Determining the Optimal Release Window for Lake-Stocked Brown Trout – Interactions between Release Size, Prey Availability, Predation Risks and Fishing Mortality

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Contents

Abstract

The major part of the annual stocking of about one million age-2 and 3 brown trout (*Salmo trutta*) in freshwaters in Finland are released into large regulated lakes, where natural brown trout reproduction has collapsed. Effective exploitation and unpredictable success characterize the brown trout lake stockings carried out during recent decades. The focus of this thesis was to identify the basic factors affecting the success of brown trout stocked for fishing and to develop practical management tools for brown trout stocking programmes and for catch allocation. The study was conducted in Lake Oulujärvi (928 km^2), one of the largest regulated lakes in Europe. Both long-term time series and short-term experimental data were used.

The results showed that the timing of stocking, together with the availability of seasonally varying suitability of prey, played a major role in determining the optimal release window for lake-stocked brown trout. Most of the brown trout studied in Lake Oulujärvi were piscivorous. They consistently preferred prey sizes smaller than 10 cm (total length, L_T) and avoided larger prey. Between small vendace *Coregonus albula* and smelt *Osmerus eperlanus* available (4-10 cm, L_T), the most abundant species was selected as prey. With regard to suitable prey availability, the best prey window for successful stocking with small-sized, 150-200 g, (age-2 and 3) brown trout was from late June to early July, when abundant 0+ vendace occupy the pelagic areas of the lake. When stocked between late May and early June brown trout should be clearly over 200 g (age-3 and 4) to be able to consume adult prey over 10 cm (L_T), and to produce favourable catches. The maximum prey length consumed by brown trout was approximately 40% of their body length.

Another important factor influencing the success of stocked brown trout was size-dependent predation. Heavy predation (50% mortality) by pike *Esox lucius* was observed on 200-300 g (age-3) brown trout within the first week after release, whereas most of the larger 400-700 g (age-4) brown trout avoided predation (5% mortality). The results suggest that if the release site cannot be chosen from the area with scarce predator populations, the refuge size from pike predation for stocked brown trout can be estimated, if the size distribution of pike population in the release area is known before stocking.

The results showed that trawls and gillnets captured a large number of small brown trout. The laboratory simulations, however, suggested that brown trout could survive, when released after 1 h swimming in a trawl. Catch chilling (to maintain the quality of fish food) induced cold shock and the resulting temporary comatose state delayed recovery for non-target (minimum landing size, MLS $\geq$40 cm, L_T) brown trout increasing their vulnerability before release. Therefore, brown trout should be removed from the yield before chilling or as soon as possible from the chilling tank and be permitted to recover before release.

Most of the small brown trout (< 40 cm, L_T) captured were killed in gillnets with small mesh sizes ($\leq$40 mm). If the restrictions on gillnet fishing cannot be carried out and the lake is heavily exploited, brown trout yields per constant investment available can be increased by stocking large fish. Large release sizes close to the MLS would be most beneficial in areas that have high exploitation as well as problems with high predation rate, lack of small prey fish and out-migration of stocked fish from the area. In addition to decreasing the vulnerability to predation, the distance between the release and recapture sites decreased with the increasing size of brown trout at release making stocking size a management tool also for regional yield allocation. However, with regard to increasing production costs with increasing stocking size of fish, the combination of stocking of small brown trout into optimal prey and predator window and with suitable fishing restrictions may be more recommendable than efforts to establish fishable brown trout stocks into unfavorable areas using large fish.

Key words: brown trout, stocking success, stocking size, predation, pike, prey, vendace, smelt, gillnet fishing, trawling.

Original articles

This thesis is based on the following original articles, referred to in the text by their Roman numerals:

I	Hyvärinen, P. & Vehanen, T. 2003. Length at release affects movement and recapture of lake-stocked brown trout. North American Journal of Fisheries Management 23:1126-1135.
II	Hyvärinen, P. & Vehanen, T. 2004. Effect of brown trout body size on post-stocking survival and pike predation. Ecology of Freshwater Fish 13: 77-84.
III	Hyvärinen, P. & Huusko A. 2004. How the variation in abundance and size distribution of two pelagic prey fish shows up in the diet of lake-stocked brown trout. (Manuscript).
IV	Hyvärinen, P. & Huusko, A. 2004. Long-term variation in brown trout, *Salmo trutta* L., stocking success in a large lake: interplay between availability of suitable prey and size at release. (Manuscript).
V	Hyvärinen, P., Heinimaa, S. & Rita H. 2004. Effects of abrupt cold shock on stress responses and recovery in brown trout exhausted by swimming. Journal of Fish Biology 64: 1015-1026.

Author's contribution:

I	The author was responsible for the research question, planning the study design and organising the data collection. The data was analysed and article was written together.
II	The article was planned together. The author was responsible for organising the data collecting, analysing the data and writing the article.
III	The article was planned together. The author was responsible for organising the data collecting, analysing the data and writing the article.
IV	The article was planned together. The author was responsible for organising the data collecting, analysing the data and writing the article.
V	The original research question was due to the author. The experimental design was planned together. The author was responsible for the practical organisation of the data collection. The author was responsible for writing the article, while H. Rita and S. Heinimaa assisted in structuring it.

Introduction

The production of hatchery-reared salmonids both for food and for stocking has increased rapidly worldwide since the 1980s (Anderson 1997). The brown trout (*Salmo trutta*) is one of the popular salmonid species; originally it was a European species, but due to stocking programmes its present distribution covers all continents (Elliott 1994). The natural production of this species has collapsed in many regions due to a lack of nursery areas, e.g. resulting from the degradation of river environments or damming of spawning rivers for hydropower production (Hurme 1969, Vehanen 1995). Another important factor reducing brood stocks and the natural reproduction of brown trout is overfishing; i.e. too many fish are captured before their first spawning (Huusko *et al*. 1990, Vehanen *et al*. 1998a). In most Finnish lakes fishable stocks of brown trout have been maintained by continuous stocking of hatchery-reared fish (Vehanen 1995). Yearly releases of age-2 and -3 brown trout during the 1990s consisted of approximately one million fish into freshwaters and one million fish into the sea.

