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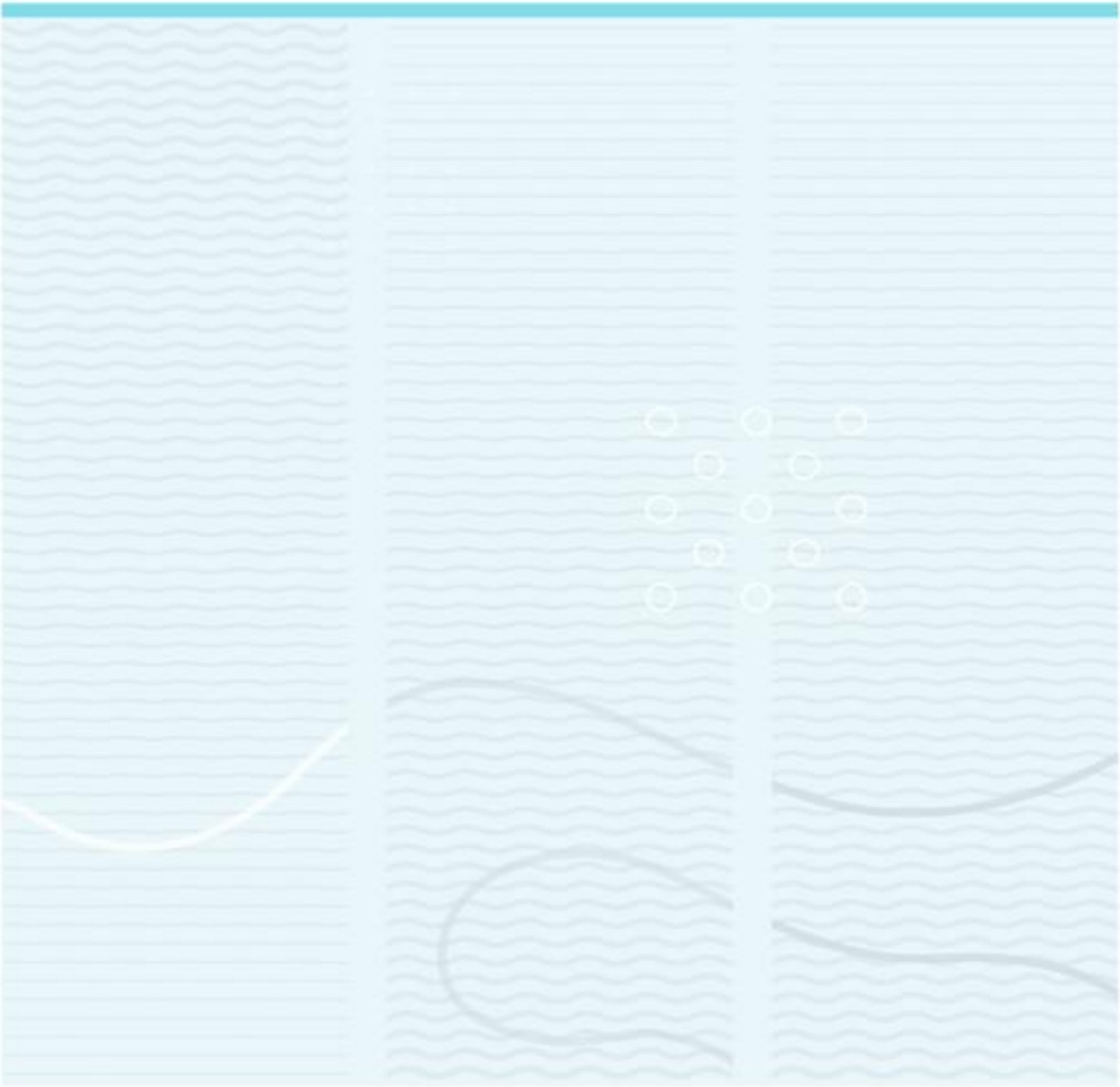
# Brown trout recruitment from natural streams with residual regulated flow

Lake population dynamics in the Upper Kova River system, Telemark



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This thesis is worth 60 study points

# Abstract

The urgent global need for more and better conservation of nature often seems to conflict with the equally pressing need for increased production of renewable and sustainable energy. Frequently played out at a local level, such interest conflicts may sometimes be resolved or mitigated with better knowledge. In this study, I investigate a local case of brown trout (*Salmo trutta*) versus hydropower, both of which are economically and socio-culturally important in Norway.

Brown trout depend on streams for spawning and recruitment. As a compensation for anticipated reduced recruitment after regulation of the Kova River system in Telemark in the late 1950s, stocking was implemented but ceased from 2015 after gillnet test fisheries documented quite high densities of brown trout (the only fish species) in three small lakes in the Upper Kova R. Based on previous fish investigations in the Upper Kova R., the present study hypothesized that natural recruitment to the three lakes was sufficient and balanced to food production, given limited local harvest and only residual flow in the summer. In other words, it was assumed that the decision to cease stocking was well-founded.

Gillnet test fishery was performed in the three lakes in mid-June 2022, following the standard NS-EN 14757 whenever possible, using Nordic multi-mesh gillnets, a roughly systematic design and with a sampling effort of 8 gillnet-nights per lake. Data collected and modes of analysis utilized reflected the twin aims of characterizing the current lake populations and addressing temporal population dynamics by comparison of the current results with the previous test fisheries in the Upper Kova R.

The results indicated that recruitment since the 2015 stocking cessation has overall been a bit too high to be balanced to food production and local harvest in the lakes Øvre- and Nedre Urdetjønn, reflected in current densities that were as high or higher than in previous gillnet test fisheries and with lower size and quality (growth and condition) of the fish. For lake Bjønntjønn, natural recruitment may currently have been too low relative to local harvest, contrary to previously documented good balance with food production, but results for this lake since the stocking cessation are more uncertain than for the other two Upper Kova R. lakes. The earlier timing of the 2022 test fishery may have lessened the comparability of some results with the previous gillnetting studies.

Firmer conclusions regarding the sufficiency of natural recruitment to the three lakes necessitate additional knowledge about Bjønntjønn in particular, both on the stream and lake populations and on the local harvest. However, the results so far indicated that the case of the Upper Kova R. may illustrate that compensatory measures such as stocking could be unnecessary or even counterproductive if based on general assumptions rather than on context-specific knowledge.

# Content

# Preface

I am grateful to the University of South-Eastern Norway (USN), Bø i Telemark, for providing all necessary accreditation and permits, equipment, and training, as well as supervision by Professor Jan Heggenes, and field assistance by Eivind Sandvik Schartum. I would like to thank them both for their invaluable contributions to my study.

My supervisor had all contact with local landowners/rights-holders and the hydropower company. Boats used in the test fishery were generously lent by local owners, and we operated them with an electric motor brought by the field assistant.

On request, one of the authors of the report from the test fishery in the same lakes in 2009 provided some individual fish data from their study. I thank him for this and for encouraging remarks.

I would also like to thank my co-student Ola Kristensen for much-needed and appreciated help, especially related to laboratory work.

My own formal responsibilities were to develop the whole Master's project in light of legal and ethical obligations, to follow USN's rules for field- and laboratory work (Institutt for natur helse og miljø, 2018a, 2018b) and other relevant standards, and to write this thesis to the best of my abilities. It has been a long and sometimes challenging process, but I have learned a lot and hope to be able to put some of it to use in future employment.

Bø i Telemark, 12.05.23

Knut Midttun

# 1 Introduction

The urgent need for increased global efforts to protect and restore nature and biodiversity often seems to conflict with the equally pressing need for more renewable and sustainable energy production integral to a grand transition in that sector (Gasparatos et al., 2017; Jackson, 2011; Ponitka & Boettner, 2020). Frequently played out at a local level, such interest conflicts may sometimes be resolved, or mitigated, with better knowledge. In the present study, I investigate a local case of brown trout (*Salmo trutta*) versus hydropower, both of which are economically and socio-culturally important in Norway.

Brown trout is widely distributed in northern boreal streams, in many countries sharing the importance it has in Norway (Lobón-Cerviá, 2018; Marttila et al., 2019). Although the species has considerable environmental tolerance and may be found in a large range of habitats (Klemetsen et al., 2003), brown trout spawning and recruitment are highly dependent on rivers and streams (Jonsson & Jonsson, 2011). Hydropower is also extensively developed in the northern boreal hemisphere, and it is the dominant supplier of electrical energy in Norway (Ministry of Petroleum and Energy, 2021; Rusten, 2013). Hydropower is often considered carbon neutral and less harmful to the environment than many energy alternatives. However, it may still have an impact on aquatic ecosystems that is important to assess and to mitigate if negative (Alfredsen et al., 2022; Gracey & Verones, 2016; Haxton & Findlay, 2008). Fish populations are affected particularly by reduced and/or residual flows in regulated rivers (Harper et al., 2020; Ugedal et al., 2008; Young et al., 2011). For salmonid fishes like brown trout, the adverse effects of hydropower may be particularly strong for early life-stages (Hayes et al., 2019; Saltveit et al., 2001), in some cases reducing survival so much that the viability of brown trout lake populations recruiting from those streams may be threatened.

The Kova River system in Telemark (Fig. 1.1) is one of many regulated rivers with brown trout populations in Norway. Unfortunately, the status of the Kova R.'s allopatric, resident brown trout populations was not investigated before regulation started in 1958. The Kova R. hydropower development included the construction of a dam establishing the upstream reservoir L. Vindsjåen (Figs. 2.1 and 2.2), from which water is tapped in the natural river to a downstream hydropower plant. Regulation entailed an inversion of the natural flow patterns. Water is stored in the reservoir during spring and summer, but no minimum water flow requirements were imposed, so the downstream river and lake system is left with residual flow during the growth and recruitment season for brown trout. It was assumed that this would result in recruitment being reduced to levels that were insufficient to sustain viable natural brown trout populations in the downstream lakes (Fig.

2.1). To compensate for this, the hydropower company was required to annually stock a number of juvenile trout into the lakes (Heggenes, 2020).

*Figure 1.1. The Kova River system (Kovavassdraget). River trajectory in dark blue, with the reservoir L. Vindsjåen in the upper left part of the river. From NVE Atlas (2023).*

However, a pilot study in 1997 (Solhøi, 1998) and a follow-up study in 2009 (Tormodsgard & Gustavsen, 2010) of the brown trout populations in three small lakes in the upper part of the Kova R. (Fig. 2.1) indicated rather high fish densities. The latter study recommended that the stocking of brown trout into these lakes should cease, if continued monitoring of natural recruitment confirmed that it was sufficient for balancing population density to food production in the lakes over time. This recommendation was sanctioned by the regional federal environmental authority, *Fylkesmannen i Telemark*, with effect from (including) 2015. Studies in 2017 and 2019 of natural recruitment in the Upper Kova R. (Heggenes, 2018, 2020), the only stream important to brown trout recruitment for those lakes, provided said confirmation with some caveats. The more important of Heggenes' caveats was that the brown trout populations in both the recruitment streams and lakes should be investigated again, also to evaluate more fully the effect of the decision to cease stocking (2018, 2020).

Based on these previous fish investigations, the present study hypothesized that natural recruitment of brown trout to the three small lakes was sufficient and balanced to food production, in spite of the recruitment river only having residual flow during the growth season after regulation, and provided that local harvest does not change substantially. Thus, “sufficient” and “balanced” were here primarily seen from a user’s or local fishery point of view. I assumed that recruitment over time could be assessed, at least to a certain extent, via estimates of lake population abundance/density and age/length structures (Borgstrøm & Hansen, 2000; Elliott, 1994). Food production in the lakes was not quantified but inferred mainly from gillnet test fishery indications regarding size, growth and condition of the fish. Analyses followed both spatial and temporal axes. Comparisons were made within and among the lakes, as well as relative to other Norwegian lakes. Time perspectives were both prospective and retrospective: data from the present study were used to point both forwards and backwards from the milestone of the 2015 stocking cessation, partly reflected in the structure of the Results chapters (4 and 5) below. With this approach, evaluation of sampling design became important, and I found it appropriate that this should also be reflected in the text.

More generally, the present study covered all three main purposes described in the Standard for freshwater sampling and analysis in Norway: assessment of ecological status (and water quality), changes over time, and effects of human influence and mitigating measures (Standard Norge, 2015b).

# 2 Brown trout and hydropower

## 2.1 Brown trout: basic characteristics and general methodology

In this general section, I outline some key, relevant aspects of what we know about brown trout and of how we may collect data to develop valid knowledge about brown trout and other wild fish populations.

*Brown trout life-histories, habitats and populations*

A natural starting point in the life cycle of brown trout is when females, in the autumn, dig a nest in a well-oxygenated, gravel-bottomed stream, often in the same area year after year (Hunter, 1991). After spawning, the fertilized eggs incubate in the substratum through winter and hatch in the spring, releasing ca. 2 cm long alevins (larval stage) that feed on their yolk sac (Jonsson & Jonsson, 2018; Klemetsen et al., 2003). The duration of both egg incubation and the alevin stage are temperature-dependent, both last longer in lower temperatures (Elliott & Hurley, 1998; Jonsson & Jonsson, 2011). For brown trout, egg incubation time is about 400 degree-days (the product of temperature and days) in temperatures up to 10 °C (Heggenes et al., 2021). At the end of the endogenous feeding stage, the alevins transit to the fry (or early parr) stage and exogenous feeding (Jonsson & Jonsson, 2018). Characteristic for the fry stage is aggressive territorial behavior with high mortality (Elliott, 1994; Milner et al., 2003). The following juvenile stage may be divided in small parr (young-of-the-year, < 7 cm) and larger parr (> 7 cm) (Heggenes et al., 1999). Potential recruits often spend their first summer(s) in the natal stream; some even remain as life-long residents (Jonsson & Jonsson, 2018). Others migrate to a lake, often when they reach a size of ca. 15 cm. These individuals may move between the lake and the stream for food, shelter and reproduction (Jonsson & Jonsson, 2011).

A crucial decision in brown trout life-histories is timing sexual maturation so as to gain a fitness advantage over competitors (Klemetsen et al., 2003). Onset of maturity is influenced by growth rate, energy stores and body size, and it varies between individuals, the sexes and populations (Jonsson & Jonsson, 2011). Onset (size or age) at maturity may be defined by variation ranges, or as the point at which 50% of a cohort has reached maturity (Jonsson & Jonsson, 2011; Nicola & Almodóvar, 2002). Maturity onset ranges between ages 1 and 10 years in freshwater populations, relatively later in cold localities, and earlier and at more variable sizes in males than in females (Klemetsen et al., 2003).

Brown trout life expectancy varies; whereas ages up to almost 40 years have been recorded (Borgstrøm & Hansen, 2000), most die much younger (Klemetsen et al., 2003). In populations with relatively stable annual recruitment, age class frequencies tend to fall progressively with increasing age. The reason for this is mortality from natural causes or harvesting, the latter especially from a certain age, when the fish have reached catchable size (Borgstrøm & Hansen, 2000).

Much of the variation in brown trout life-histories may be attributed to factors specific to the environments the populations inhabit (Jonsson & Jonsson, 2018). Biotic factors such as growth, body size and the presence of other species shape habitats and regulate brown trout populations and their densities (Jonsson & Jonsson, 2011). Environmental factors such as water temperature, depth, flow, and nutrient content are important in reproduction, recruitment and growth, as are bottom substrate and migration barriers (Jonsson & Jonsson, 2018).

Given the crucial role of streams in brown trout recruitment, understanding stream habitat use and natural, limiting processes of population control in these is important for targeted interventions and sustainable fisheries management (Armstrong et al., 2003; Milner et al., 2003). In streams, the biotic and abiotic factors interact in complex and interdependent ways, and the variability and use of habitats influence fish distribution and abundance (Armstrong et al., 2003). Exploitation of available niches varies with body size, season, and time of the day: small size is associated with shallow, swift areas with cobbled substrate, larger size with slower, deeper areas like pools; summer and nighttime are times of higher activity and wider habitat use than winter and daytime, when cover and shelter has high priority (Heggenes et al., 1999). Within a stream, even adjacent areas with habitats suitable for different life stages may show age structures that vary and deviate from the tendency of declining numbers with age in the total population (Milner et al., 2003). When densities are high relative to fish size and the population approaches carrying capacity, habitat may have a limiting effect on cohorts of stream-living salmonids (Bohlin et al., 1994). Habitat may also be a limiting factor in more specific critical periods such as the post-hatching stage (Armstrong et al., 2003). The high mortality in the fry stage is density-dependent and a regulator of abundance, whereas later stages in stream salmonids may be determined in more unpredictable and density-independent ways by factors such as extreme water temperatures or flows (Milner et al., 2003).

Water temperature is essential for growth in ectothermic organisms such as brown trout. This is especially reflected under harsh mountain conditions, where the growth season is short (Heggenes, 2020); years with little snow and early ice melting may see better length growth in brown trout (Borgstrøm & Hansen, 2000). Brown trout developmental rates are influenced by temperature from incubation onward; the critical range for growth is 3 – 26 °C, the optimal range ca. 13 – 18 °C (Elliott & Elliott, 2010; Klemetsen et al., 2003). Provided suitable temperatures, brown trout growth and body size is dictated by food, and both quantity and quality matter (Ugedal et al., 2005). Brown trout are omnivores that may be opportunistic or specialized (Jonsson & Jonsson, 2018). Diets vary between individuals but also with life stages: fry eat small benthic organisms and zooplankton, juveniles feed on insects and amphipods, and adult eat insects, crustaceans, and fish[1]. Piscivory may start in brown trout that have reached ca. 15 cm and become predominant from around 30 – 35 cm (Klemetsen et al., 2003), depending on prey fish sizes. Continued growth is contingent on opportunities for shifting to larger-sized food resources at adequate stages.

Growth is usually faster before maturity, even if mature brown trout may keep growing substantially especially in mountain lakes (Borgstrøm & Hansen, 2000). Slow, steady growth and large size correlate with late maturity and longevity, whereas fast growers are more vulnerable to predation, including fishing (Klemetsen et al., 2003). For instance in lakes with high harvest pressure, this may lead to Lee's phenomenon: as the fast-growers of catchable size have been disproportionally removed, the remaining fish (more slow-growers) do not fully represent the growth rates of these fish ages/sizes (Borgstrøm & Hansen, 2000). Whether growth in salmonids is density-dependent or not seems contested: some have concluded that it is independent, others that it is contingent on the context (Parra et al., 2011). Others again cite studies showing that high density has a negative effect on growth in both lakes and streams, possibly due to a relative lack of food and more aggressive competitive behavior among the fish (Jonsson & Jonsson, 2018; Klemetsen et al., 2003). As surplus energy can be used by brown trout for either growth or present and future reproductive investment (Berg & Fleming, 2018), it seems reasonable to assume that population density via a relationship with growth would also influence the timing of sexual maturation. Density-related growth patterns seem to be a factor in the interannual variation commonly seen in brown trout size at maturity and recruitment (Parra et al., 2011).

Accumulated growth is reflected in length and weight, the relationship of which is seen as reflecting fish condition, often quantified as k-factor (below). A k-factor of 1.0 is considered normal for brown trout, and values below/above reflect fish that are more or less lean/fat (Borgstrøm & Hansen, 2000). However, k-factor is influenced by a number of variables, such as season, sex, maturation stage, age and stomach filling[2] and certainly some forms of disease.

### *Brown trout populations: recruitment, stocking and harvests*

Brown trout populations may over time experience considerable natural variation in abundance, i.e., the sum effect of births, mortality and net migration (Milner et al., 2003). For viable populations, fish

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[1] https://www.state.nj.us/dep//fgw/pdf/fishfact/trout_brown.pdf

[2] http://bamboorods.ca/Trout%20condition%20factor.pdf

that die or emigrate must be replaced by new recruits in amounts and rates that are adequate relative to available food and other influences in varying conditions. Recruitment may be influenced by both natural processes (such as a harsh winter in alpine settings) and anthropogenic factors, or a combination thereof. Human impact on brown trout recruitment can be somewhat indirect (as with degradation or improvement of habitats), or more direct manipulation of the number and/or quality of the fish (as in stocking). The altered flow and thermal regimes resulting from hydropower development may determine riverine fish recruitment (Rolls et al., 2013) but the actual effects often seem to be context-specific. Quantification of hydropower impacts on recruitment presupposes knowledge on flows/temperatures and fish populations before and after regulation. Pre-regulation data are often not available but a couple of examples to the contrary on salmonid fishes in Norwegian contexts may illustrate a possible range of outcomes. A study on the effects of the highly contested regulation of the *Alta* river in northern Norway reported density reductions of up to 80% in juvenile Atlantic salmon (*Salmo salar*) a decade after regulation, due to stranding and increased winter mortality (Ugedal et al., 2008). In one part of the regulated *Aurlandsvassdraget* with its source in alpine western Norway, recruitment of anadromous salmonid fishes decreased by an estimated 25 – 40% after regulation, about half from reduced flow/water-covered area and half from reduced summer temperature (Ugedal et al., 2019).

If recruitment is high relative to the availability of food, the result may be dense populations dominated by small, slow-growing fish in relatively poor condition, and the opposite if recruitment is low (Heggenes, 2020). Stocking may be implemented if natural recruitment is considered too low, for instance because stream habitats have been lost or degraded due to regulation, and/or there is a food surplus for the same or some other reason (Borgstrøm & Hansen, 2000). Still a widespread practice globally, stocking is increasingly controversial because the effects can be uncertain or even harmful (Araki & Schmid, 2010). Much of the concern centers on qualitative aspects such as fish genetics and fitness, but these may also be linked to quantitative aspects, as in the fear that the abundance of wild populations may be reduced via density-dependent mortality or genetic introgression (Araki & Schmid, 2010). To ensure stocks that are adapted to the ecosystems into which they will be introduced, the use of local breeds in hatcheries has become common in both restorative and other settings. Even so, a recent review of river restoration impacts on salmonids argued that the benefits of current stocking regimes are moderate at best, predicting a paradigm shift from stocking to other, more targeted measures (Marttila et al., 2019).

Recruitment and food production are “balanced” from a user’s or fisheries perspective when the result is fast-growing fish of good quality (Heggenes, 2020). What constitutes quality for brown trout may be subjective and context-dependent, but some candidate factors are fish size, condition, health and perhaps flesh color. According to an old study based on Norwegian materials, brown trout that might be expected in gillnet mesh sizes 26 – 35 mm (lengths ca. 27 – 37 cm) or with weights > 150 grams could be considered "attractive size" (Jensen, 1979) but this would certainly be on the low side of expectations in many settings. A k-factor of around or above 1.0 would nearly by definition be necessary for brown trout to be considered as high-quality. Macro-parasites such as *Eustrongylides sp.* (below) is one example of a fish health issue that might not objectively affect flesh quality if handled appropriately but it could still affect perceived quality of the fish. Flesh color is another potential quality-indicator in a fisheries perspective, as it has been shown to influence end-users' acceptance of brown trout as a foodstuff (Rounds et al., 1992). Even if the diet reflected in flesh color should not directly influence the taste of the flesh[3], it seems uncontroversial that many consumers find red color attractive and preferable to white flesh in brown trout.

Depending on the type and scale of harvest, quantitative measures like total number and/or weight of the fish caught over time also matter in addition to quality. Both fishing pressure and mesh sizes matter in sustainable gillnet harvesting; introducing and/or adjusting a minimum mesh size may for instance have a large impact on catches (Borgstrøm & Hansen, 2000) and thus on population abundance and structures over time. In small lakes, local harvest with gillnets or even fishing rods may have a rapid and strong impact on the balance between recruitment and food production (Heggenes, 2020).

### *Monitoring fish populations: sampling design*

Parameters of interest in the present study, such as fish abundance and population structures, are in field studies usually estimated from samples. For valid inferences about populations, samples must be representative, with as little bias and error as possible. One important way to ensure this is randomization, a process whereby each individual in the population has an equal and independent chance of being sampled (Whitlock & Schluter, 2020). Within probabilistic sampling designs in fish monitoring, Radinger and colleagues distinguished between simple random, systematic, or stratified random designs (Radinger et al., 2019). In stratified random sampling, strata representing different habitat units are proportionally sampled to reduce the effect of spatial variability; in systematic sampling design, the first site is chosen randomly, and subsequent samples are regularly spaced. Although random samples are assumed in most statistical analyses, sample sites in fish monitoring

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[3] https://forskning.no/bakgrunn-hav-og-fiske-havforskningsinstituttet/denne-orreten-kan-ha-hvitt-kjott/296579

are often selected non-probabilistically, based on judgment or convenience (Radinger et al., 2019). When random samples in the field are impossible or fail despite sincere efforts, the consequences of possible biases should be addressed (Whitlock & Schluter, 2020).

