Fisheries Research 267 (2023) 106799

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Density- and size-dependent mechanisms modulate the outcome of stocking in a naturally recruiting freshwater piscivore (northern pike, *Esox lucius*): A replicated whole-lake experiment

Daniel Hühn [a,*], Daniel C. Gwinn [b], Stephanie L. Shaw [b], Josep Alós [a,c], Micheal S. Allen [b], Thilo Pagel [a], Christian Skov [d], Robert Arlinghaus [a,e]

[a] Department of Fish Biology, Fisheries and Aquaculture, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany
[b] School of Forest, Fisheries and Geomatics Science, The University of Florida, Gainesville, FL 32653-3071, USA
[c] Instituto Mediterráneo de Estudios Avanzados, IMEDEA (CSIC-UIB), C/ Miquel Marquès 21, 07190 Esporles, Illes Balears, Spain
[d] DTU AQUA, National Institute of Aquatic Resources, Technical University of Denmark, Vejlsøvej 39, 8600 Silkeborg, Denmark
[e] Division of Integrative Fisheries Management, Department for Crop and Animal Sciences, Faculty of Life Sciences, Humboldt-Universität zu Berlin, Philippstrasse 13, Haus 7, 10155 Berlin, Germany

ARTICLE INFO

Handled by B. Morales-Nin

Keywords:
Stocking
Enhancement
Additive effects
Esox lucius
Density-dependent growth
Population regulation

ABSTRACT

Despite the widespread use of stock enhancements to improve fisheries across the world, there is a lack of robust knowledge under which conditions fish stocking provides additive effects rather than merely replacing a fraction of natural recruitment. Fully controlled and replicated studies at the level of entire ecosystems are needed to provide answers. Properly monitored experimental releases also allow testing mechanisms of density- and size-dependent population regulation. In this study, the population-level outcome of stocking juvenile pike (*Esox lucius* L.) in naturally reproducing lentic stocks was investigated. We used a replicated before-after-control-impact design in 15 experimental lakes involving two stocking densities and unstocked controls. Releasing age-0 pike failed to generate additive effects at the age-2 cohort. As expected from theory, we observed density-dependent mortality and differential survival of wild and stocked pike. Stocked and wild fishes showed contrasting responses in terms of growth to variation in predator density, competitor density and the forage base, suggesting both subpopulations differed in their response to stocking-induced changes in population traits (e.g., density). Despite the lack of additive effects caused by stocking, a fraction of the stocked individuals established in the stock-enhanced cohort, indicating that replacement of wild recruits by stocked conspecifics had occurred. Depending on the origin of the stocking material, pike stocking thus has the potential for genetic hybridization, while not necessarily benefiting fisheries catch. We conclude that whenever a natural pike population exists, stocking juvenile pike will not produce additive effects in lakes and that enhanced pike populations will be strongly regulated by size- and density-dependent juvenile mortality and less by density-dependent growth.

1. Introduction

Stocking constitutes a widespread fisheries-management tool across the world, whose objectives range from meeting fisheries goals to enhance catches to conservation objectives to recover depleted or extinct species (Cowx, 1994; Lorenzen et al., 2012; Arlinghaus et al., 2016). Stock enhancement of naturally recruiting fish is a common stocking form (Lorenzen et al., 2012) and is defined as the release of fish into an ecosystem hosting background natural recruitment. It is aimed at generating additive effects by increasing the abundance or biomass, and hence catch rate or yield, of the target stock above its naturally achievable levels (Lorenzen et al., 2012). Natural recruitment may be impaired by recruitment bottlenecks (e.g., habitat limitations), where stocking based-enhancements may provide a solution to keep stock sizes and catches high. However, there is controversy whether additive effects stemming from stocking can be sustained when naturally recruiting stocks are supplemented by juvenile hatchery fishes (Hilborn, 1999; Hilborn and Eggers, 2000; Lorenzen, 2005; Radinger et al., 2023; Terui et al., 2023). In fact, theory of fish population regulation and quantitative stocking models suggest that to generate additive effects in

* Correspondence to: Potsdam Institute of Inland Fisheries, Im Königswald 2, 14469 Potsdam, Germany.
E-mail address: daniel.huehn@ifb-potsdam.de (D. Hühn).

https://doi.org/10.1016/j.fishres.2023.106799
Received 30 June 2022; Received in revised form 12 July 2023; Accepted 14 July 2023
Available online 20 August 2023

naturally recruiting populations the released fish must be larger than the life stage where size- and density-dependent compensatory mortality is most prominent and overall recruitment determined (Lorenzen, 2005; Rogers et al., 2010; Camp et al., 2014, 2017; Johnston et al., 2018; Lorenzen and Camp, 2019). Compensatory mortality is most pronounced in the larval and juvenile life stages in most fishes (Walters and Martell, 2004; Lorenzen, 2005). However, surprisingly few robustly designed stocking experiments at the scale of entire ecosystems exist (for exception, see Radinger et al., 2023) to support the theoretical prediction that stocking of fry or small juveniles into self-sustaining stocks should rarely lead to additive effects in subsequent cohorts (Walters and Martell, 2004; Hühn et al., 2014b).

The potential of fisheries data to test ecological theories, such as density- and size-dependent population regulation, has been underutilized by fisheries scholars and managers (Hutchings, 2000; Jensen et al., 2012; Lorenzen, 2014). However, the strongly manipulative character of harvesting and certain fisheries management actions (e.g., stocking) harbor large potentials for testing key mechanisms of density-dependence, evolutionary adaptation and general population regulation (Jensen et al., 2012; Lorenzen, 2014). Unfortunately, most management actions in freshwater fisheries, including stocking, are conducted rather haphazardly lacking a proper monitoring program (Post et al., 2002; Fayram et al., 2009), which limits the opportunity to learn academically from the interventions (Walters and Martell, 2004; Hansen et al., 2015). Here, we report a case where a robust before-after-control-impact-design (BACI; Green, 1979; Underwood, 1994) was used in a replicated stocking experiment in angler-managed lakes in Germany involving the experimental release of juveniles of a freshwater top piscivore, the northern pike (*Esox lucius* L.).

Density-dependence can occur in all life stages in fishes and generally affects all vital rates (Rose et al., 2001). However, density-dependent mortality occurs in the juvenile life stage (e.g., Elliott, 1994). In the adult life stage, the main density-dependent regulatory mechanisms tends to shift from mortality to a predominance of growth regulation, inter alia because size-dependent mortality is much less pronounced in adults compared to larvae and juveniles (Lorenzen and Enberg, 2002; Haugen et al., 2007; Edeline et al., 2010; Hazlerigg et al., 2012; see Lorenzen, 2005 for a review). Hence, elevated competition for food and shelter caused by unnaturally high numbers of juveniles in stock enhanced populations should lead to rapid numerical population size regulation due to compensatory mortality in juveniles. By contrast, biomass and fecundity regulation through density-dependent food limitation and resulting growth depression should be most prominent when stocking happens with adults or generally old life stages larger than bottleneck size (Rose et al., 2001; Lorenzen, 2005, 2008). In this context, ecology and evolutionary thinking merges because domesticated stocked fish will often be suboptimally adapted to the natural ecosystems into which they are released from hatcheries (Lorenzen et al., 2012). Indeed, due to physiological or behavioral maladaptation of stocked fish, for various species higher post-release natural mortality compared to wild fishes has been described (Lorenzen, 2006). The elevated density of newly stocked fish might also induce growth depression, displacement or shifts to less suitable habitats in the naturally recruiting wild cohort (Baer and Brinker, 2008), in turn potentially affecting natural mortality of wild conspecifics due to predation (Skov et al., 2003; Grønkjær et al., 2004). Coupled with the inverse size-dependency of natural mortality common to most fish species (Lorenzen, 2000, 2006), the two patterns mentioned above could in fact even reduce year class strength despite stocking (van Poorten et al., 2011). Without proper experimentation, it is not possible to reliably predict which stocking outcomes to expect for a given species as moderated by prevailing ecological conditions, size of stocked fish and stocking density (Lorenzen, 2005, 2014).

Northern pike (hereafter referred as to pike) is a circumpolar distributed top predator in many lentic and slow-flowing lake and river ecosystems of the temperate regions. The species is characterized by pronounced self-regulation through size-dependent intra- and inter-cohort cannibalism in the juvenile life stage (Kipling and Frost, 1970; Wright and Giles, 1987; Skov and Koed, 2004; Persson et al., 2006). Therefore, even highly intensive stocking of larvae or small juveniles may not bring about desired additive effects. Indeed, stock enhancement experiments using pike fry in the presence of natural reproduction failed to generate additive effects owing to strong compensatory density-dependent mortality of early life stages (Sutela et al., 2004; Jansen et al., 2013; Hühn et al., 2014b). It is possible, however, that releasing larger-sized pike, e.g. age-0 pike after the first growing season, could elevate year-class strength, which would be most likely if size-dependent recruitment bottlenecks were circumvented or in ecosystems suffering recruitment limitation due to habitat constraints (Lorenzen, 2005). In muskellunge (*Esox masquinongy*), post-stocking survival has been shown to be positively related to fish length (Szendrey and Wahl, 1996; Wahl, 1999). Previous experiments with releasing juvenile pike at lake scales failed to provide evidence for additive effects (Radinger et al., 2023), but Radinger et al. (2023) did not test different stocking rates and did not examine the underlying mechanisms of population regulation. Other work with releasing larger sized pike was inconclusive, in some cases resulting in large survival (Monk et al., 2020) and in others failing to elevate catches in a French river (Guillerault et al., 2018, 2021). Stocking outcomes in pike might be release-size dependent. Releasing large juvenile pike might provide a suitable test case for studying the success probability of stock enhancement using esocids as a model.

The first objective of this study was to test whether releasing large juvenile pike in fall of the first growing season would generate additive effects (i.e., increase cohort size) and whether the additive effects would be a function of habitat structure and other ecological variables of the recipient ecosystem (e.g., prey and predator abundance). Documenting the persistence of a strongly enhanced cohort would provide evidence of additive stocking effects when the system is pushed beyond natural recruitment limits. However, we hypothesized in line with available experiments with pike cited above that stocking pike juveniles into naturally recruiting stocks would not result in additive effects. Our second objective was to examine whether releasing large numbers of pond-reared pike would lead to density-dependent growth in wild recruits, in turn putting the wild subpopulation under pressure because survival is strongly size-dependent in juvenile pike (Haugen et al., 2007). Work on brown trout (*Salmo trutta* L.) by Baer and Brinker (2008) suggests that density-dependence in growth should not necessarily carry over to wild fishes due to their superior ability in finding food and shelter in a competitive situation compared to stocked individuals. Similar adaptation benefits of wild pike have been reported in artificially raised pike fry stocked into ponds (Hühn et al., 2014b) and in a lake study (Skov et al., 2011). We thus hypothesized that wild pike should not be growth-depressed when confronted with large numbers of pond-reared, stocked conspecifics of similar or larger size.

