

Long-term ecological studies in northern lakes—challenges, experiences, and accomplishments

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Abstract

We review three long-term research programs performed over the last four decades on the ecology and management of oligotrophic lake systems with different fish communities at 69° N in Norway. Through whole-lake perturbation experiments, intensive culling of stunted fish removed 35 tons (1984–1991) of Arctic charr *Salvelinus alpinus* in Takvatn (15 km²) and 153 tons (1981–1983, 2002–2004) of European whitefish *Coregonus lavaretus* in Stuorajavri (25 km²). In Takvatn, the overcrowded charr population decreased to 20% of the initial abundance, whereas brown trout *Salmo trutta* abundance increased. Somatic growth improved strongly in both species. In charr, ontogenetic habitat shifts broke down, the diet changed to more benthos, and plankton-borne parasites decreased. High abundance of juvenile, littoral charr provided new prey for trout, creating an alternative, predator-regulated stable state. Similar density reductions, positive effects on growth and reduced parasite loads occurred in whitefish in Stuorajavri. Despite the heavy culling, however, a new stable state did not occur and the fish community returned to the pre-culling situation. In the Pasvik watercourse, vendace *Coregonus albula* invaded around 1990 after an upstream introduction. The population of this non-native, highly specialized planktivore increased rapidly, resulting in steep density declines in zooplankton and the native planktivorous whitefish morph, and large changes in energy flow and structure and dynamics of the lacustrine food web. These programs show that long-term research is essential for understanding the ecology of manmade disturbances and providing a scientific basis for management efforts.

During the last decades, ecological research on population and community dynamics has aimed at an increased realism by integrating adaptation, population structure, and environmental heterogeneity. This research agenda has revealed that feedbacks in ecological communities are mediated by ecological interactions structured by size and stage, and involve both numerical and plastic phenotypic responses (Holt and Barfield 2012; DeRoos and Persson 2013). Further, research in community ecology has mapped the dynamic implications of multi-species interactions, focusing on community modules of a few interacting species (Holt 1997), including pathogens (Holt and Dobson 2006), but also addressing how link configurations can affect the dynamics of whole food webs (Dunne 2006). The resulting refined causal understanding of the dynamics of populations and communities has increased our predictive ability and is currently applied in management and conservation. The evidence backing this causal understanding is largely

based on long-term studies because the ecological effects of the processes involved take a long time to unfold (Strayer et al. 1986, 2006; Franklin 1989).

Long-term ecological studies are necessary to test hypotheses and investigate the impact of perturbations, but are notoriously difficult to maintain because they must last beyond the timespan of individual research projects or even scientific careers. Long-term studies spanning over decades have primarily been maintained in the context of monitoring programs targeting ecological systems that are being managed or impacted by human activities. Such long-term monitoring programs tend to restrict the scope of observation to species or functional groups that are targeted by management or are indicators of ecosystem health. Also, in such studies ecological feedback and processes operating in pristine ecosystems are often masked by the effects of human activity. Monitoring of natural reserves and protected areas have provided long-term data for more pristine ecosystems. These are often speciose systems with complex structure such as coral reefs. To unravel such complexity in the field, we need to rely on perturbation experiments. However, field experiments on a sufficient scale are rarely an option in protected areas, and so the design of

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Special Issue: Long-term Perspectives in Aquatic Research
Edited by: Stephanie Hampton, Matthew Church, John Melack and Mark Scheuerell.

perturbations are mostly left to the inscrutable plans of nature. Natural experiments have been invaluable sources of ecological insight, particularly when control systems have been available. Yet, if perturbations are not local but global, such as with climate warming, the only option for a reference system is to have very long time-series that stretch back into a cooler, or otherwise more pristine world.

In the context of conservation and management, which are becoming increasingly integrative by including more ecosystem components and processes, the lessons learned from long-term studies have been translated into adaptive monitoring (Lindenmayer and Likens 2009). The adaptive monitoring framework advocates an iterative process including well-defined scientific questions, rigorous statistical design, management relevance and a robust conceptual model for the targeted study system (e.g., population or ecosystem) as key elements in the development of efficient and successful ecological monitoring and long-term research (Lindenmayer and Likens 2010). Adaptive monitoring may further provide a strong knowledge basis for adaptive management, which has been used as an iterative resource management tool since the 1970s (Holling 1978). Integration of the adaptive monitoring and management paradigms constitutes a highly promising avenue for the management and conservation efforts needed to address the current ecological challenges emerging from anthropogenic pressure.

Here, we present some of the main findings and lessons learned from three long-term studies of subarctic lake communities spanning the last four decades. The three studies,

involving whole lake perturbation experiments, targeting fish by either culling or invasion, have addressed basic and applied issues in population and community ecology. The studies capitalize on the unique research opportunities provided by pristine, Holarctic lake ecosystems, characterized by low productivity and water temperature, strong seasonality, and few species members in relatively simple food webs. The lakes are primarily managed with regard to local sustenance fishery, and fish harvesting and introductions have been the main human influences. Fish are commonly top-consumers in these ecosystems with a strong influence on the whole food web, and perturbation of fish abundance will expectedly result in strong ecological responses across the community, mediated by size-structured interactions and indirect effects. The mechanisms behind these ecological responses, and their management implications, have been the object of close scrutiny in our lake studies for 38 yr, 35 yr, and 27 yr, respectively, adding up to a century-long experience with long-term ecological studies.