### *Test fishery with gillnets*

Test fisheries aim to make valid inferences about lake populations by using scientific principles and methods. In test fishery with gillnets, the sampling design and equipment must take into account that habitats, behaviors, fish shape and size vary with species, life stages, seasons and other factors (Standard Norge, 2015a). Gillnets are passive structures that must be placed where there is a chance that moving fish encounter them, and the fish must get entangled in ways that ensure that they end up in the catch. The properties of gillnets make them selective, particularly their mesh size, and the probability of being sampled varies with fish characteristics such as morphology and territoriality. The specific selectivity of gillnets has been estimated for several fish species (Standard Norge, 2015a). Gillnets most effectively catch fish of a certain, rather narrow length range (modal length). Mesh size and modal length are proportional in principle: small fish are trapped in small mesh, larger fish in larger mesh. As a rule-of thumb for brown trout, mesh size multiplied with 10 gives the modal length. The probability of being caught is slightly higher for fish somewhat above modal length than for fish somewhat below it (Borgstrøm & Hansen, 2000).

Two different types of gillnets are considered in NS-EN 14757 and NS 9455, the most relevant Standards for gillnet test fishery in Norway (2015a, 2015b): the recommended Nordic multi-mesh gillnets (*Nordisk oversiktsgarn*), and the expanded Jensen series (single-mesh gillnets). Multi-mesh gillnets consist of adjoined panels with different mesh sizes, in proportions and a particular order (geometric series) that aim to obtain a representative catch. The benthic variant of the Nordic gillnets is 30 meters long and 1.5 meters high (gillnet area 45 $m^2$), and is composed of 12 panels with mesh-sizes from 5 to 55 mm, covering a fish size range of 40 – 400 mm. The gillnets in the Jensen series are 25 meters long and 1.5 meters high (gillnet area 37.5 $m^2$); the standard Jensen series has 8 gillnets with mesh sizes from 21 mm to 52 mm (Jensen, 1972), and the expanded series includes gillnets with mesh size 12.5 and 16 mm. According to NS 9455, use of the expanded Jensen series is as an acceptable adaptation to Norwegian (historical) conditions (2015b), but single-mesh gillnets entail more laborious and/or less representative sampling.

Adherence to the recommendations in NS-EN 14757 ensures reliable estimates for quantitative relative abundance (catch per unit effort, CPUE), number per unit effort (NPUE), biomass (weight per unit effort, WPUE), and size distribution in temperate lakes. However, precision levels vary with sampling design. Two alternatives are presented in NS-EN 14757: time series ("standardized") and inventory design. A "standardized design" means depth-stratified randomized sampling with multi-mesh gillnets, and it ensures maximum, specified precision and statistical power. The inventory design, with a less rigorous randomization procedure, provides rougher estimates.

For the two respective sampling designs, NS-EN 14757 specifies the stratified sampling effort necessary in lakes per surface area and depth to achieve the desired precision of estimates (i.e., reflecting a study's power). The sampling effort is expressed in gillnet-nights, which is the product of the number of gillnets and the number of nights the nets have been fishing. For depth-stratified randomized design, the prescribed sampling effort enables detection of 50% changes in relative fish abundance between sampling occasions. For small, shallow lakes (< 20 ha, depths < 12 m), most relevant in the present study, the Standard suggests a total effort of 8 gillnet-nights per lake, distributing 3 + 3 + 2 gillnets in the respective 3-meter interval depth strata (2015a).

Reports reviewed in the present study on brown trout sampling with gillnets typically referred to one or both standards NS-EN 14757 and NS 9455, or to similar principles (Johnsen & Hesthagen, 2020; Lehmann et al., 2008; Solhøi, 1998; Tormodsgard & Gustavsen, 2010; Ugedal et al., 2005). Some limitation or modification of the cited Standard was reported in every case, with varying specificity as to the nature of the adaptations. Unfortunately, there was little detail in the reports about the randomization procedure employed. Gillnet location was usually marked on a map in the reports, without exact geo-coordinates or angles, and with varying details about the depths at which they were placed. The terms sampling design, time series or inventory were not used in the cited reports; one, however, referred to its use of depth-stratified sampling (Lehmann et al., 2008).

The traditional way of brown trout gillnet sampling in Norway has been a systematic rather than stratified random design, i.e., to "cover" a lake by distributing benthic gillnets (in older studies one or more Jensen series) from the shore outwards, with a minimum distance between them. In practice, the nets have then been placed mostly at depths less than 5 – 10 meters, with at least 50 – 100 meters between them (Borgstrøm & Hansen, 2000; Ugedal et al., 2005). The Nordic multi-mesh gillnets are increasingly used for test fishery in Norway, mostly the benthic type for brown trout, as they are typically benthic feeders.

### *Characterization of brown trout populations through test fishery*

Using comprehensive empirical data from 410 Norwegian lakes as well as statistical analyses, Ugedal and colleagues (2005) developed a system for characterization and classification of brown trout populations. Based on test fishery catches, lakes and their populations can be placed in one of three classes of density and of achievable fish size, yielding nine possible outcomes reflecting typical recruitment and growth conditions (categories A-I) when combined (Fig. 5.1). The intention behind having few classes was easy comparison and communication of gillnet test fishery results. However, the authors warned that outcomes should be interpreted cautiously, as rather large differences may be found within the broad categories, and because the class limits are somewhat arbitrary.

The density classification in the system contains three variables: catch in numbers per 100 $m^2$ relevant gillnet area per night (a standardized catch per unit effort, CPUE), as well as numbers and kilograms caught per gillnet series (I have translated the kilogram measure, *utbytte*, to yield). Expected yields are reached by calculating the number of fish caught with the mean fish weight (150 grams) in the empirical material used to develop the system. The two latter measures are thus expected to correspond, for instance: a medium yield for a medium catch in numbers per gillnet series. The data underlying the system was mostly based on test fishery with standard Jensen series with benthic gillnets, but the authors provide guidelines for comparisons with multi-mesh gillnets: only fish ≥ 15 cm/in mesh sizes ≥ 15.5 mm should be included from multi-mesh catches, due to the lack of mesh sizes < 21 mm in the standard Jensen series.

As for achievable fish size, the other main parameter in this system, the authors demonstrate that mean size of mature females is a useful indicator of growth conditions, as it correlates well with mean achievable maximum fish size in a lake. For this assessment, the total catch must be at least 40 – 50 individuals, and 5 – 10 mature randomly sampled females are necessary for a mean length estimate precision of ± 10 %; data from several occasions may be used if necessary to achieve this (Ugedal et al., 2005).

As part of the background for their system, Ugedal and colleagues referred to the previously mentioned study by Jensen (1979). Based on a selection of 79 Norwegian lakes, Jensen suggested that a simple measure of brown trout recruitment in a lake may be based on test fishery catches (in his study: series with benthic gillnets, single-mesh with range 19.5 – 45 mm) by dividing weight in grams caught in the mesh sizes 26 – 35 mm (catching “attractive fish”) on the number of individuals caught in mesh sizes 19.5 mm and 22.5 mm. Ratio values between 40 and 70 would indicate a “good situation”, under 40 overpopulation or stagnation, and over 70 recruitment too low relative to the “exploitable” part of the population (Jensen, 1979).

## 2.2 Hydropower and the environment

*Hydropower developments: consequences and compensations*

Most larger hydropower systems are variants of two major designs: low-head (or run-of-the-river) regulation with intake and power station in the dam, and high-head regulation with reservoirs at a high elevation and long tunnels or pipes to the power plant, the latter type being common in northern, temperate climates such as in Norway (Alfredsen et al., 2022; Heggenes et al., 2021). Impoundment and regulation of rivers for hydroelectricity purposes disrupts natural patterns of water flow and temperature in complex ways (Alfredsen et al., 2022; Austin et al., 2015; Heggenes et al., 2021; Poff et al., 1997).

In the high-head systems, of which the Kova R. is one example, water may be stored over the summer behind dams and released in the fall and winter when energy demand and prices are higher. This virtually inverts the natural water flow regime. In a dammed system utilizing a physically unaltered river course, as in the Kova R. case, mean flows are typically higher than natural in the winter during hydropower production, but lower in summer during reservoir storage. The reaches downstream of the dam will be left with residual flows, plus any minimum environmental flow if imposed, during the important growth and recruitment season for brown trout. Natural spring and/or autumn flooding does not occur either, because the water is impounded in the reservoir. The altered flow patterns may have great impact on fish: early life stages are particularly vulnerable due to a restricted repertoire of behavioral responses, but all stages may be affected, for instance by reduced habitat volumes and/or by stranding at low flows (Elliott, 1994; Warren et al., 2015).

Temporal and spatial variability in water temperature plays a crucial role in aquatic ecosystems and the distribution of river-dwelling species, and fluctuations may be natural or influenced by human activities (Caissie, 2006). Hydropower regulation may shift natural patterns of water temperatures in several ways, for example directly downstream from tunnels with hypolimnic intakes, or indirectly via flow modifications and thereby changed heat fluxes. The higher mean winter flow in northern regulated rivers entails higher temperatures and less ice formation in reaches under electricity production, while the opposite is the case in bypassed reaches with residual flows (Heggenes, Alfredsen, et al., 2018). Thermal conditions in reduced/residual flows are more affected by the sun and air temperatures and thus vary more than in systems with natural flows. Negative consequences of hydropower-related temperature shifts for fish and the food webs they depend on, seem to be greater and at least more studied than possible positive impacts (Heggenes et al., 2021).

Fish response to anthropogenic stressors, such as hydropower leading to reduced habitat availability and potentially also habitat quality, is a valuable indicator for the integrity and status of freshwater lakes and streams (Radinger et al., 2019). Attention to restorative efforts and mitigating measures compensating for regulation damage has increased over the past decades (Auestad et al., 2018). Examples of historic and current approaches include adaptive flow management (Nislow & Armstrong, 2012), minimum or environmentally-based water flows (Gillespie et al., 2015; Renöfelt et al., 2010; Saltveit, 2006), rehabilitation and/or improvement of degraded habitats (Heggenes, Røed, et al., 2018), reestablishment of connectivity/fish passage (Kraabøl, 2016; Schilt, 2007), and stocking/release of juvenile fish (Polgar et al., 2022). Regular monitoring and research on effects of such measures is crucial and should be an integral part of any project that aims to restore or improve riverine ecosystems (Griffith & McManus, 2020; Kail et al., 2015).

### *Environmental status of waterbodies and the EU Water Framework Directive*

The European Union Water Framework Directive (WFD) is implemented in Norway through the bylaw *Vannforskriften* (Vannforskriften, 2007). In this system, waterbodies are “characterized” based on primarily nature-given aspects such as location, size, and water type (Direktoratsgruppen vanndirektivet, 2018a). They are “classified” in terms of environmental status, which is the sum of ecological status (five classes, of which the two upper ones – “very good” and “good” – are considered acceptable and aimed for) and chemical status (“good” or “bad”). The ecological status is determined by the sum of biological- and supporting physical-chemical “quality elements”, which are quantified through relevant parameters and indexes. Fish is one of the biological quality elements considered important in the monitoring of freshwater ecological status and the effect of anthropogenic influences, such as hydropower regulation. Chemical classification is based on presence and levels of specified environmental toxins (Direktoratsgruppen vanndirektivet, 2018b).

In the WFD system, the standard aim of at least “good ecological status” is considered unrealistic for waterbodies that are permanently and heavily modified (Norwegian acronym: *SMVF*), for instance by substantial regulation for hydroelectricity purposes. Instead, the aim for *SMVF*s is reaching and maintaining “good ecological potential” (Departementsgruppen, 2014).

## 2.3 Study area: The Upper Kova R.

The part of the Kova R. system (REGINE unit 016.EAAZ) explored in the present study belongs to the *Kova øvre* (Upper Kova) waterbody (ID 016-262-R, REGINE unit 016.EAAD (Fig. 2.1). Located in Hjartdal municipality, the Upper Kova R. has a length of 8.9 km (Miljødirektoratatet, 2021; NVE Atlas, 2021), a catchment area of 18.9 km² (Fig. A1 2.1) with mean runoff 35.6 l/second km², and an upstream catchment area of about 63 km² with mean runoff 38 l/second km². The Upper Kova R. runs from the alpine regulation reservoir L. Vindsjåen (971 – 956 m.a.s.l.; area at highest regulated water level 4.72 km²; REGINE unit 016.EAAE; catchment area 43.9 km²) through a natural, physically unaltered course to the inlet of the dammed L. Kovvatnet (876 – 859 m.a.s.l.; area 3.57 km²; catchment area 103.1 km²). The small lakes interspersed in and defined as part of the Upper Kova R., are in order from north to south: Våtjønn (947 m.a.s.l.; area 0.211 km²; catchment area 47.7 km²), Øvre Urdetjønn (945 m.a.s.l.; area 0.032 km²/3.2 ha; catchment area 48.4 km²), Nedre Urdetjønn (942 m.a.s.l.; area 0.096 km²/9.6 ha; catchment area 49.1 km²), Bjønntjønn (920 m.a.s.l.; two sections with areas 0.018 km²/1.8 ha and 0.082 km²/8.2 ha, connected by a short riverlike reach; catchment area of lakes 100.5 km²), Berutjønn (916 m.a.s.l.; area 0.169 km²; catchment area 59.7 km²), and Reinstultjønn (913 m.a.s.l.; area 0.089 km²; catchment area 61.1 km²) (NVE Atlas, 2021).

## 2.4 Hydropower and the environment in the Upper Kova R.

*Hydrology, hydropower regulation and mitigation measures in the Upper Kova R.*

The Lake Vindsjåen watershed is all natural with no upstream man-made transfers of water into the reservoir (Fig. 2.2). Neither are there any diversions between the upstream L. Vindsjåen and the downstream (8.9 km) reservoir, except a ca. 100 m tunnel through the dam at the outlet of the Vindsjåen reservoir, i.e., the head of the Upper Kova River. The supply of water to the Kova reservoir from L. Vindsjåen thus corresponds to the lake’s catchment area. Estimated annual mean water flow in the Kova R. from L. Vindsjåen is 1.28 m³/second (Heggenes, 2020). Although no water is diverted from or transported into the watershed by the regulation, the annual flow pattern in the Upper Kova R. system is significantly changed, i.e., virtually inverted from the natural regime, and is now in line with the market-driven flow regime outlined above. Because no minimum or environmental flow requirement was imposed, the Upper Kova R. is dependent on residual flow in summer. However, due to unintended dam leakage, there has been an additional mean water supply of about 50 l/second (0.05 m³/second) through the dam. During winter, the period of electricity production is typically from December to March, and mean flow is then usually 2 – 4 m³/second (Heggenes, 2020).

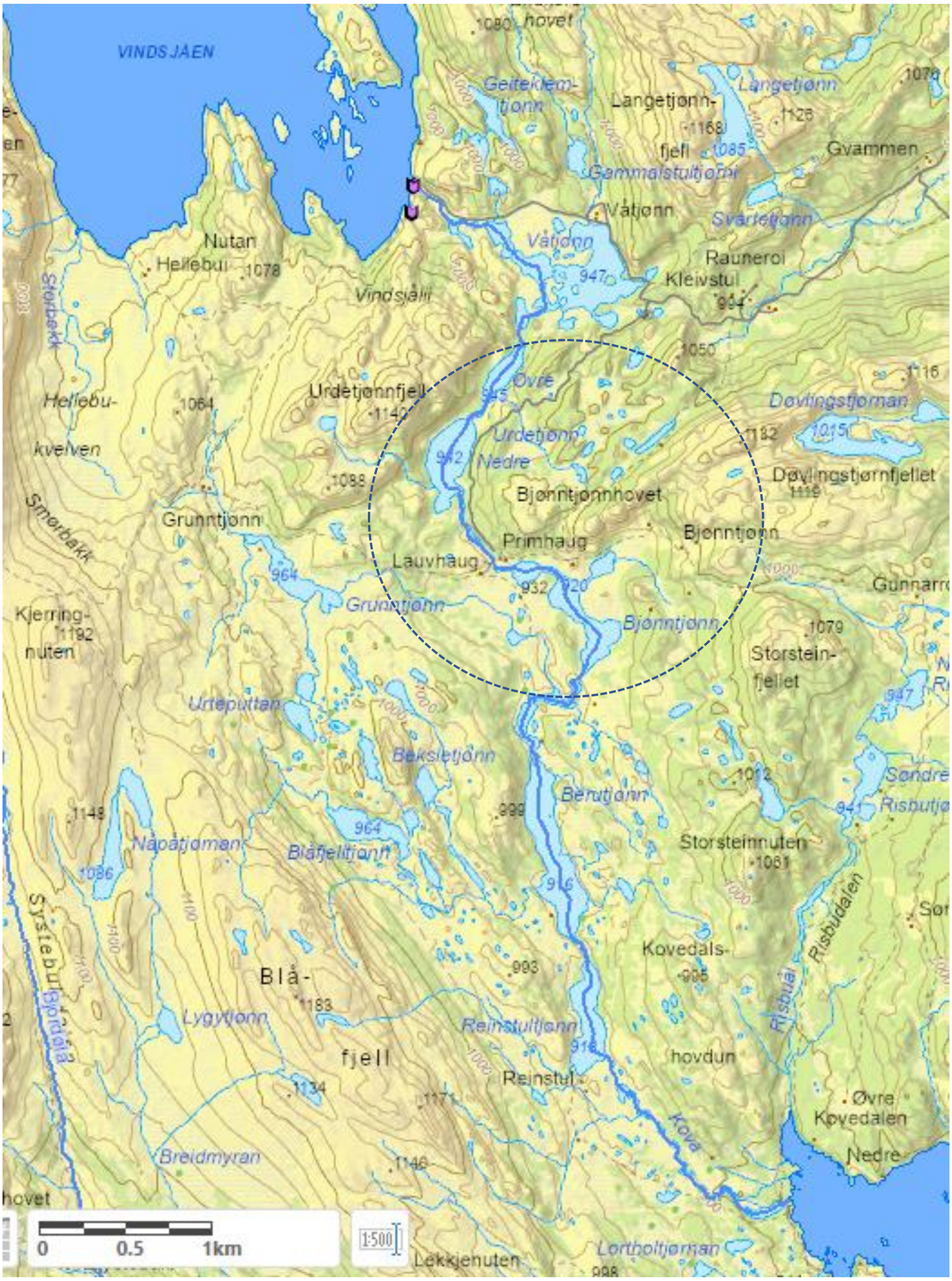

*Figure 2.1. The Upper Kova R (waterbody). The river runs from L. Vindsjåen to L. Kovvatn. The three small lakes of interest in the present study circled: Øvre Urdetjønn, Nedre Urdetjønn, and Bjønntjønn. From NVE Atlas (2022).*

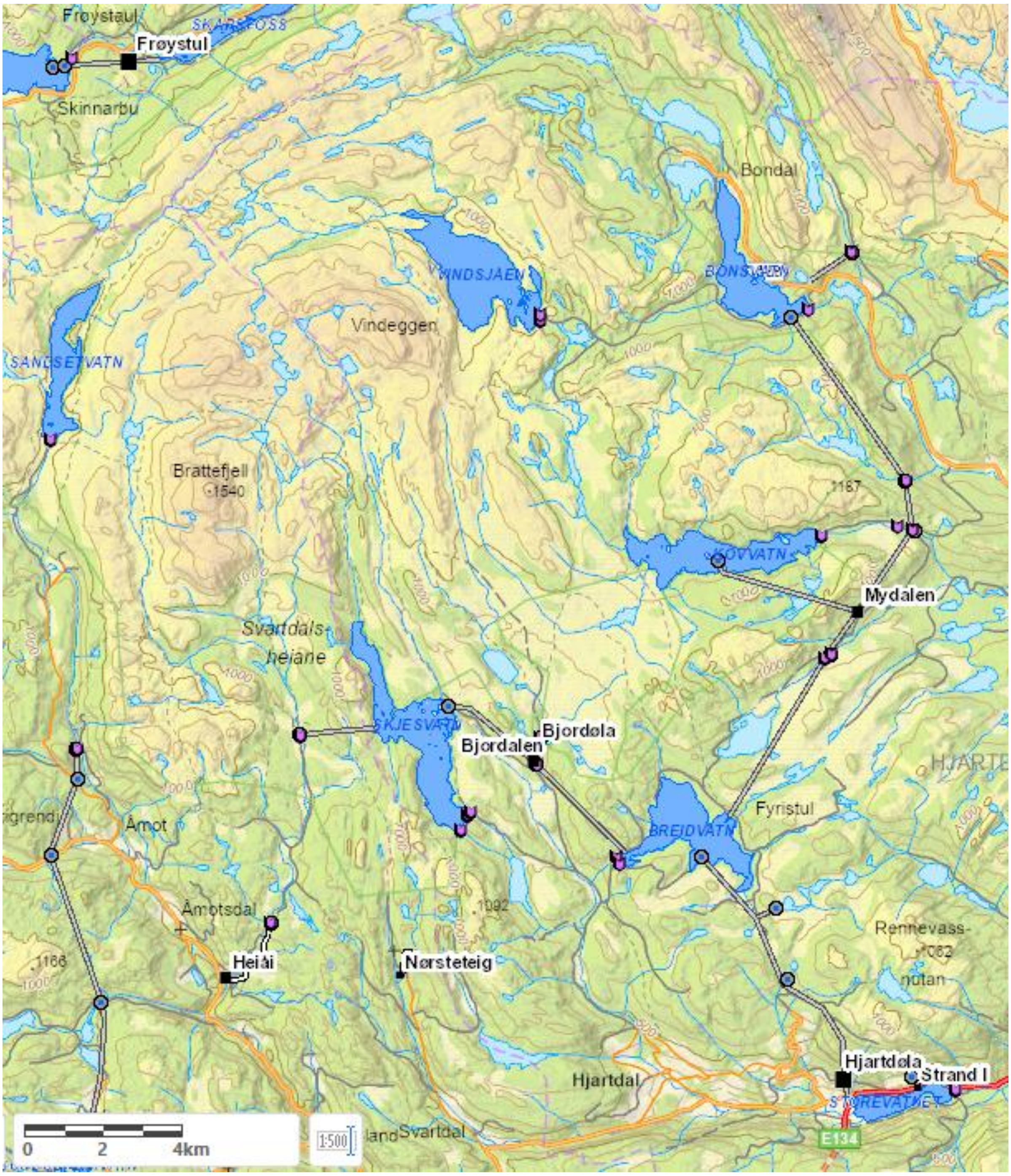

*Figure 2.2. The Kova R. system: regulation installations (dams and transfers). Lake reservoirs in dark blue. The area of particular interest in this study is the natural, physically unaltered reach between L. Vindsjåen and L. Kovvatn. From NVE Atlas (2022).*

In 2019, repairs on the dam led to higher-than-normal flows from L. Vindsjåen to the Upper Kova R. (Heggenes, 2020). In 2022, filling levels of hydropower reservoirs were unusually low in the part of Norway where the Kova R. is situated (Fig. A1 2.2), but the unintended leakage still provided the "normal" supplement to residual flow in 2022 (J. Heggenes, personal communication, April 21, 2023). Precipitation levels were probably mostly below normal in the Upper Kova area through the first half of 2022 (Fig. A1 4.12), with possible impacts not only on reservoir filling but also on the residual flows. The aggregate effect in terms of actual flows in the Upper Kova R. in 2022 are not available, as there are no flow gauging stations.

Prior to 2016, water temperatures in the Kova R. had not been investigated systematically, but Heggenes (2018, 2020) found it likely that regulation changed the natural thermal regime. Before distributing temperature loggers in the Upper Kova R. in December 2016, Heggenes' expectation was higher winter temperatures due to tapping of hypolimnic water from the L. Vindsjåen reservoir in winter, and depending on solar radiation, earlier start of the growth season and more fluctuating diurnal water temperatures through the summer. The rationale for the latter was that a reduced amount of water in a relatively wide natural riverbed would be more exposed to effects of the sun, with the water rapidly heating up during the day and cooling off at night. Data from the loggers indicated that the winter effect in 2016 – 2017 was perhaps lower than expected, whereas the predictions regarding spring and summer were confirmed (Heggenes, 2018, 2020).