The brown trout is a multiform species having at least 3 different life history types (Jonsson 1985, Huusko *et al*. 1990, Elliott 1994). Resident trout live their entire lives in streams or small lakes, whereas anadromous sea-run trout have their spawning and nursery areas in rivers, but forage in the sea. The lake-run form has a juvenile phase similar to that of the sea-run form (Soivio *et al*. 1989, Pirhonen *et al*. 1998), but it migrates to a lake instead of the sea for feeding (Jonsson 1985, Huusko *et al*. 1990, Elliott 1994). In rivers in Finland lake-run brown trout parr usually smolt and emigrate from streams into lakes after attaining total lengths (L_T) of 20-30 cm (Huusko *et al*. 1990).

There are 2 distinct ecological forms of lake-foraging brown trout. In small lakes (0.05-50 km^2) trout are rarely piscivorous, feeding mainly on invertebrates and seldom growing larger than 30 cm (L_T) (Hunt & Jones 1972, Campbell 1979, L'Abee-Lund *et al*. 1992). Several large (500-1500 km^2) oligotrophic lakes in Scandinavia and northwestern Russia are used by large growing (50-90 cm, L_T) piscivorous lake-run brown trout as foraging areas, but their nursery areas are located in rivers (Huusko *et al*. 1990, Vehanen 1995, Nyberg *et al*. 2001). Many of these large lakes are regulated for hydropower, and hatchery-reared brown trout are released for fishing to compensate for loss in natural smolt production (Huusko *et al*. 1990, Vehanen 1995). Since a large degree of unpredictability is present in the stocking results, knowledge of the mechanisms affecting the success of fish released in the lakes is needed to minimize the risks of failure in high stocking investments.

As suggested by Bilton *et al*. (1982), an optimal release window may exist that provides the most favourable conditions, such as the absence of predators at the release area and availability of proper prey, under which any stocked fish may survive and produce high yields. A previous study of lake-stocked brown trout indicated that stocking with age 2 and 3 brown trout in lakes with high yields of coregonid species such as vendace *Coregonus albula,* and low yields of northern pike *Esox lucius*, resulted in the proportionally highest trout yields (Vehanen 1995). Pike can effectively predate migratory salmonids (Larsson 1985, Jepsen *et al*. 1998). Pike were also shown to be size-selective predators that prefer relatively small prey sizes (Hart & Hamrin 1988, Nilsson & Brönmark 2000).

It is evident that large size at release in addition to rapid growth rate after release may help the stocked fish to obtain a size refuge from predation soon after release (Olson 1996, Nilsson & Brönmark 2000). The availability of suitably sized prey fish in the release area is crucial for stocked fish to obtain a favourable start in growth (Sutela & Hyvärinen 2002). However, large fluctuations may occur in the availability of suitable prey fish between seasons (Olson 1996). Therefore, the timing of stocking with optimal stocking size to coincide with availability of suitable prey resources may be crucial to favourable growth and stocking success (Pirhonen *et al*. 2003). Vehanen *et al*. (1998b) and Niva & Julkunen (1998) have reported that brown trout prefer small sized fish, especially vendace in Finnish lakes. Niva & Julkunen (1998) also showed that trout grow better with small sized prey fish than with insect food. However, it is not stated yet, whether there exists an optimal release window for stocked brown trout in a lake with complex multispecies fish community. A better understanding of brown trout prey choice and predator avoidance in the yearly and seasonally fluctuating fish community would aid in avoiding failure in stocking.

In fish stocking, the usual questions are how to maximize yield and allocate catch. Previously it has been shown that increasing the size of brown trout at released increase the recapture rate and yield (Skurdal *et al*. 1989). Since the migration behaviour of brown trout varies with fish size and life stage (Jonsson 1985, Huusko *et al*. 1990), the size of stocked brown trout and thus their migration behaviour could also be a means enabling fisheries managers to influence where the stocked fish are to be exploited. However, production costs may play an essential role when management decisions are made, and therefore they should also be taken into account in yield analyses when variously sized stocked fish are compared.

To protect natural reproduction and to decrease growth-overfishing (fish are captured before using their best growth potential) minimum landing sizes (MLSs) have been set for many valuable species. For brown trout the MLS is 40 cm (L_T) in Finland. Currently, fishermen are well aware of the purpose of this limit and usually release accidentally captured undersized alive fish immediately after capture. However, any capture process including additional handling of fish may be stressful (Barton *et al*. 1980, Olla & Davis 1992); thus the increased mortality due to lowered viability of discarded fish is a worldwide problem (e.g. Soivio *et al*. 1991, Olla *et al*. 1997, Davis *et al*. 2001).

Previously several studies have examined the viability of discarded non-target fish after trawling (Soivio *et al*., 1991; Turunen *et al.,* 1994; Olla *et al*., 1997; Davis *et al*. 2001). It has been indicated that capture by trawls increases the concentrations of blood stress indicators in released undersized brown trout, but usually does not cause instant mortality (Soivio *et al*. 1991, Turunen *et al*. 1994, Jurvelius *et al*. 2000). However, during the last 5 y Finnish freshwater trawlers have introduced a new chilling method, similar to that also used by some marine fisheries (Joensen *et al*. 2000, Careche *et al*. 2002), to maintain the high quality of food fish. Recent results indicate that live-chilling can prevent some of the negative effects on fillet quality caused by crowding stress at high fish density before slaughter (Skjervold *et al*. 2001). In Finnish freshwater trawling catch handling often contains the process that after hauling the trawl net, fishermen hoist the catch from the surface water and empty it directly into a tank containing ice and water. However, the abrupt cold shock caused by the chilling process may be an additional stressor for non-target fish before their release (Barton & Peter 1982, Tanck *et al*. 2000). If this possible additional stressor affects the viability of released brown trout, it may have a considerable influence on the brown trout population and fishery.

The primary purpose here was to identify the basic factors affecting the success of brown trout stocked for fishing into a large regulated boreal lake with a multi-species fish community and multiform fishery. Another goal was to develop management tools for stocking programmes and for harvest allocation. The basic objectives of the study were:

- to identify the interactions between stocking success, prey availability, predation and size of brown trout at release,
- to estimate the size-dependent movements and yields of stocked brown trout and
- to estimate the viability of under-sized brown trout released after trawling and chilling (the method used to maintain quality of food fish).