2. Material and methods

2.1. Study area and study lakes

The study was initially conducted in 18 man-made small gravel pit lakes and ponds (< 12 ha surface area) distributed over the middle and south part of Lower Saxony in the northwestern German lowlands (see Supplementary Table S1 for locations). We had to exclude three lakes from the final data set due to unexpected winterkills pre-stocking or ongoing gravel excavations in the vicinity of the lakes that strongly modified the ecological status, leading to non-comparable conditions over the experimental time. The final data set contained 15 lakes. The experimental lakes were managed by five recreational fishing clubs. The stocking experiment was part of a large transdisciplinary project conducted jointly by the research team and the local angling clubs over a period of five years (www.besatz-fisch.de). Choice of lakes was based on

the small size, the importance of the lakes for local recreational angling for pike and the fact that pike stocks were actively managed in the lakes in the past. Lakes were chosen to be comparable in size and depth but otherwise variation in level of exploitation (and hence adult pike population size), productivity (e.g., nutrients and prey resource base) and key habitat features, such as macrophyte coverage, was desired by design to investigate the impact of these factors on stocking outcomes, survival and growth. Availability and density of emergent and submerged aquatic vegetation and the presence of woody debris, which is a key juvenile pike habitat (Grimm, 1989; Casselman and Lewis, 1996; Matern et al., 2021; Maday et al., 2023), was visually assessed prior to conducting the stocking experiment and was further enumerated by running transects with an echo sounder (Huminbird 788cHD). In all lakes habitat surveys were conducted in September prior to the stocking experiment (Supplementary Table S1 and S2). Echo sounder and GPS (Trimble® GeoXH™ handheld, GeoExplorer® 2008 series, Athens, Georgia) information was used to assess morphological information of the study lakes in terms of area (ha), and maximum and mean depth (m) (Supplementary Table S1). At all subsequent fish surveys (see below), water transparency was measured as Secchi depth (Secchi disc, Hydrobios, Kiel, Germany), and total phosphorus (only assessed during spring overturn) and chlorophyll *a* concentrations were determined following a standard protocol (DIN EN ISO 6878). Finally, water temperature, oxygen concentration, conductivity, and pH-value were measured in the vertical dimension during all fish surveys using a multi-parameter probe (WTW Multi 340i, Weilheim, Germany) (Supplementary Table S1).

2.2. Study design and fish sampling

To test our hypotheses, we implemented a replicated experiment where we stocked two densities of advanced one summer old (age-0) pike in fall 2011 alongside unstocked control lakes. We assessed the status quo prior to stocking in terms of abundance and size structure of pike and other littoral fish species using electrofishing surveys in spring and fall 2011. Prior to the stocking experiment, we clustered lakes into lakes with supposedly "good" and "poor" pike habitat (lake type) using a threshold of 30% of the lake bottom overgrown with aquatic vegetation or other structures (e.g., woody debris, shoreline trees fallen into the water) (Casselman and Lewis, 1996) resulting in n = 7 good and n = 8 poor pike habitat lakes. Within each pike habitat type category, lakes were randomly assigned to one of the three treatments: (1) control lakes represented unstocked juvenile pike populations, (2) low stocking density (LSD, stocking of 35 age-0 pike·ha^{-1}) treatment lakes mimicked the standard stock enhancement protocol for stock enhancement of juvenile pike in Germany (Baer et al., 2007), and (3) high stocking density (HSD, 70 age-0 pike·ha^{-1}) treatment lakes represented an extreme treatment of pike stock enhancement.

We analyzed the data using a BACI design to investigate the potential additive effects of stocking on the enhanced pike cohort, represented by the age-1 cohort in 2012 (in the first year post release) and the age-2 cohort in 2013 (in the second year post release). To investigate potential additive effects and to determine relevant biotic covariates of stocking success (e.g., prey fish density, abundance of large adult cannibalistic pike, juvenile pike abundance as a measure of competitor density), fish communities were sampled during day-time using a battery-powered DC electrofishing unit (Type EFGI 4000, 4 kW, Bretschneider Spezialelektronik, Chemnitz, Germany), with one anodic handnet of 45 cm ring diameter. Lakes were sampled in March, April, and September 2011 prior to stocking, and in March and September 2012 as well as in March 2013 after stocking. According to the BACI design, 2011 represented the situation before and data from 2012 and 2013 captured the situation after the stocking intervention. Within the BACI design, the zero stocking lakes controlled for temporal changes unrelated to any treatment effect. During spring sampling, we additionally used gillnets (mesh size range 50–75 mm, knot-to-knot) to sample some large fish in the experimental lakes for marking and subsequent release. In addition, some angling took place by collaborating anglers during the electrofishing events to add fishes to the mark and recapture sample (see below). In each electrofishing event, we divided the shoreline into the same 50 or 100 m long transects depending on lake surface area. In all lakes the entire shoreline was sampled by electrofishing on each sampling event, except in one lake (Vockfeyer See) where only 13 randomly selected transects were sampled for logistical reasons to keep the electrofishing effort to one full working day per lake.

All captured fishes (pike and other fishes) were assigned to the capture method (electrofishing [transect no.], gill netting or angling), identified to species level, measured to the nearest mm total body length (TL) and weighed (Sartorius TE2101 with an accuracy of ± 0.1 g for small fishes, or Sartorius BL 12, with an accuracy of ± 1 g for larger individuals; Sartorius AG, Göttingen, Germany). A detailed analysis of the littoral fish communities can be found elsewhere (Emmrich et al., 2014). Captured pike were anesthetized and if captured for the first time individually marked with a passive integrated transponder tag (PIT, 2.15 mm in diameter, 12 mm in length; Oregon RFID, Portland, Oregon, USA) and T-bar anchor tags (TL < 400 mm TL, FD−68BC FF; TL > 400 mm TL, FD−68B; Floy Tag Inc., Seattle, Washington, USA) as described and validated in Hühn et al. (2014a). Marking studies with similar sized pike as the ones that were stocked showed a high retention rate of PIT tags of close to 100% (Hühn et al., 2014a), which is why we assumed zero tag loss in the mark-recapture portion of the present work. Further, we sampled scales above the lateral line for age determination following an established and validated protocol (Pagel et al., 2015) to be able to assign wild recruits to the corresponding year-classes.

Using the catch and age data, prior to stocking we calculated catch per unit effort (CPUE) as a measure of relative abundance expressed as the number of age-1 and age-2 pike caught per 50 m electrofishing. We estimated lake specific age-1 and age-2 pike CPUE to be able to assess a potential increase of the juvenile pike cohort due to the stocking treatments and correspondingly investigate additive effects of stocking on both cohorts.

2.3. Stocking material

Spawners to produce stocking material were caught in March 2011 from Bohtkampsee (54°12'25.92"N, 10°8′6.51"E) and Bordesholmer See (54°10'17.83"N, 10° 1′6.81"E) in northwestern Germany. Fish were stripped for eggs and sperm following standard hatchery practices in a commercial hatchery. Fertilized eggs were reared in Zuger jars until hatching, and free-swimming fry were then reared in earthen ponds on natural prey until draining in October 2011. Age-0 pike were transported to Fischfarm Wegert (52°19'53.81"N, 8°12'44.96"E) and held in three concrete tanks (2 m height × 2 m length × 1 m depth) for two days to recover. All pike were measured for TL and mass as described before, and double tagged under anesthesia (as described in Hühn et al., 2014a) between 31 October and 02 November 2011 using a PIT and a T-bar anchor tag (FD-68BC FF). Pike were allowed to recover from tagging and handling for 1 day before transportation and release into the study lakes.

Age-0 pike were transported in plastic transport bags (55 × 130 cm) containing water to one third and filled with oxygen to secure sufficient oxygen supply during transport. Transport to the study lakes lasted between 30 and 240 min. Water temperature ranged between 10.9 and 13.7 °C in the holding tanks and between 9.1 and 11.3 °C in the lakes at stocking. Water temperature in the transport bags was allowed to adapt to the lake water temperature for about 30 min before age-0 pike were randomly and manually distributed along the shoreline of the lakes. Such rapid release after transport is common in local angling clubs, and we mimicked prototypical procedures. Age-0 pike stocking was conducted between 02 and 04 November 2011. In total, we released 1875 marked age-0 pike with an average TL ± SD of 208 ± 29 mm and average mass ± SD of 49 ± 30 g.

2.4. Wild and stocked juvenile pike conditions over the experiment

To understand differences in sizes, masses and condition of stocked and wild fishes, we first analysed mean differences in length-at-age, mass, and relative condition (K_n, Le Cren, 1951) of stocked and wild age-0 pike at the time of stocking (2011) and for the survivors in the first (2012) and second (2013) year post-stocking using linear mixed-effects models (LMM), with lake as a random factor. The relative condition was calculated for each individual as $K_n = (W/W') \times 100$, where W is the individual weight and W′ is the standard length-specific mass predicted from a $\log_{10}$ transformed length-weight regression of the respective pike populations (Supplementary Table S3). To estimate the relative condition of the stocked cohort at time of stocking we used the length (TL)-weight (W) regression of the entire sample of stocked pike prior to stocking ($\log_{10}W = 2.895 \log_{10}TL - 11.635$; $R^2 = 0.87$; N = 1875; $P < 0.001$).

At the time of stocking in fall 2011, wild and stocked age-0 pike differed in total length. The average wild pike was significantly smaller than the average stocked conspecifics [mean (± SD) TL of age-0 wild pike = 139 ± 23 mm (n = 56), mean TL of stocked age-0 pike = 208 ± 29 mm (n = 1875), LMM: $F_{1,\ 1929} = 298.8$, $P < 0.001$]. Relatedly, at stocking the mean mass of stocked pike (49 ± 30 g) was three times higher compared to the mean mass of wild age-0 pike (15 ± 10 g) (LMM: $F_{1,\ 1929} = 69.68$, $P < 0.001$). By contrast, the relative condition did not differ among wild (0.95 ± 0.1) and stocked age-0 pike (1.02 ± 0.4) (LMM: $F_{1,\ 1929} = 1.329$, $P = 0.24$) at the onset of the stocking experiment.

2.5. Ecological covariates

To better explain the stocking outcomes, relevant biotic covariates that could affect the abundance of juvenile pike and the potential additive effects of stocking were estimated for each lake based on the pre-stocking lake data. In particular, the abundance of large pike (> 400 mm TL) as potential predators of the wild and stocked individuals and the intraspecific competitor density (i.e., pike of a similar size range as the stocked fish) were calculated. Pike of sizes below 400 mm TL are known to be strongly dependent on underwater vegetation and to almost exclusively use littoral zones (Grimm, 1989; Grimm and Klinge, 1996). We thus assumed wild pike < 400 mm TL to most strongly interact with stocked conspecifics and that adults > 400 mm TL would predate on smaller-sized conspecifics. Predator and wild competitor densities were calculated based on a Schnabel (1938) population size estimate in spring 2011 using data collected in the three surveys in 2011 and expressed as fish·ha^{-1}. In the treatment lakes, the competitor density was calculated as the summation of wild competitor density and the stocking density, representing all stocked and wild pike between 175 and 399 mm TL. As potential predators for the stocked pike we assigned all pike > 400 mm TL using established size-dependent victim-predator relationships in pike (Mittelbach and Persson, 1998). Additionally, we used prey fish abundance (prey fish·50 m electrofishing^{-1}) as a further ecological covariate. Electrofishing CPUE values were variable across samplings in a given lake; hence we averaged the prey fish CPUE values over all surveys conducted prior to stocking to represent the average forage base in the littoral. Finally, we calculated an index of relative abundance of suitable sized prey fish in the littoral zone, based on published relationships of prey sizes in relation to pike gape sizes following Nilsson and Brönmark (2000) for age-1 pike of a mean TL of 207 mm and of age-2 pike of a mean TL of 321 mm. Accordingly, forage fish with TL equal or below 129 mm and 151 mm were assigned as prey fish for age-1 and age-2 pike, respectively. The prey fish density was expressed as numerical abundance of suitable sized prey fish per 50 m shoreline electrofishing in the three study years pooling all samplings.