The assumption that the brown trout populations in the Upper Kova R. would be negatively affected by the hydropower regulation was related to the impact on the stream habitats on which recruitment to the lakes in the system depend. Both quantity and quality of the habitats might be reduced, including the effects of possibly decreased nutrient transport from L. Vindsjåen to the Kova R. (Heggenes, 2020). As mentioned, it was assumed that the anticipated reduced natural recruitment could be compensated by supplemental stocking. The numbers of 1-summer-old (0+) hatchery-reared brown trout released into the Kova R. as a mitigating measure after regulation was 2200 annually from 1958 to 1997 (Solhøi, 1998). Annual releases in the period 1997 – 2009 were ca. 125 in each of Øvre- and Nedre Urdetjønn, and ca. 200 in Bjønntjønn (Tormodsgard & Gustavsen, 2010). Total releases in the Upper Kova R. were gradually reduced from 1998 until stocking was abandoned altogether from and including 2015 (Heggenes, 2020).

### *Environmental status of the Upper Kova R.*

The hydropower regulation with no minimum water flow requirements has resulted in the Upper Kova R. being classified as a heavily modified water body (*SMVF*) in the WFD system (above).

According to the official characterization in *Vann-nett Portal* (2022), the Upper Kova R. is a medium size, lime deficient, clear (for humus) river located in ecoregion Sørlandet, in an intermediate climate zone. Its current environmental classification is "good ecological potential" and "undefined" chemical class, the latter due to lack of data (Vann-Nett portal, 2022). The biological quality element on which the ecological classification was based, seems to be the 2009 fish investigation by Tormodsgard and Gustavsen (2010). Unfortunately, *Vann-Nett* does not provide any details on the process behind this classification. However, based on information in the reports of Tormodsgard and Gustavsen (2010) and Solhøi (1998), I calculated CPUE (catch per 100 $m^2$ gillnet area per night) per lake in 2009/1997: Øvre Urdetjønn = 6.3/11.3, Nedre Urdetjønn = 15.7/17.0, and Bjønntjønn = 14.7/9.3. Comparing these results to Table 6.8 in the classification guide (Direktoratsgruppen vanndirektivet, 2018b), I found that the quality element fish (brown trout) density in 2009/1997 would dictate classification as "moderate"/"good" for Øvre Urdetjønn, "very good"/"very good" for Nedre Urdetjønn, and "good"/"moderate" for Bjønntjønn. The possible rules for WFD classification of a river based on gillnet test fishery results from three of the lakes that form part of the river are not clear to me. However, the mean CPUE for all three lakes taken together correspond to the class "good", both for 2009 (CPUE = 12.2), and for 2009 and 1997 taken together (CPUE = 12.4). As the Upper Kova R. is an *SMVF*, "good" in this case refers to "ecological potential". Considered this way, the results of my calculations thus appeared to be in agreement with the information in Vann-Nett portal (2022).

The official expectation for 2022 – 2027 is that the "good ecological potential" of the Upper Kova R. will be maintained, and that the chemical status, once investigated, will also be "good", thus fulfilling the minimum environmental aim for an *SMVF* waterbody (Vann-Nett portal, 2022).

## 2.5 The brown trout populations in the Upper Kova R.

*Previous fish studies in the Upper Kova R.*

The brown trout populations in the Kova R. system were not systematically investigated before or for decades after the regulation process started in 1958. A gillnet test fishery was first performed in some of its lakes including L. Vindsjåen in the mid-1980s, and in the report from this study, it was stated that brown trout is the only fish species in the Kova R. system (Kildal, 1988). From a decade later, fish studies focusing on L. Øvre Urdetjønn, L. Nedre Urdetjønn, and L. Bjønntjønn were undertaken: Solhøi's gillnet test fishery in 1997 (1998), fish investigations by Tormodsgard and Gustavsen in 2009 (2010), and stream studies on natural recruitment by Heggenes in 2017 and 2019 (2018, 2020). Tormodsgard and Gustavsen (2010) largely replicated the 1997 test fishery but added investigations of water quality (primarily with respect to acidification, through chemical markers and zoo plankton as biological indicators), and limited electrofishing to assess recruitment in inlet streams. Heggenes widened the scope on natural recruitment to the three lakes. He was also the first to report another fish species in the Kova R. system, as his electrofishing catches included the remnants of what was likely a brook lamprey (*Lampetra planeri*) (2018).

In the paragraphs below, I summarize the main points first from the gillnet test fisheries in 2009 and 1997 (2010, 1998), and next from Heggenes' studies on natural recruitment in 2017 and 2019 (2018, 2020). All information in these sections is from the cited reports, if not specified otherwise.

*Gillnet test fisheries in 2009 and 1997*

Both studies described the three lakes as small and mainly shallow (0 – 3 meters), with maximum depths around 10 meters. Neither report contains the specific depths at which the respective gillnets were set. In 2009, the depths were measured continuously with an echo-sounder, to "get an impression of mean and maximum", but unfortunately without generating any map with depth contours. Single gillnets were set outwards from shore, distributed to cover the lake in a somewhat random fashion, by calculating the minimum distance between them based on number of nets and lake circumference (P.Ø. Gustavsen, personal communication, December 19, 2021). The gillnets used in both test fisheries were standard Jensen series, with one exception. In Øvre Urdetjønn, the 1997 investigation used a reduced Jensen series, arguing that expected catches in the gillnets with the largest mesh sizes were low or null for this small lake. This entailed a smaller sampling effort than in 2009 for this lake, but this probably had no influence on the results (below). In Nedre Urdetjønn and

Bjønntjønn, the sampling effort was the same in 2009 and 1997, a standard Jensen series with eight gillnets for one night in each lake. The 2010 report contains maps for each lake which indicate locations of gillnets (with serial numbers) and other sampling stations. Unfortunately, the 1998 report has no such maps or any details about the gillnet distributions.

Both reports contain general characterizations of the lakes in terms of trout abundance (expressed as density) and population structure, occasionally compared to food production. However, I found the terminology used in these characterizations poorly harmonized, and the criteria used somewhat opaque. To supplement the verbalized expert opinions on densities in the two reports, I applied the system of Ugedal and colleagues (2005) to the available data from 2009 and 1997, as well as to the data from the 2022 test fishery (below).

The 2010 report classified the water quality as “good”, with no indication of the acidification that has been a great concern and an indirect fish exterminator in many waterbodies in southern Norway since the 1980s (Borgstrøm & Hansen, 2000). The 2010 finding on acidification seems to be in line with a recent reference in the Upper Kova R. fact sheet in *Vann-Nett Portal*, where the status of the index “acid neutralizing capacity” (ANC) is listed as “good” (2022).

Tormodsgard and Gustavsen (2010) systematically compared their results per analysis and lake with those from Solhøi’s gillnet test fishery (1998). I found some discrepancies within the 2010 report and between the 2010 authors’ reporting of the 1997 numbers and the original source, but most were minor and easily resolved. In the following paragraphs, I mostly focus on the authors’ verbally stated assessments (marked with “ ”), as the numeric results are addressed together with those from 2022 in the second Results chapter (5).

For Øvre Urdetjønn, the main conclusions of the 2009 and 1997 studies were similar: a bit “too densely” populated, with relatively small fish, generally slow growth, especially from age 5 or 6 years, a “good” mean k-factor especially for the younger/smaller fish, early onset of maturity for males, comparable patterns in the distribution of white versus red flesh (crustaceans not a main food source), and mainly natural recruitment. Read together, the studies suggested that some difference in length and age structures between the two surveys might be related temporal changes in fishing pressure, specifically slightly increased local harvest with gillnetting directed at the larger fish through selective use of relatively large gillnet mesh sizes.

For Nedre Urdetjønn, the main conclusions of the 2009 and 1997 studies differed more. Similar conclusions were: Nedre Urdetjønn had the highest density of the investigated lakes (reflected in high catch in numbers), mostly small fish (< 30 cm), with “acceptable” growth (similar patterns up to 6-year-olds), early onset of maturity for males, comparable patterns of white versus red flesh distribution, and “good” or “excellent” natural recruitment. Somewhat differing results were reported for length distributions and for fish condition. In 2009, fish 16 – 19 cm were “over-represented” (45% of the catch), and the k-factor was rated “excellent”. In 1997, the proportion of fish 16 – 19 cm was ca. 15%, and the k-factor “acceptable”. Fish size and quality were evaluated as “good” in 2009, apparently slightly “improved” from 1997. The population in 2009 was still considered a bit “too dense” relative to food resources, but cannibalism may have provided an alternative for the larger fish. Tormodsgard and Gustavsen hypothesized that the population in the lake might be enroute to an even higher density (2010).

For Bjønntjønn, many of the conclusions were in the form of direct comparisons with the other two lakes: in both 2009 and 1997, Bjønntjønn had lower density and “better quality” fish, a higher proportion of “large to small” fish, k-factor was “as good” or “better”, growth and length distribution patterns “more normal” (although size 16 – 19 cm was “overrepresented” also here), early onset of maturity for males, a similar distribution of white versus red flesh (crustaceans not a main food source), and a relatively good food availability. In 2009, natural recruitment was rated as “good and stable”. In 1997, Bjønntjønn had a higher proportion of hatchery stock in the test fishery catches than the other two lakes, but recruitment was still assumed to be “primarily natural”. Both studies seemed to attribute the “better-balanced” population in Bjønntjønn to more appropriate practices of local gillnet harvesting (pressure and mesh size) than in the other two lakes. However, the study from 1997 pointed out that a relatively high local harvest might be sustainable only up to a point in a small lake such as this one.

The above assessments on natural recruitment seemed to be inferred mainly from the proportion of gillnet test fishery catches constituted by hatchery-stock trout. It should then be pointed out that the identification of the latter was described as quite uncertain for 1997, as it depended on indirect signs of injuries on fins and opercula attributed to hatchery conditions. Identification of hatchery stock seemed more certain by 2009, judged from the consistent reference to the more reliable marker clipped adipose fins in the report of Tormodsgard and Gustavsen (2010).

### *Natural recruitment of brown trout to the three lakes*

Heggenes’ stream studies aimed at providing a comprehensive assessment of the natural recruitment to the three Upper Kova R. lakes. In addition to the logging of water temperatures, habitats were systematically surveyed and classified, and standard electrofishing (Standard Norge, 2003) was performed in 10 stream stations, covering the main in- and outlets of the lakes, a river reach location between Nedre Urdetjønn and Bjønntjønn, and three smaller inlet streams (Fig. A1 2.3).

Heggenes emphasized the importance of the unintended dam leakage for habitats and recruitment areas in the Upper Kova R., primarily for mitigating the otherwise strong reduction in water-covered area caused by the regulation but possibly also by facilitating some nutrient flow. As mentioned, the temperature logging in the period 2017 – 2019 suggested that in normal years after regulation, there were modest alterations from natural winter temperatures, but earlier temperature rise in the spring and more fluctuations through the growth and recruitment season. Overall, Heggenes found that the altered thermal regime probably entailed little change in incubation and hatching times but had an overall beneficial effect for brown trout growth.

The electrofishing results indicated relatively high densities of small recruits (0+ and parr), but few larger individuals in the streams, suggesting that most fish move from the recruitment streams into the nearby lake when they reach lengths of 13 – 15 cm. Based on average density estimated from electrofishing catches (44,7 or more/100 $m^2$), and calculated areas of recruitment habitats compared to lake size, Heggenes proposed that relative natural recruitment was greatest to Øvre Urdetjønn, least to Bjønntjønn, with Nedre Urdetjønn as an intermediate case. Recruitment to Bjønntjønn was most uncertain, due to natural barriers for migration upstream and a potential spawning area in the stream-like reach between the two lake sections (above).

Heggenes' main conclusion with caveats was "satisfactory" (sufficient or more) natural recruitment for the three lakes, best balanced to food production in Bjønntjønn, a bit less so for Nedre Urdetjønn, and with recruitment a bit too high for Øvre Urdetjønn. Representativity was perhaps the main caveat. Only two investigations within a two-year interval is a small number, especially given the large natural variation in conditions for brown trout recruitment in precarious mountain areas. Moreover, Heggenes pointed out that the higher-than-normal flow from L. Vindsjåen in 2019 might have led to inflated recruitment that season. For more reliable knowledge, he recommended continued monitoring through similar stream investigations over time and followed this up with electrofishing in the late summer of 2022.

The above recruitment assessments provide important clues but cannot be directly converted into density predictions for the lakes that recruit from the investigated stream habitats. As mentioned, gillnet harvesting is one potentially very dynamic factor that may have great impact on the brown trout populations in these lakes. Knowledge on the local harvesting practices is limited, but it has been suggested that the activity is low in Øvre Urdetjønn, a bit higher in Nedre Urdetjønn, and highest in Bjønntjønn (Heggenes, 2020).

The amount of natural recruitment to the three lakes cannot be fully ascertained until the effect of the stocking has faded out. Given the cessation of stocking from 2015 and the age range 4 – 10 years for the trout caught in 2009, it seems probable that the released hatchery-stock individuals will have disappeared from the three lakes by 2025 or before. As even a ten-year cycle between gillnet samplings is considered long (Tormodsgard & Gustavsen, 2010), a gillnet test fishery in 2022 seemed appropriately timed.

# 3 Methods

## 3.1 Literature review and search strategy

The main background for the present study was found in the reports from the previous fish studies in the Upper Kova R. (Heggenes, 2020; Solhøi, 1998; Tormodsgard & Gustavsen, 2010) and the two most relevant Standards for test fishery with gillnets (Standard Norge, 2015a, 2015b). In addition, I searched the databases Oria, Scopus, and Web of Science with combinations of key words and phrases such as “ørret”, “prøvefiske”, “brown trout”, “sampling”, “multi-mesh”, “gillnet*”, “recruitment”, “hatchery” and “stocking”, “hydropower”, “streams”, and “brown trout ecology”, considering also literature cited in the most relevant search results.

## 3.2 Equipment and software used

Locations of gillnets and for some water measurements were registered with a Garmin 62s GPS[4]. Depths were measured with a handheld Plastimo Echotest II Depth Sounder[5]. Measurements with calibrated handheld devices were made with PeakTech 5305[6] for pH/water temperature and HACH Pocket Pro Low Range[7] for conductivity/water temperature. Data for more extensive water profiles were logged with an YSI EXO2 Multiparameter Sonde[8]. Water temperatures from June – October 2022 were measured continuously with HOBO Water Temperature Pro v2 Data Logger[9].

Field data from the GPS were transferred to Excel format from gpx-files, and coordinate data from the multiparameter logger were converted to decimals through an online service (RapidTables, 2022). Both were converted to the UTM system through another online service (LatLong.net, 2012-2022), before being plotted as points in maps created in QGIS 3.16.14 with Topografisk Norgeskart 4 as the WMS layer (QGIS Development Team, 2021). Other maps were generated through an online service available to the general public (NVE Atlas, 2021).

Diagrams were generated and statistical analyses run in R version 4.1.2 through the packages Rcmdr and RcmdrPlugin.NMBU (R core team, 2021) and in MS Excel. Otoliths were studied and documented

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[4] https://www.garmin.com/nb-NO/p/63801

[5] https://www.plastimo.com/en/sondeur-echotest-ii.html

[6] https://peaktechthai.com/en/products/environmental-measuring-instruments/water-measuring-instruments/peaktech%C2%AE-5305.html

[7] https://www.hach.com/p-pocket-testers/9531400

[8] https://www.ysi.com/exo2

[9] https://www.onsetcomp.com/products/data-loggers/u22-001

with a Zeiss Stemi 305 microscope with 5:1 zoom[10] with an ocular Wi-Fi camera (product information available in Chinese only) connected to a Ucam Plus app (Liang, 2022), with subsequent age estimation performed in ImageJ (Rasband, 2020) with ObjectJ plugin (Vischer & Nastase, 2022).

## 3.3 Sampling, data collection and registration

Principles and relevant methods described in NS-EN 14757 were followed whenever possible. An account of major points and modifications follow directly below and in other appropriate sections of the main text. In Appendix 2, I have included some reflections on ethics underlying the methods (A2 1), as well as some elaboration on methodology that I considered relevant for compliance with the Standard's transparency principles but that were too detailed to fit in the main text (A2 2-3).

As one major objective in the present study was to disclose any temporal changes in population dynamics in the three Upper Kova R. lakes, the types of data collected were made compatible to the investigations of Tormodsgard and Gustavsen in 2009 and Solhøi in 1997. Though similar in methodology, the present study was not an exact replication of the previous test fisheries: gillnet type was updated and different (above), the zooplankton collection (2009) was deemed less informative and therefore unnecessary, electrofishing (2009) was to be implemented in a separate study by Heggenes later in 2022, the material used for fish age analysis (below) was somewhat different (2009: mainly otoliths, supplemented with scales; 1997: scales only), and water quality data collected was slightly different, as the acidification concern addressed in 2009 is now fortunately less relevant in this geographical area.

*Plan before fieldwork*

Prior to fieldwork, it was decided that benthic Nordic multi-mesh gillnets would be used (A2 2.1), with a fishing effort of eight gillnet-nights per lake (eight gillnets for one night). The latter was in accordance with Table A.1 in NS-EN 14757 (for shallow lakes < 20 ha), and comparable to 2009/1997.

As systematic information about lake depths was unavailable and assumed practically unattainable, the strict depth-stratified randomized sampling recommended in NS-EN 14757 was not possible. Instead, we decided to roughly replicate the gillnet locations indicated for the 2009 test fishery (A2 2.1). Based on general knowledge and available information from that survey, the sampling design of

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[10] https://www.zeiss.com/microscopy/en/products/light-microscopes/stereo-and-zoom-microscopes/stemi-305.html

the present study may be classified as systematic (above), or perhaps an intermediate variant of the "inventory" and "standardized" designs described in the Standard (2015a). All water measurements were to be made on-site.

### *Fieldwork and field data*

Fieldwork was undertaken in the period June 20 – 22 (2022) for logistical reasons. Ideally, it should have been conducted later (July 15 – August 31) to comply with NS-EN 14757 and for better comparison with the Upper Kova R. test fisheries in 2009 and 1997 (conducted at the end of August/beginning of September). The levels of snow in the preceding winter (2021-2022) (Fig. A1 3.1) may have entailed early ice-melting in the area, but I assumed that mid-June was still near the start of the growth season of the fish. Weather conditions were good for test fishery, with temperatures in the range of 10 – 15° C, overcast skies, little precipitation, and light, northwesterly winds (A2 2.1).

All gillnets were set in the evening and lifted before noon the next day, with an average fishing time of ca. 17 hours (A2 2.1). Single gillnets were set outwards and roughly perpendicular to the shoreline, and GPS coordinates and depth were registered at each gillnet end (Table A1 3.1). On-site depth measurements indicated that our approach led to some of the gillnets crossing the standard 3-meter strata, and that others were partly or entirely set in water shallower than the gillnet height (A2 2.3).

After lifting the gillnets, the length (mm) and weight (grams) of individual fish were measured and registered *in situ*, along with the mesh size in which it was caught and an assessment of the adipose fin for stock status (A2 2.2). In the field, all catches were kept as cool as possible in boxes with numerous freezing elements. All fish were deposited whole, sorted by gillnet and lake, in a deep freezer at USN in Bø by the late evening of June 22.

Superficially assessing the water level in the lakes, we saw no obvious signs along the shorelines of lower-than-normal conditions. Our searches for maximum depths were unsystematic, guided by locations given in the report from the 2009 test fishery and topographical features onshore. Locations for assessment of water visibility were chosen after a quick search with a handheld device for possible maximum lake depth. Deeper areas were found when searching locations for measurements with the multiparameter logger, which was operated by the field assistant. Water temperature, pH and conductivity were measured with handheld devices in lake inlets and outlets.

Based on recorded depths and sketches of all gillnets (A2 2.3), I later constructed a rough depth profile for each lake. The main results of this exercise, along with the locations of the gillnets and for water measurements with the multiparameter logger, were plotted on maps (Figs. 3.1-3.3).

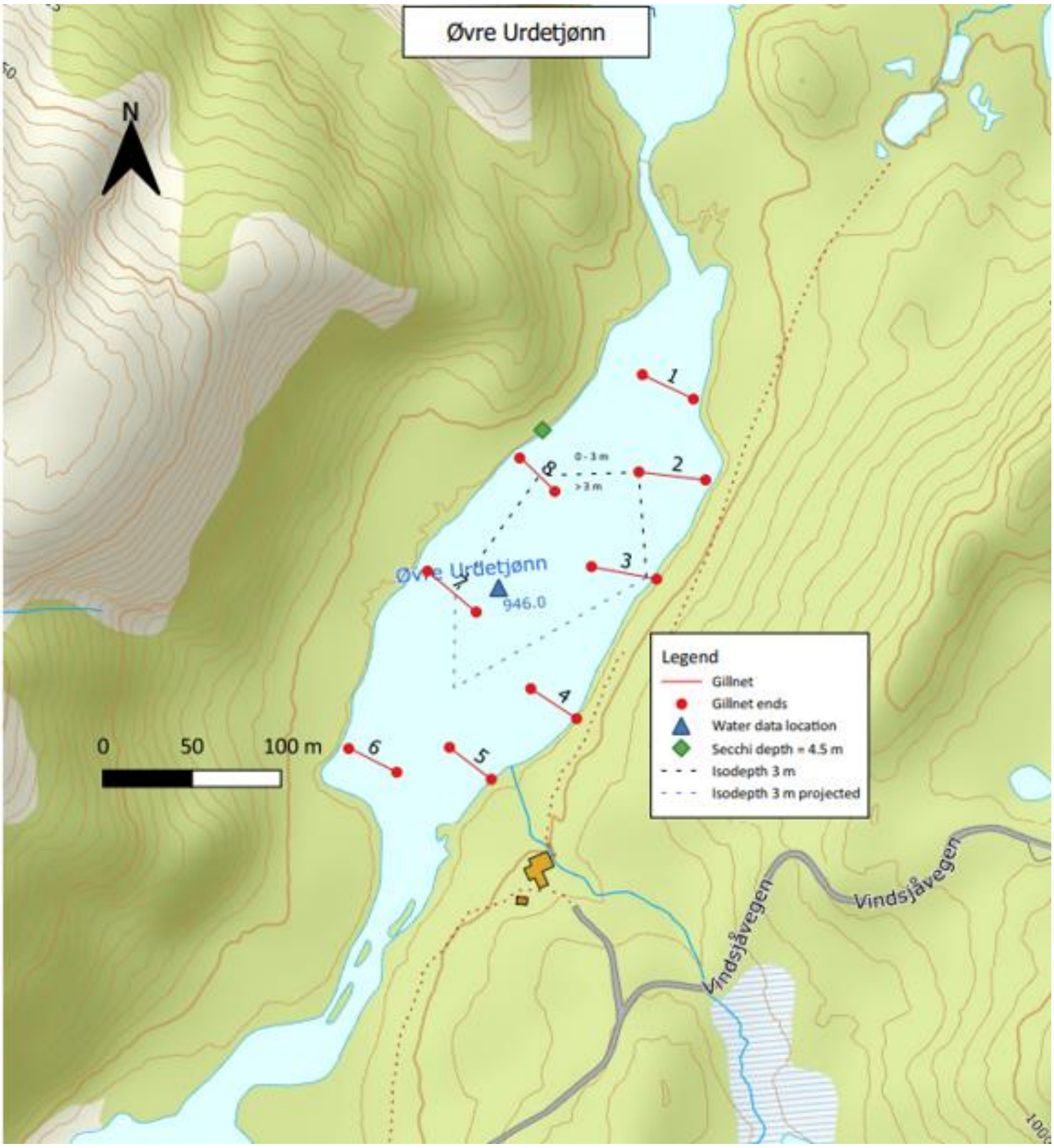


*Figure 3.1. L. Øvre Urdetjønn: locations of 2022 test fishery gillnets (with serial numbers) and water sampling sites. Location for Secchi depth probably reflects GPS imprecision. Apparent varying lengths of gillnets may be due to GPS imprecision or imperfectly set nets. Map generated in QGIS (2021).*