The three long-term research programs

The three long-term ecological studies include (1) Lake Takvatn (69°N, 19°E; annual sampling since 1980), (2) Lake Stuorajavri (69°N, 23°E; mostly annual or biennial sampling since 1981), and (3) two lake localities in the Pasvik watercourse (69°N, 29°E; annual sampling since 1991). These subarctic lakes located in northern Norway (Fig. 1) are oligotrophic and dimictic, with a 6–7 months period of ice-cover. In all three

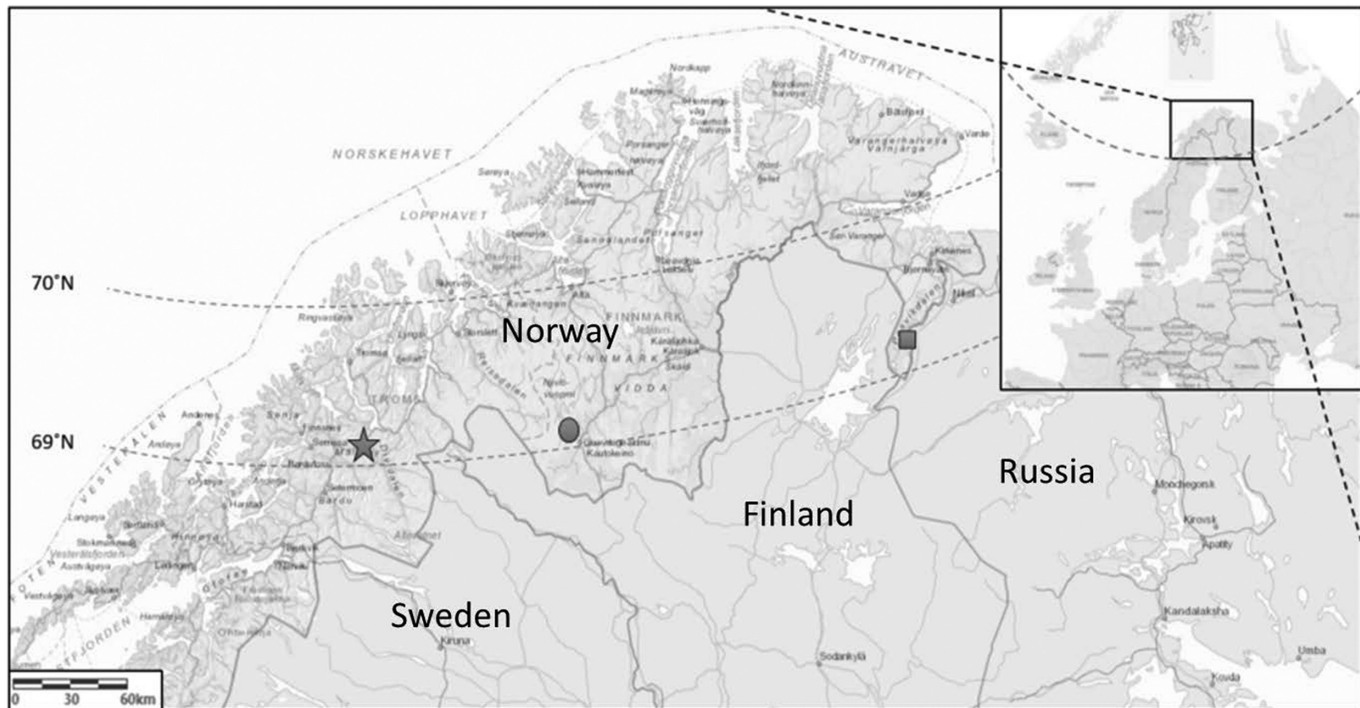


Fig. 1. Location of Takvatn (star), Stuorajavri (circle), and Pasvik watercourse (square) in northern Norway. In the overview map of northern Europe (top right corner), the Arctic circle is marked with a stippled line.

systems, the main focus has been on the fish communities, including population biology and dynamics, trophic ecology and interactions, as well as fish parasites. The fish sampling has been standardized using multimesh gillnets in the littoral, pelagic, and profundal habitats. Additionally, the crustacean zooplankton community and more occasionally the benthic macroinvertebrate community have been sampled.