2.6. Additive effects of stocking in the age-1 and age-2 pike cohorts one and two years after stocking

To assess additive effects of stocking, we modeled the electrofishing catch of age-1 and age-2 pike as a function of relevant covariates (stocking treatment, predator and prey fish abundance, and lake type as represented by the categorical pike habitat quality variable mentioned before) with a generalized linear model that assumed the catch data conformed to a Poisson distribution (Kéry, 2010). Our models accounted for temporal changes in unstocked controls and for variation in initial pike stock sizes before the commencement of the experiment. For the *i*th sample (each transect is a sample $i = 1,\ldots, 137$; see Supplementary Table S1 for lake specific number of samples), the single parameter for the Poisson distribution (mean λ) was modeled as a $\log_e$-scale function of multiple covariates. The effort expended for each sampling event (i.e., total electrofishing transect distance) was included in the model as an offset to account for differences in catch among samples due to inevitable variation in the sampling process (Kéry, 2010) due to varying lake sizes. We included seven covariates in the model to account for the effects of two levels of stocking densities (*LSD, HSD*), before and after stocking effects (*year*), seasonal effects related to the timing of sampling (*season*), effects of lake type (*habitat*), effects of prey fish density (*prey*), and effects of predator density (*predator*). Competitor density was confounded with the dependent variable and not used in this particular model. The full model was specified as:

$$\begin{aligned}
\log(CPUE_i) = {} & \beta_{0,j} + \beta_1 LSD + \beta_2 HSD + \beta_3 year + \beta_4 season + \beta_5 habitat \\
& + \beta_6 prey + \beta_7 predator \\
& + \beta_8 LSD \times year + \beta_9 HSD \times year \\
& + \beta_{10} season \times LSD \times year + \beta_{11} season \times HSD \times year \\
& + \beta_{12} habitat \times LSD \times year + \beta_{13} habitat \times HSD \times year \\
& + \beta_{14} prey \times T1 \times time + \beta_{15} prey \times T2 \times time \\
& + \beta_{16} predator \times LSD \times year + \beta_{17} predator \times HSD \times year \\
& + \beta_{18} season \times habitat \times LSD \times year + \beta_{19} season \times habitat \times HSD \times year \\
& + \beta_{20} prey \times habitat \times LSD \times year + \beta_{21} prey \times habitat \times HSD \times year \\
& + \beta_{22} predator \times habitat \times LSD \times year + \beta_{23} predator \times habitat \times HSD \\
& \times year + \varepsilon_i
\end{aligned}$$

where β_1 through β_{23} represent the fixed effects associated with the covariates and interactions among covariates. The parameter $\beta_{0,j}$ represents the intercept of the model for lake *j* ($j = 1,\ldots,15$), which was modeled as a random effect across lakes. This parameter was assumed to be a random variable drawn from a normal distribution, $\beta_{0,j} \sim \text{Normal}\ (\beta_{0,\mu}, \beta_{0,\sigma})$, where $\beta_{0,\mu}$ and $\beta_{0,\sigma}$ represent the mean and standard deviation of the intercept parameters across lakes. Specifying the intercept ($\beta_{0,j}$) as a random effect among lakes and the covariate effects ($\beta_1,\ldots,\beta_7$) as fixed effects made the assumption explicit that the base-line mean pike catches at each lake may be inherently different, while the effects of the covariates on catch are equivalent among lakes. To model unexplained extra-Poisson variation in the catch data we included a normally distributed random variable (ε_i) with mean equal to zero and a latent standard deviation (σ_ε) estimated in the model (i.e. $\varepsilon_i \sim \text{Normal}(0, \sigma_\varepsilon)$). Including the random variable ε_i models the Poisson mean varying according to a lognormal distribution among samples, which is a common procedure for modeling extra-Poisson variation similar to the negative binomial distribution (Kéry, 2010). Thus, the model specified with the fixed effects, random effects, and normally distributed overdispersion parameter can be categorized as a

Poisson-lognormal mixture model (Bulmer, 1974; Kéry, 2010).

The BACI stocking experiment followed a design in the spirits of Stewart-Oaten et al. (1986) and Carpenter et al. (1989). Hence, each parameter in the model was analogous to a hypothesis test, where the support for the alternate hypothesis of a non-zero effect estimate can be measured by the inclusion of the parameter in the 'best' model. Thus, we framed the hypotheses tests as a problem of parameter selection. For this study we focused on the hypotheses associated with the interaction effects of the model because they represented the potential effects of stocking (β_8 and β_9) and how other variables moderated the potential effects of stocking ($\beta_{10},\ldots,\beta_{23}$). We modeled the probability that each parameter was included in the best model as a measure of support for the associated hypotheses by using a mixture modeling approach in which each parameter was multiplied by an "inclusion parameter" (Royle and Dorazio, 2008). The inclusion parameters (w_v for all v variables in the model) were latent binary variables distributed as Bernoulli trials with an uninformative prior probability of 0.5 (i.e., equal probability that the variable was included or excluded from the model). The mean of the posterior samples of the inclusion parameters corresponded to the probability that the given variable is included in the best model and indicated the support for the associated hypothesis. Furthermore, the product of the posterior sample of the inclusion parameters (w_v) and the posterior sample of the associated effect parameter ($\beta_1,\ldots,\beta_{23}$) represented the model averaged posterior distribution of the covariate effects, accounting for both model and parameter uncertainty (Burnham and Anderson, 1998). Barbieri and Berger (2004) determined that models including all parameters with inclusion probabilities ≥ 0.5 produced optimal predictive properties. Thus, all parameters with a posterior inclusion probability ≥ 0.5 were included in the final model.

Posterior probability distributions of the model parameters were estimated using a Monte Carlo-Markov chain (MCMC) algorithm implemented in JAGS (Plummer, 2003). We called JAGS from R (R Development Core Team, 2009) with the library RJAGS (http://mcmc-jags.sourceforge.net). All prior distributions of effect parameters ($\beta_1,\ldots,\beta_{23}$ and $\beta_{0,\mu}$) were specified as flat normal distributions with mean equal to zero and standard deviation equal to one hundred and were specified for the parameters on the $\log_e$ scale such that they would have no influence on the posterior probability distributions. Prior distributions of the standard deviation parameters (σ_ε and $\beta_{0,\sigma}$) were modeled as uninformative Gamma distributions with a value of 0.01 specified for each shape parameter. Inference was drawn from 90,000 posterior samples taken from 3 chains of 300,000 samples thinned to every 10. We allowed a burn in of 30,000 samples to remove the effects of initial values. Convergence cannot be diagnosed when modeling inclusion parameters, so we diagnosed convergence for the full model with inclusion parameters fixed at a value of one (prior probability of inclusion $= 1$) by visual inspection of the MCMC chains for adequate mixing and stationarity and by using the Gelman-Rubin statistic (with values < 1.1 indicating convergence; Gelman et al., 2004; Kéry, 2010). Model fit was evaluated by estimating a Bayesian p-value (Kéry, 2010). Bayesian p-values are a posterior predictive check where a value of 0.5 indicated perfect model fit while values approaching 0 or 1 indicated over dispersion and under dispersion of the data relative to the model. Generally, values between 0.2 and 0.8 indicated adequate fit.

2.7. Ecological determinants of growth in stocked and wild fishes, stocking-induced growth depression on wild juvenile pike and size-dependent cannibalism

We first investigated the ecological determinants of growth in the wild and stocked age-0 pike in the first year post-stocking (2012) using the mark-recapture data. To that end, we computed the change in TL (ΔTL) for each recaptured fish from spring to fall post-stocking in 2012 as a measure of individual growth rate in wild and stocked individuals. In this analysis, we excluded lakes with less than three observations (i.e., $<$ three recaptures) of individual pike resulting in a final data set of 74 wild and 54 stocked age-1 pike out of 10 lakes. We fitted a LMM to investigate differences in ΔTL in the first year post stocking between origin (wild vs. stocked) as a function of a set of explanatory covariates including the treatment (control vs. LSD vs. HSD), predator density, competitor density, prey fish density, and habitat quality as well as interactions. We fitted the most parsimonious LMM using stepwise exclusion of non-significant fixed effects based on the Akaike Information Criterion (Akaike, 1973) for small sample sizes (AICc, Sugiura, 1978). We first considered the random structure of the LMM assuming lake ID nested in treatment because the observations on ΔTL originated from individuals striving in different lakes assigned to three treatments. However, the random structure of the most parsimonious LMM including individual lakes as random effect produced a superior model fit based on AICc compared to the alternative of nesting lakes in treatment, and we thus choose individual lakes as random effects. Because predator density and prey fish density were strongly correlated ($\beta = 0.80110$, $P < 0.001$) we used the residuals of prey fish density regressed on predator density instead of the absolute prey fish density data to avoid potential co-linearity in the LMM. In addition, habitat type was tested as a substitute for prey fish and predator density in separate models due to strong correlations between covariates. We refer to this model as growth rate model in the results.

The above model was based on individual-level growth rate data from spring to fall in 2012, but the model did not answer if stocking induces a change in the growth rate (i.e., ΔTL) in wild cohorts as a potential result of the enhanced intra-cohort density- and size-dependent mortality caused by stocking. We also wanted to examine the potential for stocking-induced growth depression in wild fishes. Answering this question required observations about the growth of wild fish before and after stocking while controlling for potential environmental-related changes in the growth using observations of wild fish growth in unstocked control lakes. To that end, we constructed separate models following a BACI design to investigate whether stocking led to a growth depression of wild pike relative to the development of the length of wild pike in the unstocked controls while controlling for several ecological covariates. Because we were not successful in sampling wild pike at high numerical abundances in the year of stocking, to increase sample size the TL of individual wild pike caught in fall in the first year post-stocking (2012) or in spring in the second year post-stocking (2013) was back-calculated to spring post-stocking (2012) from growth information contained on the scales (based on the scale-proportion hypothesis, Francis, 1990; see Supplementary Table S3 for lake specific regressions of scale size and TL). We excluded lakes with less than three length observations before or after the stocking event from the data set, leaving n = 7 lakes. Subsequently, we compared the TL of age-0 wild pike with the length of wild pike of age-1 one year post-stocking using LMM and accounting for treatment effects and effects of ecological covariates. The full model included predator density, residuals of prey fish density, and competitor density as covariates, with lake as random factor. Similar as described above, nesting lake in treatment as random factor produced a poorer model fit based on the AICc compared to treating lake as random factor. In addition, habitat type was tested as a substitute for prey fish and predator density in a second model due to strong correlations between covariates. Best fitting models were determined after stepwise exclusion of non-significant variables based on AICc. We refer to this second growth model as the length model in the results.

We also examined evidence of inverse size-dependent mortality from stocking to one year post-stocking by comparing the distribution of the TLs of both stocked and wild-captured age-0 pike at time of stocking in fall of 2011 with the back-calculated age-0 size distribution from fish captured in 2012 and 2013. To answer this question, we fitted origin-independent LMM to see whether either the surviving wild or the surviving stocked fishes at age-1 in 2012 were significantly larger at the time of stocking in fall of 2011 as age-0 fishes compared to the average

Table 1
Posterior probability summaries of parameters for covariate effects on relative abundance of age-1 pike. Parameter mean, standard deviation (SD) and 95% confidence intervals are based on model averaged posterior samples. "LSD" = low stocking density and "HSD" = high stocking density, base = control group; "year" = year post stocking, base = year pre stocking; "season" base = spring; "lake type" base = poor habitat quality; prey = prey fish CPUE; predator = predator density. Bold parameters were included in the finale model.