Material and methods

Study area

The study was conducted in Lake Oulujärvi (I, III, IV) in central Finland and in the Kajaaninjoki River (II) which descends to this lake from the southeast (Fig. 1). Lake Oulujärvi is one of the largest lakes in Finland, with a surface area of about 928 km^2. The colour of the water is generally below 80 mg/l Pt and the total phosphorus level is below 20 µg/l (PSV Ltd. 2002). The mean depth of the lake is 7.6 m, the maximum is 36 m, and the mean annual variation in water level is 1.9 m. Located in the far-northern seasonal environment, the lake is ice-covered from November to May. In summer, the surface water temperature reaches just over 20 °C. Lake Oulujärvi has been regulated for hydropower since 1951, when the largest rivers flowing both into and out of the lake were dammed for hydropower generation; following this the natural reproduction of lake-run brown trout soon collapsed (Hurme 1969). The Kajaaninjoki River is regulated for hydropower production, with the power plant situated 9 km upstream from the river's outlet at Lake Oulujärvi. During the study period (II), the mean discharge of the river was 55.8 m^3/s.

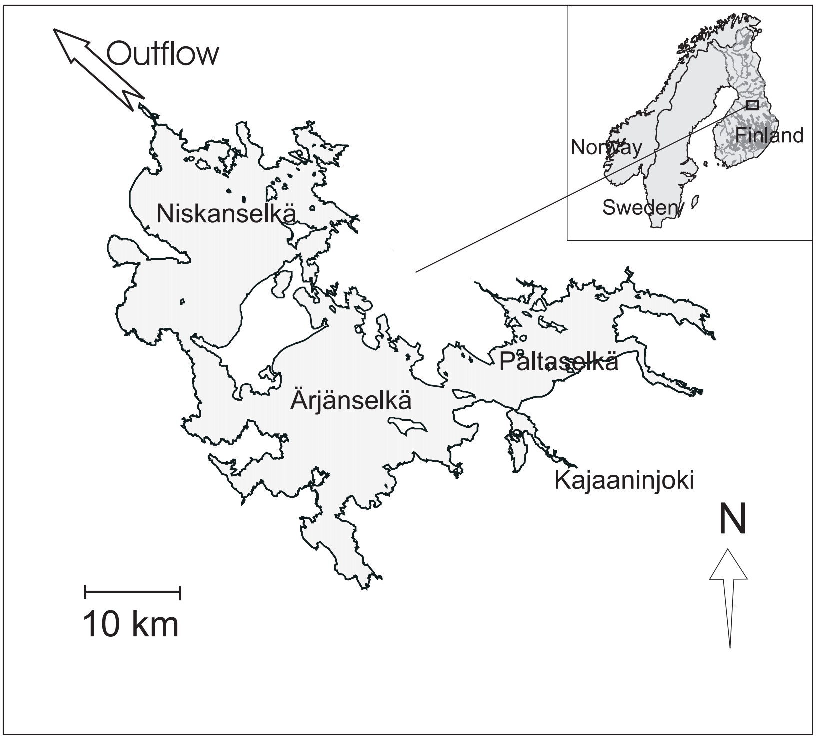

Fig. 1. Map of study area: Lake Oulujärvi and the Kajaaninjoki River. Paltaselkä, Ärjänselkä and Niskanselkä are the principal basins of the lake.

The lake is divided into 3 basins, separated by straits. Paltaselkä, the eastern basin of the lake, is affected by wastewater from the city of Kajaani and a paper mill situated there. The nutrient content and colour values of the water are higher in this basin than in the other two basins (Ärjänselkä and Niskanselkä) of the lake. The lake drains from the Niskanselkä Basin through the Oulujoki River to the Gulf of Bothnia.

The fish species present in the lake include (in alphabetical order) bleak *Alburnus alburnus,* bream *Abramis brama*, brown trout, bullhead *Cottus gobio*, burbot *Lota lota*, crucian carp *Carassius carassius*, dace *Leuciscus leuciscus*, eel *Anguilla anguilla*, landlocked salmon *Salmo salar*, minnow *Phoxinus phoxinus*, nine-spined stickleback *Pungitius pungitius*, northern pike, perch *Perca fluviatilis*, pike-perch *Sander lucioperca*, roach *Rutilus rutilus*, ruff *Gymnocephalus cernuus*, smelt *Osmerus eperlanus*, stone loach *Barbatula barbatula*, vendace and whitefish *Coregonus lavaretus* (Tolvanen 1915, Salojärvi 1992). The brown trout population of Lake Oulujärvi is sustained by yearly releases of age-2 and -3 hatchery fish. The annual mean weight of brown trout at release has varied between 60 and 280 g and the mean L_T between 18 and 30 cm (during 1974-2001, IV).

The total catch in Lake Oulujärvi varied between 500 and 800 t/y during the 1990s (PSV Ltd. 1996, 2001). The annual vendace catch varied between 250 and 350 t, pike catch between 80 and 90 t, smelt catch between 70 and 120 t and brown trout catch between 7 and 16 t (PSV ltd. 1996, 2001). Vendace predominates in the Niskanselkä and Ärjänselkä Basins catches, while perch, roach, and pike catches have been higher in the Paltaselkä Basin. The main gear used are gillnets, lures, fykenets, trawls and seines. The total fishing effort with gillnets in 2000 was 870 000 net-days, corresponding to 9 net-days per hectare. The total effort by angling and trolling was 33 000 fishing days. During the ice-free season a total of 34 fykenets and 9 trawls were used. In addition, 9 seines were used mainly in winter (PSV Ltd. 2001). Due to the vicinity of the city of Kajaani, the fishing pressure in the Paltaselkä Basin was higher than in the Ärjänselkä and Niskanselkä Basins (PSV Ltd 2001).

Effect of release size and site on recaptures of brown trout (I)

Tag (Carlin) recapture data were used to examine whether stocking yield, movement patterns and recapture time are dependent on brown trout length (15-50 cm, L_T) at release or the release site. Three separate basins (Niskanselkä, Ärjänselkä and Paltaselkä) in Lake Oulujärvi with different fish communities and fishing pressure were compared as release sites.

Seven size-groups were established from different ages of fish as follows: 150-199 mm (age-1 and 2), 200-249 mm (age-2), 250-299 mm (age-2 and -3), 300-349 mm (age-3), 350-399 mm (age-3 and -4), 400-449 mm (age-4 and -5) and 450-499 mm (age-4 and -5). In each size-group the relative yield (kg) and recapture rate (number of fish recaptured) per 1 000 brown trout stocked were calculated separately. The production costs of the stocked fish were taken into account by converting a sum of 100 000 euros to the numbers of differently sized fish produced with that amount. Recaptures were then calculated per number of fish produced by 100 000 euros. The sum of 100 000 euros was chosen as a constant investment for fish stocking based on the mean production costs of brown trout stocked in Lake Oulujärvi per year. The yield and recapture rate per 1 000 stocked fish and per 100 000 euros were calculated both for the yield from all recaptures and for those fish recaptured at the legal size (≥ 40 cm, L_T).