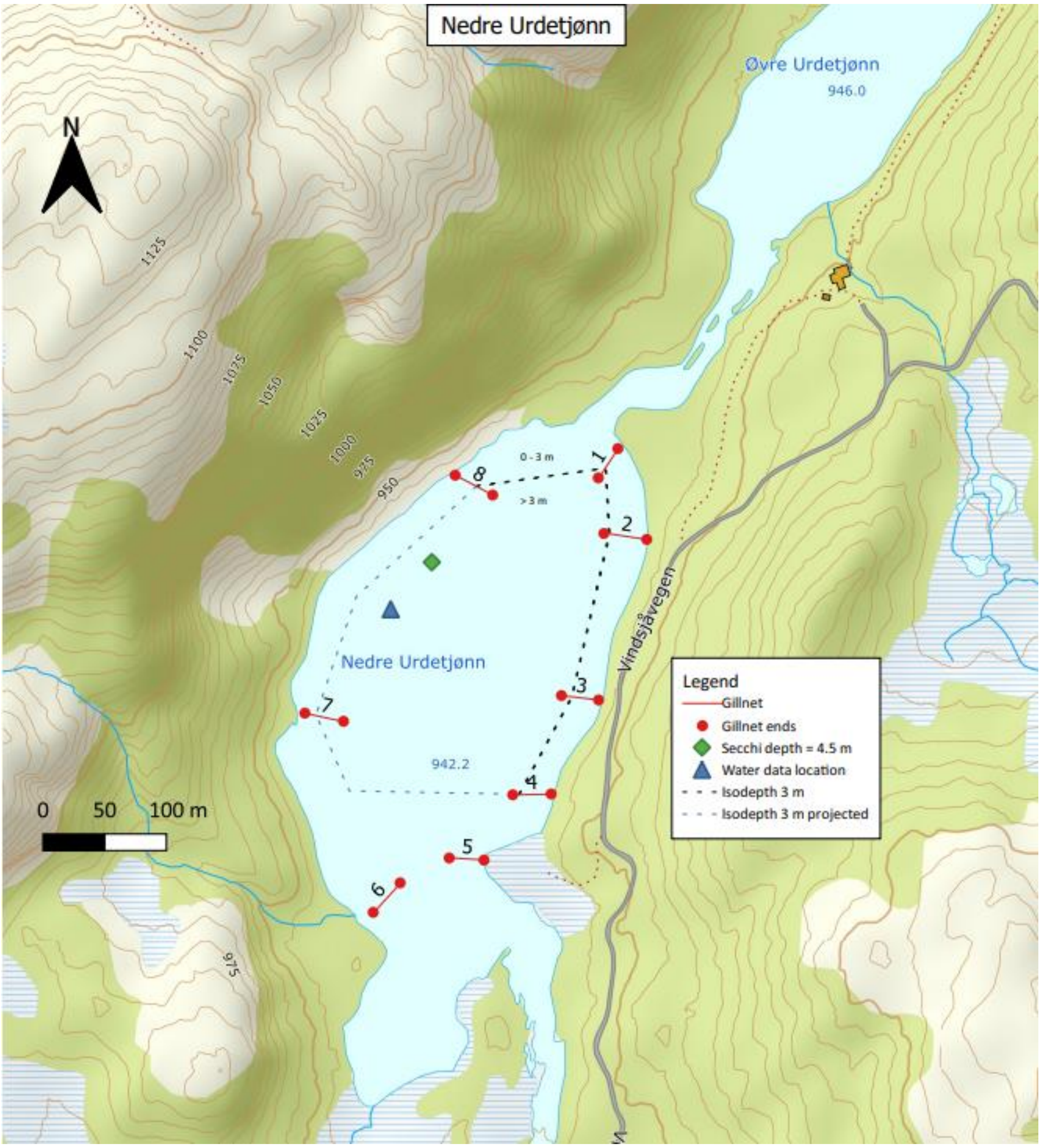


*Figure 3.2. L. Nedre Urdetjønn: locations of 2022 test fishery gillnets (with serial numbers) and water sampling sites. Apparent varying lengths of gillnets may be due to GPS imprecision or imperfectly set nets. Map generated in QGIS (2021).*

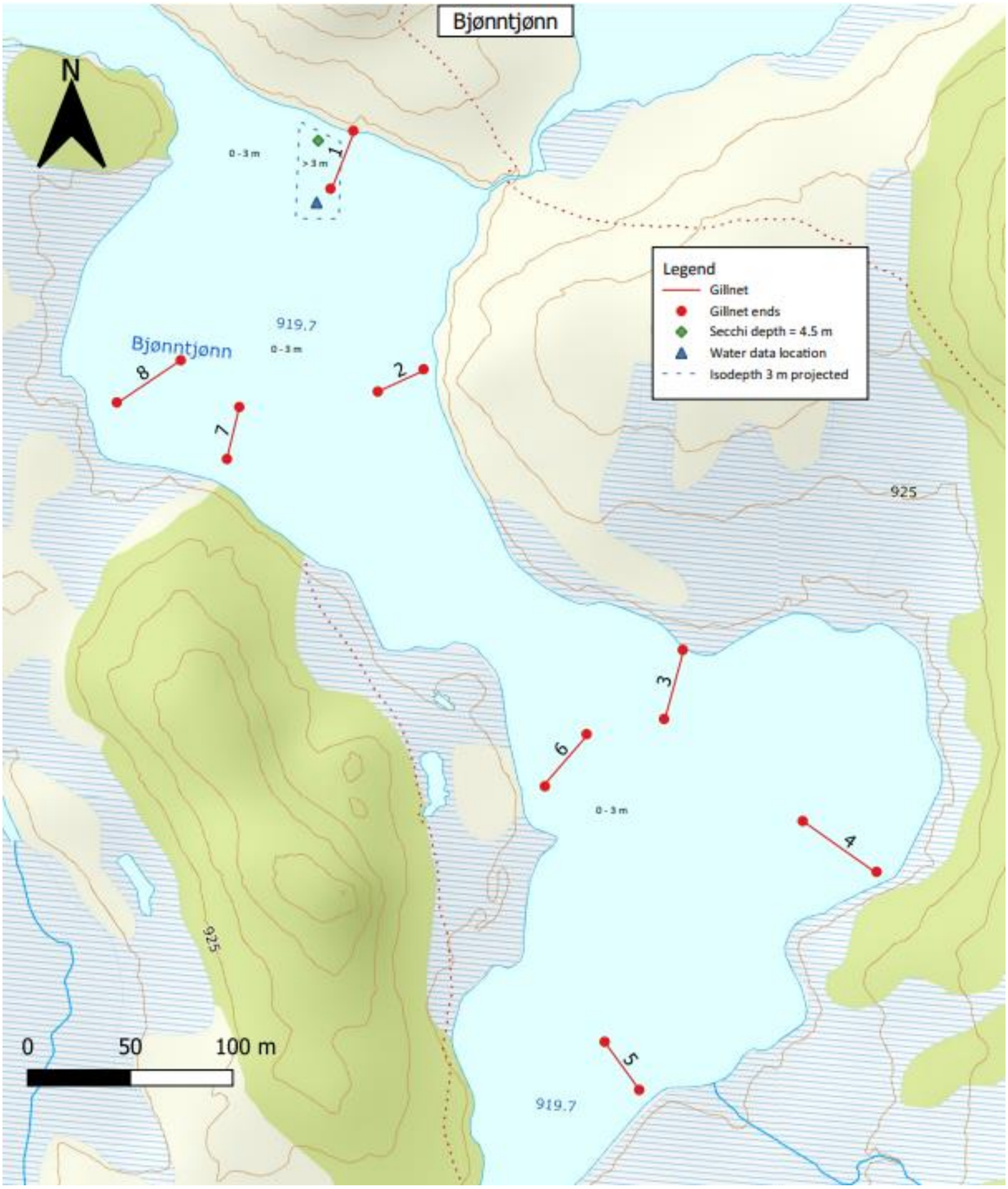


*Figure 3.3. L. Bjønntjønn: locations of 2022 test fishery gillnets (with serial numbers) and water sampling sites. Gillnet #4 set in location not used in the 2009 test fishery. Apparent varying lengths of gillnets may be due to GPS imprecision or imperfectly set nets. Map generated in QGIS (2021).*

The data from the multiparameter logger received post-field suggested certain operational and measurement problems. The end result was relatively little information from the full water column (especially for L. Bjønntjønn) and implausible conductivity data across the lakes that unfortunately had to be discarded altogether (A2 2.4). For reference, ranges of recorded conductivity values in µS/cm were: Øvre Urdetjønn 62 – 84, Nedre Urdetjønn 48 – 61, Bjønntjønn 94 – 128.

*Laboratory work*

In the laboratory, data on age, sex, maturation stage, stomach filling, and flesh color were collected from thawed, whole fish. Due to limited experience and for transparency, I implemented a system for quantified subjective evaluation of the process and quality of the data collected in the lab (A2 2.5). The main conclusions from this exercise were that my fish age estimates from all three lakes should be interpreted with caution, and that some of the data from Bjønntjønn (especially sex and maturation stage) unfortunately would have limited value in later analyses.

Individual length and weight measurements were repeated in the laboratory (A2 2.6), and the adipose fin was reassessed (and confirmed) for stock status. The field measurements (with one individual exception for length) were used in all analyses (A2 2.6).

For age determination (and subsequent analyses), otoliths were used (A2 2.7), in line with recommendation in NS-EN 14757. Otoliths were extracted from all individuals, and at least one per individual was burnt and cut in two with a scalpel. Before concluding on any individual’s age, the otolith-based estimates were compared to the body length in a non-blinded manner.

Determination of sex and sexual maturity was done according to a standard scheme (Fig. A1 3.2) (Miljølare.no, Undated): each fish was classified as being in one of several sex-specific maturation stages, corresponding primarily to gonads being shorter (values 1 – 2: immature) or longer (3 – 5: mature fish set to spawn this season) than half the length of the abdominal cavity (A2 2.8).

Stomach filling was assessed by visual and tactile assessment of food or remains thereof in the esophagus and ventricle. In this, I replicated the scale (values 0 – 5) used in the 1997 test fishery (this analysis was not done on the 2009 survey), with the value 0 corresponding to “empty”, and 5 to distended/bursting.

Flesh color was classified as white, light red, or red (A2 2.9).

## 3.4 Data analyses and displays

As indicated, I divided my analytical efforts in two main parts, reflected in the two separate Results chapters. In the first (chapter 4), the complete data from the 2022 test fishery were the basis when considering appropriate statistical and other analyses. For Bjønntjønn, low numbers and the mentioned data quality challenges limited some analytical options. In the second Results chapter (5), the 2022 data corrected for mesh size differences (below) were used for comparison with the previous gillnet test fisheries in the three lakes, reporting these results together across the three surveys. Although the latter is unconventional, I found it pedagogical and appropriate in this case. In chapter 5, I mostly replicated the structure, analyses and presentation modes from the previous gillnet test fishery reports. However, as those reports contain no statistical analyses or even measures of spread, I supplemented with some of these where relevant and possible (some individual fish data were available from 2009).

For all statistical analyses, I assumed that samples were random. Conventional significance levels ($\alpha = 0.05$) and confidence intervals (95 %) were applied. Parametric analyses (independent samples t-test or one-way analysis of variance, ANOVA) were run when assumptions were satisfactorily met (A2 3.1). When normal distribution was in doubt, I log- and square root-transformed (A2 3.1) one or both variables before considering a nonparametric alternative (two-sample Wilcoxon or Kruskal-Wallis). For one-way ANOVA with resulting P-value < 0.05, post-test multiple comparison of means analyses (Tukey tests) were run. For linear regression analysis, plots in Rcmdr NMBU were used to check assumptions and confidence intervals. For $\chi^2$ tests, critical values for the $\chi^2$ distribution were found in Statistical Table A in the cited textbook on the analysis of biological data (Whitlock & Schluter, 2020).

Figures and tables that I considered most central for the overall study hypothesis were included in the main text. Those I found to be of a more supplementary nature were placed in the Appendices. Generating figures and tables, I was conscious of the principle of “showing the data” (Whitlock & Schluter, 2020). However, in comparisons, especially when lacking individual data and/or with unbalanced sample sizes, I often found it more illustrative to use aggregates or relative numbers.

As prescribed in NS-EN 14757, the number per unit effort (NPUE) and weight (kg) per unit effort (WPUE) were calculated as arithmetic means of catches per gillnet night (2015a). Catch per unit effort (CPUE) was calculated from the number of fish caught per 100 $m^2$ (relevant) gillnet area per night (Hårsaker et al., 2021; Ugedal et al., 2005). Mean and variance of CPUE were calculated for the entire lake in each case (A2 3.2). For all comparisons of the 2022 test fishery with gillnet test fisheries using single-mesh Jensen series, the data correction guidelines of Ugedal and colleagues (2005) for such comparisons were applied to the best of my understanding (A2 3.3).

As the timing of fieldwork seemed relevant for some of the comparisons with the previous Upper Kova R. (and other end-of-season) test fisheries, I attempted to predict what mean length, weight and k-factor the fish caught in the 2022 test fishery might have had towards the end of the growth season. For this, I developed a simple projection model (A2 3.4); some results of putting the model to use were included in the Results.

Throughout the present study, I used standard nomenclature for reference to fish age: years were counted in lived winters, a +-sign added for post-summer catches (as in 0+ for summer-old fish) (A2 3.5). In the comparisons of growth (age-length) with the previous Upper Kova R. gillnet test fisheries, I replicated the approach from the 2009, with plots displaying mean length at age (empirical values) and maximum and minimum length of each age class represented by error bars.

To calculate k-factor, I used Fulton's formula:

$$K = 100W/L^3 \tag{3.1}$$

where K is condition, W is weight in grams and L length in centimeters (Nash et al., 2006).

In the linear regression analyses of length-weight relationships, I used the formula:

$$Log\ W = Log\ a + b\ Log\ L \tag{3.2}$$

where W is weight in grams, L is length in centimeters, and a (intercept) and b (slope) are constants (Borgstrøm & Hansen, 2000; Muddasir et al., 2018).

In the analysis of size at maturity based on the complete data from the 2022 test fishery (Tables A1 4.7-4.8), I defined the cohorts based on the 30 mm intervals used elsewhere in the present study.

Analyzing the data on stomach filling, I replicated the approach from 1997, reporting the proportion of the total catches per lake constituted by fish placed in category 0 (empty), and the mean value for the remaining fish (using the categories they were placed in (1 – 5) as numeric values).

As the complete data from the multiparameter water logger had limited information value (above), I selected the data sequences that seemed most realistic and representative for the water column per lake to generate conventional displays for each of the three reliable water variables plotted against depth (Figs. A1 4.13-4.15). Plots displaying water temperature and solar radiation (illuminance) (Michael et al., 2020) for the three lakes in the period June – October 2022 (Figs. A1 4.16-4.18) were generously provided by Heggenes (J. Heggenes, personal communication, December 8, 2022). The data for these were from loggers placed in the main inlet to Øvre Urdetjønn, and in the outlets of Nedre Urdetjønn and Bjønntjønn.

# 4 Results within and across the lakes 2022

In this first Results chapter, the current trout populations in the three lakes are characterized based on the complete data from the 2022 gillnet test fishery. When supplemented with data sets of the most important individual fish variables per lake (Tables A1 4.1-4.3), this provides benchmarks for future test fisheries with multi-mesh gillnets in these lakes. The most important results relative to the overall study hypothesis are presented first, i.e., estimates of abundance/density (total and per stock status), population structures of age and length, growth (age-length) and overall fish condition (k-factor). Next follows supplementary results, on fish distribution per depth stratum and catch per mesh size, fish weight, macro-parasite findings, k-factor per age, sex and macro-parasite status, sex and maturity, stomach filling and flesh color. Relatively few data especially for Bjønntjønn limited some analytical options.

## 4.1 Abundance/density, fish age, -size, -growth and -condition

*Overall catch summary: estimates on abundance and density*

The fishing effort in the 2022 test fishery in the three Upper Kova R. lakes was 8 gillnet-nights per lake, representing a randomized gillnet sampling area of 360 $m^2$ in Øvre Urdetjønn and Bjønntjønn and 345 $m^2$ in Nedre Urdetjønn (A2 2.1). Brown trout was the only species. The number of fish caught were 57 in Øvre Urdetjønn (2 of hatchery stock), 58 in Nedre Urdetjønn (0 of hatchery stock), and 23 in Bjønntjønn (1 of hatchery stock), the total fish weights were 4.9, 5.3, and 2.6 kilograms.

Overall, the catch results indicated that relative abundance was similar in Øvre- and Nedre Urdetjønn but lower in Bjønntjønn, and that density in numbers (abundance per lake surface area) was possibly higher in Øvre Urdetjønn than in the other two lakes (Discussion for caveats about the latter analysis mode).

*Fish number and weight per gillnet-night (NPUE and WPUE)*

The NPUE and WPUE (above) values for Bjønntjønn were about half of those for Øvre- and Nedre Urdetjønn, which were similar (Table 4.1). Overlaps in 95 % confidence intervals indicated substantial variation in the data. Statistical testing supported that NPUE was significantly lower for Bjønntjønn than for the other two lakes (one-way ANOVA: $F = 5.45$, $df = 2$, $P_{0.05} = 0.012$). No difference in WPUE was found among the lakes (Kruskal-Wallis (KW) $\chi^2 = 3.26$, $df = 2$, $P > 0.05$).

Correcting for lake surface area, mean NPUE and WPUE per hectare were highest for Øvre Urdetjønn, about three times higher than for Nedre Urdetjønn and five times higher than for Bjønntjønn (Table 4.1). Statistical testing showed significant differences among the lakes in both NPUE and WPUE per hectare lake surface area (NPUE per hectare lake surface area: KW $\chi^2 = 15.79$, df = 2, $P < 0.001$; WPUE per hectare lake surface area: KW $\chi^2 = 8.95$, df = 2, $P < 0.05$). Plots of means suggested that the significant difference in NPUE per hectare was for Øvre Urdetjønn compared to both other two lakes (Fig. A1 4.1), and in WPUE per hectare probably for Øvre Urdetjønn compared to Bjønntjønn (Fig. A1 4.2).

*Table 4.1. Three Upper Kova lakes: catches in number and weight per unit effort (NPUE and WPUE) based on the 2022 test fishery. NPUE: number of fish per gillnet-night, WPUE: weight (kg) of fish per gillnet-night. SD: standard deviation, CI: confidence interval. Per ha: NPUE and WPUE means/hectare lake surface area. FE (GnN): fishing effort, in gillnet-nights.*

| Lake | Variable | Mean | Min | Max | SD | 95 % CI | Per ha | n | FE (GnN) |
|---|---|---|---|---|---|---|---|---|---|
| Øvre Urdetjønn | NPUE | 7.1 | 3.0 | 13.0 | 3.1 | 4.5 - 9.7 | 2.23 | 57 | 8 |
| Nedre Urdetjønn | NPUE | 7.6 | 1.1 | 12.9 | 4.1 | 4.2 - 11.0 | 0.79 | 58 | 8 |
| Bjønntjønn | NPUE | 2.9 | 0.0 | 6.0 | 1.9 | 1.3 - 4.5 | 0.35 | 23 | 8 |
| Øvre Urdetjønn | WPUE | 0.6 | 0.2 | 1.1 | 0.3 | 0.3 - 0.9 | 0.19 | 57 | 8 |
| Nedre Urdetjønn | WPUE | 0.7 | 0.1 | 1.4 | 0.5 | 0.3 - 1.1 | 0.07 | 58 | 8 |
| Bjønntjønn | WPUE | 0.3 | 0.0 | 0.9 | 0.3 | 0.0 - 0.6 | 0.04 | 23 | 8 |

### *Relative abundance (mean catch per unit effort, CPUE)*

Relative abundance indicated by mean CPUE was significantly lower in Bjønntjønn and the same in the other two lakes (one-way ANOVA: F = 5.38, df = 2, $P_{0.05} = 0.013$). The slight difference from the NPUE results above were due to the somewhat smaller total gillnet area for Nedre Urdetjønn.

Mean CPUE per hectare lake surface area was highest for Øvre Urdetjønn, about three times higher than for Nedre Urdetjønn and five times higher than for Bjønntjønn (Table A1 4.4). Statistical testing indicated a significant difference among the lakes (KW $\chi^2 = 15.95$, df = 2, $P < 0.001$). A plot of means suggested that CPUE per hectare for Øvre Urdetjønn was different from both of the other lakes (Fig. A1 4.3).

### *Catch of stocked hatchery fish*

Most of the fish in the lakes were natural recruits, as judged from the catches. In all, only three individuals had a clipped adipose fin, i.e., were stocked hatchery fish, constituting 3.5% of the catch in Øvre Urdetjønn and 4.3% in Bjønntjønn. Age estimates for the stocked individuals in Øvre

Urdetjønn were 7 and 8 years (lengths 288 mm and 289 mm), and 3 years (length 160 mm) for the one in Bjønntjønn, the latter thus being born after the 2015 stocking cessation (Discussion).

*Fish age distributions*

The overall pattern in the age distributions was falling frequencies with increasing age but with some exceptions (Fig. 4.1). More specifically, the patterns looked bimodal for Øvre- and Nedre Urdetjønn (maximum at age 3-4 years, possible dip at 6, secondary mode 7-8 years), and perhaps unimodal for the bulk of the catch in Bjønntjønn (mode 4 years, i.e., not for the youngest class), with a few old outliers (Fig. 4.1). Ages ranged from 3 to 13 years, with the youngest classes dominating, especially in Bjønntjønn (ages 3 and 4 years combined: 60% of the catch in Øvre- and Nedre Urdetjønn, 80% in Bjønntjønn). Possible effects on the age structures from the cessation of stocking starting from 2015, i.e., signs of systematically reduced recruitment, were not directly evident in the data (Fig. A1 4.4).

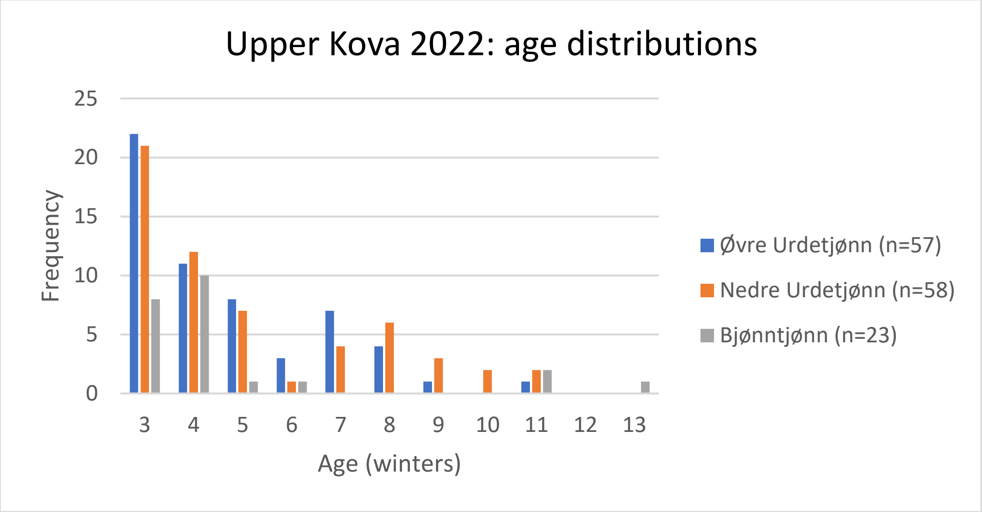
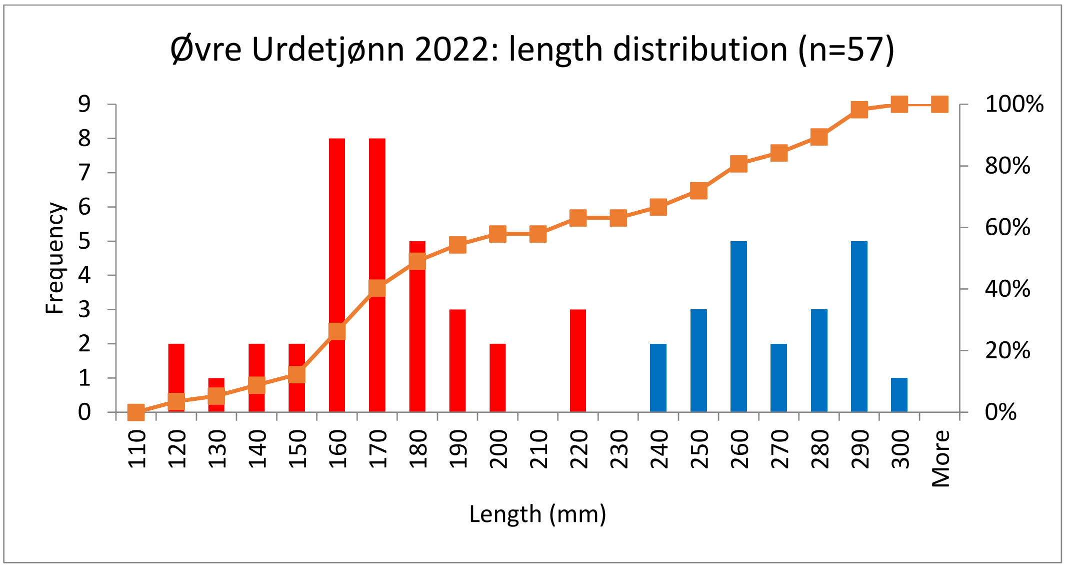
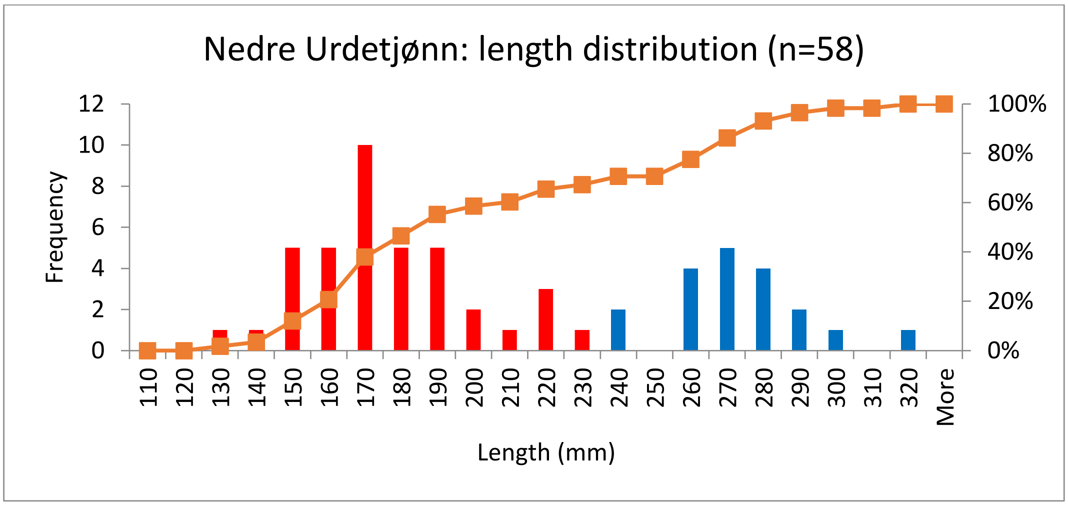


*Figure 4.1. Three Upper Kova lakes: frequency distributions of fish age based on the 2022 test fishery.*

*Fish length distributions*

The frequency distributions of fish lengths (Fig. 4.2) roughly mirrored the age distributions: bimodal tendencies for Øvre- and Nedre Urdetjønn (maximum mode 160-170 mm, minimum at ca. 210 mm, secondary mode at ca. 260 mm), and for Bjønntjønn, variable but roughly symmetric (mode 160 mm) for the bulk of the catch, with some long outliers. As for relative proportions of smaller to larger fish, the ratio < 240 mm : > 240 mm were about 2 : 1 in Øvre- and Nedre Urdetjønn, and 4 : 1 in Bjønntjønn. Median length was around 180 – 190 mm across the lakes (Fig. 4.2).





