2005; Boersma & Wiltshire 2006; Wacker & Martin-Creuzburg 2007).

What have we learned?

So, what have we learned, and where do we go from here? One thing that we have learned is that despite multiple efforts to separate out the food quality determining factors, and rank them in order of importance, this has not been successful. Most importantly, aquatic environments are very dynamic with a large variety of phytoplankton species (Brett & Müller-Navarra 1997), and in some cases strong seasonality that changes the supply and demand of food (Boersma et al. 2001). Further, grazers' demands vary with taxonomy (Hessen & Lyche 1991; Elser et al. 2003), ontogeny (Meunier et al. 2016), as well as external factors such as temperature (Laspoumaderes et al. 2022), so there is no such general rule.

In addition, in many cases, the three quality determining factors are interlinked; for example, nutrient-limited algae often have thicker cell walls (Van Donk et al. 1997), and changing biochemistry (Bi et al. 2017). Thus, efforts to identify the most important factor(s) determining food quality have led to much discussion and controversy in the literature (reviewed in Boersma & Meunier 2020), and a formal meta-analysis presented in Thomas et al. (2022). The link between the elemental composition and the biochemical composition is so tight that separating them is not useful. For example, phosphorus limitation in many algae will change the spectrum of essential components of the food, and simultaneously create an excess of available carbon. As the herbivore has to deal with the excess carbon and the scarcity of essential biochemicals at the same time, both of these mechanisms will change the quality of the food for the consumer.

In our future work, we should try to include all the factors, and refrain from advocating one-factor solutions. Interactions between more than one potential resource, for example by one resource being important for the uptake of the other one, may result in resources being co-limiting. Both the increase of the limiting resource, as well as the increase of the resource that is important for the uptake of the limiting resource will increase growth (Sperfeld et al. 2012). Other cases of co-limitation might exist as well; these have been described in great detail by Sperfeld et al. (2016).

Lasting heritage and where to go

So, what is Winfried Lampert's legacy in this field? Using the reductionist and mechanistic approaches that Winfried often advocated, we have been able to identify the factors that shape planktonic communities, or more specifically the trophic interactions between phytoplankton and zooplankton. We have also learned that there are limits as single factor explanations are often too simple. Hence, it is time to integrate the simple one-factor approaches into more complicated models to understand the interactions between all drivers and stressors of aquatic environments (Adrian et al. 2022).

(3) Chemical communication

Winfried Lampert's initial work at the MPIL in Plön had a strong focus on ecophysiology. Soon, the work on *Daphnia* did not only include the effects of environmental conditions and resources such as temperature or food defining its fundamental niche, but also different kinds of biotic interactions shaping the fundamental niche towards a realized niche, such as competition or predation.

With the increasing research focus on the importance of biotic interactions, it became evident that direct trophic interactions such as predation are accompanied by "non-trophic" interactions (e.g., variability of chemical stimuli in lakes). Such non-trophic interactions are usually diminishing the effects of predation on prey and therefore have strong feedback links to the trophic flows, prey abundances and population dynamics.

As noted above, a famous example within Winfried's early research portfolio was his mechanistic approach to find the ultimate explanation for the diel vertical migration (DVM) of *Daphnia* (Lampert 1993). DVM is a typical case, where a direct trophic interaction between fish and *Daphnia* is strongly affected by a non-trophic interaction. For example, a chemical stimulus released by fish (kairomones) might be involved, whereby *Daphnia* senses the presence of fish and initiates an escape behavior to avoid the negative consequences (i.e., being eaten) of the direct trophic interaction. Additionally, it was already known from earlier studies that predator-released chemicals can induce changes not only in behavior but also in morphology of planktonic organisms such as in ciliates, rotifers or *Daphnia* (summarized in Tollrian & Harvell 1999); see a number of contributions in this special issue (e.g. Horstmann et al. 2022; Kiehnau & Weider 2022; Mikulski & Pijanowska 2022; Pijanowska et al. 2022).