Takvatn

Takvatn has a surface area of 15 km², a catchment area of 66 km² and a maximum depth of 80 m (Klemetsen et al. 1989). Brown trout (*S. trutta*) was the only fish species in the lake until the 1930s. The trout population declined due to extensive fishing, and Arctic charr (*S. alpinus*) was introduced in 1930 (Klemetsen et al. 1989). By 1980, the density of the Arctic charr population had increased and was in an overcrowded state dominated by small-sized, mature, and parasitized charr (Klemetsen et al. 2002). Three-spined stickleback (*Gasterosteus aculeatus*) was introduced in 1950 and at present forms a fluctuating but dense population in the lake. Intensive stock reduction of Arctic charr using baited funnel traps took place from 1984 to 1991, and totally > 690,000 charr (~ 35 metric tons) were removed (Amundsen et al. 1993; Klemetsen et al. 2002). By 1990, the intensive culling had reduced the density of charr to 20%, whereas the density of trout had increased and at present makes up about 50% of the littoral catches (Fig. 2). The long-term effects are higher somatic growth of both species, altered population structure and a profound change in habitat use of charr from utilizing all macro-habitats in an ontogenetic habitat shift (Klemetsen et al. 1989) to chiefly inhabiting the benthic zone (Klemetsen et al. 2002; Persson et al. 2007). The diets of charr and trout have also changed as charr eat less zooplankton and both species include more large-sized benthos (e.g., *Gammarus*) and fish as prey (Knudsen et al. 1996; Klemetsen et al. 2002).

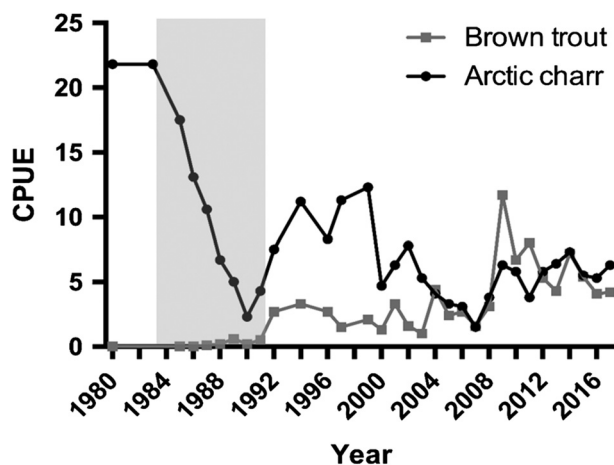


Fig. 2. Relative abundance (catch per unit effort (CPUE) standardized from August samples) of brown trout and Arctic charr in the littoral zone in Takvatn from 1980 to 2017. The hatched gray area indicates the culling period.

This has resulted in alterations of the food-transmitted parasite infections in the salmonid hosts (Knudsen et al. 2002; Amundsen et al. 2013; Henriksen et al. 2016; Kuhn et al. 2016a,b). Over the last decade, the density of charr and trout has remained relatively constant (Fig. 2).

Stuorajavri

As in Takvatn, the long-term study in Stuorajavri (25 km²; max. depth 30 m) was initiated to follow up the effects of a large-scale fish removal experiment. European whitefish (*C. lavaretus*) is by far the dominating fish species in Stuorajavri and constitutes > 90% of the catchable stock, which also include perch (*Perca fluviatilis*), pike (*Esox lucius*), and burbot (*Lota lota*) and a few other species. In an attempt to improve the status of the overcrowded, stunted and heavily parasitized whitefish stock with the aim of initiating a commercial fishery, 101 metric tons of fish were removed from the lake over the years 1981–1983 mainly by gillnets. The catches mostly consisted of whitefish (96 tons), but culling of pike was particularly encouraged as pike is the final host of *Trienophorus crassus*, a cestode parasite with a larval stage that encysts in the whitefish flesh (Amundsen and Kristoffersen 1990). Later, a less extensive fish removal effort was conducted in 2002–2004 when about 52 tons of fish were harvested.

The effects of these management efforts have been followed by annual or biennial samplings from 1981. An important result from the first studies was the documentation of two sympatric whitefish morphs, which can be separated by the gillraker number and exhibit highly different ecological adaptations (Amundsen 1988a; Siwertsson et al. 2012). From gillrakers and growth patterns, these have been termed “large sparsely rakered” (LSR) and “densely rakered” (DR) morphs (Siwertsson et al. 2010). A third, slow-growing profundal morph has later been identified and termed “small sparsely rakered” (SSR) (Präbel et al. 2013a). In the initial years after the first stock depletion, the growth rate of the whitefish highly improved (Amundsen 1988b). The age distribution changed toward a dominance of younger fish, and the 1982-year-class was particularly strong for both morphs. Prior to the fish removal, the incidence of plerocercoid larvae of the cestode *T. crassus* in the whitefish was very high (Amundsen 1988b), but the culling resulted in a dramatic decline in the abundance of this parasite (Amundsen and Kristoffersen 1990). It was hoped that the improved conditions would encourage initiation of a commercial fishery, but this did not come about. The exploitation was negligible after 1983, and during the following time period the whitefish stock gradually returned toward the pre-removal situation with respect to growth, population structure, and parasite infection (Amundsen et al. 2002).

Pasvik watercourse

The Pasvik watercourse (142 km² total surface area) originates from Lake Inari (1102 km²) in Finland and forms the border between Norway and Russia for 120 km before

ending in the Barents Sea. The watercourse holds 15 fish species of which eight are important in lake systems with polymorphic whitefish, and perch and pike as the dominant native species. Despite being located in a region with pristine nature, the watercourse is exposed to multiple anthropogenic stressors. Due to several major dam constructions for hydropower production, most rapids and waterfalls have disappeared, and consecutive lakes and reservoirs now dominate the former river system. Major metallurgic smelters with large emissions of heavy metals and sulfur dioxide are located nearby the lower parts (Amundsen et al. 1997, 2011). A large catchment area (21,000 km²) makes the watercourse a potential sink for atmospheric fallouts of long-transported pollutants. A major ecological impact was induced around 1990 through the invasion of vendace (*C. albula*), a non-native fish species that was translocated and introduced in Lake Inari around 1960 (Amundsen et al. 1999; Præbel et al. 2013b). Recent climate warming has affected the watercourse through increased air and water temperatures and precipitation and runoff.