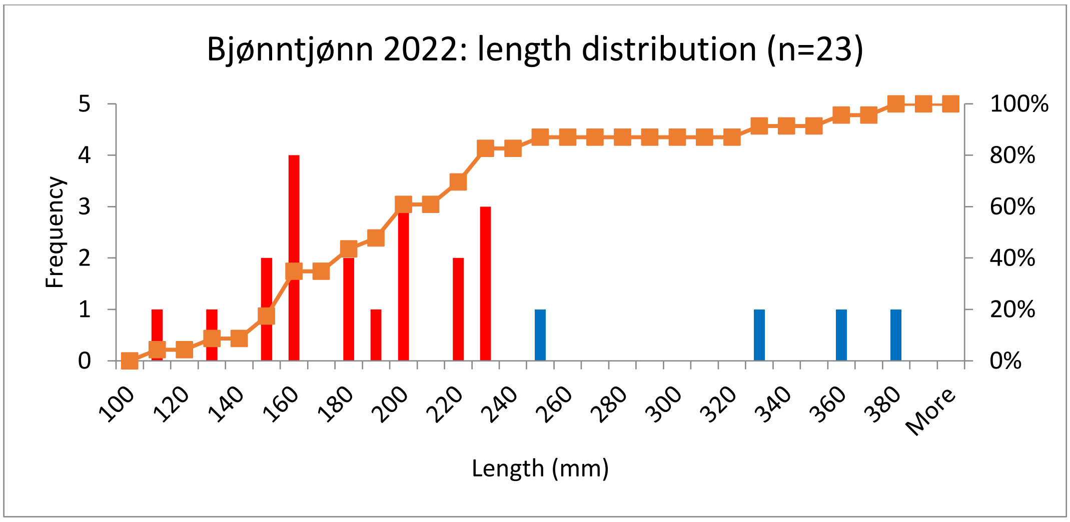


*Figure 4.2. Three Upper Kova lakes: frequency distribution of fish lengths based on the 2022 test fishery. Length intervals: 10 mm. The blue bars represent fish with lengths ≥ 240 mm, ~ "attractive size" based on my adaptation of Jensen, 1979. The cumulative curve (in orange) indicates the proportion of fish under/over a given length, 50 % corresponding to the median.*

*Fish growth*

Growth based on empirical age-length appeared broadly similar across the lakes, on average somewhat below a growth rate of 50 mm per year up to medium-range ages (6 – 7 years) and with slower growth (around or less than 20 mm per year) for fish older than this, at least for Øvre- and Nedre Urdetjønn (Fig. 4.3). However, the details revealed substantial variation that made further generalization across the lakes difficult, possibly influenced by few data (especially for Bjønntjønn) and unbalanced numbers for most age classes among the lakes (Table A1 4.5).

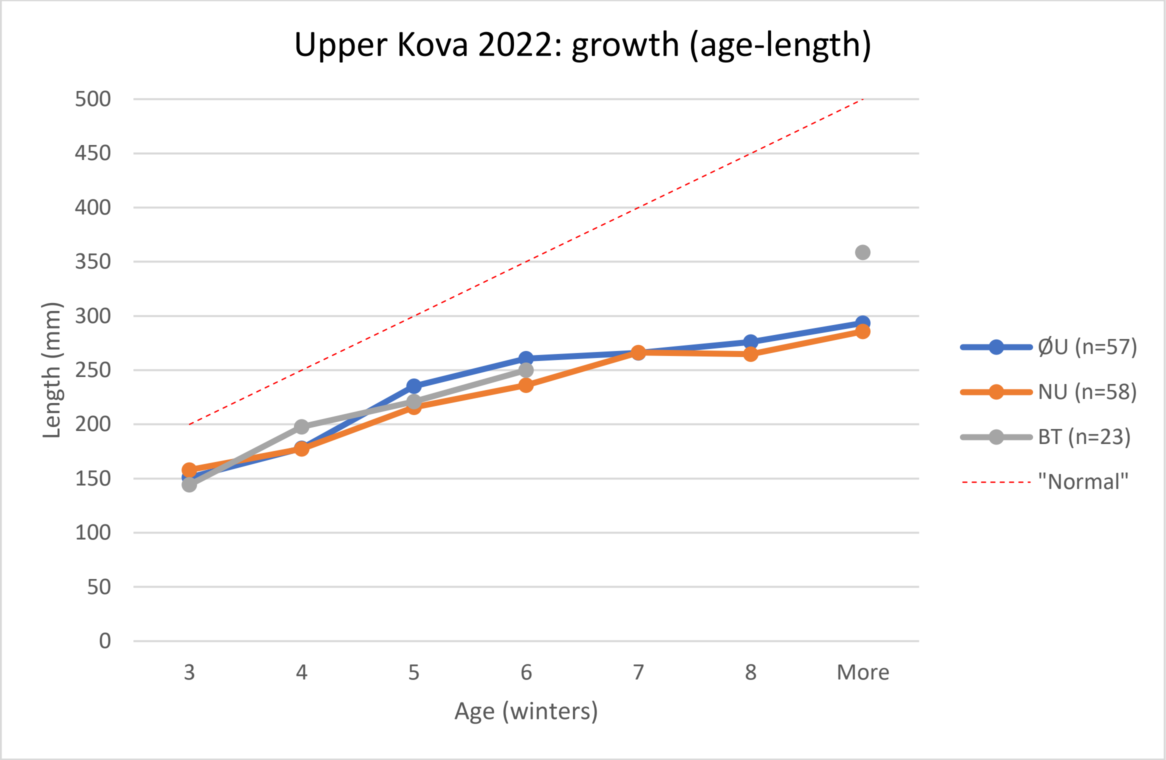


*Figure 4.3. Three Upper Kova lakes: growth (empirical age-length) based on the 2022 test fishery. Dots represent mean length for age class, joined with lines where consecutive age classed were represented in the catches. Red dashed line ("Normal"): stable growth rate of 50 mm/year. ØU: Øvre Urdetjønn, NU: Nedre Urdetjønn, BT: Bjønntjønn.*

The growth patterns were broadly similar for Øvre- and Nedre Urdetjønn but with considerable variation around mean lengths within some of the age classes, especially for Øvre Urdetjønn (Fig. A1 4.5, top and middle). These two lakes were similar in that the strongest growth was indicated from age 4 to 5 years (ca. 40 – 55 mm) and in that mean lengths were nearly identical between the lakes at age 3, 4, 7 and 11 years. Reduced growth was most pronounced from age 6 years in Øvre Urdetjønn and age 7 years in Nedre Urdetjønn. The data for Bjønntjønn were too few to generalize reliably about overall growth patterns, but they indicated that growth was strongest from age 3 to 4 years. If the few data points from age 4 years upwards should be close to representative for this lake, growth appeared to be quite stable, with an average rate of about 20 mm per year (Fig. A1 4.5, bottom).

Little difference was suggested between males and females in growth based on age-length (not reported, since the data for this analysis were few even from Øvre- and Nedre Urdetjønn).

Applying the projected end-of-season lengths (A2 3.4) would increase the mean length of most age classes, shifting the growth trajectories upwards towards the line indicating stable growth of 50 mm per year, especially evident for the youngest age classes (Fig. A1 4.6).

*Fish condition (k-factor)*

The k-factor (Formula 3.1) median value was under 1.0 per lake, with considerable spread especially in Øvre- and Nedre Urdetjønn (Fig. 4.4) but relatively narrow confidence intervals across the lakes (Fig. A1 4.7). K-factor for all fish was significantly lower in Øvre Urdetjønn than in Bjønntjønn (one-way ANOVA: F = 5.9, df = 2, P < 0.01).

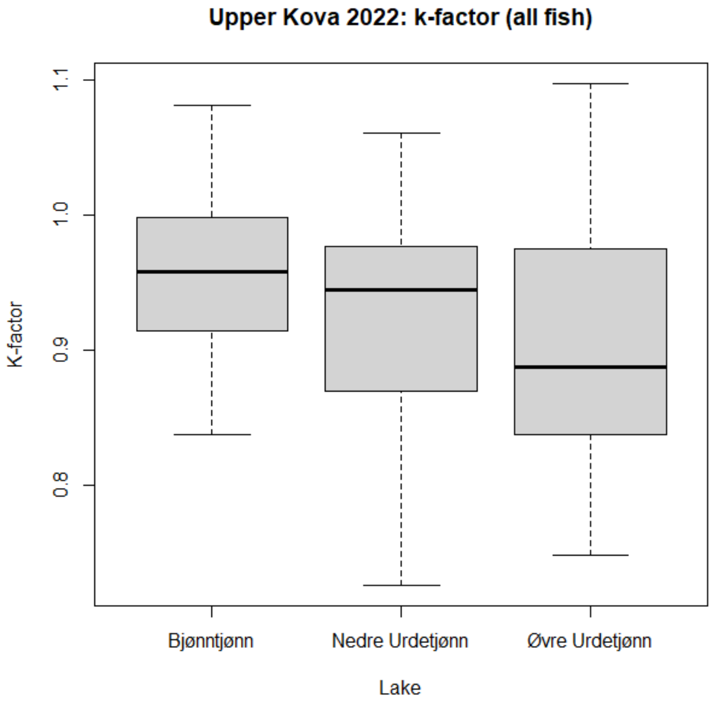


*Figure 4.4. Three Upper Kova lakes: k-factor of all fish per lake based on the 2022 test fishery. The line in the boxes represents the median, the walls the upper quartile (75% of the length values) and lower quartile (25% of the length values), and the lines the minimum and maximum lengths. Bjønntjønn: n=23, Nedre Urdetjønn: n=58, Øvre Urdetjønn: n=57.*

Tendencies of decreasing k-factor with length in Øvre- and Nedre Urdetjønn (Fig. 4.5) were statistically significant but with relatively little predictive power in linear regression analysis (Øvre Urdetjønn: F = 10.1 on 1 and 55 df, $P < 0.01$; adjusted $R^2 = 0.14$; Nedre Urdetjønn: F = 19.3 on 1 and 56 df, $P < 0.001$; adjusted $R^2 = 0.24$).

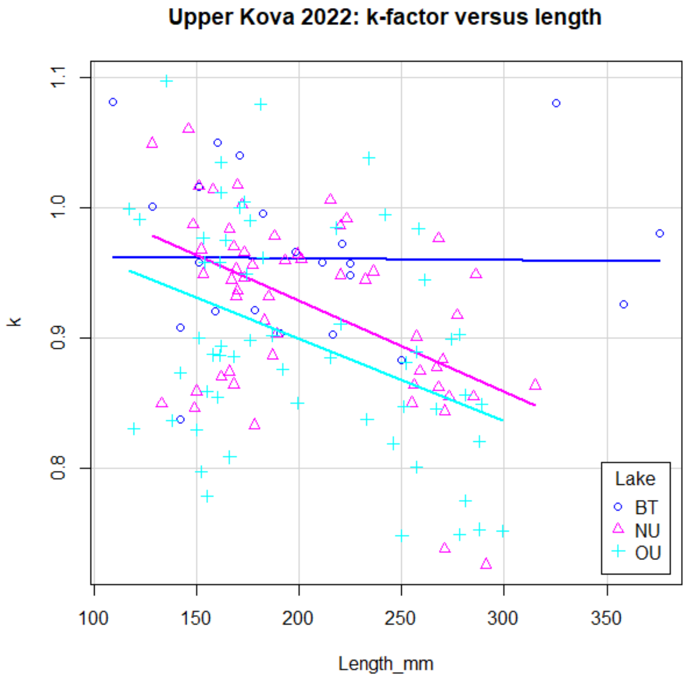


*Figure 4.5. Three Upper Kova lakes: k-factor versus length (mm) based on the 2022 test fishery. BT: Bjønntjønn (n=23), NU: Nedre Urdetjønn (n=58), OU: Øvre Urdetjønn (n=57).*

For k-factors of four fish size classes approximately balanced for numbers per lake (Table A1 4.6), statistical testing and post-test assessment indicated that the largest size class (> 250 mm) had the lowest k-factor within Øvre- and Nedre Urdetjønn, significantly lower than the class 160 – 190 mm in Øvre Urdetjønn (KW $\chi^2 = 14.0$, df = 3, $P < 0.01$), and possibly lower than all three other classes in Nedre Urdetjønn (KW $\chi^2 = 19.3$, df = 3, $P < 0.001$). The data for Bjønntjønn were too few for such formal analysis, but if anything, the means suggested an almost reverse situation there, with the largest size class having at least as high k-factor as the other classes in the lake (Table A1 4.6). Comparing the separate size classes across the lakes, k-factor of the largest fish class (> 250 mm) was significantly higher in Bjønntjønn than in the other two lakes (KW $\chi^2 = 7.1$, df = 2, $P_{0.05} = 0.028$) and there was no difference among the lakes in the k-factors of the other size classes (< 160 mm: KW $\chi^2 = 6.0$, df = 2, $P > 0.05$; 160-190 mm: KW $\chi^2 = 2.5$, df = 2, $P > 0.05$; 190-250 mm: KW $\chi^2 = 5.0$, df = 2, $P > 0.05$).

## 4.2 Supplementary results

*Depth distribution based on catch per depth stratum*

The catches of the 2022 test fishery indicated that fish were more abundant in the shallowest depth stratum (0 – 3 m) than in the deeper one (3 – 6 m) in Øvre- and Nedre Urdetjønn, judged by ratios over 1.0 when dividing the proportion of total fish caught in each depth stratum on the proportion of total gillnet area fishing in the corresponding stratum (Table 4.2). The results for Bjønntjønn should be interpreted with caution, due to low catch and small area with estimated depths 3 – 6 m.

Possible bias in population estimates that might result from disproportionate placement of gillnets relative to lake depths was also considered (Table 4.2: Gn area vs. Lake). These results indicated that a somewhat high proportion of the gillnets were set in the shallowest depth stratum in Nedre Urdetjønn (Table 4.2), but caveats must be made for low precision in this analysis.

*Table 4.2. Three Upper Kova lakes: fish distribution per depth based on the 2022 test fishery. Gn area: proportion of total gillnet area fishing in the respective strata. Catch: proportion of total catch caught in the respective strata. Lake: roughly estimated proportion of the lake with respective depths (Figs. 3.1-3.3).*

| Lake | Depth | Gn area (%) | Catch (%) | Catch/Gn area | Lake (%) |
|---|---|---|---|---|---|
| Øvre Urdetjønn | 0 - 3 m | 66 | 82 | 1.3 | 68 |
| Nedre Urdetjønn | 0 - 3 m | 70 | 79 | 1.1 | 56 |
| Bjønntjønn | 0 - 3 m | 94 | 87 | 0.9 | 97.5 |
| Øvre Urdetjønn | 3 - 6 m | 34 | 18 | 0.5 | 32 |
| Nedre Urdetjønn | 3 - 6 m | 30 | 21 | 0.7 | 44 |
| Bjønntjønn | 3 - 6 m | 6 | 13 | 2.1 | 2.5 |

*Catch per mesh size*

Catches per mesh size in terms of number, weight and lengths of fish were analyzed per single mesh size, and for number and weight through my adaptation of Jensen (1979) regarding “attractively sized fish” (above).

Catches per mesh size largely mirrored the reported length and weight distributions. In numbers caught, ratios for mesh sizes ≤ 19.5 mm : ≥ 24 mm were about 2 : 1 in Øvre- and Nedre Urdetjønn (highest number in 15.5 mm), and almost 3 : 1 in Bjønntjønn (highest number in 19.5 mm) (Table 4.3; Fig. A1 4.8, top). The larger mesh sizes (≥ 24 mm) caught the highest numbers of fish > 150 grams but less than a quarter of the total number per lake had achieved this weight at the time of the 2022 test fishery (Table 4.3). In biomass (total fish weight caught), the yield was largest in mesh size 24 mm in Øvre- and Nedre Urdetjønn, while no single mesh size stood out in Bjønntjønn (Fig. A1 4.8, bottom).

*Table 4.3. Three Upper Kova lakes: catch per mesh category (≤ 19.5 mm vs. ≥ 24 mm) in the 2022 test fishery. Catch of total number of fish (%) per mesh category and proportion (%) of fish within each mesh category with weights > 150 grams (fish of assumed "attractive weight" in accordance with Jensen, 1979.*

| | **Mesh size ≤ 19.5 mm** | | **Mesh size ≥ 24 mm** | | **All mesh sizes** |
|---|---|---|---|---|---|
| | **Of total** | **> 150 grams** | **Of total** | **> 150 grams** | **> 150 grams** |
| Øvre Urdetjønn | 65 % | 8 % | 35 % | 50 % | 23 % |
| Nedre Urdetjønn | 69 % | 5 % | 31 % | 67 % | 24 % |
| Bjønntjønn | 74 % | 6 % | 26 % | 33 % | 13 % |

Fish length and mesh size correlated significantly in linear regression analysis, but with rather low predictive power (Øvre Urdetjønn: F = 15.6 on 1 and 55 df, P < 0.001, adjusted $R^2$ = 0.21; Nedre Urdetjønn: F = 16.3 on 1 and 56 df, P < 0.001, adjusted $R^2$ = 0.21; Bjønntjønn: F = 5.3 on 1 and 21 df, $P_{0.05}$ = 0.03, adjusted $R^2$ = 0.16).

*Fish weights*

The frequency distributions of fish weight (Fig. A1 4.9) roughly mirrored the length distributions: bimodal tendencies for Øvre- and Nedre Urdetjønn (modes 40 – 60 grams and 170 – 180 grams), and for Bjønntjønn approximately uniform for the bulk of the fish (mostly with weights less than 100 grams), with a few outliers on the heavy end. The ratio of fish < 150 grams : > 150 grams was approximately 4 : 1 across the lakes. The high proportion of small fish (and a few substantially larger individuals) was reflected in median weight being around only 60 grams across the lakes (Fig. A1 4.9), as opposed to mean weights of 125 grams in Bjønntjønn and about 180 grams in the other two lakes.

*Macro-parasites in catches*

Macro-parasites *Eustrongylides sp.* (Fig. A1 4.10) were without systematic scrutiny observed in the abdominal cavity of four female fish in Øvre Urdetjønn, and in eight fish (four of each sex) in Nedre Urdetjønn.

*K-factor per age, sex and relative to parasite status*

Tendencies of decreasing k-factor with age in Øvre- and Nedre Urdetjønn (Fig. A1 4.11) were statistically significant but with modest predictive power in linear regression analysis (Øvre Urdetjønn: F = 13.9 on 1 and 55 df, P < 0.001; adjusted $R^2$ = 0.19; Nedre Urdetjønn: F = 26.3 on 1 and 56 df, P < 0.001; adjusted $R^2$ = 0.31).

There was no difference in k-factor between males and females within Øvre- and Nedre Urdetjønn, judged from independent samples t-test (Welch test) (Øvre Urdetjønn: $t = 0.48$, $df = 52.7$, $P > 0.05$; Nedre Urdetjønn: $t = 0.03$, $df = 53.7$, $P > 0.05$). This analysis was omitted for Bjønntjønn due to low numbers and larger uncertainty in sex determination (above).

Mean k-factor of the fish with detected macro-parasites was lower than for the assumed non-infected fish, statistically significant for both Øvre Urdetjønn (Two-sample Wilcoxon: $W = 166$, $P_{0.05} = 0.04$) and Nedre Urdetjønn (Two-sample Wilcoxon: $W = 326$, $P < 0.01$).

*Sex ratios and sexual maturity*

An overweight of females in Øvre Urdetjønn (ratio 1.3) and of males in Nedre Urdetjønn (ratio 1.2) was indicated by the 2022 test fishery (Fig. 4.6). In both lakes, empirical age and size ranges of mature fish were wider for males than for females (Table 4.4).