Parameter		Mean	SD	Credibility interval		Probability of inclusion
				2.50%	97.50%	
LSD	bet[1]	0.18	0.40	-0.40	1.23	0.42
HSD	**bet [2]**	**-0.47**	**0.57**	**-1.74**	**0.20**	**0.60**
Year	bet[3]	0	0.13	-0.33	0.37	0.23
Season	**bet [4]**	**-0.55**	**0.22**	**-0.92**	**0**	**0.96**
Lake type	bet[5]	-0.03	0.30	-0.82	0.61	0.32
Prey	**bet [6]**	**0.40**	**0.37**	**0**	**1.11**	**0.68**
Predator	**bet [7]**	**0.29**	**0.34**	**0**	**1.02**	**0.57**
LSD:year	**bet [8]**	**0.73**	**0.47**	**0**	**1.63**	**0.86**
HSD:year	**bet [9]**	**2.32**	**0.44**	**1.40**	**3.15**	**0.99**
Season:LSD:year	bet[10]	-0.21	0.35	-1.11	0.13	0.44
Season:HSD:year	**bet [11]**	**-0.65**	**0.46**	**-1.52**	**0**	**0.81**
Lake type:LSD:year	bet[12]	-0.21	0.43	-1.27	0.45	0.46
Lake type:HSD:year	bet[13]	0.07	0.47	-0.87	1.36	0.41
Prey:LSD:year	bet[14]	-0.06	0.28	-0.82	0.50	0.33
Prey:HSD:year	**bet [15]**	**-0.88**	**0.34**	**-1.38**	**0**	**0.94**
Pred:LSD:year	**bet [16]**	**-0.60**	**0.51**	**-1.70**	**0**	**0.76**
Pred:HSD:year	**bet [17]**	**-0.40**	**0.61**	**-2.04**	**0.14**	**0.53**
Season: lake type:LSD:year	bet[18]	-0.03	0.27	-0.74	0.60	0.33
Season: lake type:HSD:year	bet[19]	-0.12	0.37	-1.11	0.54	0.39
Prey: lake type:LSD:year	bet[20]	0.10	0.66	-1.31	1.76	0.49
Prey: lake type:HSD:year	bet[21]	0	0.63	-1.45	1.49	0.47
Pred: lake type:LSD:year	bet[22]	0.07	0.46	-0.85	1.26	0.46
Pred: lake type:HSD:year	bet[23]	0.14	0.51	-0.69	1.62	0.41

size of the fishes in 2011 (7 lakes included in the wild pike analysis and 7 lakes in the stocked pike analysis). We used the data of the length-model mentioned in the preceding paragraph and included the significant covariates revealed by the previous length-model (in particular lake type and competitor density, see Supplementary Table S4), with lake as random factor, to test whether the back-constructed age-0 size distribution from survivors differed from the subpopulation's size distribution of age-0 fish at the time of stocking.

All three LMM's were fitted using the package nlme in the software R (R Core Team 2013) version 3.0.2. A type-1 error probability of $\alpha = 0.05$ was used, and in all cases the distribution of the residuals were checked for normality and homogeneity of the variances for proper fitting.

3. Results

3.1. Additive effects of stocking on age-1 and age-2 pike abundance

Average pre-stocking CPUE ± SD (2011) ranged from 0.35 ± 0.59 to 0.48 ± 0.53 age-1 pike·50 m^{-1} in spring and 0.17 ± 0.09 to 0.37 ± 0.67 age-1 pike·50 m^{-1} in fall averaged across all 15 study lakes. Average spring CPUE ± SD in the year post-stocking (2012) was 0.21 ± 0.19 in the control lakes, and 1.08 ± 0.95 and 1.39 ± 0.73 age-1 pike·50 m^{-1} in the LSD and HSD lakes, respectively. In both stocking treatments (LSD and HSD), we observed mean CPUE values above 1 age-1 pike·50 m^{-1}, which represented a significantly increased age-1 pike abundance over control lakes in the first year post stocking, indicating a stocking-induced additive effect at the age-1 cohort level (Table 1, Fig. 1). Relative to the age-1 pike population size estimates pre-stocking in spring, stocking caused, on average, a 5.4 and 48.8 fold increase of the age-1 pike population size in the LSD and HSD treatments, respectively (see Supplementary Table S2 for raw values).

Mean CPUE values in fall post-stocking, one year after release, ranged between 0.19 ± 0.19 and 0.37 ± 0.29 age-1 pike·50 m^{-1} across treatment and control lakes, suggesting that age-1 abundance had dropped to pre-stocking levels within one year post stocking. Model-estimated parameter inclusion probabilities suggested support for a transient additive effect of stock enhancement at the age-1 cohort level that was only present in the short term in spring post stocking in fall (Table 1). The positive interaction effect between treatment (LSD, HSD) and year (pre- vs. post-stocking) (β_8 and β_9) indicated that the abundance of age-1 pike significantly increased by stocking 35 age-1 pike·ha^{-1} (LSD, $\beta = 0.76$, Pr = 0.86) and 70 age-1 pike·ha^{-1} (HSD, $\beta = 2.32$, Pr = 0.99) relative to controls. However, the main effect of *season* was negatively related to the CPUE of age-1 pike (Fig. 1, Table 1, $\beta = -0.55$, Pr = 0.96), indicating either consistently higher abundances of age-1 pike in the littoral zones in spring compared to fall and/or a season-dependent catchability effect. When examining the relevant three-way interactions, however, the additive effects of stocking at the age-1 cohort level were only pronounced in spring immediately after the fall stocking. Afterwards, the pike populations regulated back to pre-stocking levels in fall one year after the stocking event. In particular, the negative sign of the three-way interaction season × treatment × year (LSD: $\beta = -0.21$, Pr = 0.44; HSD: $\beta = -0.65$, Pr = 0.81) indicated a strong decline in CPUE of age-1 pike over time in both stocking treatments compared to controls. Although this decline in CPUE was not significant in the LSD treatment, we concluded that stocking failed to generate a long-lasting additive effect on the age-1 cohort because such effects would have been indicated by a significantly positive three-way interaction of season × treatment × year. Such positive interaction would have indicated that the abundance trend of pike in stocked lakes did not change after the spring boost in CPUE over time or be positive relative to trends in controls. However, we found a negative three-way interaction, indicating a stronger reduction in abundance in stocked lakes across seasons relative to the seasonally varying abundance change in controls.

The average CPUE ± SD of age-2 pike pre-stocking ranged from 0.15 ± 0.16 to 0.21 ± 0.29 pike·50 m^{-1} in spring and from 0.03 ± 0.05 to 0.07 ± 0.12 pike·50 m^{-1} in fall across treatments groups (Fig. 2). As in the age-1 cohort, the model-estimated inclusion of the main effect of *season* ($\beta = -1.03$, Pr = 0.93) indicated seasonality of juvenile pike catchability or changing abundance of age-2 pike in the littoral zones. Mean age-2 CPUE values in spring after the enhancement effect ranged from 0.08 ± 0.06 to 0.23 ± 0.24 pike·50 m^{-1}. Model-estimated parameter inclusion probabilities provided no support for stock enhancing effects caused by stocking in the age-2 pike cohort (Table 2, Fig. 2). In fact, the interaction between treatment (LSD or HSD) and year

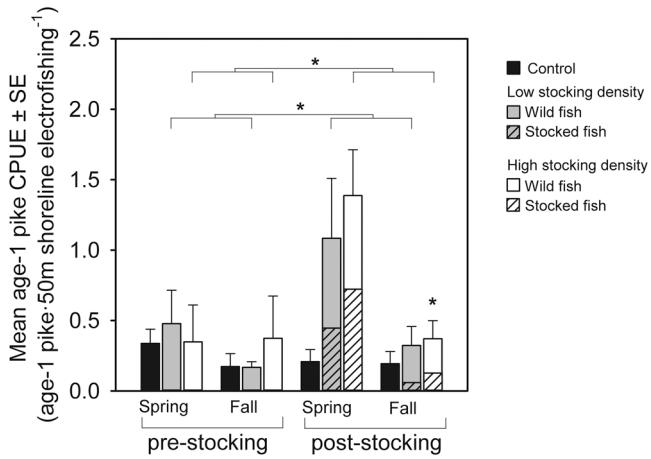

Fig. 1. Mean CPUE of age-1 pike ± SE (age-1 pike·50 m shoreline electrofishing^{-1}) in spring and fall in the year pre- and post-stocking (following a before-after-control-impact design) and the composition of the cohort in terms of wild and stocked individuals. Low stocking density (LSD, 35 age-0 pike·ha^{-1}), high stocking density (HSD, 70 age-0 pike·ha^{-1}). * indicates significant differences of treatment groups (LSD or HSD) relative to control (for full model, see Table 1).

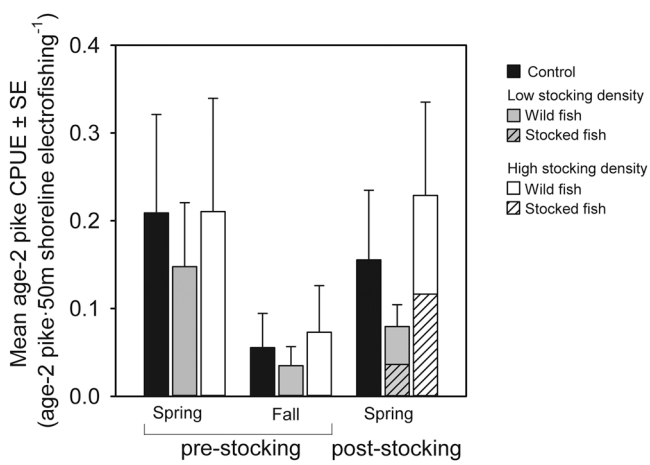

Fig. 2. Mean CPUE of age-2 pike ± SE (age-2 pike·50 m shoreline electrofishing^{-1}) in spring and fall in the year pre- and post-stocking (following a before-after-control-impact design) along with the composition of the cohort in terms of wild and stocked fishes. Low stocking density (LSD, 35 age-0 pike·ha^{-1}), high stocking density (HSD, 70 age-0 pike·ha^{-1}). * indicates significant differences of treatment groups (LSD or HSD) relative to control (for model estimates, see Table 2).

was excluded from the age-2 pike CPUE model (LSD, $\beta = -0.62$, Pr = 0.48; HSD, $\beta = -0.01$, Pr = 0.22), indicating no additive effect of age-0 pike stocking at the age-2 cohort level. Hence, density-dependent population regulation through compensatory juvenile mortality had fully re-equilibrated the age-2 cohort to pre-stocking levels despite massive increases in potential recruitment through stocking.

Juvenile pike habitat quality did not influence the outcome of stocking at the age-1 level, irrespective of stocking density (Table 1), suggesting that the juvenile pike cohort responded within the carrying capacity offered by essential habitat features within each lake. By contrast, the posterior probability of inclusion parameters indicated that both prey fish abundance and predator density (i.e., adult pike density) affected the stock enhancement effect at the age-1 cohort level. As indicated by a significant three-way interaction between predator density × treatment × year, the presence of large numbers of predators had a negative effect on the change of abundance of age-1 pike post-stocking in both the LSD ($\beta = -0.60$, Pr = 0.76) and the HSD treatment groups ($\beta = -0.40$, Pr = 0.53; Table 1, Supplementary Fig. S1) compared to controls. This was interpreted as evidence for density-dependent population size regulation of the age-1 cohort through inter-cohort cannibalism. Although, the model-averaged 95% credible intervals of the three-way interaction predator × HSD × year (β_{17}) included zero, the inclusion probability of 0.53 indicated support for this hypothesis (Table 1). In contrast to predator density, the prey fish density had no effect on the change of abundance post stocking in the LSD treatment group (β_{14}, Pr = 0.33). By contrast, the decline of abundance in the HSD treatment group post-stocking relative to controls was negatively related to the prey fish availability ($\beta = -0.88$, Pr = 0.94; Supplementary Fig. S1). Hence, larger CPUE post stocking were observed in systems with lower prey availability, which on first sight seems counterintuitive, but can likely be explained with catchability effects (see discussion).