Analysis of covariance was used to analyse the effect of the release basin (factor) and the mean length of the size-group at release (covariate) on yield and recapture rate (per 1 000 stocked fish and per 100 000 euros), mean recapture time and mean distance moved. The effect of fish length at release on distribution of recaptures using different types of gear was evaluated.

Size-dependent predation on brown trout (II)

Radiotelemetry was used to compare northern pike predation on 2 size-groups (age-3 and -4) of brown trout stocked in the Kajaaninjoki River. A general model predicting the relative vulnerabilities of differently sized prey fishes to predation (Hambright *et al.* 1991) was used to estimate the relative vulnerabilities of differently sized brown trout and the threshold stocking size of brown trout able to avoid pike predation. Radiotracking was used to locate and observe the tagged brown trout and their predators, and diving to determine the causes of death for brown trout. The movements of radiotagged brown trout and distribution of radiotagged pike in the release area were monitored to evaluate the possibility that brown trout and pike habitats could have overlapped. A stationary tracking station in the river outlet monitored the movements of the tagged fish from river to lake.

Size-selective foraging by brown trout (III)

Virtual population analysis (VPA) (Pope 1972) was carried out to estimate the population sizes of vendace and smelt, 2 potential prey species of brown trout, in 3 periods (winter (January-April), summer (June-August), and autumn (September-December)). The aim was to estimate the intra-annual changes occurring in prey availability in Lake Oulujärvi. The interseasonal reduction in fish numbers in each age-group was assumed to be linear. The size structures (between 40 and 160 mm) of the prey populations (vendace and smelt) were monitored from mid May to late October by taking 2 weekly samples from the pelagic trawl catch in 2001 and 2002. The number of fish in each age-group obtained with VPA was divided into 20-mm size-classes based on these catch samples.

Brown trout were sampled from the trawl, trolling and gillnet catches. The stomachs of brown trout were investigated in the laboratory. Prey size selection by brown trout during the open-water season (divided into 3 periods: May-June, July-August, September-October) was determined with the electivity index (D) of Jacobs (1974),

$$D = (r - p)\ (r + p - 2rp)\ -1,$$

where r is the proportion of a prey size interval (in the 20-mm size-classes) eaten by brown trout and p the proportion of prey size interval (in 20-mm size-classes) available to them. Values between –1 and 1 can be obtained in the index, where –1 indicates total avoidance and +1 total preference.

Factors affecting long-term variation in brown trout stocking success (IV)

The index of brown trout stocking success (S) in Lake Oulujärvi was developed from the available stocking, catch-effort and tag-recapture (Carlin) data from 1974 to 2003 according to the following formula:

$$S_i = 10/N_i\,(A_0C_i + A_1C_{i+1} + A_2C_{i+2}).$$

Where C = catch per unit effort, i = the release year, N = the number of brown trout released, $A_{0\text{-}2}$ = percentage of age (years spent in lake) -group in catch (kg).

A forward stepwise regression technique was used to examine the relationships between stocking success and 5 independent predictors. The time series was divided into 2 periods, with the mean annual stocking day occurring between late May and early June (mean date May 29, 1974-1991) for period 1 and between late June and early July (mean date July 9, 1992-2001) for period 2. The model was first developed separately for the 2 periods with different stocking seasons and then also for the entire time series. The 5 independent variables used to search for the interannual variation in stocking success were 1) stocking rate, 2) mean brown trout weight at release, 3) biomass of adult vendace during brown trout release season, 4) biomass of 0+ vendace and 5) predator-CPUE: combined pike, burbot and pike-perch CPUE represented as the relative abundance of these predator species.

Effect of chilling on the viability of brown trout released after trawling (V)

The effect of additional stress induced by chilling (the method fishermen use to maintain high quality of food fish) after simulated trawling stress was examined in a laboratory experiment. To simulate swimming in a trawl, age-3 brown trout were made to swim against a flow of 0.5 m/s for 60 min. To simulate chilling the fish were kept for 10 min in a tank containing ice and water. To simulate combined stressors representing the whole catch treatment in the trawler, the fish were first made to swim followed by chilling. Changes in the concentration of blood plasma cortisol, lactate and glucose values of brown trout were used as stress indicators. The recovery of stressed fish was observed as a reduction of these blood chemicals. The data were subjected to an analysis of variance (ANOVA) with treatment (swimming, cold shock and combined stressors) and the recovery time (10, 20, 60, 240 and 1440 min). Additional comparisons of means were performed using Tukey's test.

Results and discussion

Importance of availability of suitable prey for stocking success

Effects of seasonal variation

On the basis of the brown trout stomach analysis (III), vendace was the principal prey species for brown trout in Lake Oulujärvi. The great importance of vendace for brown trout was supported by results (IV), indicating that the abundance and size structure of vendace populations were the most important factors accounting for the long-term (27 y) variation in brown trout stocking success. The large proportion of vendace in brown trout diet have been found earlier by Vehanen *et al*. (1998a) and Niva (1999) and Heikinheimo (2001). The present study showed that the importance of vendace and other factors affecting consumption by brown trout (III), and stocking success (IV) were heavily influenced by stocking season. For brown trout released in early summer (late May – early June), the adult vendace biomass together with the mean size of brown trout at release accounted for a major part of the interannual variation in brown trout stocking success (IV). For brown trout released in summer (late June - early July), the total biomass of the vendace population accounted for the major proportion of the variation in stocking success, with 0+ vendace recruits playing a major role (IV); this was also observed in the stomach contents (III). In spring brown trout foraged on adult prey, but as soon as a new year-class of 0+ vendace entered the pelagic area, brown trout shifted to foraging on this prey (III).