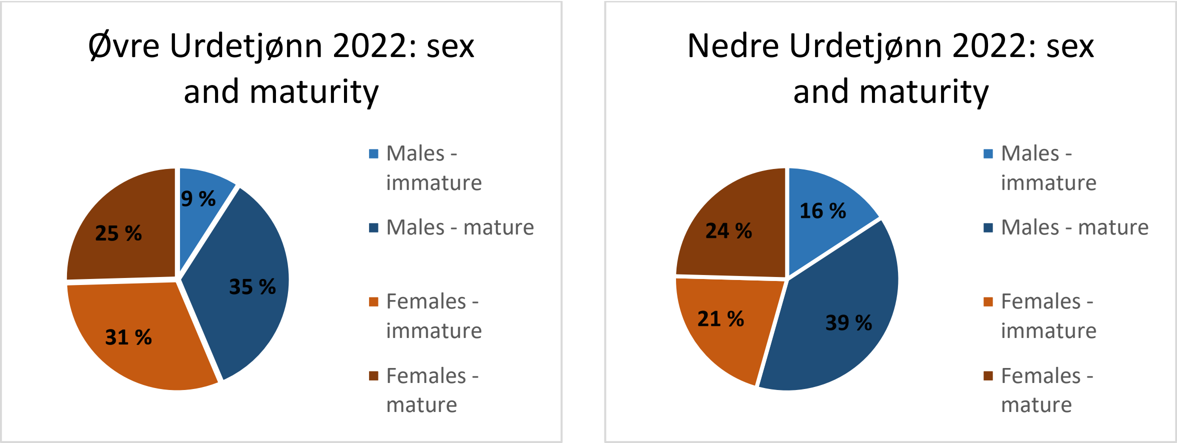


*Figure 4.6. Two Upper Kova lakes: proportion of males and females and maturity status (% within pie slices) of total catch based on the 2022 test fishery. Øvre Urdetjønn: n=55, Nedre Urdetjønn: n=57.*

*Table 4.4. Øvre Urdetjønn (ØU) and Nedre Urdetjønn (NU): maturity status (proportion in % of total within sex) with associated ranges of length and age based on the 2022 test fishery.*

| **ØU** | **Immature** | | | | **Mature** | | | |
|---|---|---|---|---|---|---|---|---|
| **Sex** | **n** | **Prop. (%)** | **Length (mm)** | **Age (years)** | **n** | **Prop. (%)** | **Length (mm)** | **Age (years)** |
| Male | 5 | 21 | 117-199 | 3-4 | 19 | 79 | 135-299 | 3-11 |
| Female | 17 | 55 | 119-261 | 3-7 | 14 | 45 | 218-288 | 5-9 |
| **NU** | **Immature** | | | | **Mature** | | | |
| **Sex** | **n** | **Prop. (%)** | **Length (mm)** | **Age (years)** | **n** | **Prop. (%)** | **Length (mm)** | **Age (years)** |
| Male | 9 | 29 | 146-215 | 3-5 | 22 | 71 | 158-315 | 3-11 |
| Female | 12 | 46 | 128-223 | 3-5 | 14 | 54 | 178-291 | 4-9 |

Defining onset of maturity as the size (30 mm intervals/classes) or age at which 50% of a cohort is mature, earlier maturity in males compared to females was indicated for both Øvre Urdetjønn (onset in males at 130-160 mm/3 years, in females at 190-220 mm/5 years) (Tables A1 4.7 and A1 4.9) and for Nedre Urdetjønn. For the latter lake, the data indicated smaller sex differences in age at maturity (onset in males at 160-190 mm/3 years, in females at 220-250 mm/4 years) (Tables A1 4.8-4.9). Caveats must be made for the scarcity of data in these analyses, especially for size at maturity.

For Bjønntjønn, the only reasonably certain data on sex and maturity were (at least) two mature females and one mature male, all three among the longest and oldest fish in the catch made in this lake.

### *Stomach filling*

According to the analysis on stomach filling, eating just prior to being caught in the 2022 test fishery was apparently most prominent in Nedre Urdetjønn, and least so in Bjønntjønn (Table 4.5).

*Table 4.5. Three Upper Kova lakes: stomach filling in the 2022 test fishery. Stomach filling: the degree to which the esophagus and the ventricle contained food, ranging from 0 (empty) to 5 (distended/bursting). Proportion (%) with value 0 in the total catch. Mean: arithmetic mean of values for fish with food in the stomach (value range 1-5).*

| | **Empty (0)** | | **Remaining (1-5)** | | |
|---|---|---|---|---|---|
| **Lake** | **n** | **Proportion (%)** | **n** | **Mean** | **Total catch** |
| Øvre Urdetjønn | 8 | 14 | 49 | 2.2 | 57 |
| Nedre Urdetjønn | 3 | 5 | 55 | 2.3 | 58 |
| Bjønntjønn | 6 | 26 | 17 | 1.4 | 23 |

### *Flesh color*

The 2022 test fishery indicated that over 90% of the fish per lake could have white flesh, with small differences among the lakes; the only individual classified as having red flesh was the largest individual in the catches (Table A1 4.10). The probability of having non-white flesh appeared to increase with length, which was significantly higher for fish with light red flesh than with white flesh in both Øvre Urdetjønn (Two-sample Wilcoxon: W = 42, P < 0.05) and Nedre Urdetjønn (Two-sample Wilcoxon: W = 29, P < 0.05).

## 4.3 Physical conditions: water quality variables and depths

Overall, the results on water quality were as expected for the latitude and season in small, shallow and oligotroph mountain lakes in a regulated river with residual flow. As for assumed major influences on the residual flow in 2022, the averaged air temperatures in the Kova R. region were above normal from January through March, and about normal from May to mid-October, while precipitation was mostly substantially below normal from January to July (Fig. A1 4.12).

Visibility judged with Secchi disk was approximately 4.5 meters across the lakes, with modest lake depth as a possibly limiting factor for measurement of maximal visibility in Bjønntjønn. The ranges of water temperature, dissolved oxygen (mg/L and saturation), and pH recorded by multiparameter logger in the 2022 test fishery (1-2 attempts per lake) were largely similar across the lakes when differing maximum water depths are taken into account (Table 4.6, Figs. A1 4.13-4.15).

*Table 4.6. Three Upper Kova lakes: water quality (value ranges) based on the 2022 test fishery. Measurements made with multi-parameter logger with 1-2 attempts per lake. DO: dissolved oxygen. *: excluding one aberrant lower value. Conductivity not reported due to implausible values registered.*

| | **Temp (° C)** | | **DO (mg/L)** | | **DO (%)** | | **pH** | | **Depth (m)** |
|---|---|---|---|---|---|---|---|---|---|
| **Lake** | **Min** | **Max** | **Min** | **Max** | **Min** | **Max** | **Min** | **Max** | **Max** |
| Øvre Urdetjønn | 10.8 | 12.6 | 7.9* | 9.8 | 72* | 91 | 6.4 | 6.8 | 6.6 |
| Nedre Urdetjønn | 9.1 | 13.0 | 8.2 | 9.8 | 71 | 91 | 6.3 | 6.8 | 9.2 |
| Bjønntjønn | 12.1 | 13.9 | 9.4 | 9.7 | 88 | 91 | 6.6 | 6.8 | 4.4 |

The devices logging water temperature and solar radiation (illuminance) in the period June – October 2022 were positioned in the main inlet to Øvre Urdetjønn, and in the main outlets of the other two lakes, in similar locations as in 2017 – 2019. The plotted data for 2022 (J. Heggenes, personal communication, December 6, 2022) showed water temperatures with similar outer bounds for the three locations: 7 – 8 °C (approximate daily mean) at the start of June, rising to a maximum of 20 – 21 °C sometime in the summer, and falling to a minimum of about 3 °C at the end of October (Figs. A1 4.16-4.18). Two types of water temperature fluctuations were evident: diurnal, and some broader dips reflecting processes stretching over days or weeks. The diurnal fluctuations appeared to be strongest at the Nedre Urdetjønn location (Fig. A1 4.17).

# 5 Results across time: 2022 versus 2009 and 1997

In this chapter, results from our test fishery in 2022 are compared to the Upper Kova R. gillnet test fisheries in 2009 and 1997 to assess possible temporal changes in population dynamics, contrasting thus also the current situation with presumed exclusive natural recruitment to situations with natural recruitment supplemented by stocking. Here, it was natural to largely replicate the analyses, structure and formats of the reports from those surveys (2010, 1998). For these comparisons, the 2022 data had to be corrected because of the different gillnet types used (primarily the lack of mesh size < 21 mm in 2009/1997), and the consequence was that about 1/3 of the catches in Øvre- and Nedre Urdetjønn and 1/4 of the catch in Bjønntjønn in 2022 were excluded from all analyses in this chapter. As I strived to present these comparative data without much reflection about possible explanations for the observed phenomena, I classified it as a results chapter, seeing it as an appropriate bridge to the subsequent Discussion.

The limited sampling effort across time (~ 8 gillnet-nights per lake in all three surveys) and the earlier timing of the 2022 test fishery should be kept in mind throughout the chapter. As mentioned, I tried to develop a model that corrected for the seasonal factor (A2 3.4) and illustrate briefly the outcome of its use in some of the sections below. As in the previous Results chapter (4), Bjønntjønn is not necessarily mentioned when the combination of relatively few and somewhat uncertain data from 2022 (A2 2.5) provided a too weak basis for analysis and assessments. Lack of individual fish data from the 1997 test fishery limited the options for statistical comparisons with this survey.

## 5.1 Characterization of the brown trout populations based on catches

*Characterization and classification according to Ugedal et al. (2005)*

The classification principles of Ugedal and colleagues (2005) for density and for achievable fish size (reflecting growth conditions) were used to analyze the relevant data from the three gillnet test fisheries in the three Upper Kova R. lakes.

Comparing 2022 to the previous test fisheries, the numbers indicated that relative abundance (mean CPUE) was currently higher in Øvre- and Nedre Urdetjønn and lower in Bjønntjønn, the latter especially when compared to 2009 (Table 5.1). Classes of density (based on CPUE), catch and yield (*utbytte*) per lake were mostly the same across the years; exceptions to this, when comparing 2022 to the previous test fisheries, were that density appeared to be higher in Øvre Urdetjønn, catch in numbers lower in Nedre Urdetjønn, and yield in weight (much) lower in Bjønntjønn (Table 5.1). All three lakes appeared to have growth conditions apt to produce medium size fish (25 – 35 cm) over time, judged from the relatively sparse available data (Table A1 5.1).

*Table 5.1. Three Upper Kova lakes: density classifications (Ugedal et al., 2005) based on catches in three gillnet test fisheries. CPUE: mean number of fish per 100 m² relevant gillnet area. Number of fish and weight (kg): catch per standard Jensen series/8 multi-mesh gillnets (corrected data).*

| **Lake** | **Year** | **CPUE** | **Density class** | **Number of fish** | **Catch class** | **Weight (kg)** | **Yield class** |
|---|---|---|---|---|---|---|---|
| Øvre Urdetjønn | 2022 | 21.0 | Dense | 44 | Medium | 4.1 | Medium |
| Øvre Urdetjønn | 2009 | 6.3 | Medium | 19 | Medium | 2.8 | Medium |
| Øvre Urdetjønn | 1997 | 11.3 | Medium | 34 | Medium | 4.8 | Medium |
| Nedre Urdetjønn | 2022 | 21.9 | Dense | 44 | Medium | 4.7 | Medium |
| Nedre Urdetjønn | 2009 | 15.7 | Dense | 47 | High | 6.9 | Medium |
| Nedre Urdetjønn | 1997 | 17.0 | Dense | 51 | High | 6.7 | Medium |
| Bjønntjønn | 2022 | 8.1 | Medium | 17 | Medium | 1.8 | Low |
| Bjønntjønn | 2009 | 14.7 | Medium | 44 | Medium | 8.7 | High |
| Bjønntjønn | 1997 | 9.3 | Medium | 28 | Medium | 4.8 | Medium |

Based on the combined results for density and achievable size/growth conditions per survey, the three lakes would be placed in the Ugedal system’s (Fig. 5.1) middle category *E* (Øvre Urdetjønn in 2009 and 1997, and Bjønntjønn in all three surveys) or the category *F* (Øvre Urdetjønn in 2022, Nedre Urdetjønn in all three surveys).

For lakes in category *E*, the recruitment is described as “satisfactory”, but growth may be limited by scarcity of larger prey; in category *F*, “recruitment conditions” are “good”, and there is an “acceptable” (*brukbar*) balance between the amount of recruitment and food production. In both categories, fish longer than 300 mm can be common but weight over one kilogram rare. Conditions in category *E* lakes are commonly seen in Norway, both in the high- and lowlands. In category *F*, brown trout is often the only fish species (Ugedal et al., 2005).

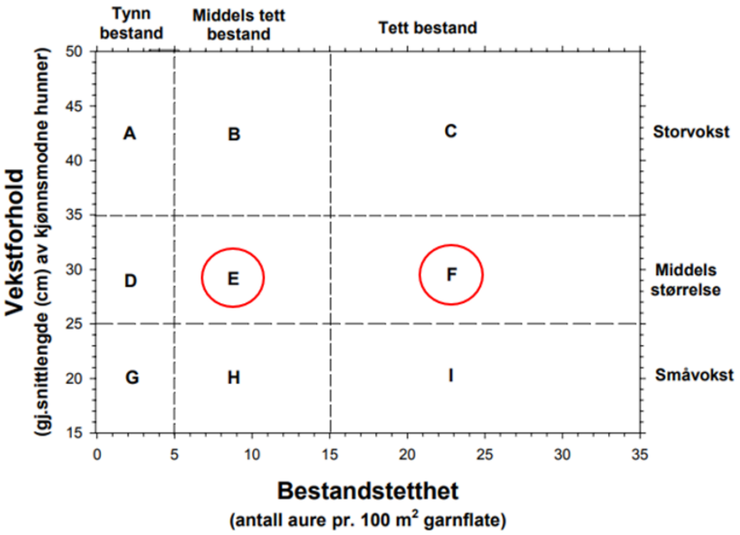


*Figure 5.1. Brown trout lake categories in Ugedal et al. (2005, Fig. 16) based on density and growth conditions. X-axis: density (number of trout per 100 m² gillnet area; thin, medium, dense); Y-axis: growth conditions reflected in medium length (cm) of mature females (large, medium, small). Categories assigned to the Upper Kova lakes on the basis of results from the test fisheries across time ringed in red.*

### *Classification according to the Water Framework Directive (WFD)/Vannforskriften*

The same analysis for WFD environmental classification as above (for 2009/1997) was applied to the corrected data from the 2022 test fishery. The mean CPUE for the lakes combined (CPUE = 16.9) dictates *very good* ecological potential, in other words, apparently better than the current official classification *good* (Vann-Nett portal, 2022). Per lake, the corrected CPUEs correspond to *very good* ecological potential for Øvre- and Nedre Urdetjønn, and *moderate* potential for Bjønntjønn. Compared to the calculated CPUEs for the previous gillnet test fisheries, the 2022 results would appear to dictate a better status for Øvre Urdetjønn, the same status for Nedre Urdetjønn, and a worse (versus 2009) or the same (versus 1997) status for Bjønntjønn.

### *Catch per mesh size category (numbers and weight)*

Catches per mesh size were analyzed for number (relative, i.e., proportion of total catch) and weight of the fish, as in the previous survey reports. To allow comparison across the test fisheries, the mesh sizes of the two different types of gillnets used were placed in six different categories (Table 5.2). The gillnet area per mesh category was 20% larger in 2009/1997 than in 2022.

*Table 5.2. Mesh size categories (A-F) for comparison of catches with different gillnet types. Categories based on Ugedal et al., 2005, used in this study for comparisons between Nordic multi-mesh gillnets (2022) and standard Jensen series (2009/1997).*

| Year | A | B | C | D | E | F |
|---|---|---|---|---|---|---|
| 2022 | 15.5 mm & 19.5 mm | 24 mm | 29 mm | 35 mm | 43 mm | 55 mm |
| 2009/1997 | 21 mm & 21 mm | 26 mm | 29 mm | 35 mm | 39 mm | 45 mm & 52 mm |

Overall, the catches per mesh size category reflected reported population structures, as expected. In terms of relative number of fish caught per mesh category, the patterns were similar in 2022 and the two previous gillnet test fisheries in Øvre- and Nedre Urdetjønn: in $\chi^2$ goodness of fit testing with three alternatives per lake, a null hypothesis of no difference was not rejected in eight out of nine alternatives (Table A1 5.2). Empirically, the highest proportion of fish was caught in the smallest mesh category (A) in all cases, except in Øvre Urdetjønn in 2009 (Fig. A1 5.1).

There was considerable empirical variation across the test fisheries and lakes in terms of fish weight per mesh category. However, when the results of the three gillnet surveys were summed up, there was a clear tendency that each of the three smallest categories (≤ 29 mm) yielded more (by a factor of about 3 – 5) than each of the three largest categories (Table A1 5.3).

*Catch of stocked hatchery fish*

The Upper Kova R. gillnet test fisheries suggested that recruitment was primarily natural even when there was supplementary stocking, reflected in the mostly low proportion (< 10%) of hatchery-stock trout in the catches across the lakes and per survey (Table A1 5.4). In the 2022 test fishery, the proportion of hatchery stock was lower than the combined mean for 2009 and 1997 (representing the period with supplementary stocking) across the lakes (Table A1 5.4).

## 5.2 Analyses based on individual fish data

*Fish length and weight: proportion of fish < 220 mm, mean weight and k-factor*

Comparing the observed results from 2022 to the previous test fisheries for aspects of the variables length, weight and k-factor highlighted in those surveys, there was a higher proportion of small fish in Øvre Urdetjønn and Bjønntjønn in 2022, and mean fish weight and k-factor was currently lower in all three lakes (Table 5.3). The numbers in parenthesis in Table 5.3 represent the outcome of putting to use the second version of the model developed to project end-of-season lengths and weights (A2 3.4). To exemplify how these projections might be interpreted, about 35 – 66% of the per-lake difference in mean fish weight between the gillnet test fisheries in 2022 and 2009/1997 might be "explained" by the timing of the fieldwork (Table A1 5.5).

*Table 5.3. Three Kova lakes: length, weight, and k-factor based on three gillnet test fisheries. Numbers in parentheses are projections based on an attempt to correct for the early timing of the 2022 test fishery. Results for 2009 and 1997 are from tables in report from the former (2010), * indicates that clearly erroneous results in the 2010 tables have been replaced here with the correct values provided elsewhere in that report.*

| Lake | Year | Proportion < 220 mm (%) | Mean weight (grams) | Mean k-factor | n |
|---|---|---|---|---|---|
| Øvre Urdetjønn | 2022 | 59 (43) | 92 (120) | 0.90 (0.96) | 44 |
| Øvre Urdetjønn | 2009 | 47 | 148 | 1.20 | 19 |
| Øvre Urdetjønn | 1997 | 49 | 141 | 0.99 | 34 |
| Nedre Urdetjønn | 2022 | 59 (48) | 102 (126) | 0.91 (0.96) | 44 |
| Nedre Urdetjønn | 2009 | 63 | 147 | 1.16 | 47 |
| Nedre Urdetjønn | 1997 | 60 | 131 | 0.99 | 51 |
| Bjønntjønn | 2022 | 71 (64) | 108 (138) | 0.96 (1.04) | 17 |
| Bjønntjønn | 2009 | 41* | 218 | 1.06* | 44 |
| Bjønntjønn | 1997 | 32 | 170 | 0.99 | 28 |

### *Fish lengths*

Comparing the 2022 catches (in mid-June) to the other two gillnet test fisheries (in primo September/ultimo August), observed fish lengths were currently mostly shorter, reflected in mean and range, and partly in the proportion constituted by the smallest of three fish size classes defined in the previous test fisheries (Table A1 5.6). However, comparing 2022 to 2009 with two-sample Wilcoxon tests, the fish were currently significantly shorter only in Bjønntjønn (Bjønntjønn: W = 543.5, $P_{0.05}$ = 0.007; Øvre Urdetjønn: W = 517.5, $P_{0.05}$ = 0.14; Nedre Urdetjønn: W = 1048, $P_{0.05}$ = 0.91).

The lower proportion of the largest size class (> 250 mm) in the 2022 test fishery in Bjønntjønn stood out in the comparative empirical size results (ca. 10% versus almost 50%) (Table A1 5.6). Converting proportions to counts and running Fisher's Exact Tests, a significant difference among the three gillnet test fisheries based on the three size classes was indicated for Nedre Urdetjønn (Øvre Urdetjønn: $P_{0.05}$ = 0.19, Nedre Urdetjønn: $P_{0.05}$ = 0.03, Bjønntjønn: $P_{0.05}$ = 0.064).

Although there was a general tendency of decreasing frequencies with length across the lakes and surveys, there were several exceptions to this (below) when the distributions were displayed with the 30 mm intervals used in the reports from the previous test fisheries (Fig. A1 5.2).

Across the gillnet test fisheries in Øvre Urdetjønn, few individuals > 300 mm were caught, and the proportion of fish < 190 mm was highest in 2022 (ca. 50% versus < ca. 15% in 2009/1997) (Fig. A1 5.2, top). The length distributions appeared bimodal in 2022 and 1997 (modes in 2022: 160-190 mm and 250-280 mm; modes in 1997: 190-220 mm and 250-280 mm), in both years with the highest proportion in the smaller length classes. For 2009, the distribution looked more symmetric except for one possible outlier in the 310-340 mm interval but the catch was relatively low (Fig. A1 5.2, top).

In Nedre Urdetjønn, the proportion of fish > 300 mm was also low overall across the gillnet test fisheries, but a few larger individuals were caught in 2009; the proportion of fish < 190 mm was similar in 2022 and 2009 (ca. 50%) and higher than in 1997 (ca. 15%) (Fig. A1 5.2, middle). The length distributions for 2022 and 1997 appeared bimodal also for this lake (modes in 2022: 160-190 mm and 250-280 mm; modes in 1997: 250-280 mm and 190-220 mm). The pattern for 2009 was asymmetric, with a positive skew and long tail (Fig. A1 5.2, middle).

In Bjønntjønn, the proportion of fish > 300 mm caught in the 2022 and 2009 (especially) surveys was higher than in the other two lakes; the proportion of fish < 190 mm was higher in 2022 (ca. 40%) than in the other two surveys (< 20%) (Fig. A1 5.2, bottom). For 2022, the length distribution of most individuals (up to 250 mm) was roughly symmetric (mode 190-220 mm), with a couple of larger individuals. In comparison, the length distributions for 2009 and 1997 were asymmetric, possibly bimodal, with the highest proportion in the interval 190-220 mm for both surveys (Fig. A1 5.2, bottom).

### *Fish weights*

Comparing the 2022 test fishery to the 2009 survey, the observed weights were overall lower, and they were more varied for the bulk of the fish in Øvre- and Nedre Urdetjønn (Fig. A1 5.3). In two-sample Wilcoxon tests, the fish weights in Øvre Urdetjønn and Bjønntjønn were significantly lower in 2022 compared to 2009 (Øvre Urdetjønn: $W = 614.5$, $P_{0.05} = 0.003$; Bjønntjønn: $W = 573.5$, $P_{0.05} = 0.0014$; Nedre Urdetjønn: $W = 1260$, $P_{0.05} = 0.07$).

Comparing the projected end-of-season weights for 2022 (A2 3.4) to the weights in 2009 with two-sample Wilcoxon tests, the differences were no longer statistically significant for any of the lakes (Øvre Urdetjønn: $W = 501$, $P_{0.05} = 0.22$; Nedre Urdetjønn: $W = 925$, $P_{0.05} = 0.39$; Bjønntjønn: $W = 470$, $P_{0.05} = 0.12$).

### *Fish condition (k-factor)*

As shown above, the mean k-factor for all fish was under 1.0 in 2022, over 1.0 in 2009, and close to 1.0 in 1997 (Table 5.3; Table A1 5.7 for values of spread and confidence). For 2022 with the corrected data, k-factor was significantly higher in Bjønntjønn than in Øvre Urdetjønn (one-way ANOVA: F = 4.3, df = 2, $P_{0.05} = 0.015$). For 2009, significant variation was indicated among the lakes (Kruskal-Wallis $\chi^2 = 35.8$, df = 2, $P < 0.001$), probably related to a lower mean k-factor in Bjønntjønn than in the other two lakes (Table A1 5.7).

Comparing the 2022 test fishery to the 2009 survey with two-sample Wilcoxon tests, the mean k-factor for all fish was significantly lower in each lake (Øvre Urdetjønn: W = 831, $P < 0.001$; Nedre Urdetjønn: W = 1966, $P < 0.001$, and Bjønntjønn: W = 638, $P < 0.001$). Using the projected lengths and weights for end-of-season 2022 had little influence on these results for Øvre- and Nedre Urdetjønn but for Bjønntjønn, the difference in k-factor between 2022 and 2009 was no longer significant (Øvre Urdetjønn: W = 815, $P < 0.001$; Nedre Urdetjønn: W = 1844, $P < 0.001$, and Bjønntjønn: W = 437, $P > 0.05$).

Tendencies of k-factor versus fish length per lake were addressed in the 2009 and 1997 survey reports. Based on the data per lake from 2022 and 2009, linear regression analysis indicated that k-factor decreased significantly with length in three of the six cases: for Øvre Urdetjønn in 2022, and for Nedre Urdetjønn in both surveys (Figs. A1 5.4-5.5; Table A1 5.8). However, as reflected in generally low $R^2$-values and the plots, the data points were mostly quite scattered around the regression line, especially for Øvre Urdetjønn and Bjønntjønn.

### *Fish age*

The three gillnet test fisheries suggested that most of the fish in the three Upper Kova R. lakes were young (2 – 4 years/winters old) but otherwise, there was considerable variation in the age distributions. Fish aged 2 winters (2+) were only caught in the lakes in the 1997 test fishery, when they represented over 30% of the catches in Øvre- and Nedre Urdetjønn.

Across the lakes and surveys, the overall tendency was that the proportion of total catch decreased with age (positive skew) but with some exceptions both on the low end and among medium-aged fish, the latter creating bimodal impressions in some cases (Fig. A1 5.6; below).