The Pasvik long-term studies started in 1991, aiming to address the possible ecological impacts of the vendace invasion and provide information about heavy metal contaminations in fish (Amundsen et al. 1997, 1999). Several lake localities along the watercourse were studied over the first few years, but subsequently two of these, in the upper and lower parts, respectively, were selected for the long-term efforts. With a few exceptions, the two lake sites have been sampled annually from 1991 to present. The studies were designed from a food-web perspective with a top-down approach particularly addressing the fish community and their trophic ecology, interactions and prey resources. Important outcomes of the long-term studies include a documentation of successful establishment and development of the invading vendace (e.g., Amundsen et al. 1999, 2012; Bøhn et al. 2004), and multiple effects of the invasion on zooplankton and fish communities (Bøhn and Amundsen 1998, 2001; Bøhn et al. 2008; Amundsen et al. 2009b; Sandlund et al. 2013). Heavy metals like Ni, Cu, and Cd show elevated levels in fish from localities nearby the metallurgic smelters, but steeply decline with increasing distance from the pollution sources (Amundsen et al. 1997, 2011). For most elements, no temporal changes in contamination levels are evident, but a distinct increase in the Hg contents in fish has been revealed over the last couple of decades, especially for predatory fishes like perch, pike and brown trout (Amundsen 2015).

Structured populations, community dynamics, and management

Our long-term studies have provided valuable insights into structured population dynamics and direct and indirect effects of ecological interactions in aquatic communities. Fish populations are typically size structured, and larger

species, including salmonids like trout and charr, undergo ontogenetic niche shifts that change the character of interactions experienced during the life cycle (DeRoos and Persson 2013). The resulting intraspecific and interspecific interactions are size-, and often stage-, structured. Such structured interactions have interesting dynamic implications, and are candidate mechanisms for alternative stable states in population abundance (De Roos and Persson 2013). Salmonid populations living in high latitude lakes may display bistability, raising the question of whether size-structured interactions, within or between species, are responsible for the phenomenon. The answer to this question matters for managers, as fish in an overcrowded state do not appeal to fishers due to their stunted growth and heavy parasite load. Fish parasites are interesting in their own terms, and predicting their response to perturbation of their host abundance is not straightforward due to their complex life cycles and indirect effects involving other hosts. Such indirect effects of ecological interactions make invasion biology a challenging field. Trying to assess the community impact of a fish invasion is the ultimate exercise in adaptive monitoring with steadily growing and changing lists of target species. Below, we highlight three topics to which our long-term studies have contributed by identifying ecological mechanisms that have also helped inform management. We start by discussing the role of size-structured interactions for population dynamics and bistability in light of our culling experiments. We then expand the discussion to the dynamics of fish and their parasites, considering the indirect effects of interactions. Finally, we discuss direct and indirect effects of interactions in an aquatic community invaded by a planktivorous fish species.

Size-structured interactions

Novel knowledge of mechanisms in size-structured populations and processes leading to alternative stable states in fish populations have been provided by the Takvatn long-term study (De Roos and Persson 2013). Predator-prey interactions, in this case between brown trout and Arctic charr, were found to be important in regulating fish population abundance and community structure (Persson et al. 2007, 2013). In the stunted, pre-culling state in Takvatn, the littoral prey (charr) was dominated by individuals larger than the preferred prey size of the predator (trout) (Klemetsen et al. 2002). The ontogenetic habitat shift of charr confined smaller, more suitable prey fish to the profundal zone, which is a habitat trout rarely visit. The unimodal size-distribution of the charr in the littoral habitat not only outcompeted juveniles of its own population, but also juveniles of the predator. This led to a state where the predator was almost totally excluded from the lake. With the strongly reduced density of charr in the post-culling situation, the recruitment, survival and growth of the prey juveniles and adults increased, leading to a broader size-distribution of fish prey, resulting in a higher proportion of the prey being within