In addition to vendace, brown trout also preyed on smelt in Lake Oulujärvi (III). Occasionally, when the density of small sized (4-10 cm, L_T) smelt, was equal to that of similarly sized vendace, brown trout exploited them indiscriminately (III). However, when the smelt density (4-10 cm, L_T) was lower than that of vendace, brown trout foraged on vendace almost exlusively (III) and vice versa smelt was preferred, when smelt density was higher than that of vendace. Evidently, it was not profitable for a piscivorous brown trout to exploit prey at low densities, but shift to an alternative more dense prey species. This data lend support to the type III form of functional response (Holling 1965) in the brown trout-prey interaction, namely S-shaped rise to a plateau with increasing prey density. Previously also Heikinheimo (2000) speculated that type III response for brown trout-vendace interaction is more probable than type II (negatively accelearated rise to a plateau). However, Heikinheimo *et al*. (2002) found type II functional predator-prey response for brown trout on the basis of the data collected from Lake Päijänne. Heikinheimo (2001) also estimated that type II response could cause a total collapse in the vendace stock. Instead, the present results (III) suggest that brown trout selected their target prey based on the relative density of the potential suitably sized prey species with type III response. This sort of foraging behaviour suggests clearly lower risk of overgrazing than type II at least, when alternative prey (smelt) are available for stocked brown trout even though high seasonal variation occurs in principal prey (vendace) size and availability.

Brown trout size – prey size relations

In the present study (III) the maximum prey length (mainly vendace and smelt) consumed by brown trout was 40% of their body length, when the length of brown trout was below 30 cm (L_T). This is also in accordance with the previous results of L'Abee-Lund *et al.* (1992) and Damsgård (1995). In Lake Oulujärvi all the brown trout sampled consistently preferred prey from the smallest vendace and smelt size-groups available, whatever the season or available prey size structure and density (III). In general, fish predators are usually referred to as gape-limited foragers, with the upper limit for their prey size being set by predator gape or oesophagus dimensions (Wankowski 1979, Hambright *et al*. 1991, Olson 1996). The gape-limitation is related to diameter of food particle (Wankowski & Thorpe 1979), and usually this determinative diameter is the depth of prey fish (Hambright *et al*. 1991, Nilsson & Brönmark 2000). Wankowski & Thorpe (1979) showed that Atlantic salmon, *Salmo salar*, had highest growth rate when food particle size was 2.2 –2.6 % of length (4.2 – 20.3 cm). Supposing similar relation with brown trout, optimal prey particle size would be approximately 4-8 mm for 20-30 cm (typical stocking size) brown trout. Brown trout ingest vendace head first (Vehanen *et al*. 1998b), thus the optimal size of vendace is determined by the body depth diameter of vendace. The body depth (d) and L_T are linearly related (Hambright et al. 1991) and for vendace the depth of 4-8 mm corresponds 4-6 cm in L_T ($d=0.21L_T - 5.2$, $R^2 = 0.92$, N = 272, P. Hyvärinen, unpublished data from Lake Oulujärvi). In conclusion, for a 20 – 30 cm stocked brown trout an optimal prey size of vendace is approximately 4 – 6 cm L_T (20% of brown trout L_T) and maximal 8-12 cm L_T (40% of brown trout L_T). In Lake Oulujärvi 4 – 6 cm L_T vendace were available between late June and early July (III) thus suggesting also optimal stocking season for 20 – 30 cm brown trout during this period.

In Lake Oulujärvi 27-y time-series data (IV) showed that the mean weight of brown trout at release was important for stocking success when the fish were released in spring (late May-early June), but was not if the fish were released in summer (late June-early July). The results from the stomach analysis (III) indicated that this was coupled with the availability of suitably sized prey. The size of adult vendace was large, about 10 cm or more (L_t), almost throughout the study period (1974-2002, III, IV), thus being in the upper range (8-12 cm L_T) of edible prey for age-2 and -3 stocked brown trout (20 – 30 cm L_T) (III). Based on the papers III and IV only the largest brown trout individuals stocked in spring were able to take advantage of relatively large-sized vendace. This probably lowered survival potential of small trout through weak growth leading to size-at-release-dependence in survival (II) and in stocking success (I, IV). However, the alternative prey, small sized smelt, may have been available, when small vendace were scarce (III). Unfortunately, due to lack of long-term data such as with vendace (IV), the effects of fluctuation in the smelt population on the brown trout stocking success was not possible to study in Lake Oulujärvi.

Previously it has been shown that variation in prey growth (bluegill *Lepomis macrochirus*) can strongly affect on the predator growth (large-mouth bass *Micropterus salmoides*) (Olson 1996). When prey had high growth rate, predators were restricted to forage only on the youngest prey (Olson 1996). The results of Niva & Julkunen (1998) indicated that brown trout switched to alternative prey (nine-spined stickleback *Pungitius pungitius*) if the density of small-sized vendace fell in a small lake in northern Finland. These results are also in accordance with the findings here (III) except that the alternative prey were smelt.

In Lake Oulujärvi, brown trout stocking success was highest during the years of abundant vendace population (IV). The growth rate and condition of vendace show high density-dependence (Auvinen 1994, Salmi & Huusko 1995). Therefore, individuals of abundant vendace year-classes are likely to be more and longer vulnerable to predation (III) by stocked brown trout than those of sparse year-classes, thus enhancing stocking success.

I conclude that if small brown trout that were released in early summer (late May-early June, 1974-1991, IV) lacked suitably sized prey (III) during the first weeks after release, their start in growth and stocking success would be poor (IV). Improving food resources one month later in summer by the recruitment of a new year-class of 0+ vendace was not able to rescue the stocking result for that year (IV). The success of a cohort of stocked brown trout was dependent essentially on the abundance of available prey at release (III, IV), together with a suitable size ratio between prey and stocked fish, allowing for successful foraging (III, IV).

Summer stockings (late June-early July) in Lake Oulujärvi during 1992-2001 (IV) match well the time period during which 0+ vendace occupy the pelagic area of the lake and form a dense mass of suitably sized (4 – 6 cm L_T) prey for newly stocked brown trout (III). Based on the results from papers III and IV I conclude that most of the newly stocked brown trout released in summer (1992-2001) were large enough to consume 0+ vendace, which permitted a good start for growth and thus favourable stocking success (IV).

Practical recommendations

In practical management work, it can be difficult to obtain good estimate of the state of prey populations. If vendace are present in the stocked lake and are effectively exploited, catch and effort data are often available for estimating the relative abundance (CPUE) of the adult vendace population. The abundance of 3-week-old vendace in mid-June correlates with the abundance of vendace recruits in September (Karjalainen *et al*. 2002) and yearly estimations of it would be a useful tool for management decision-making. However, the problem is that managers seldom have opportunities to obtain this type of data. In practice, the opportunities for predicting the forthcoming year-class strength of vendace are found in lakes, where strong vendace year-classes occur every second year (Marjomäki *et al*. 2004). This has also been the case in Lake Oulujärvi since 1994 (IV). If this type of year-class fluctuation occurs regularly, I recommend that small brown trout be stocked between late June and early July during those years when 0+ vendace are assumed to occur abundantly, whereas large brown trout are recommended for release in early summer (late May-early June) during those years between strong vendace year-classes.