Surprisingly, relative to control lakes the abundance of age-2 pike even decreased post-stocking in the LSD treatment in lakes characterized by good habitat structure, as indicated by the inclusion of the three-way interaction habitat × LSD × year ($\beta = -0.93$, Pr = 0.62). There was no similar effect in the HSD treatment. Prey fish availability correlated negatively with post-stocking changes in age-2 pike CPUE in the LSD treatment, but the inclusion probability was only moderate at 0.57 ($\beta_{12} = -1.15$, Pr = 0.57), while prey fish availability strongly positively affected age-2 CPUE in the HSD treatment ($\beta_{13} = 1.43$, Pr = 0.67; Supplementary Fig. S2) post-stocking relative to controls. Relative to control lakes, predator density negatively affected the age-2 pike CPUE post-stocking in the HSD treatment lakes, as indicated by the inclusion of the three-way interaction predator density × HSD × year ($\beta = -1.86$, Pr = 0.89). Overall the results provided evidence of the absence of stock enhancing effects of age-0 pike stocking at the age-2 pike cohort level two years after stocking and a moderating role of selected ecological factors related to the forage base and presence of predators affecting stocking outcomes. Hence, although there was no main effect of stocking on the age-2 pike abundance, the interaction effects with ecological covariates revealed that under certain cases - high stocking density, high prey fish availability, and low predator density - there was a small positive enhancement effect on the age-2 cohort in exceptional lakes (Supplementary Fig. S2). Despite the absence of general additive effects of stocking in the age-2 pike cohort, stocked pike constituted approximately one half of the age-2 pike year class irrespective of stocking treatment (Fig. 2), indicating a strong replacement effect of wild recruits by stocked pike with no additive effects on total population size.

3.2. Ecological determinants of growth in stocked and wild cohorts, stocking-induced growth depression on wild juvenile pike and size-dependent cannibalism

At the start of the experiment, wild age-0 pike were significantly smaller on average compared to stocked conspecifics across all lakes (see material and methods). Significant size differences between wild and stocked pike post stocking remained (Fig. 3), with wild pike being consistently smaller, on average, compared to stocked pike in fall 2012 (age-1; LMM: $F_{1,\ 126} = 147$, $P < 0.001$) and spring 2013 (age-2; LMM: $F_{1,47} = 91.55$, $P < 0.001$). These data indicated that surviving stocked pike maintained their size advantage over the study period compared to wild conspecifics. By contrast, there were no differences in pike relative condition between wild and stocked individuals neither in fall 2012 (LMM: $F_{1,\ 126} = 1.276$, $P = 0.26$) nor in spring 2013 (LMM: $F_{1,\ 47} = 0.027$, $P = 0.87$).

Based on the AICc model ranking, the final model explaining change in TL of wild and stocked age-1 pike in the year post stocking (our so-called growth rate model) included the interaction terms origin × predator density, origin × competitor density, and treatment as fixed factors, with lake as random factor (Table 3). When examining the statistical significance of coefficients, the change in total length over the first growing season post stocking was not affected by stocking

Table 2
Posterior probability summaries of parameters for covariate effects on relative abundance of age-2 pike. Parameter mean, standard deviation (SD) and 95% confidence intervals are based on model averaged posterior samples. "LSD" = low stocking density and "HSD" = high stocking density, base = control group; "year" = year with expected stocking effect, base = year pre expected stocking effect; "season" base = spring; "lake type" base = poor habitat quality. Bold parameters were included in the finale model.

Parameter		Mean	SD	Credibility interval		Probability of inclusion
				2.50%	97.50%	
LSD	bet[1]	0.01	0.23	-0.45	0.58	0.14
HSD	bet[2]	-0.02	0.26	-0.67	0.43	0.15
Year	bet[3]	-0.07	0.26	-0.92	0.14	0.18
Season	**bet[4]**	**-1.03**	**0.41**	**-1.74**	**0**	**0.93**
lake type	bet[5]	0.01	0.82	-0.80	1.08	0.07
Prey	bet[6]	0	0.04	-0.06	0	0.05
Predator	**bet[7]**	**0.72**	**0.31**	**0**	**1.34**	**0.94**
LSD:year	bet[8]	-0.62	1.03	-3.12	0.69	0.48
HSD:year	bet[9]	-0.01	0.50	-1.30	1.02	0.22
Lake type:LSD:year	**bet[10]**	**-0.93**	**1.05**	**-3.13**	**0.27**	**0.62**
Lake type:HSD:year	bet[11]	0.59	0.96	-0.18	3.04	0.44
Prey:LSD:year	**bet[12]**	**-1.15**	**1.44**	**-4.68**	**0**	**0.57**
Prey:HSD:year	**bet[13]**	**1.43**	**1.44**	**0**	**4.51**	**0.67**
Pred:LSD:year	bet[14]	0.01	0.77	-1.65	2.13	0.28
Pred:HSD:year	**bet[15]**	**-1.86**	**1.13**	**-4.18**	**0**	**0.89**
Prey: lake type:LSD:year	bet[16]	-0.18	1.06	-3.06	1.99	0.33
Prey: lake type:HSD:year	bet[17]	0.16	1.11	-2.19	2.98	0.36
Pred: lake type:LSD:year	bet[18]	-0.18	1.05	-3.00	1.98	0.33
Pred: lake type:HSD:year	bet[19]	0.16	1.09	-2.23	2.93	0.36

treatment (Table 4), despite treatment being a component of the best fitting model (Table 3). Furthermore, growth rates were statistically similar between wild and stocked pike, as indicated by the non-significant main effect of origin (Table 4). However, it was found that the growth rate of stocked pike in the year post-stocking was significantly and negatively related to predator density and significantly elevated in lakes hosting high competitor densities (Table 4, Supplementary Fig. S3), as indicated by the significant interaction terms origin × predator density ($t = -3.55$, df = 85.61, $P < 0.001$) and origin × competitor density ($t = 3.48$, df = 80.87, $P < 0.001$). The situation was opposite for the wild cohort, where growth rates were greater in systems hosting more adult pike as predators and lower in lakes with higher numbers of competitors of the same cohort, in turn suggesting density-dependent growth (Table 4, Supplementary Fig. S3). Overall, the ecological determinants driving growth rate were different in wild and stocked fishes, suggesting that both subpopulations reacted differently to ecological gradients relating to food, shelter and predation and that there was no evidence of treatment-induced growth depression in the wild cohort.

To further examine whether stocking led to changes in the size of the surviving wild cohort, we compared the TL of wild pike pre- and post-stocking in a LMM using a BACI design (our so-called length model). Based on the AICc model ranking, two length models were equally supported by the data, one including lake type as main effect and one including competitor density in addition to a year × treatment interaction (Supplementary Tables S4, S5, and S6). As expected, the mean TL of surviving wild pike increased significantly from stocking to o ne year after stocking (Supplementary Table S5, LMM: df = 242.22, t = 8.33, $P < 0.001$). Moreover, we found that the TL of wild pike in the year post-stocking was significantly larger in lakes belonging to the high stocking

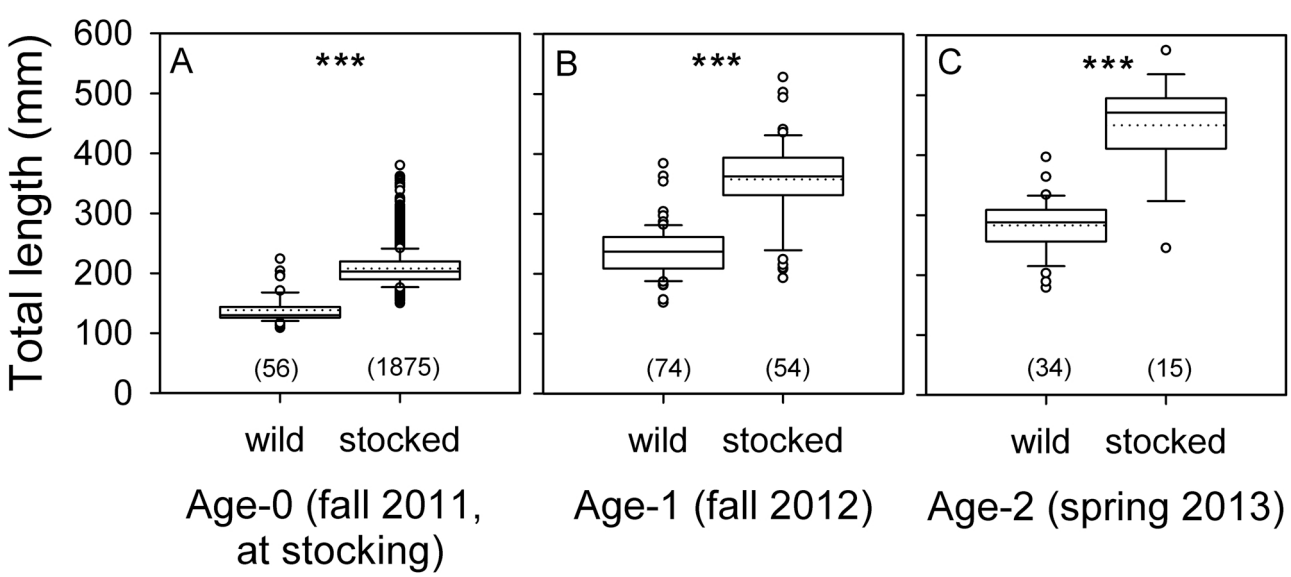

Fig. 3. Comparison of total length between wild and stocked age-0 (at stocking, fall 2011; A), age-1 (one year after stocking, fall 2012; B) and age-2 (one and a half year after stocking, spring 2013; C) pike based on raw data. Boxplots show 25–75th percentiles (box) with median (solid line), mean (dotted line) and outliers (circles). Whiskers represent the 95% range. Numbers in parentheses represent number of caught pike at sampling. * indicates significant differences between wild and stocked pike at $\alpha < 0.001$.

Table 3
Ranking of models modeling growth rate differences (Δ TL, individual-level data) of wild and stocked fish in the year post-stocking based on AICc. As fixed factor we tested origin of fish (wild vs. stocked) and the covariates treatment group (control, low stocking densities [LSD, 35 age-0 pike·ha^{-1}], and high stocking densities [HSD, 75 age-0 pike·ha^{-1}]), predator density (pike > 400 mm TL·ha^{-1}), competitor density (all pike between 175 and 400 mm TL·ha^{-1}), and residuals of prey fish density (preyres; prey fish·50 shoreline electrofishing^{-1}). In a second model lake type (poor vs. good habitat) substituting prey fish density and predator density was used due to strong correlations between covariates. Lake was included as random factor as expressed by "1|lake".

Model: Δ TL ~	AICc	Δ AICc
1) predator density × origin + competitor density × origin + treatment + (1|lake)	1306.6	0
2) preyres × origin + predator density × origin + competitor density × origin + treatment + (1|lake)	1309.8	3.2
3) predator density × origin + competitor density × origin + (1|lake)	1319.8	13.2
4) lake type × origin + competitor density × origin+ (1|lake)	1321.7	15.1
5) origin + (1|lake)	1328.0	21.4
6) predator density × origin + (1|lake)	1328.9	22.3

density treatment group compared to the control group as indicated by the significant interaction term year × HSD (Table 5, Fig. 4). These data added further weight to the lack of evidence of stocking-induced growth depression when judged by the TL of surviving wild juveniles. Although according to AICc-based ranking, the best fitting models included lake type and competitor density (Supplementary Table S4) as covariates of the TL variation of wild pike, none of these covariates were significant explanatory values (Supplementary Tables S5 and S6).

Any variation in TL of the wild cohort among years might have been caused by growth rate changes, selective mortality of individuals varying in growth rate (and hence in risk-taking) or by size-selective mortality of the smallest segments of the cohort. To test whether inverse size-dependent mortality was present in the wild cohort from the period before stocking to the one year after stocking, we compared the length distribution of the age-0 wild pike cohort before stocking with the back-calculated age-0 length distribution of the surviving wild fishes one year after stocking. The analyses revealed no significant size differences among the wild pike at the time of stocking compared to those that survived the stocking event (Table 5). The same model constructed for the stocked cohort lead to the same results as observed in the wild pike cohort (Table 5). Overall, the comparisons of length distributions of the age-0 pike before stocking with the back-calculated age-0 length distribution of the surviving fishes one year after stocking, indicated that inverse size-dependent mortality was neither present in the wild nor in the stocked pike cohort.