the preferable prey-size range of the predatory trout (Persson et al. 2007). With reduced intraspecific competition in the culled Arctic charr population (Amundsen et al. 2007), juvenile charr now stayed in the rich feeding areas of the littoral zone despite the increased predation risk. The increased availability of preferable fish prey led to enhanced somatic growth and survival and increased density of the predator (Persson et al. 2007, 2013). More important, the self-regulatory maintenance of a new state of the system created an alternative stable situation where both the predator and the prey were present. The difference in charr size distribution induced by food-dependent growth was pivotal for creating the alternative stable state (Persson et al. 2007). The first years after the culling perturbation both populations oscillated in abundance and at some point, the culling seemed to fail in creating an alternative stable state. This, however, proved to be only a transient phase in the process followed by a new stable state regulated by predation from trout (Persson et al. 2007, 2013). The transition to the new stable state was also facilitated by cannibalism from large-sized charr (Amundsen 1994). In Stourajavri, contrary to Takvatn, the fish removal program failed to tip the whitefish population to an alternative stable state with consistent lower abundance, improved growth and reduced parasite infection. This shows that strong recruitment following stock depletion may quickly return fish populations to overcrowded, stunted conditions on cessation of the intensive fishing, demonstrating a strong resilience of the overcrowded equilibrium state. In summary, the long-term adaptive monitoring of the Takvatn and Stourajavri systems not only allowed to document the endpoint of the culling experiments, but also permitted to identify the mechanisms and processes responsible for the alternative stable states in these size-structured fish populations. The causal understanding inspired solutions for the management of fish populations with critical thresholds, consisting in culling small fish when a population tends to an overcrowded state (Persson et al. 2007).

Host–parasite interactions

Freshwater fishes are intermediate and final hosts to many food-transmitted parasites with complex life cycles. The first intermediate host for these parasites are mainly pelagic copepods or benthic species like amphipods and insect larvae. In addition, some parasites can re-establish in piscivorous fish. The culling experiments in Takvatn and Stourajavri provided unique opportunities to study how fish abundance affects parasite transmission rates and abundances. Meta-analyses and short-term studies have shown a link between parasite abundance and host densities (Arneberg et al. 1998; Arneberg 2002; Hechinger and Lafferty 2005). From our long-term studies, it appears that parasite burdens in freshwater fishes may be governed by both intraspecific and interspecific interactions between hosts, rather than host densities per se. After the mass removal of fish (Stourajavri and Takvatn studies), the prevalence of copepod-transmitted tapeworm species (*T. crassus* and *Diphyllbothrium* spp.) declined in the second intermediate whitefish and charr hosts (Fig. 3; Amundsen and Kristoffersen 1990; Henriksen 2014). However, the abundance of a nematode, *Cystidicola farionis*, that uses charr as final host and the benthic amphipod *Gammarus lacustris* as intermediate host, increased in Takvatn charr (Giæver et al. 1991; Knudsen et al. 2002). In both cases, the density of fish seems to have influenced parasites burdens indirectly through a shift in host diet from pelagic to benthic prey items. In addition, it was documented that the culling of pike, the final host of *T. crassus*, also contributed significantly to the reduction of this parasite in whitefish (Amundsen and Kristoffersen 1990). Some of the long-term changes in parasite abundance can be attributed to shifts in the trophic status of the fish community (e.g., degree of zooplanktivory or piscivory). Prior to the trout comeback in Takvatn, ~ 20% of the charr were either cannibalistic or preyed on sticklebacks (Amundsen 1994), suffering high infections of *Diphyllbothrium* parasites (Kristoffersen 1993; Henriksen 2014). Over the last 20 yr, trout has been the

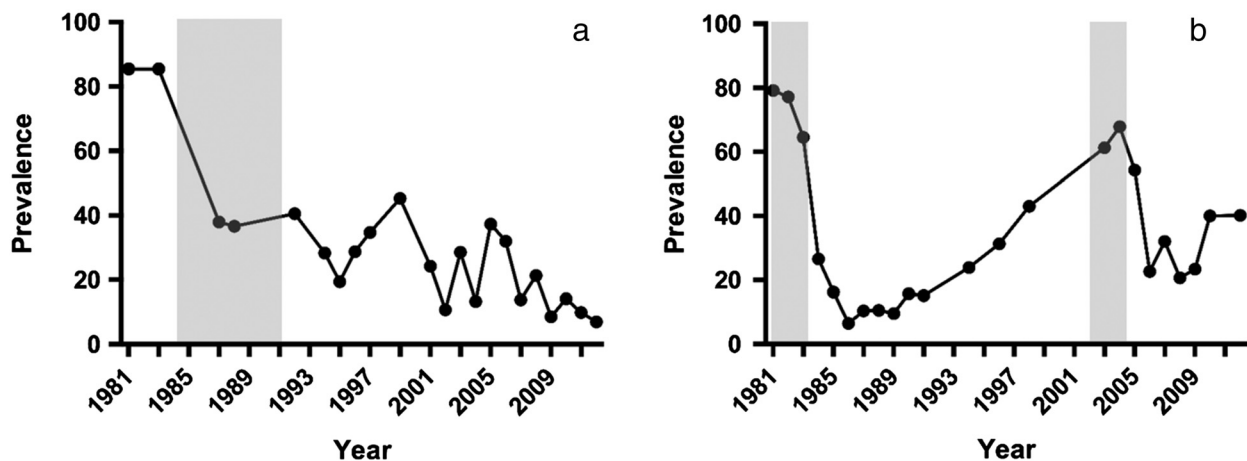


Fig. 3. Prevalence of *D. dendriticum* in Arctic charr in Takvatn (a) and prevalence of *T. crassus* in LSR whitefish in Stourajavri (b) from 1981 to 2012. The hatched gray areas indicate the culling periods.