To elucidate the different roles of trophic and non-trophic elements of complex fish-*Daphnia* interactions, and as mentioned above, Winfried had an impressive research tool – the twin plankton towers (Lampert & Loose 1992) that mimicked 11.5-m water columns in a lake. The towers overcame many shortcomings of typical large size (i.e., mesocosm) experimental units, where there is often a high degree of mimicking nature on the one side, but at the same time only limited control over environmental conditions. The "cost" of overcoming to some degree the usual trade-off between "nature-like"/complexity and experimental control (that is still unsurpassed) was that only two of the huge and very complex systems could be installed. Hence, the need for some experiments to have large numbers of replicates and at the same time did not need the full size and complexity of the towers resulted soon in small scale "copies" of the towers that allowed high replication and the investigation of individual *Daphnia* – the so called "Plankton Organs (Dawidowicz & Loose 1992; Gliwicz et al. 2006; Dawidowicz et al. 2023).

What have we learned?

Following the effects of kairomones on individual organisms allowed the measurement of reaction norms of plasticity not only in behavior, but also in other phenotypic traits such as life-history and morphological responses to kairomones. Hence, a main aspect of the research done on chemical communication at the MPIL was about the consequences of chemical communication for the recipient. Quantifying the dimensions of the responses to chemical stimuli (i.e., phenotypic plasticity), was central to experimental designs. Many experiments focused on the effect(s) of predator-released chemicals on reaction norms of morphological parameters (body size, tail-spines and other protective structures) and life-history traits such as age at first reproduction or reproductive output (Stibor & Lüning 1994; Boersma et al. 1998). Additionally, this individual-based approach allowed also the study of instar-dependent or maternal effects of responses to kairomones and their interactions with environmental conditions (temperature, light) and resources (Riessen & Gilbert 2019). *Daphnia* was already well-known for its impressive phenotypic plasticity and the study of reaction norms since the work of Woltereck (1909). The above-mentioned experiments contributed to a deeper understanding of proximate and ultimate causes behind this phenomenon.

Another important aspect was to assess the costs of the defenses induced by kairomones. Such costs were central for the eco-evolutionary explanation as to why defenses are inducible and not permanent (i.e., constitutive). It soon became clear that such costs may not be easily measured within the same experimental environment, usually showing only a small snapshot of the potential environmental conditions and resources the animals experience in the field. Hence, experimental designs included also the "environmental" context of effects and costs of kairomone-induced defenses in a large variety of experimental environments (Horstmann et al. 2022; Pijanowska et al. 2022).

The "individual" approach also led to investigate "clonal" differences in reaction norms to kairomones. Different genotypes showed differences in their responses, and it was sometimes possible to relate the predator environment of a *Daphnia* clone (e.g., fishless ponds or lakes with strong fish predation, clones existing before and after introduction of fish) to the direction and strength of its responses to predator kairomones. The reaction to kairomones was a definite adaptive factor that differed between clones with different evolutionary histories (De Meester & Weider 1999; Kiehnau & Weider 2022).

It was only logical that the initial work on *Daphnia* as a prey was extended towards the prey of *Daphnia*. For example, colony formation of the green algae *Scendesmus* was experimentally shown to be inducible by water inhabited previously by *Daphnia* (Lürling & Van Donk 1996; Wiltshire & Lampert 1999). Additionally, modern developments in imaging and -omics- approaches in recent years have allowed much more detailed insights into the underlying mechanisms of the different responses to kairomones (for example Oliver et al. 2022).

The work on chemical communication explored extensively the concepts of life-history and trade-offs and illustrated the shift from ecophysiology towards eco-evolutionary research questions at the MPIL during Winfried Lampert's time.

Whereas the eco-evolutionary direction in the research agenda on chemical communication at the MPIL was followed in depth, the community approach was not followed to the same degree. Inducible variable traits (behavior, life-history, morphology) of a prey resulting from predator kairomones can have effects on the resources of the prey itself (trait-mediated indirect interactions; Werner & Peacor 2003). One reason that this approach was not explored in detail at the MPIL was that the kairomones were not characterized yet. In the early 1990s, when the research on chemical communication started to "bloom", it was expected that kairomone structure would soon be available, which would allow more rigid experimentation. One of us (H. Stibor) can personally remember good advice (1995) from Winfried Lampert to stop working on chemical communication for 1 or 2 years because then the chemical nature of the kairomones would be identified. However, it took nearly 30 years to achieve substantial progress in kairomone identification, thus keeping many researchers busy for entire careers (Weiss et al. 2018; Hahn et al. 2019; Pohnert 2019; Pijanowska et al. 2020). Hence, early experiments used either water from tanks containing high numbers of predators or some purified extracts from such tank water, still consisting of a mixture of unknown substances. Especially in experiments with plankton communities with fast-growing algae at the base of the food web, adding tank water inhabited by high numbers of predators also adds other substances (i.e., fecal material) than only kairomones. This made it difficult to relate observed differences in food web dynamics to a kairomone *per se*.