4. Discussion

Our whole lake experimental study revealed insights of importance for both fisheries management and basic population biology in relation the study objectives. In relation to the management consideration of whether stock enhancement with pike works or not (objective 1), our replicated experiment clearly showed stocking large juvenile pike cannot be expected to produce predictable benefits for fisheries, with rare exceptions at high stocking densities in lakes with an exceptional forage base and few cannibalistic adult pike. Our work agrees with previous studies involving the stocking of pike fry and pike fingerlings (Grimm, 1983; Vuorinen et al., 1998; Sutela et al., 2004; Skov et al., 2011; Jansen et al., 2013; Hühn et al., 2014b; Radinger et al., 2023) that also failed to generate consistent additive effects of stock enhancement when the releases happened in naturally reproducing stocks. Our findings are particularly noteworthy giving the dramatic elevation of recruitment of several hundred to over 1000% in particular lakes above natural levels due to the release of large age-0 pike. Based on our work and the findings cited above we can conclude that whenever a natural pike population exists, neither stocking of fry nor large juvenile pike will produce stable additive effects and will unlikely elevate catches.

From a fundamental scientific perspective of population regulation in fishes, our study confirmed five patterns predicted from theory or previous empirical work on a variety of fishes. First, we documented a rapid self-regulation of an artificially enhanced age-0 pike cohort and only weak evidence for density-dependent growth to further contribute to population regulation. These findings fully agree with theory of fish population regulation in stock enhanced systems (Lorenzen, 2005) and long-term studies on the pike population of Lake Windermere (UK) (Haugen et al., 2006, 2007). Secondly, our research confirmed the general maladaptation of stocked fishes as revealed by their low survival rates post-stocking, despite the stocked fish being significantly larger than the wild fish at stocking. Moreover, we found that stocked and wild fishes showed different reactions to key ecological factors (in particular predator and competitor densities), suggesting both subpopulations were behaviorally unique and phenotypically different (in line with Monk et al., 2020). Our findings of substantial fitness costs of artificial insemination and rearing, even for pike bred in semi-natural conditions in ponds, fully agrees with previous work on the subject (Lorenzen, 2000, 2005, 2006; Lorenzen et al., 2012; Szczepkowski et al., 2012), including controlled studies on pike fry (Hühn et al., 2014b), that all documented that "domesticated phenotypes" fair less well than their wild conspecifics under natural conditions. Third, because we did not find a lasting increase of the enhanced cohort, stocking of pike did not destabilize the natural pike population or lead to a population cycles as reported from other cannibalistic species (Persson et al., 2003, 2004, 2007). Similarly, the stability of absolute cohort size, albeit at a different composition in terms of origin of the pike population post stocking, did not seem to foster an ecological regime shift similar to the one found in other top predatory cannibalistic freshwater species in response to stocking (Carpenter et al., 2011) or harvesting (Persson et al., 2007). Our work instead confirmed that pike populations are characterized by rather stable dynamics and high degree of cannibalism-driven self--regulation compared to other cannibalistic fish species with smaller predation windows (e.g. perch, *Perca fluviatilis*, van Kooten et al., 2010). Fourth, from a biodiversity perspective our results indicated that some stocked pike will establish after stocking and partially replace wild recruits and that these survivors display similar growth rates and condition than their wild conspecifics. Depending on the choice of the stocking material and the relative size of stocked versus wild fishes, the partial establishment of stocked individuals can affect the gene pool of the stock-enhanced ecosystem due to hybridization with wild conspecifics (Laikre e al, 2010; van Poorten et al., 2011; Monk et al., 2020; Eschbach et al., 2021). Hence, pike stocking might have negative consequences in the long term through genetic effects without producing additive effects for fisheries or conservation. Finally, roughly half of the stock-enhanced cohort was composed of stocked fishes at the end of the experiment. Thus, stocking also negatively affected the wild cohort through elevating their natural mortality, but not through stocking-induced growth depression. Hence, in line with Radinger et al. (2023), we can overall conclude that juvenile pike stocking produces no benefit for fisheries, while carrying substantial ecological costs and genetic risks.

Our study confirms the theoretically supported hypothesis that stock enhancement over carrying capacity in naturally reproducing stocks with fish sizes that still undergo important mortality regulation is bound to fail (Lorenzen, 2005; Rogers et al., 2010; Radinger et al., 2023). We found that the unnaturally high abundance of juvenile pike after

Table 4
Parameter estimates of the best fitting model from Table 3 using a linear mixed-effects model testing the change in total length (individual-level growth rate data) from spring to fall in the year post-stocking from age-0 pike to age-1 pike of either wild or stocked origin. "Origin" base = wild pike; "LSD" = low stocking density and "HSD" = high stocking density, base = control group. Significant effects are in bold.

Effect	Estimate	SE	df	*t*	*P*
Intercept	**159.09**	**37.13**	**9.75**	**4.29**	**0.002**
Predator density	3.46	2.04	10.97	1.7	0.117
Origin	-2.69	17.45	45.55	-0.15	0.878
Competitor density	-2.01	1.05	14.67	-1.92	0.075
LSD	-43.23	30.83	6.93	-1.4	0.204
HSD	-48.58	35.88	7.65	-1.35	0.214
Origin × predator density	**-9.08**	**2.56**	**85.61**	**-3.55**	**< 0.001**
Origin × competitor density	**4.57**	**1.31**	**80.87**	**3.48**	**< 0.001**

stocking was rapidly regulated to pre-stocking levels within 18 months post stocking. However, we also observed a short-term increased abundance of age-1 pike in spring post stocking and that this effect increased with stocking density. Hence, a monitoring program tailored at the age-1 cohort would have concluded differently about the stock enhancement potential of pike stocking and the intraspecific self-regulation potential of natural pike populations. The importance of multi-year observation of stocking outcomes has previously been noted for other top predatory freshwater fishes (e.g., Diana and Wahl, 2008) and this suggestion is underscored by our work.

Although we did not assess stomach contents to prove cannibalism control directly, two lines of evidence support the hypothesis that the juvenile mortality regulation was mainly driven by cannibalism in our study. First, we found the presence of predators, in our case the abundance of large pike (≥ 400 mm TL), to negatively affect the strength of the enhanced age-1 and age-2 pike cohorts (see Supplementary Fig. S1 and S2). This result is in line with theoretical studies (e.g., Persson et al., 2004) and empirical observations in pike (e.g., Kipling and Frost, 1970; Haugen et al., 2007). Second, although the degree of macrophyte coverage did not affect the stocking outcome, we found the survival of juvenile wild pike to be somewhat larger in lakes with greater degree of structured habitat (results not reported), which is known to reduce cannibalism in this species (Grimm, 1981; Eklöv, 1997; Skov et al., 2003; Skov and Koed, 2004). However, we also found that large predator abundances only negatively affected the growth of stocked fishes, but not of wild fishes. In contrast, the growth of surviving individuals was even positively, rather than negatively, correlated with adult pike abundance, similar to previous reports from Lake Windermere for wild pike, which suggest selective mortality of smaller-growing segments of the population (Haugen et al., 2007). We thus propose that cannibalism

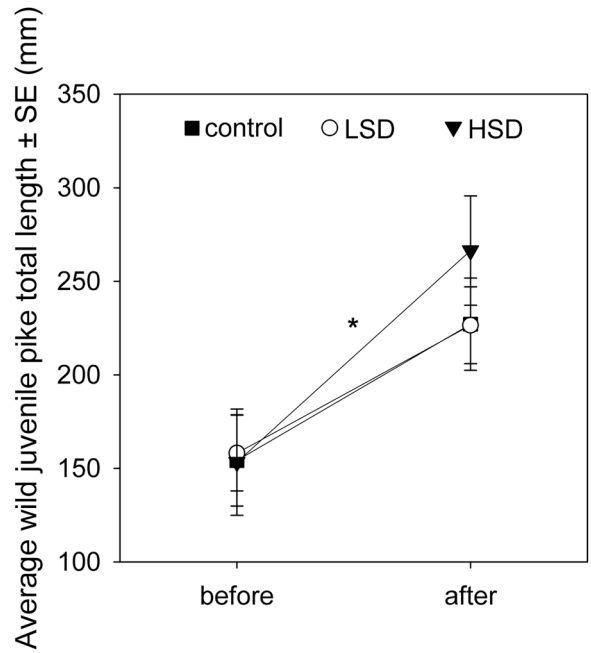

Fig. 4. Model estimated effect of stocking low densities (LSD, 35 age-0 pike ha-1) and high densities (HSD, 75 age-0 pike ha-1) on length at age of wild juvenile pike at age-0 in the year before stocking and age-1 in the year after stocking (mm). * indicates significant differences in length changes of the HSD treatment group relative to control (for model details, see Table 5).

was the main probable mechanism that prevented the stocked fishes to establish successfully, while wild fishes were more resilient to variation in adult pike abundance.

We did not detect an effect of available refuges and hence the general quality of juvenile pike habitat on the outcome of our stocking experiment. Although the degree of vegetation is known to determine a lake's carrying capacity for pike (Grimm, 1989), our results suggest that each lake has a lake-specific carrying capacity for juveniles that cannot be increased by stocking individuals in sizes where pike are still strongly bound to underwater vegetation (Bry, 1996; Grimm and Klinge, 1996). The sizes stocked in our study were apparently not large enough to have surpassed the lake-specific juvenile habitat bottlenecks, and we also did not found evidence for a refuge effect (Nilsson and Persson, 2013) facilitating a greater establishment of stocked fishes in good quality lakes. It has been reported before that a lake's juvenile pike density is constrained by the amount of refuges (Grimm, 1989; Skov and Koed, 2004). At equilibrium, in each lake the system will be saturated by wild recruits and hence the addition of stocked fishes will increase

Table 5
Linear mixed-effects model outputs comparing length at stocking of age-0 pike and back-calculated length at age-0 at stocking from surviving age-1 pike caught in fall post-stocking for wild and stocked fish. The fixed effect "treatment" is represented in the stocked fish model as low stocking densities (LSD, 35 age-0 pike·ha^{-1}) and high stocking densities (HSD, 75 age-0 pike·ha^{-1}), and in the wild fish model as control, LSD, and HSD. Stocked pike model: "survivor" = back-calculated length at age-0 at stocking from surviving age-1 pike (2012), base = length of age-0 pike at stocking 2011; "HSD" = high stocking density, base = low stocking density; wild pike model: "survivor" = back-calculated length at age-0 at stocking from surviving age-1 pike (2012), base = length of age-0 pike at stocking 2011; "LSD" = low stocking density and "HSD" = high stocking density, base = control group. Significant effects are in bold.

Model	Effect	Estimate	SE	df	*t*	*P*
Stocked pike	**Intercept**	**204.28**	**3.01**	**4.10**	**67.83**	**< 0.000**
	Survivor	7.46	6.31	1160.70	1.18	0.237
	HSD	0.64	4.05	4.30	0.16	0.881
	Survivor × HSD	3.22	7.97	1161.10	0.41	0.686
Wild pike	**Intercept**	**156.06**	**13.91**	**5.70**	**11.22**	**< 0.001**
	Survivor	-0.80	12.25	1415.70	-0.07	0.948
	LSD	41.85	16.65	4.20	2.51	0.063
	HSD	41.95	17.93	4.00	2.34	0.080
	Survivor × LSD	-18.51	13.10	1417.20	-1.41	0.158
	Survivor × HSD	3.45	14.02	1418.00	0.25	0.805

competition and elevate mortality also in the wild life stages (Hühn et al., 2014b). The net result seems to be a self-regulation to juvenile carrying capacity so that habitat structure itself did not exert a significant effect on stock enhancement outcomes.