Importance of predation on stocking success

Potential long term effects of predation

Based on the results of both long-term (27 y) time-series data (IV) and the radiotelemetry experiment (II), one of the most important cause of natural mortality for stocked brown trout in Lake Oulujärvi has been predation. The increasing trend (IV) in abundance of predators (pike, pike-perch and burbot) within the last 3 decades (1974-2001) indicated an increasing probability for stocked brown trout to undergo predation in Lake Oulujärvi (IV). This was supported by the results from regression analysis for the 2 successive periods studied: during 1974-1991, when no clear increase in predator-CPUE (combined CPUE for pike, pike-perch and burbot) occurred, no significant effect of predator-CPUE on brown trout stocking success was found, but during 1992-2001 there was a clear increase in predator-CPUE and a negative effect on trout stocking success (IV). In general the predation pressure is dependent on the abundance of potential predators, and the conditions under which the predators encounter prey (DeAngelis & Petersen 2001). This interaction can be influenced by many factors such as the energy requirements of predators (Heikinheimo & Korhonen 1996), the overlap between the predator spawning season and migration of salmonids in the area (Jepsen *et al*. 2000), the availability of alternative prey species (III) and the brown trout itself: its size in relation to the size of predators (II) and previous experience with predators (Olla & Davis 1989, Järvi & Uglem 1993).

Brown trout stocking (late May-early June) in 1974-1991 probably overlapped the pike spawning period in Lake Oulujärvi, whereas pike had already spawned when the brown trout were released (late June- early July) in 1992-2001 (IV). This may be the reason why predator abundance did not affect brown trout stocking success during 1974-1991, but affected it negatively during 1992-2001 (IV). Previously Jepsen *et al*. (2000) suggested that the overlap between the pike spawning period and the brown trout smolt run prevented pike from preying on brown trout, because at that time pike were not moving in the migration routes of the brown trout. However, contrasting results (II) indicated that although the brown trout were released at the pike spawning time (June 4) in the Kajaaninjoki River, no refuge from pike predation existed for small brown trout. Instead, I conclude that in Lake Oulujärvi the difference between the results on the effects of predator abundance from regression analysis in the 2 successive periods (1974-1991 and 1992-2001) indicated the high difference in level of predator abundance between these periods (IV) rather than difference in overlap of pike spawning and brown trout stocking season between the compared periods.

The heavy predation by northern pike on newly released brown trout was observed in the radiotelemetry study in the Kajaaninjoki River (II). Predation by other potential predators (burbot and pike-perch) on brown trout was not examined using radiotelemetry (II), but their possible negative effect on brown trout stocking success was included in the combined abundance (CPUE) of these 3 predators in the time-series analysis (IV). In previous studies, burbot and pike-perch also preyed on small-sized salmonids (Larsson 1985, Jepsen *et al*. 1998).

The brown trout stocked in Lake Oulujärvi (I-IV) were naive hatchery-reared fish having no previous experience of predators before their release, which can be one explanation for the high predation rate. Olla & Davis (1989) suggested that fish having already experienced encounters with predators survived better than naive fish, when both were exposed to predators at the same time. Thus, training the small stocked fish to avoid predators could be a successful method for stocking programmes (Järvi & Uglem 1993). However, regardless of the fact that wild fish are usually more experienced with predators than hatchery fish are, there are indications that predation may be fateful also for wild salmonids during their smolt migration (Larsson 1985, Dieperink *et al*. 2001).

Size-dependent predation by pike

Heavy predation by pike was observed in the Kajaaninjoki River on age-3 (200-300 g) brown trout within the first week after release, whereas larger (400-700 g) age-4 brown trout avoided predation (II). Also the positive correlation between body size at the time of release and the recapture rate found (I) reflect an advantage of the large size of brown trout at release that enables them to avoid predation. The body depth of the stocked age-4 brown trout was greater than the estimated gape size of most pike present in the Kajaaninjoki River, and therefore these fish were estimated to enjoy an almost absolute size refuge from pike predation (II). A slight observed predation rate on these fish also indicated that the estimation was realistic (II). The stocked age-3 brown trout were estimated to be vulnerable to almost half the members in the pike population, and the observed heavy predation rate likewise supported the estimation (II). These results indicate that using the present rearing methods and stocking predator-naive brown trout, high predation rate can be decreased by stocking larger fish. Threshold refuge size and relative vulnerability for stocked trout from pike predation can be estimated by the relation between pike gape size and brown trout body depth (II). In the laboratory pike has been shown to prefer smaller prey than their gape limited (Nilsson & Brönmark 2000). However, in the Kajaaninjoki River (II) pike foraged brown trout from the upper edge of their gape size limit, which may be due to high vulnerability of predator-naive stocked fish (Olla & Davis 1989).

For the small-sized brown trout (20-30 cm, L_T), the recapture rate decreased as the distance between stocking site (Niskanselkä Basin vs. Paltaselkä Basin) and good foraging area increased (I) suggesting increasing natural mortality. It is probable that small brown trout, which had to move further to find favourable foraging areas (from Paltaselkä Basin to Niskanselkä Basin), were longer exposed to predation than fish stocked closer to the good foraging areas (Niskanselkä Basin) and thus suffered higher natural mortality than fish undergoing shorter migrations (I). Based on the results (IV), small-sized brown trout succeeded well, as long as small-sized vendace were abundant at release (early July). They were not forced to migrate long distances to find suitably sized prey (0+ vendace) (I, III), and they probably also grew rapidly, thus attaining the size refuge from predation soon after release, which enabled favourable survival rate and stocking success (IV). On a smaller scale, similar conclusions were made in the Kajaaninjoki River study (II), where heavy size-dependent predation was observed for those stocked fish remaining in the area of dense pike population. Almost half the stocked fish emigrated from the river and survived within 3 d of release (II). Of those fish remaining in the river for a longer period all, except one age-3 (26-32 cm, L_T) brown trout were eaten by pike, whereas all but one age-4 (35-39 cm, L_T) brown trout avoided predation (II).