top-predator in the aquatic system (Persson et al. 2007; Amundsen et al. 2009a, 2013) utilizing sticklebacks and charr as prey, whereas the extent of piscivory in charr is low (Eloranta et al. 2013). As a consequence of preying on sticklebacks, large-sized trout now harbor far higher intensities of *Diphyllbothrium* spp. than charr (Henriksen et al. 2016; Kuhn et al. 2016a). This is supported by studies where we have integrated detailed information about parasites into the food web of Takvatn. A high linkage density (i.e., a high number of predator and prey) of a species increases exposure to parasites (Amundsen et al. 2009a). In this context, the introduced stickleback serves as a hub for food-transmitted parasites in the system, increasing transmission rates to both fish and bird predators (Amundsen et al. 2009a, 2013). Understanding the links between prey, predators and parasites in the ecosystem thus allows for a rigorous investigation of how specific host-parasite relationships change over time.

According to Kennedy (2009), parasite communities of freshwater fish must be seen as unregulated, unstable stochastic assemblages until more long-term studies are provided. The new stable state in the salmonid community in Takvatn (Persson et al. 2007) is also reflected in the parasite community of charr, which appears to be stable over a 20 yr period following the culling experiment (Kuhn et al. 2016b). This contrasts the situation in Stuorajavri, where the density of whitefish and their parasite burdens returned to the pre-perturbed state a decade after the first culling period ended (Amundsen et al. 2002). These two experiments taught us that parasites may respond rapidly to ecosystem perturbations. However, the stability of these responses depends on the long-term ecosystem effects.

Parasites can be a challenge for the management of freshwater fish populations. Our long-term investigations have provided novel knowledge on culling as a management strategy to reduce the infections of unwanted parasites. In both Takvatn and Stuorajavri, the culling of fish resulted in a desired decrease in the problematic parasites *Diphyllbothrium dendriticum* (Takvatn, charr) and *T. crassus* (Stuorajavri, whitefish) (Fig. 3). In Takvatn, the system reached a new stable state with low numbers of *D. dendriticum* (Henriksen 2014). In Stuorajavri, however, a more prolonged culling effort should probably have been conducted in order to sustain the positive effects on reduced *T. crassus* infections (Amundsen and Kristoffersen 1990; Amundsen et al. 2002).

Ecosystem effects of an invading specialist

The long-term studies in Pasvik have documented an ecological drama with many players and episodes following the invasion and successful establishment of vendace in the watercourse. The vendace quickly spread throughout the whole watercourse and showed a rapid population increase (Fig. 4), especially in the upper part where the invader within few years became the numerically dominant fish species in the pelagic (Amundsen et al. 1999, 2012; Bøhn et al. 2008).

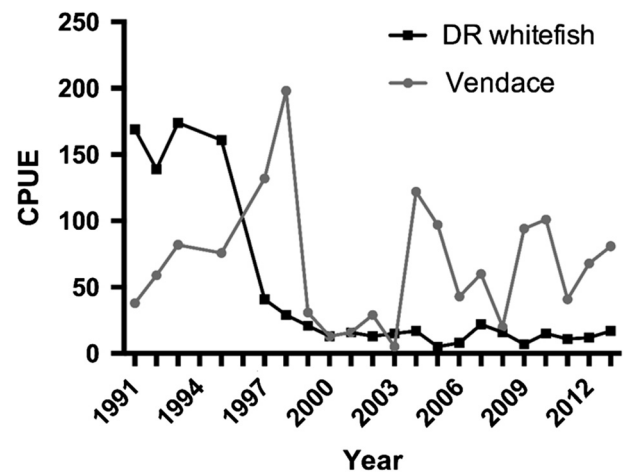


Fig. 4. Relative abundance (catch per unit effort (CPUE) standardized from September samples) of vendace and DR whitefish in the upper locality in the Pasvik watercourse from 1991 to 2013.

Over the first few years following the invasion of this highly specialized planktivore, the overall abundance of crustacean zooplankton abruptly declined and has remained at approximately 20% of the preinvasion level (Bøhn and Amundsen 1998; Amundsen et al. 2009b), chiefly diminishing zooplankton as a food resource for other fish species, in particular whitefish. Similar as documented in Stuorajavri, the whitefish in Pasvik is polymorphic, with a pelagic, zooplanktivore densely rakered (DR) morph and a littoral, benthivore large sparsely rakered (LSR) morph as the dominant morphotypes (Amundsen et al. 1999; Siwertsson et al. 2010). Simultaneously with the abrupt decline in zooplankton density, the DR whitefish morph was competitively relegated to the benthic habitats (Bøhn and Amundsen 2001), after which the population density dramatically declined to around 20% of the preinvasion level (Bøhn et al. 2008) and has remained low (Sandlund et al. 2013; Amundsen 2015; unpubl.) (Fig. 4). Zooplankton used to be the dominant food of DR whitefish (Bøhn and Amundsen 1998; Amundsen et al. 1999), but over the first couple of years after the vendace arrival, the zooplankton contribution in the whitefish diet strongly diminished (Bøhn and Amundsen 1998, 2001), whereas it has remained the prime food of vendace (Bøhn et al. 2008; Kahilainen et al. 2011; Liso et al. 2013). The major decline in the density of the DR whitefish morph after its relegation from the pelagic habitat was partly related to competition with the LSR morph and other benthos specialists, but mostly to a strong predation pressure from piscivorous fish in the benthic habitats (Bøhn et al. 2002, 2008; Amundsen et al. 2003). Besides these ecological consequences, the invasion of vendace may also induce evolutionary effects as the relegation of DR whitefish from the pelagic to the littoral habitat has apparently also resulted in a breakdown of the reproductive isolation between the DR and LSR whitefish morphs (Bhat et al. 2014). More specifically, genetic studies have revealed an increased frequency of