A counterintuitive finding was that the decline in age-1 pike abundance in the first year post stocking was stronger in lakes hosting large forage bases (Supplementary Fig. S1). However, this effect was only pronounced in the extreme enhancement treatment (HSD) in the age-1 cohort and reversed to an expected positive effect of prey fish density on pike abundance at the age-2 cohort. We propose that the counterintuitive finding in the first study year was caused by an artificially elevated catchability of pike in the HSD treatment lakes. The HSD treatment led to an unnaturally elevated cohort size of age-1 pike two orders of magnitude over natural levels, which likely fostered competition for food and shelter in the stocked fishes (Skov et al., 2011). It is likely that the stocked and potentially also the wild fishes suffered from food limitation and density-dependent stress in their search for shelter in the high stocking treatment (Skov et al., 2011), in turn elevating the exposure of survivors to the electrofishing gear in the first year post stocking. After the spring boom in the pike abundance, the populations rapidly equilibrated to pre-stocking levels over the summer of the first year, which was particularly pronounced in the HSD treatment lakes. As a result, in the age-2 cohort the expected positive relationship of prey fish availability and the relative abundance of pike was seen also in the HSD treatment lakes (Supplementary Fig. S2) as expected from theory and in agreement with field studies in Lake Windermere (Haugen et al., 2007).

Previous laboratory work on pike has revealed that the presence of high abundances of similar sized conspecifics alters stress levels in pike, leading to growth depression despite constant availability of food (Edeline et al., 2010). We also documented a decline in growth of wild pike juveniles when faced with large competitor densities. Similar effects have also been reported in Lake Windermere (Haugen et al., 2007), representing one additional mechanism of social stress-induced density-dependent growth depression in this species unrelated to general food availability. Relatedly, growth of stocked pike was smaller in lakes hosting plenty of adult pike probably because the large pike fostered risk-sensitive foraging by forcing the stocked fishes to use refuges rather than spending time in vulnerable arenas (Skov and Koed, 2004; Nilsson, 2006; Skov et al., 2011; Ahrens et al., 2012). However, to our surprise growth of stocked pike increased with increasing competitor densities in a given lake.

We found additive effects of stocking to rapidly diminish from spring to fall of the year post stocking, strongly indicating elevated mortality of the stocked fishes. The decline in performance of hatchery-reared fishes in complex natural environments has been repeatedly observed, including in pike fry (Skov et al., 2011; Hühn et al., 2014b). It is supposed to be caused by an increased susceptibility of released cultured (which may involve pond-raised animals) fish to predation due to morphological features, the utilization of high predation risk habitats, generally bold behavior and poorly developed anti-predator behavior (e.g., Olla et al., 1998; Brockmark and Johnsson, 2010; Brockmark et al., 2010; Hyvärinen and Rodewald, 2013; reviewed in Lorenzen et al., 2012). Therefore, effects of domestication and lack of ecological adaptation can cumulatively explain the higher mortality of pond-reared pike in the present experiment.

Because the carrying capacity of an ecosystem is represented by the total environment including abundance of predators, parasites and competitors (Myers, 2002) it is not surprising that prey fish availability (positively) and predator abundance (negatively) determined the survival of pond-reared age-1 pike in expected directions. However, what is insightful are the differences in ecological factors driving survival and growth in stocked and wild fishes, which often worked in opposite directions. Anti-predator behavior of wild fish is better developed compared to stocked fish (Olla et al., 1998). It is likely that refuges in the self-sustaining populations were already occupied by wild pike recruits. Consequently, released pike likely had problems to outcompete wild fish that occupied refuges (Skov et al., 2011) despite them being on average larger than the wild conspecifics. Moreover, the effects of predator and competitor densities on the growth rate of (surviving) wild and stocked fishes worked in opposing directions as elaborated before, cumulatively suggesting that stocked fish represented specific behavioral and possibly physiological phenotypes with strikingly different reactions to natural ecological factors.

We found evidence for density and general food dependence in growth and survival in the wild pike cohort as indicated by negative effects of competitor density on growth rate. However, there was no effect of stocking treatment on the growth rates of wild pike. The absence of stocking-induced growth depression in the wild pike suggested that the enhanced cohorts and especially the stocked cohort was not released in sizes below the transition phase from density-dependent mortality regulation in pre-recruits to density-dependent growth regulation in recruited fish (Lorenzen, 2005). Overall, we found pike to be resilient in terms of growth to the stocking intervention, possibly because treatment and competitor densities were not correlated.

We found growth rates of surviving stocked and wild fishes to be similar, indicating that once a critical bottleneck is surpassed stocked fishes can do reasonably well compared to wild conspecifics. Our results did not agree with previous work on pike fry by Hühn et al. (2014b) who reported that stocked pike fry only achieved half of the total length at the end of summer compared to wild conspecifics when forced into competition. However, in addition to the lack of correlation of stocking density and competitor density mentioned before, our stocked fishes were also significantly larger at the time of stocking compared to the wild conspecifics. Moreover, we found surviving stocked fishes maintaining their size advantage over the study period. Even small size-advantages are highly relevant in cannibalistic pike (Skov et al., 2003; Grønkjær et al., 2004) and can lead to competitive superiority (Nilsson, 2006). Precisely for that reason it is insightful that the survival of the larger, stocked fishes was nevertheless low, indicating that while the general growth rates shown by surviving stocked fishes might were the same as the wild ones, their overall fitness was nevertheless strongly inferior. Other work with adult pike has previously shown that the reproductive fitness of stocked fishes is about half compared to wild fishes (Monk et al., 2020).

Despite the poorer performance of stocked fishes overall, the surviving stocked fish performed extremely well in terms of growth and total length attained relative to same aged wild conspecifics. In pike, large size can turn into better competitive abilities in the quest for food and refuges (Skov et al., 2002). The larger size of stocked over wild pike likely promoted the partial replacement of smaller wild by larger stocked individuals (Lorenzen, 2005). Such replacement is in the end simply a numbers game: if enough fish are stocked, even a larger mortality in stocked compared to wild fishes can still lead to many stocked fishes surviving, who in turn affect survival of the smallest size classes of the wild conspecifics. In our experiment, despite the larger natural mortality pond-reared pike constituted approximately one half to the age-2 pike cohorts 18 months after the stocking experiment. When these fish reach maturity, it is likely that they cross-breed with the wild conspecifics as documented recently (Monk et al., 2020). Such introgression of foreign genes can be a serious risk to genetic biodiversity (Bekkevold et al., 2015; Eschbach et al., 2021) without having a measurable impact on fishing quality due to unaltered abundance despite intensive stocking.

5. Conclusions

Our stocking experiment highlighted the strong size- and density-dependence in juvenile mortality and importance of ecological adaptation of hatchery fishes to wild conditions for driving stocking outcomes. Our work also suggests that intra- and particularly inter-cohort predation, rather than intra-cohort food competition, is a major regulatory

factor driving the establishment of introduced pike, which is in line with a meta-analysis on fish invasions in ecosystems (Alofs and Jackson, 2014) and previous work in pike (Haugen et al., 2007). Given this study and previous research on pike fry (Hühn et al., 2014b), achieving a positive stock enhancement effect of pike stocking is likely only possible when releasing adult, recruited fish who no longer suffer density-dependent mortality (Lorenzen, 2005; Arlinghaus et al., 2015; Monk et al., 2020), but even such stockings have been found to fail in a French river system (Guillerault et al., 2018, 2021). Other forms of pike stocking are unlikely to generate fisheries benefits (Radinger et al., 2023), while negatively affecting the wild population and possibly the gene pool of the stock-enhanced population (Arlinghaus et al., 2015). This is because, depending on the origin of the released fish, interbreeding of stocked and wild fish will lead introgression and to the loss of genetic diversity through genetic swamping (Laikre et al., 2010). Given the fundamental properties of population regulation confirmed in the present experiment in line with stocking theory (Lorenzen, 2005), we can ultimately conclude that the stocking of pike, and possibly ecologically related predatory species such as muskellunge or pike-perch (*Sander lucioperca*), is unlikely to be wise investment of money if the goal is to elevate stock sizes and produce additive population effects while minimizing genetic and other ecological risks (e.g., spread of disease). Finally, our research involving an active adaptive management experiment of stocking is an example of how important insights for management can be combined with relevant tests of ecological and evolutionary theories in the spirits of Hutchings (2014) and Lorenzen (2014). Because fish stocking is bound to stay as an important fisheries management tool (Lorenzen, 2014; Arlinghaus et al., 2022), the scientific community may be taking advantage of the inevitable and engage in proper monitoring of ongoing releases to test fundamental ecological and evolutionary hypotheses about population regulation.

CRediT authorship contribution statement

Daniel Hühn: Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft. **Daniel C. Gwinn:** Formal analysis, Writing – review & editing. **Stephanie L. Shaw:** Formal analysis, Writing – review & editing. **Josep Alós:** Formal analysis, Writing – review & editing. **Micheal S. Allen:** Conceptualization, Formal analysis, Writing – review & editing. **Thilo Pagel:** Investigation, Methodology, Writing – review & editing. **Christian Skov:** Conceptualization, Methodology, Supervision, Writing – review & editing. **Robert Arlinghaus:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgments

We thank two anonymous reviewers for their valuable comments. We acknowledge the angling clubs SFV Helmstedt und Umgebung e.V., SFV "Früh Auf" Bramsche e.V., ASV "Gut Fang" Stapel e.V., VFG Schönewörde und Umgebung e.V. and FV Peine-Ilsede und Umgebung e. V. for provision of lakes and help. In addition, we acknowledge M. E. Beck, N. Bremer, J. Briege, E.-V. Cyrus, E. Eschbach, J. Hilsberg, A. McFall, M. Morkritzki, S. Schälicke and A. Türck for their technical support and substantial help during field work. For analyses of total phosphorus and chlorophyll a concentration, we thank E. Zwirnmann and B. Meinck from the Department of Chemical Analytics and Biogeochemistry at the Leibniz Institute of Freshwater Ecology and Inland Fisheries. We acknowledge the statistical support by M. Fujitani in the analysis of growth. Finally, we thank H.-H. Arzbach from the Lower Saxony State Office for Consumer Protection and Food Safety department of Inland Fisheries for the kind permit for electrofishing. Funding for the presented study was granted by the Federal Ministry of Education and Research (BMBF) within the Program on Social–Ecological Research and the project Besatzfisch (http://www.besatz-fisch.de) to D.H., T.P., R.A. (grant No. 01UU0907). The experiment was approved through an animal care permit (permit No. 33.9-42502-04-11/0392) granted by the Lower Saxony State Office for Consumer Protection and Food Safety, according to the German Animal Protection Act.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2023.106799.

References

Ahrens, R.N.M., Walters, C.J., Christensen, V., 2012. Foraging arena theory. Fish Fish. 13, 41–59.

Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle, in: Petrov, B.N., Csaki, F. (Eds.), International symposium on information theory. Akaďemiai Kiado, Budapest, Hungary, pp. 267–281.

Alofs, K.M., Jackson, D.A., 2014. Meta-analysis suggests biotic resistance in freshwater environments is driven by consumption rather than competition. Ecol. 95, 3259–3270.

Arlinghaus, R., Cyrus, E.-M., Eschbach, E., Fujitani, M., Hühn, D., Johnston, F., Pagel, T., Riepe, C., 2015. Hand in Hand für eine nachhaltige Angelfischerei: Ergebnisse und Empfehlungen aus fünf Jahren praxisorientierter Forschung zu Fischbesatz und seinen Alternativen. Berichte des IGB, Heft 28/2015. [Striving together for sustainable fish stocking: Results and recommendations after five years practice oriented research on fish stocking measures and alternatives management tools.].

Arlinghaus, R., Lorenzen, K., Johnson, B.M., Cooke, S.J., Cowx, I.G., 2016. Management of freshwater fisheries: addressing habitat, people and fishes, in: Craig, J.F. (Eds.), Freshwater fisheries ecology. Wiley, Chichester, pp. 557–579.

Arlinghaus, R., Riepe, C., Theis, S., Pagel, T., Fujitani, M., 2022. Dysfunctional information feedbacks cause the emergence of management panaceas in social-ecological systems: the case of fish stocking in inland recreational fisheries. J. Outdoor Recreat. Tour. 38, 100475.