For Øvre Urdetjønn (Fig. A1 5.6, top), the age distributions all looked bimodal but with moderate overlap of the modes and dips (2022: maximum mode 3 years, dip at 6; 2009: maximum mode 4-5 years, dip at 6; 1997: maximum mode at 3 years, possible dip at 4). The 2022 and 2009 surveys indicated age structures in the lakes that were right-shifted and stretched out (more age classes represented) compared to 1997, the latter with many 2-year-olds and no fish older than 6 winters (Fig. A1 5.6, top).

For Nedre Urdetjønn (Fig. A1 5.6, middle), the age distribution in 2022 looked bimodal (maximum mode 3-4 years and dip at 6) and right-skewed in 2009 and 1997 (mode 3 years in 2009 and 2 years in 1997). The 2022 results were quite stretched out compared to 2009 and especially to 1997. The 1997 distribution looked even more compact (fewer age classes represented) than in Øvre Urdetjønn due to a lack of fish more than 5 winters old (Fig. A1 5.6, middle).

For Bjønntjønn (Fig. A1 5.6, bottom), the suggested overall age distribution for 2022 (mode 4) should be interpreted extra cautiously, as two of the age classes only contained one individual each (5 and 6 years) and the ages of the outliers were more uncertain. The patterns for 2009 and 1997 were right-skewed (mode 3 years), again more compact in the latter due to the lack of fish older than 5 winters (Fig. A1 5.6, bottom).

*Fish growth (age-length)*

Across the gillnet test fisheries and lakes (Figs. A1 5.7-5.8), 1997 was the year where average length growth appeared to be closest to a relatively stable 50 mm per year for most of the age classes represented. Further overall comparison of growth based on age-length results from 2022 to the other test fisheries was difficult due to the combined effects of seasonality and few and/or more uncertain data (age estimates) in 2022. Compared to 1997, the results from 2009 indicated more variation and slower overall growth in Øvre- and Nedre Urdetjønn. The data and displays from 1997 and even more markedly from 2009 suggested growth rates under 50 mm per year in the recruitment streams, followed by a couple of years with higher growth rates in the lakes, before onset of slower growth again (except for Bjønntjønn in 2009).

For Øvre Urdetjønn, the three surveys indicated slowed growth from age 5 or 6 years, with reasonably similar overall growth curve trajectories for 2022 and 2009, both slower than for 1997 (Fig. A1 5.7, top). These overall patterns were roughly similar for Nedre Urdetjønn; one exception was that slower growth looked somewhat less pronounced, in 2009 even shifting to apparently accelerated growth for older fish (possibly due to cannibalism) (Fig. A1 5.7, bottom).

For Bjønntjønn (Fig. A1 5.8), the 2009 and 1997 test fisheries indicated a regular and persistent growth at a rate of ca. 50 mm per year for the fish in the lake, with little sign of slowed growth or spurts. Thus, it could perhaps be said that this was the lake where the results from 2022 showed the greatest difference from the previous surveys, if the few data suggesting a relatively stable growth rate of only about 20 mm per year should be lent any weight (Fig. A1 5.8).

The mean length of 3-year-olds was lower across the lakes in the 2022 test fishery than in the previous ones. As indicated, the different timing of the test fisheries could be a contributing factor to this; using my end-of-season projected lengths for 2022 (A2 3.4) would shift the mean length of 3-year-olds and the rest of the growth curves for the 2022 survey upwards, perhaps most illustratively in the case of Øvre Urdetjønn, with its continuous data/curve (Fig. A1 5.9).

### *Sex ratios and sexual maturity*

The proportion of males and females in the catches of the three gillnet test fisheries was in the range of 40 – 60% (Fig. A1 5.10). Statistical testing indicated that differences in sex ratios across lakes and surveys were random (Test of independence, likelihood ratio: $\chi^2 = 5.45$, df = 7, $P_{0.05} = 0.61$).

The three gillnet test fisheries suggested that 50% or more of the males would be mature across the lakes, with higher proportions of males that were mature than proportions of females that had reached maturity (Fig. A1 5.11). For Øvre- and Nedre Urdetjønn, the proportion of females that had reached maturity appeared to be higher in 2022 (at about 50% or above) than in the other two surveys (under 50 %). For Bjønntjønn, the proportion of mature females was close to 50% in 1997, higher than in 2009 (Fig. A1 5.11).

All three gillnet test fisheries indicated that males matured at lower lengths than females, when defining onset as the point at which 50% or more of the fish in three size classes had reached maturity (Table A1 5.9). Half or more of the males under 220 mm in the catches were mature, whereas most mature females were over 220 mm. Maturity in females appeared to set in at somewhat higher lengths in Bjønntjønn than in the other two lakes, judged from the 2009 and 1997 data. Comparing the 2022 test fishery in Øvre- and Nedre Urdetjønn to the other two surveys, length at maturity appeared similar for males and possibly somewhat shorter (earlier) for females (Table A1 5.9).

### *Stomach filling*

Comparing 2022 to 1997, a greater proportion of the fish appeared to have eaten just prior to being caught in Øvre- and Nedre Urdetjønn, reflected in both variables assessed; for Bjønntjønn, the proportion of fish with empty stomachs was nearly the same in the two surveys, whereas the stomachs that did contain food were less filled on average in 2022 than in 1997 (Table A1 5.10).

*Flesh color*

All three gillnet test fisheries indicated that white flesh dominates across the lakes: three quarters or more of the caught fish had white flesh in 2022 and 1997, and about one half to three quarters of them in 2009. The proportion of light red flesh was higher than red flesh across the lakes in time; the proportion of the latter was low (< 10%) or zero in all surveys (Table A1 5.11).

The probability of having flesh color other than white appeared to increase with length across the gillnet test fisheries. Nearly all fish under 220 mm had white flesh in all three surveys (Tables A1 5.12-5.14). In Øvre Urdetjønn, there were some individuals with white flesh in all length classes (30 mm intervals) (Table A1 5.12). In Nedre Urdetjønn, nearly all the relatively few individuals in the length classes over 310 mm had light red or red flesh (Table A1 5.13). Some or all fish in length classes longer than 220 mm had flesh color other than white in Bjønntjønn in 2009 and 1997, with a single exception (Table A1 5.14).

## 5.3 Physical lake conditions: comparative water variables and depths

Comparable water quality data from the 2022 and 2009 test fisheries were limited and not analyzed in any detail. The respective samples were drawn in the lakes in 2022, and in streams in 2009 (common location for Øvre- and Nedre Urdetjønn, separate stream for Bjønntjønn).

Conductivity values measured with handheld device in the 2022 test fishery were about half the size of the reported values from 2009, while the pH values for 2022 (measured with multi-parameter logger near the surface) were somewhat higher than in 2009 (Table A1 5.15). Both conductivity and pH values were similar across the three lakes in the two separate test fisheries.

Surface water temperatures measured with handheld devices were similar across the lakes in the 2022 survey (Table A1 5.15), and not reported for 2009.

The maximum depth measured in Bjønntjønn in the 2022 test fishery was in a different location and only about half the maximum depth reported for the lake in 2009. In the area marked with maximum depth (8 meters) on a map in the report from the 2009 test fishery (2010, p. 30), we measured no depths greater than about four meters in the 2022 test fishery (Table A1 5.15).

# 6 Discussion

The present study hypothesized that natural recruitment of brown trout to three small Upper Kova R. lakes was balanced to food production, given limited local harvest and residual regulated flow in the recruitment streams through the growth and recruitment season. Below, I discuss to what extent the hypothesis was supported by the findings in the 2022 test fishery, relating the current results for the lakes first to general knowledge on brown trout and to lakes with brown trout populations elsewhere in Norway, and next to the findings in the previous Upper Kova R. fish studies. If not specified otherwise, the external information sources have been referred previously, mostly in chapter 2. The relatively limited fishing effort/possibility of sampling error/few data particularly from Bjønntjønn and the early timing of the 2022 test fishery should be kept in mind also throughout the Discussion.

How the core elements in the present study's overall hypothesis are understood depends on whose interests one has in mind. Whether natural recruitment is "sufficient" and balanced to food production may be different seen from a human point of view than from a broader ecological one (let alone from that of a collective of fish individuals, had it been accessible to us). To exemplify, the simple WFD fish index for ecological classification briefly addressed above seems to suggest that the higher (relative) abundance, the better, while densities may be "too high" from a human perspective (below). In the present study, the overall hypothesis was explored primarily from a user's (human) point of view, excluding catch-and-release and other trophy/maximum size-oriented practices. Thus, the central research question was whether the amount of recruitment appeared to be at an appropriate level, without the aid of stocking, to produce over time an attractive number, size and quality of brown trout that may be harvested sustainably with gillnets in the three Upper Kova R. lakes.

## 6.1 Comparison of the results to general knowledge and to other Norwegian lakes

The 2022 results for Øvre- and Nedre Urdetjønn indicated that recruitment was somewhat high but reasonably balanced to food production and local harvest, reflected in currently high densities and proportions of small fish, with overall slow growth and somewhat poor fish condition on average (with caveats for season).

For Bjønntjønn, the overall results from 2022 were more uncertain due to few data and some methodological challenges. If representative, the results suggested that there could currently be a previously undocumented imbalance between recruitment, food production and local harvest.

### *Abundance/density*

The 2022 results within the catch variables highlighted in the Standard NS-EN 14757 (NPUE, WPUE, CPUE) indicated that brown trout relative abundance in number and biomass was currently similar in Øvre- and Nedre Urdetjønn and about twice as high as in Bjønntjønn, though the latter difference was statistically significant only for fish number. Common sense might have it that approximately the same number of fish caught in two differently sized lakes (here: Øvre- and Nedre Urdetjønn) could indicate a higher density in the substantially smaller lake. However, my exploration of taking lake surface area into account did not necessarily provide a reliable estimate for absolute abundances (density). According to the gillnetting Standard, relative abundance cannot be generally transformed to "… absolute abundance values (e.g. number of fish per ha, or biomass per ha)" (p. 18), because the "catchability constant" may vary for instance with environmental factors (2015a).

The need to relate relative abundances to the density assessments/rankings central to my overall study hypothesis was solved by the apparently somewhat different assumptions in the characterization system of Ugedal and colleagues (2005). Here, I found support in explicit criteria and the estimates from the 2022 test fishery to state not only that the population density in Bjønntjønn could be considered lower than in the other two Upper Kova R. lakes but also that its density appeared to be about average compared to a large number of other Norwegian lakes. Similarly, it could be claimed that the population densities in Øvre- and Nedre Urdetjønn appeared to be higher than average for the same selection of Norwegian brown trout lakes. The broadness and somewhat arbitrary cut-offs between the three density classes in the Ugedal system that may be criticized is at the same time a strength of the system, allowing easy and practical comparison across a variety of conditions, time and sampling methods.

As for other current results that might support the above density assessments, early maturity especially in males may as mentioned be a response to perceived high densities. Given the cited range and tendencies for maturity onset in brown trout in general, it seems reasonable to state that the 2022 test fishery suggested early maturity onset in at least males in Øvre- and Nedre Urdetjønn, in other words, as might be expected in lakes with somewhat high population densities.

### *Age distribution and recruitment over time*

Overall and across the lakes, the age structures suggested by the 2022 test fishery corresponded roughly but not perfectly to the general expectation of progressively sinking numbers per age class in populations with stable recruitment over time. For Øvre- and Nedre Urdetjønn, the results indicated that a good proportion of the probably inflated 2019-generation in the main recruitment stream had survived the competitive fry stage and later made their way to the lakes. What seemed to beg an explanation for these two lakes was the low number of 6-year-olds in both cases, seen in relation to the relatively higher proportion of fish older than this. Leaving the uncertainty in my age estimates aside here (cf. Potential sources of error), the catch in numbers for these generations were so small that sampling error could be the main explanation, i.e., that the true age distributions were not necessarily bimodal. However, especially given the similar patterns in the two lakes, an alternative hypothesis for the few 6-year-olds could be reduced recruitment due to environmental factors such as extreme weather and/or flow-related events in 2016, even if I have no data to back this up. Another possibility was that this particular age class had reached catchable size, combined with gillnetting with selective mesh sizes targeting these lengths, but this seemed less likely given the presumed limited harvest in these lakes. As for the latter, the relatively high proportion of older fish could be interpreted as supporting this premise (limited local harvest) in the overall study hypothesis.

For Bjønntjønn, the main question seemed to be if the age distribution was representative for the current lake population. The lower proportion of 3-year-olds than 4-year-olds could be explained by some of the former class remaining in the nursery streams, not unlikely, as this lake has a wide inlet delta. If the rest of the suggested age distribution should be close to representative, many age classes were hardly or not represented at all. In this case, it would seem hard not to interpret the pattern as reflecting a current imbalance between recruitment and food production (i.e., a surplus of the latter), probably influenced by local harvest (“attractive lengths” below).

Regarding effects of stocking on the age structures, I considered if this could somehow have boosted the proportion of survivors in the generations backwards in time from 2014 but found it hard to see any direct consequences of the shift in stocking regime in the limited data from the lakes. This is perhaps not surprising given the assessment in the previous gillnet test fisheries that recruitment was primarily natural even when supplemental stocking was taking place. That the premise of exclusive natural recruitment from 2015 underlying my overall study hypothesis was apparently challenged by the 3-year-old caught in Bjønntjønn was intriguing but the extent of any illegitimate stocking cannot be estimated from the 2022 test fishery. If validated by future catches, illegitimate stocking is certainly an issue to be followed up by relevant stakeholders.

*Length distributions*

The roughly corresponding patterns in age and length distributions across the lakes and the similarities between Øvre- and Nedre Urdetjønn were as expected and illustrated both with 10 mm (Results) and 30 mm length intervals (not presented). Interpreting the dips in lengths 190 – 250 mm in Øvre- and Nedre Urdetjønn and 250 – 310 mm in Bjønntjønn (evident with 30 mm intervals) as related to local harvest with selective mesh sizes (perhaps somewhat larger mesh size in Bjønntjønn) seems more reasonable than from the age distributions alone. Even if limited, local harvest may have a strong impact in small lakes, in this case, particularly for Øvre Urdetjønn. Larger individuals to the right of the dips could represent slow-growers less vulnerable to harvest-related mortality. Alternatively, the dips could be a consequence of small sample size/numbers and relatively few fish by chance being on the inside of the intervals used (i.e., a kind of artifact related to the mode of analysis), but I find this somewhat less likely given the apparent similarity of the bimodal patterns for age and length in both of these two lakes. For Bjønntjønn, the dip/absent size classes corresponds well with Jensen's "attractively sized fish" expected in mesh sizes 26 – 35 mm (1979), while the dips were clearly on the lower side of such attractiveness for the other two Upper Kova R. lakes. Overall, the length distribution patterns seemed to reflect well the assumptions regarding relative local harvest pressure in the three lakes: higher in Bjønntjønn than in the other two lakes.

*Growth*

Based on the 2022 test fishery, Øvre- and Nedre Urdetjønn appeared to have growth conditions and achievable brown trout sizes that were about average compared to the large number of Norwegian lakes underlying the system of Ugedal and colleagues (2005), while the data for Bjønntjønn were too few for this analysis. As regulation may have resulted in alterations in water temperature that were overall beneficial for brown trout (Heggenes, 2020), a relative scarcity of food seems a likely contributing factor to the limits on achievable body size and the generally slow age-length growth suggested by the current results for Øvre- and Nedre Urdetjønn. The few data and my modes of analysis did not allow formal testing of whether the observed growth patterns might be correlated with (dependent or not on) the population densities. However, as a more general assessment, it seems likely that the current high densities in Øvre- and Nedre Urdetjønn could be a limiting factor for the overall growth possibilities in those lakes.

As for the apparent slower growth from age 6 and 7 years in Øvre- and Nedre Urdetjønn, respectively, it is possible that this tendency was exaggerated by Lee's phenomenon, but high local harvest was as mentioned a relatively unlikely reason for this in those two lakes. It seems more probable that slower growth was associated with onset of maturity, as is commonly seen in brown trout. The 2022 data seemed too few for formal analysis of growth per sex but compared to the growth rate for the interval 4 to 5 years in Øvre- and Nedre Urdetjønn (all fish), the slower rates in the age classes directly below (interval 3 – 4 years) and above (interval 5 – 6 years) corresponded to maturity onset for males (age 3 years in both lakes) and roughly also for females (age 5 years in Øvre Urdetjønn).

For Bjønntjønn, the few data and many age classes poorly or not represented made assessments of growth difficult. If drawing a line between the few data points were permissible, growth would appear to be more stable than in the other two Upper Kova R. lakes, but with a suggested growth rate (20 mm/year) perplexingly low compared to an assumed normal of 50 mm/year (indicated in the previous gillnet test fisheries for this lake, below). Here, the low numbers (only one individual per age class 5 and 6 years) combined with uncertainties in my age estimates (for instance overestimation of the age for the three largest individuals) would have a particularly large impact, suggesting a growth rate that might be far from representative.

My attempt to correct lengths for the early timing of the 2022 test fishery should be treated with caution but the general upward shift of lengths reflected in the growth curves (Fig. A1 4.6) was as expected. In addition, my prediction model seemed to have a certain smoothing and equalizing effect on the growth rates for the youngest age classes across the lakes (Fig. A1 4.6), but I did not explore this further given the uncertainties regarding my prediction model.

### *Fish condition (k-factor)*

Mean k-factors across the lakes somewhat below the general expectation of 1.0 for brown trout and higher in Bjønntjønn than in Øvre Urdetjønn seemed as expected in light of the results on density and perhaps growth in the 2022 test fishery. Below, I briefly assess how representative the k-factor values might be by looking at the variables examined that could have influenced or biased the results compared to the “normal” value. Starting with season, I would expect the average individual to be on the lean side in the spring and to “fatten up” (increased “flesh weight”) through the growth season, thus my attempt to project length and weight for better comparison with end-of-season test fisheries. That the 2022 season-corrected mean k-factors were close to the brown trout normal is not proof of the validity of my projection model but at least the resulting values seemed plausible in light of overall results and previous gillnet test fisheries in the lakes (below).

Next, my analyses indicated that longer and older fish contributed relatively more to the sub-normal mean k-factors in Øvre- and Nedre Urdetjønn than smaller and younger fish, suggesting for instance that the former might have had more problems finding sufficient amounts or types of food than the latter in those lakes. Whether this would be transitory or true over time, I do not know, but it seems possible that these small and mostly shallow lakes have relatively more appropriate feeding opportunities for smaller fish, perhaps particularly at an early stage in the growth season with rapid warming of the water in the shallower parts. Should the few data from Bjønntjønn be representative for k-factor related to the length classes I defined, the results could indicate that feeding opportunities were as good for larger fish as for smaller ones in this lake. If so and comparing the three lakes, this could appear to be somewhat contrary to one of the expectations from the lake categories assigned through use of the system of Ugedal and colleagues (2005) (cf. Results 5.1: relative scarcity of larger prey in lake category *E*), perhaps illustrating a limitation related to the broad strokes in that system. As for the results on stomach filling, they are of little help in assessing the food availability over time reflected in fish condition, as this variable only represents a "snap-shot" perspective on the conditions at the time and thus cannot serve as a more general measure of food production in the lakes.

The uneven sex ratios in Øvre- and Nedre Urdetjønn could have skewed the averages within the lakes and reduced the validity of overall k-factor comparisons between the lakes had there been a difference in k-factor between the sexes, but this was not indicated by the analyses. As for maturation stage and k-factor, I would expect that mature females (especially), on average experience an added weight (and k-factor) gain related to gonadal development as spawning approaches. This was not accounted for in my projection model, which was only based on measured lengths and weights at the time of the 2022 test fishery in mid-June. Interestingly, k-factor at that time was higher for immature fish than for mature fish in the catches, possibly reflecting the energy investment in the shift to maturity, if not coincidental.

Stomach filling seemed to contribute little to k-factor overall; if anything, an inverse relation was suggested by looking at this variable in isolation, as relatively more fish appeared to have eaten just prior to being caught in Øvre Urdetjønn (with lower average k-factor) than in Bjønntjønn. Finally, further analysis of the fish with detected macro-parasites showed that they were longer than average for the catches, and that the difference in k-factor between infected and assumed non-infected fish was no longer significant when corrected for length.

Given the limitations on the above length-growth assessments imposed by my somewhat uncertain age estimates, I briefly explored the possibility of formal growth analysis based on the more reliable results of length and weight (in addition to k-factor). In length-weight relationship (LWR) analysis, length and weight are log-transformed and linear regression run (Formula 3.2; Fig. A1 6.1), and a b-value (slope of the line) of 3.0 is considered normal for brown trout (Borgstrøm & Hansen, 2000; Muddasir et al., 2018). As a measure of weight growth, LWR analysis might add little mathematically or substantially to appropriate k-factor analysis but given my particular constraints it seemed to represent a possibility for some modest methodological triangulation (linear regression versus one-way ANOVA). Although both modes of analysis reassuringly concurred with indicated values per lake at the time of the test fishery somewhat below the expectation for brown trout (LWR: b < 3.0; k-factor: means < 1.0), I found it interesting that the interpretation of plots with confidence intervals (Fig. 6.1) differed slightly: LWR analysis indicated that weight growth at or above the general expectation was plausible for Bjønntjønn, and that the outcome of statistical testing for LWR differences among the lakes was uncertain based on the plot alone (Fig. 6.1, left), while k-factor analysis indicated that values above 1.0 were not plausible for any of the lakes at the time, and that k-factor of all fish was significantly lower in Øvre Urdetjønn compared to Bjønntjønn (Fig. 6.1, right).

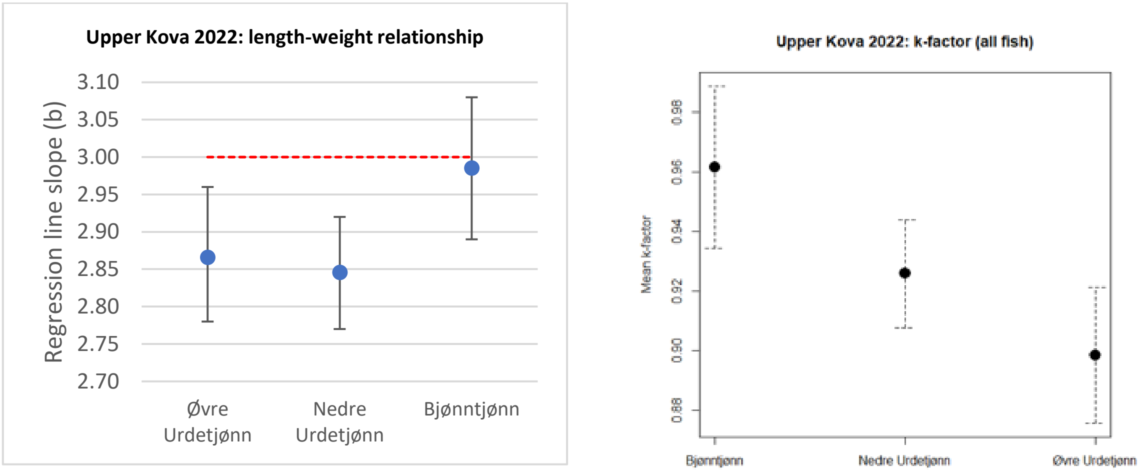


*Figure 6.1. Three Upper Kova lakes: length-weight relationship (LWR) and k-factor based on the 2022 test fishery. LWR (left panel): results expressed by regression slope of the line (b), with 3.0 as normal value. K-factor (right panel): mean value for all fish, with 1.0 as normal value. Both analyses: results per lake, error bars representing 95% confidence intervals.*

### *Balance of recruitment to food production and harvests: a snap-shot user's perspective*

Applying the system of Ugedal and colleagues (2005) to the 2022 test fishery results indicated that there was an acceptable balance between recruitment and food production in Øvre- and Nedre Urdetjønn at the time, and that recruitment in Bjønntjønn was satisfactory (Results 5.1). Turning perhaps even more explicitly to the user's perspective on recruitment and harvest potential in the three lakes, my attempt to adapt and apply the rules of Jensen (1979) to the 2022 catches should probably not be given too much weight, partly because the rules are not validated for test fishery with multi-mesh gillnets (to my knowledge). Still, for reference, my calculations resulted in ratio values around 60 – 75 (Table A1 6.1) based on the 2022 data corrected as for the comparisons with single-mesh gillnet series elsewhere in the present study. Indirectly compared to the 79 lakes that constituted the empirical basis for Jensen's rules, the results suggested a relatively "good situation" across the three Upper Kova R. lakes regarding the balance between recruitment and "attractively sized fish" (the "exploitable" part of the population). For Øvre- and Nedre Urdetjønn, this appeared to correspond reasonably well with the lake category *F* assigned through the system of Ugedal and colleagues (2005), which I interpreted as lakes where natural recruitment is so good that it may be a bit too high (i.e., more than "sufficient" in this case) for an optimal balance with food production. For Bjønntjønn and with caveats for few data and probably larger influence from local harvest, I found it more questionable that the tentative classifications mandated by both the Jensen (1979) and the Ugedal system (2005) were adequate current descriptions for the lake based on the 2022 test fishery.