Practical recommendations

In practical management work, the relative abundances of predator populations can be estimated with CPUE, if suitable catch and effort data are available. The present results (IV) showed the negative effects of predation in Lake Oulujärvi, since the combined CPUE of pike, burbot and pike-perch was over 1 kg per lifted gillnet (approximately 30 m long and 2 m high). Previously it has been shown that there is a large regional and seasonal variation in CPUE of these predators in Lake Oulujärvi thus indicating also high variation in predator density in different areas (Hyvärinen & Salojärvi 1991, PSV Ltd. 2002). This enables the predator-CPUE to be used as a tool for choosing stocking areas with low predation risk (predator-CPUE clearly below 1 kg per net). For purposes of estimating the relative vulnerability of different-sized brown trout or for estimating the threshold refuge size (II), the size distribution of predator populations in the release area can be obtained by measuring the L_T of predators captured. To obtain a representative estimate from the population size-structure, samples from unselective gears such as trap nets are recommended.

Viability of brown trout released after trawling and chilling

Recovery of released brown trout

Based on the results here (V), brown trout can survive when released after exhaustion by (simulated) swimming in a trawl followed by chilling (the method used to maintain the quality of food fish). However, chilling (10 min in a mixture of water and ice) induced cold shock and the resulting temporary comatose state, as evidenced by a lack of movement and no reaction to being touched. This increased vulnerability of non-target brown trout before their release. Blood cortisol and glucose measures also indicated a delayed recovery caused by cold shock (V). In the present study, stressors by swimming in a trawl were simulated in the hatchery conditions. In real trawling the time the fish spent inside the trawl net, the swimming speed and the distress during the trawl may vary considerably. This variation depends, for example, on the time the fish entered the trawl net, the amount of other fish in the net, and the location of the fish in relation to other fish in the net. In spite of these differences compared to real circumstances, stress responses comparable with trawled brown trout (Soivio *et al.* 1991, Turunen *et al.* 1994) were obtained here in the hatchery experiment, which of course, also was the purpose of the simulation.

Since the chilling method studied here was introduced in Lake Oulujärvi in 1998, brown trout stocking success also showed a decreasing trend (IV) regardless of the relatively favourable strong vendace population occurring in the stocking area (IV). The present results suggest that the simultaneously increasing predator populations (pike, burbot and pike-perch) have increased the predation level on stocked brown trout (IV). In addition, the increasing predator populations and decreasing stocking success (IV), coinciding with the introduction of the new chilling method in trawlers (V) may have been connected. In previous studies the condition of the prey fish was crucial to its ability to avoid predation (Olla & Davis 1992).

Based on the laboratory experiment (V), the brown trout showed 100 % survival after exposure to chilling, which suggests the presence of low or no negative effects on brown trout yield induced by this handling. However, the comatose state induced by and the delayed recovery of the stress (on the base of blood cortisol and glucose concentrations) shown after chilling increased the period during which the discarded brown trout are vulnerable to predation after release, which may have increased the mortality rate by predation (II, IV). In the laboratory experiment (V), brown trout exposed 10 min in ice and water regained consciousness in 10 min and the internal temperature (14 °C) they had before chilling in 20 min. Recent results (Farrell *et al.* 2001) showed that a 1-2-h recovery for captured salmonids before their release significantly decreased postcapture mortality. I recommend that brown trout after trawling and chilling should be permitted to recover approximately 1 h and at least for the time required to regain consciousness before release.

However, if the fish are to recover successfully, they must be treated gently and the additional tank for recovery must contain good-quality water (see also Farrell *et al*. 2001).

Number of trawled brown trout

A total of 360, 1300, 1120 brown trout below legal size (< 40 cm, L_T) were estimated to have been captured and released by trawlers in Lake Oulujärvi in 2001, 2002 and 2003, respectively (P. Hyvärinen, unpublished data). This is approximately 1-4% of the yearly number of brown trout stocked in Lake Oulujärvi at that time (IV). No estimation of the total brown trout catch from Lake Oulujärvi in 2001-2003 was available; thus, direct comparisons between trawled and released fish and total brown trout yield were not obtained. However, in 2000 the estimated total brown trout yield was 7700 kg, (about 10 000 captured fish; PSV Ltd. 2001). With regard to these catch numbers, I suggest that the maximum loss in catch would be approximately 3-13 % provided that all the fish would have been killed caused by trawling and the handling in the ship. The brown trout gillnet-CPUE in 2001 and 2003 was lower and in 2002 higher than in 2000 (paper IV), suggesting somewhat parallel changes in total yield between these years. In any case the results here indicate that such a decrease (67%) in stocking success as was found between 1997 and 2001 (IV) cannot be explained only by the additional mortality possibly caused by the new chilling method in trawlers (V).

Stocking size as a management tool

Size-related yields and stocking costs

Stocking size was one of the most important factors affecting stocking success of brown trout in lake Oulujärvi (I- IV). Both the relative yield and recapture rate (per 1 000 fish released) significantly increased with increasing fish length at release (I). The advantage of large stocking size was related to better feeding opportunities (III, IV) and lowered risk of predation (II), leading to higher survival rate and stocking success (I, IV). An important finding in this study was that the effect of release size on total recaptures and yields was highly dependent on the release site and season (I, IV). The relationship between stocking success and release size is known from many previous studies with salmonids (e.g. Skurdal *et al*. 1989, Salminen *et al*. 1995, Vehanen 1995). However, this information is not necessarily sufficient for a fisheries manager to make practical decisions on the size of the fishes to be stocked. Instead, when the production costs of different-sized fish are taken into account, when evaluating stocking results, cost data are more useful to decision-makers. In lake Oulujärvi (I), the positive relation between recapture rate (per 1000 fish released) and fish length at release turned negative, when recaptures were calculated per number of fish produced and released by constant investment (100 000 euros) and fish were released to a good foraging area (Niskanselkä). Thus, when recapture rates were calculated in relation to the constant number of stocked fish, recaptures were lowest for smallest fish, but when recapture rates were calculated per varying number of fish produced per constant investment, recapture rates were highest for smallest fish. Different ways of presentation led into different conclusions. Thus, the financial point of view is essential, when different valued stocked fish are compared and practical management decisions are made.

Stocking size affects yield proportion in different gear

The time that stocked brown trout spent in the lake between release and capture was short (I), which resulted in the larger size on release, the larger the fish were at capture. Thus, it also follows that when only fish recaptured at the legal size (≥ 40 cm, L_T) were considered, the yield and recapture rate remained very small for small fish at release, indicating heavy mortality of brown trout under the legal size (I). The majority (60%) of the captured fish from the fish stocked at 20-30 cm (L_T) were caught in gillnets, mostly (70%) with small mesh sizes (≤ 40 mm) (I). Increasing the stocking size decreased the proportion captured in gillnets with small mesh sizes (≤ 40 mm) and increased the proportion captured in fykenets. The highest catch (50 %) in fykenets was obtained, when stocked brown trout were > 45 cm (L_T).