hybrids between the DR and LSR whitefish morphs from 34% in 1993 to nearly 100% by 2008. This suggests a potential “speciation in reverse” scenario following the benthic habitat shift of the DR morph (Bhat et al. 2014).

The vendace population in the Pasvik watercourse is slow-growing and small-sized (Bøhn et al. 2004), having adopted a pioneer life-history strategy of early maturation and short generation time that has been instrumental for the successful invasion and establishment (Amundsen et al. 2012). However, the initial rapid population increase of vendace was followed by a typical fluctuating “boom-and-bust” development with large variations in population density (Fig. 4; Salonen et al. 2007; Sandlund et al. 2013). These fluctuations are apparently related to intraspecific competitive interactions (Bøhn et al. 2008; Amundsen et al. 2012; Sandlund et al. 2013). Despite these fluctuations, the overall strong population buildup of vendace has strongly influenced the trophic network in Pasvik lakes (Bøhn et al. 2008). Besides being the key zooplankton predator in the watercourse, the small-sized vendace has also become the main prey of brown trout, the prime top predator in the pelagic network (Jensen et al. 2004, 2008). Typical benthic-dwelling predators like pike and burbot have also started to feed on vendace. Moreover, the invasion has influenced the energy flow and the structure and dynamics of the lacustrine food web (Bøhn et al. 2008) with possible consequences for e.g., accumulation and biomagnification of pollutants (Amundsen et al. 1997; Amundsen 2015).

Coda

The above three topics could only be addressed thanks to the long-term character of the studies. Some of the community responses investigated may take decades to fully unfold. In addition, dynamic properties of populations of interest for management and conservation, such as the return tendency after perturbation, or engineering resilience, are measured over many years. Moreover, it takes many years to be able to assess the outcomes of management decisions. The mechanistic focus of our long-term studies has benefited management by providing simple but promising heuristics such as culling of small individuals to avert overcrowding or fish stock reductions to diminish parasite load.

Adaptive approaches

Even though the three long-term research programs were initiated well before the adaptive monitoring paradigm was advised (Lindenmayer and Likens 2009), similar adaptive approaches were largely implemented in the strategy of these efforts. The initiations of the programs were related to management problems and actions, including experimental density manipulations of stunted fish populations in Takvatn and Stuurajavri and system impacts from biological invasion and environmental pollution in Pasvik. Conceptual frameworks

for the study systems were established with special reference to the large-scale ecological perturbations that occurred in the three systems. In Takvatn and Stuurajavri, these frameworks were primarily focusing on the targeted fish populations, i.e., Arctic charr and European whitefish, respectively, and their anticipated responses to the density manipulations in terms of changes in population ecology, trophic interactions, prey resources, and parasite infection (e.g., Amundsen et al. 1993, 2002, 2007; Klemetsen et al. 2002; Persson et al. 2007, 2013). For the Pasvik studies, the conceptual framework was food-web and ecosystem based, addressing both the ecological impacts of the invading species on the trophic network (e.g., Bøhn and Amundsen 1998, 2001; Amundsen et al. 1999, 2009b; Bøhn et al. 2008; Sandlund et al. 2013) and the potential role of biomagnification of pollutants (Amundsen et al. 1997, 2011).

Based on the specific management challenges and conceptual frameworks, several initial objectives were established for the respective systems. Hence, all three long-term studies are question- and hypothesis-driven as advocated by the adaptive monitoring paradigm (Lindenmayer and Likens 2009). The execution of the long-term studies have further been highly iterative, as novel questions emerging from the study outcomes have successively been implemented as new objectives, either through new specific research efforts or by adjusting and expanding the adopted study design. New methods like stable isotope and genetic analyses have also been added when feasible. Importantly, however, the basic study design has chiefly been kept unchanged, which represents a prerequisite for any long-term study effort. Nevertheless, some necessary adjustments may be identified and adopted through the adaptive framework, and the development of new methods and technologies may also invoke some tentative trade-offs for the long-term sampling strategy.

All three programs have included a strong integration of basic and applied research. In particular, management-induced manipulations have been combined with hypothesis-driven scientific endeavors, utilizing the various system perturbations as large-scale experiments from which ecological mechanisms and transient dynamics can be explored. Hence, the studies have aimed on the one hand to elucidate specific scientific objectives, and on the other hand to provide information for the management and conservation of these systems. To facilitate the latter, findings and advices have regularly been conveyed to managers and local practitioners through reports and popular science publications and oral presentations at public meetings. A close contact between researchers and managers has further been emphasized, partly resulting in successful implementation of the principles of adaptive management. The Takvatn program constitutes the best example in this respect. The fish culling experiment was designed and implemented in close collaboration between scientists and practitioners, and in the subsequent decades, all fishing regulation and other

management actions have been based on advices generated from the long-term studies. The long-term study approach and the close contact and collaboration between scientists and local stakeholders have been instrumental for the successful implementation of the rehabilitation and management efforts in Takvatn.