Lasting heritage and where to go

Chapters about the importance and role of chemical communication are now standard within ecological textbooks (see also several contributions to this special issue), very often using plankton examples to illustrate major principles. However, with recent progress in kairomone identification, more rigid and controlled experiments at the community level are possible. In addition, also an "up-scaling" to field situations could be done. Knowing the kairomones and being able to quantify them will allow the construction of "maps of fear" in natural aquatic environments and link such "maps" to the behavior, life history, or morphology of prey living in these systems. This would allow bringing results from experimentation into the "wild", thereby adding an important "final" step to the analyses of the (seasonal) importance and relevance of chemical communication in aquatic systems.

(4) Evolutionary Ecology /Ecological Genetics

Many of the research topics that have been highlighted in this tribute article, along with many of the papers in this special issue (Kerfoot & Boriss 2022; Kiehnau & Weider 2022; Pijanowska et al. 2022) have a common theme of the importance of evolutionary processes that were stimulated by the positive and productive atmosphere that was generated at the MPIL under the long-term direction of Winfried Lampert. The vision and inter-connections of what Winfried achieved over the course of his career and his impact on aquatic/ecological science is seen not only in the primary literature that centered on field and laboratory experimentation, but also in the numerous invited review articles, books and special publications (see Stibor et al. 2021 for an extended bibliography of Winfried Lampert's work).

What have we learned?

As indicated in Figure 1, Winfried Lampert supported all efforts to integrate physiology, ecology, evolution, and population/ecological genetics into the overall framework of much of the work conducted at the MPIL during his tenure as Director (and beyond). Utilizing the somewhat unique breeding mode (cyclical parthenogenesis) of his beloved *Daphnia* (see more below) that allowed for the experimentation on genetically-distinct clones (genotypes), we have learned much about the genetic-environmental interactions of aquatic organisms to different abiotic stressors such as hypoxia (Weider & Lampert 1985), thermal stress (Mitchell & Lampert 2000), as well as biotic ones, including predation pressure (Pijanowska et al. 1993; De Meester et al. 1995), and algal toxins (Hairston et al. 1999; Hairston et al. 2001).

In addition, the study of spatial and temporal population genetic structure of aquatic organisms was fostered in the Lampert group over the years (Lampert & Wolf 1986; Mort & Wolf 1986; Weider 1989; Zeller et al. 2006, 2008), which expanded our knowledge of the underlying roles played by selection, drift, migration, and mutation in structuring these populations. This included the characterization and assessment of the importance of interspecific hybridization and introgression in these systems (Wolf & Mort 1986)

A further area of evolutionary ecology, termed "resurrection ecology" (Kiehnau & Weider 2022), was fully supported at the MPIL during the Lampert years, which resulted in a number of high-impact publications that examined temporal evolutionary dynamics in zooplankton (primarily *Daphnia*) systems (Weider et al. 1997; Hairston et al. 1999; Kerfoot et al. 1999; Hairston et al. 2001). This greatly expanded our ability to examine how organisms can respond to shifting environmental conditions over the course of decades (or even centuries – e.g. Frisch et al. 2014).

Lasting Heritage and where to go

Winfried Lampert was decades ahead of his time when he initially established his Arbeitsgruppe Planktonökologie (Plankton Ecology Working Group) and subsequent Department of Ecophysiology at the MPIL in the early/mid-1980s. This included the hiring of scientists in research disciplines (e.g., population/ecological genetics; evolutionary/theoretical ecology) that might be viewed as non-traditional for an aquatic biology institution. His vision established a foundational history of the importance of evolutionary biology/ecology and genetics as applied to aquatic (primarily planktonic) systems and it permeated the MPIL for decades and continued throughout Winfried's tenure as Director. As Winfried approached his retirement in 2006, it was his vision that inspired the creation of the Max Planck Institute for Evolutionary Biology (the successor to the MPIL in Plön) in the mid-2000s – truly a lasting legacy (Lampert 2007).