In Lake Oulujärvi and other large lakes (stocked age-2 and -3) brown trout can grow to 60-90 cm (L_T) in 3-6 y (Vehanen *et al.* 1998a, c, Huusko *et al.* 1990). Thus, proper technical fishing regulations such as gillnet mesh size regulation could considerably increase the profitability of brown trout stockings, especially with small fish having the highest growth potentials. Based on the present results the most problematic mesh sizes are ≤ 40 mm with the present MLS (minimum landing size, 40 cm L_T). However, if MLS was set to 50 cm (L_T), which would result in a higher total yield, suitable minimum allowable mesh size for gillnets would be 60 mm (Huusko & Hyvärinen 1994, Hyvärinen *et al.* 2000). However, the proportion of other gear in the total brown trout catch would increase, due to regulations on the use of gill nets; e.g. in Lake Oulujärvi fishermen using fyke nets would probably obtain the largest benefit due to gillnet regulations (I). Therefore, when decisions on the size of stocked fish and fishing regulations are made to obtain better total yields from brown trout stockings, managers need to know the structure of the fisheries in the whole area used by brown trout and realize the effects of these measures on yield allocation with different gears.

Using stocking size for regional yield allocation

The 3 separate basins (Paltaselkä, Ärjänselkä and Niskanselkä) in Lake Oulujärvi have been managed as separate stocking units. Fishermen have also assumed that fish released in certain areas will be captured from the same areas (Vehanen *et al.* 1998c) and this is also the case in some other lakes in Finland (Vehanen 1995). The present results

(I) show that the distance between the release site and recapture site decreased with increasing size of brown trout. Small brown trout (< 40 cm, L_T) moved towards that part of the lake in which the highest densities of pelagic prey fish are found, whereas large brown trout (≥ 40 cm, L_T) were captured near their release sites, independent of their release area (I). Similar negative relationships between migration distance and release size, probably affected by differing migration behaviour of different-sized fish were found previously, when salmon were stocked in the Gulf of Bothnia (Salminen *et al*. 1994). Thus, as suggested by Salminen *et al*. (1994) for salmon in the case of Gulf of Bothnia, the stocking size could be used as a suitable management tool for regional allocation also for brown trout yield and fishery in large lakes as found here (I).

Conclusions

Matching the optimal prey window at release for brown trout

The present study showed that the timing of stocking, together with the availability of seasonally varying suitability of prey, played a major role in determining the optimal release window for lake-stocked brown trout (III, IV). I conclude that small-sized (< 200 g) brown trout should be stocked only in lakes where small-sized (< 10 cm, L_T) prey are also abundant at the release time and in the release area (I, III, IV). If vendace are present in the fish community, the best release window for successful brown trout stocking is from late June to early July, when 0+ vendace occupy the pelagic areas of the lake (III, IV). In this case brown trout as small as 150-200 g may be successful (IV). If brown trout are released in spring and the adult prey available are larger than 10 cm (L_T), the stocking size should be larger, with the trout weighing clearly over 200 g (IV), because the large size widens the size range of suitable prey. The maximal prey length consumed by brown trout was approximately 40% of brown trout L_T (III) and the optimal clearly less than that (approximately 20%). If a strong year-class occurs regularly every second year in the stocked lake, I recommend that small brown trout be stocked between late June and early July in those years when 0+ vendace are assumed to be abundant, whereas more large brown trout should be released in early summer (late May-early June) in the years between the strong vendace year-classes.

Matching the optimal predator window at release for brown trout

The age-3 (200-300 g) brown trout were highly vulnerable to predation in the Kajaaninjoki River within the first week after release, whereas age-4 brown trout (400-700 g) enjoyed an almost absolute size refuge from predation (II). I recommend that small brown trout be released into areas where predators are scarce (mean gillnet CPUE clearly below 1 kg/net). They should also be released near favourable foraging areas to ensure a favourable start for growth and, thus, a refuge from predation soon after release (I-IV). If this is not possible, heavy predation by pike can be decreased by stocking brown trout large enough to enjoy the size refuge from predators at the release site (II). The threshold refuge size for brown trout and the relative vulnerability of different sized fish to pike predation can be estimated (II), as long as the size distribution of the pike population in the stocking area is known before stocking.

Solving the problematic fisheries management of brown trout

The number (360-1300 fish) of undersized (< 40 cm L_T) brown trout captured by trawls in Lake Oulujärvi was relatively low, but it may be of some significance for the fishery, if all the fish released would be killed. Although the simulation including chilling (to maintain the quality of food fish) after exhaustion by swimming in a trawl did not cause any instant mortality, it induced a comatose state and delayed recovery (V), which increased the time the released fish were vulnerable to predation. Therefore I recommend that undersized fish should be removed from the yield before chilling or as soon as possible from the chilling tank and be allowed to recover approximately 1 h and at least for the time necessary to regain consciousness before being released back into the lake. However, if the fish are to recover successfully, they must be treated gently and the additional tank for recovery must contain good-quality water.

The majority of the captured brown trout stocked at small sizes (20-30 cm, L_T) were caught by small-mesh-sized (≤ 40 mm) gill nets soon after release (I). To obtain better results from brown trout stockings using the present release sizes (20-30 cm, L_T), regulations covering gillnet fishing (mesh size ≤ 40 mm) are needed. If effective regulations for fishing cannot be carried out and the lake is heavily exploited, the yield per constant investment could be increased by stocking brown trout that are close to or over their present legal landing size (40 cm, L_T). Stocking large brown trout would be most beneficial in areas such as the Paltaselkä Basin (I) or the Kajaaninjoki River, where high predation rates have decreased stocking success (II) and small brown trout have also migrated to the other areas, reducing the profit for fishermen operating in the release area (I). The distance between the release site and recapture site decreased with the increasing stocking size of brown trout, especially when stocked into foraging areas unfavourable to small brown trout, as was the case in the Paltaselkä Basin (I, III). However, in regard to increasing production costs with increasing size of fish the combination including stockings of small brown trout into optimal prey and predator window with suitable fishing restrictions may be more recommendable than efforts to establish fishable brown trout stocks into unfavorable areas using large fish.

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