For a brief exploration of the results from the 2022 test fishery in light of the user's desired "fast-growing fish of good quality" (above), I first tried to envision how a naïve (to the Upper Kova R. lakes) local gillnetter with relatively short-term perspectives might assess the current brown trout populations relative to general expectations for brown trout (directly below). At the end of section 6.2, I try to supplement this picture from the perspective of an imagined "longitudinal" Upper Kova gillnet fisher, i.e., someone with experience from these lakes and with the aim of sustainable local harvests through knowledge-based management.

Overall for the naïve harvester, I imagine the current proportion of fish of attractive length and weight and associated growth rates, as well as perhaps flesh color and macro-parasites in some of larger fish, might be perceived as somewhat unsatisfactory across the lakes. Fish condition especially for larger individuals in Øvre- and Nedre Urdetjønn might also be somewhat below expectations, while condition and the chances for sporadic individuals larger than average "attractive size" could appear better in Bjønntjønn. For the best catch here and now, gillnetting in relatively shallow waters (0 – 3 m) with mesh sizes ≥ 24 mm would probably seem most promising in terms of total weight (but with no guarantee for attractively sized individuals in length and/or weight), while mesh sizes < 24 mm might secure the largest number of fish. Postponing the harvest until late summer or autumn of 2022 might have improved the average k-factor but possibly not increased the number and proportion of attractively sized fish very much.

*The brown trout populations and water quantity/quality in the Upper Kova R.*

Precise quantification of the effects on brown trout recruitment and growth from the altered flow (reduced water-covered area in the main recruitment streams) and thermal regimes following regulation of the Kova R. would not be possible due to the lack of reliable pre-regulation data on fish, flows and temperatures. Post-regulation, there has surely been interannual variation in all of these parameters; Heggenes documented aspects of them in his stream studies (2018, 2020) undertaken after the cessation of stocking from 2015, while the test fisheries in 1997 and 2009 did not explicitly address the possible effects of these altered flows and temperatures on the brown trout populations in three Upper Kova R. lakes.

As mentioned, information on actual water flows in the Upper Kova R. is limited. For 2022, I assume that the precipitation levels may have entailed lower than normal residual flow through the recruitment and growth season, with potential negative effects for the fish in the streams and lakes.

The outer bounds of the water temperature logging in the Upper Kova R. (2017 – 2022) represented a period covering the full lifetime of individuals up to 5 years old and about half the lifetime of the oldest fish caught in the 2022 test fishery. The patterns of water temperatures in 2022 looked about average for this five-year period, superficially assessed, more specifically like an intermediate of the conditions reported by Heggenes (2020) for 2018 ("unusually warm") and the "cooler 2017 and 2019" (the latter also influenced by the higher-than-usual flows due to dam repair). As in the earlier documented years, and as expected for the Upper Kova R., the 2022 water temperature plots (Figs. A1 4.16-4.18) illustrated how varying solar radiation caused strong diurnal fluctuations through the growth and recruitment season. The relatively stronger amplitudes at the Nedre Urdetjønn location observed in 2022 were also seen in 2017. According to Heggenes (2020), the phenomenon was then probably due to a larger area of water having been exposed to solar radiation for a longer time at that location compared to for instance the Øvre Urdetjønn location, and I assume this would be as plausible an explanation for 2022.

The net effect of all influences resulted in recorded water temperatures from spring to autumn 2022 all within the cited critical range for brown trout growth and feeding (3 – 26° C). Periods encompassing days with temperatures (approximate daily means) within the cited optimal range for brown trout growth and feeding (13 – 16° C) covered about 9 weeks in Øvre- and Nedre Urdetjønn (ultimo June to primo September) and about 12 weeks in Bjønntjønn (mid-June to mid-September). However, within the same periods, Bjønntjønn also experienced about twice as many ca. one-week-long periods with approximate mean daily temperatures somewhat above the optimum, possibly countering some of the potentially beneficial effect of a longer period containing days with optimal temperatures.

Other reported results from water measurements, made during the test fishery in mid-June 2022, were about as expected and overall within the cited critical/tolerance ranges for brown trout in nearly the entire water column across the lakes. Overall, the water-covered area of the recruitment streams and the three lakes in the Upper Kova R. is limited but the characteristics of the water seem to be well suited for brown trout.

## 6.2 Comparison of results across the lakes in time

In this section, I briefly address temporal population dynamics by discussing the 2022 results first against the previous gillnet test fisheries in the Upper Kova R. (before the stocking cessation in 2015) and in view of the assessments in Heggenes' stream studies (2018, 2020). Given the high variability in brown trout recruitment and populations even from natural causes alone, the limited sampling size and number of surveys in the present case do not allow inference of robust tendencies over time. For an assessment of the current status, I still found it relevant to analyze similarities and differences suggested by the separate surveys, as they integrated some aspects of conditions in the lakes spanning the period from the early 1990s to the present day, potentially with relevance also for the time to come.

Before moving to assessments per lake, an overall summary could be that the balance of recruitment to food production (and local harvest) across the lakes appeared to be no better or somewhat worse currently than in the situations documented by the previous fish studies in the Upper Kova R. This was perhaps contrary to the anticipated effects of the stocking cessation from 2015. As Heggenes pointed out in his stream studies (2020), the area of the lakes recruiting from the streams is so small that even the reduced water-covered area of the latter (due to regulation but with the important unintended dam leakage) may be sufficient or more in normal years, at least in Øvre- and Nedre Urdetjønn. Based on this, I assume it was expected that the stocking cessation might have positive consequences especially for these two lakes (lower population density and better size/quality of the fish). Such a development was not evident in the results from the 2022 test fishery but as pointed out above, natural interannual variation may be great, and the comparative assessment of results over time especially related to fish length and weight was challenging due to the different timing of the test fisheries. As indicated above, the early timing of the 2022 test fishery was probably a main reason at least for generally lower k-factors in the present survey compared to the previous test fisheries in the Upper Kova R. The results on stomach filling could also have been strongly influenced by season, weather and temperatures, but since they also have limited information value, I have not given these results much weight or any place below.

For Øvre Urdetjønn, the 2022 test fishery indicated that the previously documented tendencies of too high recruitment relative to food production were currently as strong or stronger even with exclusive natural recruitment, judged by the results on density, maturity onset in males, proportion of smaller fish (< 220 mm), length growth (including patterns of slowed growth), and fish condition. For this lake, it is possible that some of the difference across time in fish lengths and weights (lower in 2022) not explained by season could reflect effects of increased competition for food resources with higher density. Differences in length and age distributions between 1997 and 2009 (the latter: right-shifted "dip" in length frequencies and higher proportion of old fish) attributed to changes in local harvest appeared in 2022 to have shifted back to or beyond the 1997 situation for lengths (left-shift), while the relative proportion of older fish appeared to remain high in 2022. Possible explanations for the 2022 dip in length distribution were discussed above (6.1); the apparent left-shift of the 2022 length-dip compared to 2009 (especially) could also be related to mesh sizes used in local harvest but I have no direct information about changes in harvest practice that might corroborate this.

For Nedre Urdetjønn, the results across time were similar to those for Øvre Urdetjønn: the 2022 test fishery suggested that the previously documented tendency of recruitment being somewhat high relative to food production was currently as strong or stronger with exclusive natural recruitment, judged by the results on density, maturity onset in males, proportion of smaller fish (< 220 mm), length growth (including patterns of slowed growth), and fish condition. The indicators of fish size and quality (at least k-factor) assessed as better in 2009 than in 1997 appeared in 2022 to have changed to values more similar to or poorer than in 1997. Also as for Øvre Urdetjønn, it is possible that some of the difference across time in lengths and weights not explained by season could reflect effects of increased competition for food resources with higher density. The entire 2009 population had most likely been replaced by 2022 but the dynamics behind the 2009 prediction of increasing population density in this lake may have persisted.

For Bjønntjønn, the relatively few data from the 2022 test fishery could be seen as repeating the previous assessments of lower density and higher fish quality (in 2022 judged by k-factor) than in the other two Upper Kova R. lakes. However, the previously documented better balance of recruitment to food production reflected in "more normal" patterns of growth and length distributions were not evident in the 2022 data, rather to the contrary for the proportion of large to small fish. As mentioned, overall growth based on age-length was difficult to assess for 2022, given the scarcity of data and few age classes represented. Several reasons for the possibly deteriorated population status are conceivable and discussed above and below, but it does seem appropriate here with a reminder of the 1997 warning that the mentioned balance could be vulnerable to higher gillnetting pressure in a small lake such as this one.

Heggenes' ranking of the three Upper Kova R. lakes in terms of the amount of natural recruitment seemed to be reflected well in the lake populations as characterized by the 2022 test fishery, especially if lake surface area is taken into account: highest to Øvre Urdetjønn and probably lowest to Bjønntjønn, and possibly overall satisfactory to all three lakes but depending on the local harvest especially for Bjønntjønn. As illustrated above, it is not as evident that Heggenes' assessments of the balance of recruitment to food production at the time of his investigations would be valid across the lakes in 2022. The case of Øvre Urdetjønn seems to correspond quite well but the overall similar results for this lake and Nedre Urdetjønn makes is difficult to differentiate between these two lakes in terms of balance to food production (both: recruitment "a bit too high" in my narrative). However, if lake size is again taken into account, it seems logical that the natural recruitment "over-capacity" could be relatively higher in Øvre Urdetjønn, implying a somewhat better balance to food production in the three times larger Nedre Urdetjønn.

For Bjønntjønn, if the 2022 test fishery results should be representative for the population, my overall assessment would be that recruitment was currently not balanced to food production (food surplus due to relative scarcity of medium-large fish). Influenced by the warnings from both Solhøi (1998) and Heggenes (2020) about the potential for large and rapid impacts of increased harvest pressure especially in this lake, I assume that local harvests may have contributed to the current situation. If so and given the catch of a 3-year of possible hatchery origin in this lake, the thought naturally comes to mind that someone might have tried to improve the situation with non-sanctioned measures, but I refrain from further speculation about this scenario as I have no information to back it up. More reliable knowledge on the natural recruitment to the lake is expected from Heggenes' electrofishing in the late summer of 2022, so this should provide a more robust basis for assessment at least of that part of the equation.

### *Balance of recruitment to food production: a longer-term user's perspective*

As signaled above, I round off this section with an attempt to imagine how a local harvester might interpret the results of the 2022 test fishery in light of the previous Upper Kova R. fish studies and his/her personal gillnetting experience in the lakes, and with respect to the possibility for sustained, future catches. From experience, the harvester's expectations would perhaps be less based on general brown trout standards and more on what might be realistic in terms of growth rates and fish quality in these particular lakes.

Since I don't know anything about the actual catches or experiences in local harvests, inferences from the results of the Upper Kova R. fish studies will have to suffice. They indicate that mesh sizes ≤ 29 mm might be expected to secure the highest yield in total weight, while mesh sizes of 21 mm or somewhat below would probably result in the highest number of fish caught. Across the lakes, fish up to nearly 35 cm in good condition and with light red flesh need be no rarity, perhaps especially in the late summer, while individuals with deep red flesh and weighing around 1 kg would probably be more exceptional. Historical results showed that Bjønntjønn may sustain fish with stable growth of about 50 mm/year across the population and a sound ratio of attractively sized fish to recruits, probably also without supplemental stocking, as long as local harvest pressure was relatively modest and appropriate mesh sizes used. For Nedre- and particularly Øvre Urdetjønn, expectations regarding growth and condition especially for larger fish (except cannibals) would probably have to be more moderate than for Bjønntjønn, unless a systematic and adaptive management scheme aimed at reducing somewhat the overall densities and perhaps the proportion of smaller fish were implemented in those two lakes.

Overall, I suspect that for this hypothetical fisher, the 2022 test fishery results might be unsurprising but somewhat disappointing for Øvre- and Nedre Urdetjønn, and unsatisfactory or even causing some concern for Bjønntjønn. For all three Upper Kova R. lakes and in somewhat different ways, the key to viable brown trout populations and sustainable, satisfactory catches over time seem to lie in local harvest practices and management (and continued supplemental flow from the unintended dam leak or otherwise, below).

## 6.3 Potential sources of error

In the present study, I tried to emphasize whenever possible data that integrate conditions over time (such as length, weight and k-factor) rather than data with a "snap-shot" character (such as CPUE), that are more prone to sampling error with fishing efforts as low as in the present case. As certain snap-shot data were still relevant in some analyses essential to the overall study hypothesis (including the comparisons with other test fisheries), it seems all the more important to dwell a bit on possible errors and biases related to estimates based on such data from the 2022 test fishery.

The decision to use multi-mesh gillnets in the present study did not guarantee catches that were representative for the population structures. Small fish are often underrepresented and large fish overrepresented even with this equipment, but any such effects are hard to predict, as this tendency might be directly opposite in some contexts (Borgstrøm & Hansen, 2000). Our use of a roughly systematic sampling design instead of the gillnetting Standard's recommended depth-stratified randomization (2015a) could have influenced the catches in a number of ways (difficult to quantify) and even lessened the appropriateness of the statistical analyses undertaken. A simple test of the 2022 results against a random (Poisson) distribution indicated that catch could be highly dependent on the location of the gillnets, as clumped dispersion was indicated at least for two of the lakes (Øvre Urdetjønn: $\chi^2 = 13.0$, df = 6, $P < 0.05$, ratio variance/mean = 1.4; Nedre Urdetjønn: $\chi^2 = 28.8$, df = 6, $P < 0.001$, ratio variance/mean = 2.0) (Table A1 6.2). However, I assume that the multi-mesh gillnets used in 2022 were less vulnerable to non-representative catches due to a less than perfectly randomized localization than the single-mesh nets used in the previous Upper Kova R. test fisheries. Based on the present study's unsystematic depth measurements and my crude depth models and analyses, it is possible that the 2022 test fishery catch in Nedre Urdetjønn might overestimate somewhat the abundance in this lake due to a slightly overproportionate placement of gillnets in shallow areas.

Even though the fishing effort in the 2022 test fishery was based on recommendations in the gillnetting Standard (2015a) and comparable to the previous Upper Kova R. gillnet test fisheries, it was still limited, so sampling error may have influenced the results in all three surveys. However, higher sample size would not only have increased the work load but also run the risk of overwhelming capacity, i.e., having too large an impact on at least parts of the populations in such small lakes. The effective fishing effort in 2022 could also be discussed, as fishing time was perhaps longer than average (17 hours, versus a perhaps more conventional 12 hours) and many gillnets (or parts of them) were placed at shallower depths than their height (about 10 – 30% of the total gillnet area per lake). I had no available models to realistically estimate the impact of these aberrations. However, basic arithmetic and linear assumptions indicated that these two factors might have approximately cancelled each other out overall, so I decided not to implement any catch corrections on this basis.

If there should be systematic seasonal differences in how the fish use and thus are distributed in the three Upper Kova R. lakes, the early timing of the 2022 test fishery could have lessened the comparability of catches with the previous gillnet test fisheries, even with gillnets in approximately the same positions. Furthermore, catches could be higher than average at the start of the growth season because the fish more actively seek food than for instance in high summer, so the timing of the 2022 test fishery could potentially entail an overestimation of abundances in this respect compared to test fisheries later in the season. Seasonal differences in the size of individual fish and thus shifting catchability in given mesh sizes further complicates the matter but it seems that an appropriate number of multi-mesh gillnets “covering” a lake would be less vulnerable to this effect than single-mesh gillnets would have been.

The CPUE results from the 2022 test fishery were based on catch in each gillnet. As each gillnet is only 45 m² and CPUE was defined as catch per 100 m² gillnet area per night, this seemed to entail a sort of extrapolation. Extrapolation can introduce a considerable element of error, as we can’t know if catch in each gillnet would approximately double by doubling its gillnet area. Mathematically, it seemed less of a problem in my analyses, as the calculated means based on each gillnet were the same as when calculating means from total catch and -gillnet area (which was > 100 m²). Comparing CPUE across the lakes with simple one-way ANOVA as I did may have entailed assuming that the unknown catchability constant was equal in the three lakes, but more advanced statistical modes of analysis were unfortunately beyond my current capacity.

Possible seasonal effects on length and weight have been amply addressed elsewhere in the present study (A2 3.4). As for the differences in length and weight measured in the field and in the laboratory, I find it likely that they were not due to measurement error but rather reflected actual post-field changes in the fish (mainly freezing and thawing), as the level and direction of deviance were reasonably consistent.

In the age determination process, several low-quality images (weakly depicted rings/sclerites marking winter zones) combined with my inexperience led to uncertain and possibly some erroneous age estimates, perhaps especially overestimating the age of some older individuals. With low-quality images, I may have been too strongly influenced by the length measurements I used as a control in the age estimation, thus perhaps also exaggerating the correlation between the factors age and length and their distributions (Table A1 6.3; Fig. A1 6.2 and Table A1 6.4). If I had included for analyses only the individuals with the most certain age estimates, the population age structure suggested for Nedre Urdetjønn (A2 2.7) did not seem plausible, so I discarded this option. As indicated elsewhere, uncertainty and errors in the age estimates unfortunately had repercussions for the length growth analyses crucial to the present study.

The higher uncertainty and possible errors signaled for some of the data on sex and maturation stage for Bjønntjønn were probably a result of my inexperience, possibly aggravated by a seasonal component at least for the smaller fish (A2 2.5).

All the instruments used for water measurements in the 2022 test fishery were reportedly calibrated before use. Thus, I assume that the unreliable data described above were primarily due to operational challenges and so were probably a consequence of human measurement error.

In the comparisons with the previous Upper Kova R. gillnet test fisheries, the results would naturally be influenced by any factual errors in the reports (above) and other available data from those surveys, as well as by any errors I might have made re-using their materials. I strived to avoid misrepresentations of the latter kind but had some legitimate precision challenges for instance related to their unfortunate choice to present many key results in 3D bar charts with units of 5 (%) on the y-axis.

A key decision prior to all comparisons with the previous Upper Kova R. gillnet test fisheries was related to which data from the present study should be included. If my interpretation of the guidelines of Ugedal and colleagues (2005) should be incorrect (I excluded all fish caught in mesh size < 15.5 mm, including fish > 150 mm, *and* any fish < 150 mm), this could have had a rather large impact in the overall rather small data set from the 2022 test fishery. Added to this challenge was my inexperience in removing caught fish from the gillnets, as the possibility of some erroneous panel/mesh size registrations affecting data inclusion cannot be excluded.

## 6.4 Future studies and management

For more robust assessments regarding the balance of natural recruitment to food production and the decision to stop supplemental stocking in the Upper Kova R., there is a need for more knowledge on the these brown trout populations and perhaps also on local harvest, especially for Bjønntjønn.

Science-based knowledge should be acquired through continued monitoring in both the recruitment streams and in the lakes. Heggenes' follow-up stream studies in 2022 will be an important contribution to the former, increasing the chance of representative baseline data. For the lakes, a longer time-series of test fisheries with multi-mesh gillnets and competent analysis is needed. For Bjønntjønn, the possibility of illegitimate stocking should also be kept in mind. Frequent test fisheries could overwhelm the capacity of such small lakes even with limited fishing efforts, so an appropriate time for a next survey might be when it is reasonably certain that there are no more individuals left from the pre-2015 stocking. Information on local harvests (catches and practices) could be a useful supplement to the knowledge pool if there are sufficient resources and interest in collecting and systematizing such data.

If minimum or environmental flows should not be relevant in any revision of terms for the regulation of the Kova R., it seems important for sufficient natural recruitment in the Upper Kova R. that the unintended leakage through the dam at L. Vindsjåen is allowed to continue. If the results from the 2022 test fishery should be mirrored by local harvest results and future test fisheries, a user's or fisheries perspective would entail somewhat different management considerations and decisions for the three lakes. For Øvre- and Nedre Urdetjønn, natural recruitment is probably sufficient in normal years, and somewhat higher local harvest with some smaller mesh sizes might be beneficial. For Bjønntjønn, the sustainability of the local harvest pressure and practice over the past decade might have to be considered. Beyond the scope of this study to assess properly, it could perhaps even be asked if some controlled supplemental stocking would have to be reintroduced to make full use of the lake's production potential for brown trout, securing local harvest catches that are satisfactory over time.

# 7 Conclusions

*Summary of main findings*

Overall, the findings based on the 2022 test fishery in the three Upper Kova R. lakes appeared to resonate well with the tentative assessments on brown trout recruitment and relative densities in Heggenes' stream studies (2018, 2020), including natural recruitment as a potential bottleneck for Bjønntjønn depending on the local harvest.

For Øvre- and Nedre Urdetjønn, the 2022 results indicated that brown trout densities were currently high (as high or higher than in the previous Upper Kova R. surveys and higher than average for a large selection of other Norwegian lakes) – possibly corroborated by early maturity onset in males; recruitment appeared to have been relatively stable and local harvest limited over time (reflected in bimodal age/size structures where fish aged 6 years/with lengths 190 – 250 mm were poorly represented); as also documented previously, overall growth was slow (with current growth rates somewhat below 50 mm/year up to age 6 or 7 years, and slower after this, the latter coinciding roughly with maturity onset in females); and the mean k-factor was below the brown trout normal (1.0) and results in the previous surveys, lowest for the largest fish (> 250 mm) in both lakes.

For Bjønntjønn, the results had to be interpreted more cautiously due to fewer data and some methodological challenges. If representative, the 2022 results indicated that the population was currently medium dense (as in the previous Upper Kova R. surveys and similar to average values for the same selection of Norwegian lakes as above), yet still with early maturity onset in males; growth and recruitment over time was difficult to assess, as most age classes > 4 years (and lengths 250 – 310 mm) were poorly or not represented, contrary to the previous surveys (which showed broader/continuous representation and stable growth rates of around 50 mm/year for all age classes) and with local harvest as a likely contributing factor; a few larger individuals (≥ 360 mm) inhabited this lake, and the mean k-factor was closer to the brown trout normal and results in the previous surveys, especially for the largest fish.

Individual fish lengths and k-factors would probably have been higher on average towards the end of growth season than at the time of the 2022 test fishery; attempts at seasonal correction made the 2022 results related to these variables more comparable and similar to those of the previous, end-of season surveys in the Upper Kova R.

*Concluding remarks related to the overall study hypothesis*

The mid-June 2022 test fishery indicated that since the stocking cessation from 2015:

- Natural recruitment had overall been more than sufficient for Øvre- and Nedre Urdetjønn, resulting in brown trout populations that in a user's perspective were currently a bit too dense to be balanced to food production. This was reflected in relatively slow growth, fish size and quality somewhat below general preferences (with caveats for season), and possibly also in the indications of limited local harvest.
- Natural recruitment may not have been sufficient to maintain the previously documented good balance to food production, better growth, fish size and quality in Bjønntjønn. It seems likely that such a change could reflect higher expectations and pressure of local harvest for attractively sized fish, but the conclusions for this lake were more uncertain due to fewer data and methodological challenges, as well as the possibility of some illegitimate stocking.

In the absence of requirements of minimum or environmental flows in the regulated Kova R., the sufficiency of natural brown trout recruitment to the three Upper Kova lakes is probably contingent on continued leakage from the dam at L. Vindsjåen supplementing residual flow.

Particularly for Bjønntjønn, more knowledge on the brown trout populations in the recruitment streams and in the lake is necessary to better assess the consequences of the 2015 stocking cessation in light of the available recruitment area and local harvest.

Based on findings so far, the case of brown trout versus hydropower in the Upper Kova R. illustrates that compensatory measures such as stocking may be unnecessary or even counterproductive when based on general assumptions rather than context-specific knowledge; for small lakes, even quite limited water-covered areas in recruitment streams may be sufficient in a user's perspective, as long as local harvest is adapted to the capacity of the stream-lake systems to produce fish that can secure attractive catches over time.

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## Figures

## Tables