The four above mentioned research fields started as "individual" research fields but soon borders between them started to get "blurred". For example, kairomone effects were soon seen from an eco-evolutionary perspective and food quality became an important aspect to understand bottom up – top down effects in a causal way. Different research fields affected each other, leading to better and more complex insights into ecological dynamics. Hence, it is therefore not surprising and a sign of this fruitful development that most of the publications collected within this special issue can be linked to several of the described research fields (e.g. Caceres & Stewart Merrill 2022; Von Elert & Otte 2022; Balkoni et al. 2023; Schachtl et al. 2023).

Beside the major conceptual aspects mentioned above, Winfried Lampert also had a major impact on the use of a single taxonomic genus, *Daphnia*, for both field and laboratory studies. *Daphnia* became – due to the work of Winfried Lampert – both, an important model organism to study ecophysiology and evolutionary ecology questions within laboratory environments, but also a key organism to study dynamics of pelagic freshwater systems *in situ*. With ongoing developments in genetic/genomic analyses, *Daphnia* became also an "ecogenomic" model organism linking genes to communities and ecosystems (Miner et al. 2012). Perhaps, Winfried Lampert's contributions to the "visibility" of *Daphnia* as a key model organism were best summarized in a review by Colin Reynolds:

(5) Daphnia as a model organism and a key player of pelagic freshwater systems

Colin Reynolds review of Winfried's 2011 *Daphnia* book (Reynolds 2011):

Few freshwater organisms are better recognised by aquatic biologists, or are more symbolically representative of freshwater habitats, than the cladoceran, Daphnia. Several species share the same general body-plan, featuring a short, segmented body and a compressed carapace that part-encloses several pairs of flattened limbs, called phyllopods. Co-ordinated rhythmic beating of the phyllopods generates a current within the carapace chamber, from -which food particles are strained by the marginal filtering setae and then channelled back to the animal's mouth. Partly because this turns out to be a highly efficient means of removing and concentrating appropriately-sized foods from the water and partly because the animals are able to grow rapidly and recruit subsequent generations, Daphnia can be a major consumer of phytoplankton (algae and bacteria). At the same time, however, individual animals are not inconspicuous to predatory young fish or, on occasions, to older fish of those species that remain planktivorous specialists for much of their lives. As a consequence, populations of Daphnia are frequently pivotal to energy transfer through aquatic food webs. In turn, the impacts on species selection in freshwaters, on system function and upon perceived water quality, are known to be far reaching.

Whereas Winfried Lampert did most of his work with *Daphnia*, the conceptual aspects of these studies were soon transferred to other study systems including other organisms within freshwater or marine systems. Hence, this transfer is also seen in this special issue dealing with concepts that can be related to Winfried Lampert but including a variety of taxonomic groups

The work of Winfried Lampert was mostly "data limited", meaning that the number of possible replicates within experiments or the number of doable measurements or laboratory analyses limited the study design and the statistical analyses. Hence, such limitations forced a careful planning of the experiments and to think in depth about the conceptual hypotheses that should be tested with an experiment. Recent developments in automated sensor technologies, biological imaging, gene sequencing, remote sensing – to name just a few – resulted in so called "Big Data" approaches, where often not the amount of data, but their processing is limiting a study design. Additionally, big data analyses are often accompanied by automated pattern recognition by A.I. approaches. These developments offer new fantastic insight and we are sure that Winfried would have enjoyed and included these opportunities within his work. However, a conceptual understanding of causality in observed patterns still needs experimentation and proper experimental designs. Curiosity is probably one of the best drivers of such approaches and Winfried Lampert's work is still an excellent example of how fruitful and long-lasting curiosity-driven research can be. Or, to use Reynolds' words again:

Winfried Lampert was close being a "model researcher" — one, when given the advantage of good laboratory conditions and adequate support, who displays the logic to understand observations, to deduce possible explanations and to reject invalidated hypotheses through experiment. As the best approximation of the truth is progressively resolved, so good communication skills broaden transmission and deepen debate. In the end, we are all gainers.

Finally, we hope the readers of this special issue will gain a greater understanding and appreciation of the long-lasting impact and legacy that Winfried Lampert's scientific contributions and achievements have made to the integrated study of aquatic systems. His legacy will continue as future research studies utilize the foundational work that he set in place.

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