Benefits and challenges of long-term studies

The increasing ecological knowledge generated by the three long-term studies has proved to be a good platform for new research initiatives also along other branches of biological disciplines. One such branch is the implementation of modern population genetics in the studies of the polymorphic whitefish in northern Fennoscandia, including Stuorajavri and Pasvik, to elucidate whether the split into several morphs has an allopatric or sympatric origin (e.g., Østbye et al. 2006; Præbel et al. 2013a,c). Further, Bhat et al. (2014) utilized historical fish samples to examine whether the vendace invasion in the Pasvik watercourse have resulted in increased hybridization between the native whitefish morphs.

Over recent decades, the research in Takvatn has gradually expanded from the population and community levels to comprise a food-web approach including parasites. The published output has so far focused on the pelagic food web (Amundsen et al. 2009a, 2013), but a comprehensive exploration of the total parasite-entangled web has in recent years been emphasized, including also the diversity and abundance of zoobenthos and water birds (Klemetsen and Elliott 2010; Klemetsen and Knudsen 2013; Frainer et al. 2016). A spin off from this work has been a novel documentation of the diversity of trematodes in Takvatn by employing modern molecular analyses (Soldánová et al. 2017). The results show that the digenean diversity is high in this otherwise depauperate northern freshwater ecosystem, suggesting that sub-Arctic and Arctic ecosystems may be characterized by unique trematode assemblages.

Another highly promising research benefit is that the extensive data sets from these long-term studies can be utilized as an important baseline for studies of possible effects of climate change and other environmental impacts. Such efforts are now under development. Long-term studies also provide a great arena for national and international cooperation, which has been an important characteristic and a necessity for the successful implementation of our study programs.

The main challenge in running long-term ecological research programs is the difficulty of finding long-term funding. The present adaptive monitoring programs are all funded in short-term perspectives (2–4 yr as typical for most research funding), either by small institution-based research funding or by various external funding agencies. Time-limited Ph.D. and postdoc fellows supported by e.g., the Norwegian Research Council have worked on the programs, but following up long-

term studies have usually not high priority by external funders, including research councils. The best way to counteract this is to build up and keep a core of long-term competence through continuous training and a permanent and qualified technical and research staff. Only then can the planning, sampling, and analyses, which are particularly demanding in adaptive long-term studies, be efficient and sustain consistent high scientific quality. A research and teaching institution like a university has several benefits in this respect. Students have always been involved in our programs, from regular field-based undergraduate courses that may provide supportive sampling efforts, to a multitude of bachelor, master, and doctoral theses that have provided comprehensive contributions. This aspect of research-based teaching cannot be underestimated. Consistently, we find that enthusiasm boosts when students are heavily involved and learn that their contribution, small or large, is part of a program with long-term perspectives.

Ideally, because of the challenges related to the time-consuming processes and continuous personnel and economical requirements, the responsibility to run such long-term data series should be shifted from the research group to the institutional (or national) level. It is a paradox that management authorities acknowledge how valuable such long-term ecosystem-based data series are, while funding for long-term studies still is very difficult to find.

Concluding remarks

The last four decades have seen an impressive progress in causal understanding of the dynamics of aquatic populations and communities; knowledge that has been put to test in applications dealing with unprecedented environmental pressures driven by human activities. Long-term studies not only provide the only means to address empirically the slow outcomes of ecological processes, but also allow us to accumulate the necessary detailed knowledge on the natural history of aquatic systems. Our own long-term studies have helped elucidate the importance of structured interactions and their indirect effects for metastable fish populations (i.e., populations that can reach alternative equilibria via perturbations) and for communities of fish and their prey and parasites. Studying the long-term effects of perturbations in pristine ecosystems with relatively simple food webs has proved invaluable to identify the mechanisms responsible for the observed dynamics and translate these into management practice. Our causal understanding is the result of a fruitful dialogue between theory and long-term observation, but it owes also much to the detailed knowledge of species and their relationships and ecosystems. Such precious knowledge of natural history, which allows us to move between the general and the specific in ecology, is accumulated over many years of research and observations in the field.

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Acknowledgments

We gratefully thank all that have contributed in these long-term efforts, including our research technicians Laina Dalsbø, Jan Evjen, Cesilie Bye, and Karin Strand Johannessen, national and international collaborators, colleagues and students, and our local partners and helpers at Takvatn, Stuorajavri, and the Pasvik watercourse. In particular, we like to thank UiT The Arctic University of Norway for the continuous support of our long-term studies. We are also grateful for financial support from the Norwegian research council (most recently, projects no. 213610, 183984, and 186320), EU research funds, and national and regional environmental management agencies and departments.

Conflict of Interest

None declared.

Submitted 22 January 2018

Revised 3 May 2018

Accepted 17 May 2018

Associate editor: Mark Scheuerell