Baer, J., Brinker, A., 2008. Are growth and recapture of hatchery-reared and resident brown trout (*Salmo trutta* L.) density dependent after stocking? Ecol. Freshw. Fish. 17, 455–464.

Baer, J., George, V., Hanfland, S., Lemcke, R., Meyer, L., Zahn, S., 2007. Gute fachliche Praxis fischereilicher Besatzmaßnahmen. Schriftenreihe des Verbandes Deutscher Fischereiverwaltungsbeamter und Fischereiwissenschaftler e. V. 14. [Best pracitce guidelines for stocking.].

Barbieri, M.M., Berger, J.O., 2004. Optimal predictive model selection. Ann. Stat. 32, 870–897.

Bekkevold, D., Jacobsen, L., Hemmer-Hansen, J., Berg, S., Skov, C., 2015. From regionally predictable to locally complex population structure in a freshwater top predator: river systems are not always the unit of connectivity in northern pike *Esox lucius*. Ecol. Freshw. Fish. 24, 305–316.

Brockmark, S., Adriaenssens, B., Johnsson, J.I., 2010. Less is more: density influences the development of behavioural life skills in trout. Proc. Royal Soc. B 277, 3035–3043.

Brockmark, S., Johnsson, J.I., 2010. Reduced hatchery rearing density increases social dominance, postrelease growth, and survival in brown trout (*Salmo trutta*). Can. J. Fish. Aquat. Sci. 67, 288–295.

Bry, C., 1996. Role of vegetation in the life cycle of pike, in: Craig, J.F. (Eds.), Pike: biology and exploitation, Fish and Fisheries Series, No, 19. Chapman and Hall, London, UK, pp. 45–67.

Bulmer, M.G., 1974. On fitting the poisson lognormal distribution to species-abundance data. Biom. 30, 101–110.

Burnham, K.P., Anderson, D.R., 1998. Model selection and inference: a practical information theoretic approach. Springer-Verlag, New York.

Camp, E., Larkin, S., Ahrens, R., Lorenzen, K., 2017. Trade-offs between socioeconomic and conservation management objectives in stock enhancement of marine recreational fisheries. Fish. Res. 186, 446–459.

Camp, E.V., Lorenzen, K., Ahrens, R.N., Allen, M.S., 2014. Stock enhancement to address multiple recreational fisheries objectives: an integrated model applied to red drum *Sciaenops ocellatus* in Florida. J. Fish. Biol. 85, 1868–1889.

Carpenter, S.R., Cole, J.J., Pace, M.L., Batt, R., Brock, W.A., Cline, T., Coloso, J., Hodgson, J.R., Kitchell, J.F., Seekell, D.A., Smith, L., Weidel, B., 2011. Early warnings of regime shifts: a whole-ecosystem experiment. Science 332, 1079–1082.

Carpenter, S.R., Frost, T.M., Heisey, D., Kratz, T.K., 1989. Randomized intervention analysis and the interpretation of whole-ecosystem experiments. Ecol. 70, 1142–1152.

Casselman, J.M., Lewis, C.A., 1996. Habitat requirements of northern pike (*Esox lucius*). Can. J. Fish. Aquat. Sci. 53, 161–174.

Cowx, I.G., 1994. Stocking strategies. Fish. Manag. Ecol. 1, 15–30.

Diana, M.J., Wahl, D.H., 2008. Long-term stocking success of largemouth bass and the relationship to natural populations, in: Allen, M.S., Sammons, S., Maceina, M.J. (Eds.), Balancing fisheries management and water uses for impounded river systems. American Fisheries Society Symposium 62, Bethesda, Maryland, pp. 413–426.

Edeline, E., Haugen, T.O., Weltzien, F.-A., Claessen, D., Winfield, I.J., Stenseth, N.C., Vøllestad, L.A., 2010. Body downsizing caused by non-consumptive social stress severely depresses population growth rate. Proc. R. Soc. B 277, 843–851.

Eklöv, P., 1997. Effects of habitat complexity and prey abundance on the spatial and temporal distributions of perch (*Perca fluviatilis*) and pike (*Esox lucius*). Can. J. Fish. Aquat. Sci. 54, 1520–1531.

Elliott, J.M., 1994. Quantitative ecology and the brown trout. Oxford University Press.

Emmrich, M., Schälicke, S., Hühn, D., Lewin, W.-C., Arlinghaus, R., 2014. No differences between littoral fish community structure of small natural and gravel pit lakes in the northern German lowlands. Limnologica 46, 84–93.

Eschbach, E., Nolte, A.W., Kohlmann, K., Alós, J., Schöning, S., Arlinghaus, R., 2021. Genetic population structure of a top predatory fish (northern pike, *Esox lucius*) covaries with anthropogenic alteration of freshwater ecosystems. Freshw. Biol. 66, 884–901.

Fayram, A.H., Schenborn, D.A., Hennessy, J.M., Nate, N.A., Schmalz, P.J., 2009. Exploring the conflict between broad scale and local inland fisheries management: the risks to agency credibility. Fisheries 34, 232–236.

Francis, R.I.C.C., 1990. Back-calculation of fish length: a critical review. J. Fish. Biol. 36, 883–902.

Gelman, A., Carlin, J.B., Stern, H.S., Rubin, D.B., 2004. Bayesian data analysis. Chapman and Hall, Boca Raton.

Green, R.H., 1979. Sampling design and statistical methods for environmental biologists. John Wiley and Sons, New York, NY.

Grimm, M.P., 1981. The composition of northern pike (*Esox lucius* L.) populations in four shallow waters in the Netherlands, with special reference to factors influencing 0+ pike biomass. Aquac. Res. 12, 61–76.

Grimm, M.P., 1983. Regulation of biomasses of small (<41 cm) northern pike (*Esox lucius* L.), with special reference to the contribution of individuals stocked as fingerlings (4–6 cm). Aquac. Res. 14, 115–134.

Grimm, M.P., 1989. Northern pike (*Esox lucius* L.) and aquatic vegetation, tools in the management of fisheries and water quality in shallow waters. Hydrobiol. Bull. 23, 59–65.

Grimm, M.P., Klinge, M., 1996. Pike and some aspects of its dependence on vegetation, in: Craig, J.F. (Eds.), Pike biology and exploitation. Chapman and Hall, London, UK, pp. 125–156.

Grønkjær, P., Skov, C., Berg, S., 2004. Otolith-based analysis of survival and size-selective mortality of stocked 0+ year pike related to time of stocking. J. Fish. Biol. 64, 1625–1637.

Guillerault, N., Loot, G., Blanchet, S., Millet, P., Musseau, C., Cucherousset, J., Santoul, F., 2021. Efficiency of Northern pike (*Esox lucius*) stocking in metropolitan France at large spatial and temporal scales. Fish. Manag. Ecol. 28, 486–495.

Guillerault, N., Loot, G., Blanchet, S., Santoul, F., 2018. Catch-related and genetic outcome of adult northern pike *Esox lucius* stocking in a large river system. J. Fish. Biol. 93, 1107–1112.

Hansen, G.J.A., Gaeta, J.W., Hansen, J.F., Carpenter, S.R., 2015. Learning to manage and managing to learn: sustaining freshwater recreational fisheries in a changing environment. Fisheries 40, 56–64.

Haugen, T.O., Winfield, I.J., Vøllestad, L.A., Fletcher, J.M., James, J.B., Stenseth, N.C., 2006. The ideal free pike: 50 years of fitness-maximizing dispersal in Windermere. Proc. R. Soc. B 273, 2917–2924.

Haugen, T.O., Winfield, I.J., Vøllestad, L.A., Fletcher, J.M., James, J.B., Stenseth, N.C., 2007. Density dependence and density independence in the demography and dispersal of pike over four decades. Ecol. Monogr. 77, 483–502.

Hazlerigg, C.R.E., Lorenzen, K., Thorbek, P., Wheeler, J.R., Tyler, C.R., 2012. Density-dependent processes in the life history of fishes: evidence from laboratory populations of zebrafish *Danio rerio*. PLoS One. 7, e37550.

Hilborn, R., 1999. Confessions of a reformed hatchery basher. Fisheries 24, 31–33.

Hilborn, R., Eggers, D., 2000. A review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska. Trans. Am. Fish. Soc. 129, 333–350.

Hühn, D., Klefoth, T., Pagel, T., Zajicek, P., Arlinghaus, R., 2014a. Impacts of external and surgery-based tagging techniques on small northern pike under field conditions. N. Am. J. Fish. Manag. 34, 322–334.

Hühn, D., Lübke, K., Skov, C., Arlinghaus, R., 2014b. Natural recruitment, density-dependent juvenile survival, and the potential for additive effects of stock enhancement: an experimental evaluation of stocking northern pike (*Esox lucius* L.) fry. Can. J. Fish. Aquat. Sci. 71, 1508–1519.

Hutchings, J.A., 2000. Numerical assessment in the front seat, ecology and evolution in the back seat: time to change drivers in fisheries and aquatic sciences? Mar. Ecol. Prog. Ser. 208, 299–303.

Hutchings, J.A., 2014. Unintentional selection, unanticipated insights: introductions, stocking and the evolutionary ecology of fishes. J. Fish. Biol. 85, 1907–1926.

Hyvärinen, P., Rodewald, P., 2013. Enriched rearing improves survival of hatchery-reared Atlantic salmon smolts during migration in the River Tornionjoki. Can. J. Fish. Aquat. Sci. 70, 1386–1395.

Jansen, T., Arlinghaus, R., Als, T.D., Skov, C., 2013. Voluntary angler logbooks reveal long-term changes in a lentic pike, *Esox lucius*, population. Fish. Manag. Ecol. 20, 125–136.

Jensen, O.P., Branch, T.A., Hilborn, R., 2012. Marine fisheries as ecological experiments. Theor. Ecol. 5, 3–22.

Johnston, F.D., Allen, M.S., Beardmore, B., Riepe, C., Pagel, T., Hühn, D., Arlinghaus, R., 2018. How ecological processes shape the outcomes of stock enhancement and harvest regulations in recreational fisheries. Ecol. Appl. 28, 2033–2054.

Kéry, M., 2010. Introduction to WinBUGS for ecologists: bayesian approach to regression. ANOVA, mixed models and related analyses. Academic Press.

Kipling, C., Frost, W.E., 1970. A study of the mortality, population numbers, year class strengths, production and food consumption of pike, *Esox lucius* L., in Windermere from 1944 to 1962. J. Anim. Ecol. 39, 115–157.

Laikre, L., Schwartz, M.K., Waples, R.S., Ryman, N., The GeM Working Group, 2010. Compromising genetic diversity in the wild: unmonitored largescale release of plants and animals. Trends Ecol. Evol. 25, 520–529.

Le Cren, E.D., 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). J. Anim. Ecol. 20, 201–219.

Lorenzen, K., 2000. Allometry of natural mortality as a basis for assessing optimal release size in fish-stocking programmes. Can. J. Fish. Aquat. Sci. 57, 2374–2381.

Lorenzen, K., 2005. Population dynamics and potential of fisheries stock enhancement: practical theory for assessment and policy analysis. Proc. Royal Soc. B 360, 171–189. https://doi.org/10.1098/rstb.2004.1570.

Lorenzen, K., 2006. Population management in fisheries enhancement: gaining key information from release experiments through use of a size-dependent mortality model. Fish. Res. 80, 19–27.

Lorenzen, K., 2008. Understanding and managing enhancement fisheries systems. Rev. Fish. Sci. 16, 10–23.

Lorenzen, K., 2014. Understanding and managing enhancements: why fisheries scientists should care. J. Fish. Biol. 85, 1807–1829.

Lorenzen, K., Beveridge, M.C.M., Mangel, M., 2012. Cultured fish: integrative biology and management of domestication and interactions with wild fish. Biol. Rev. 87, 639–660.

Lorenzen, K., Camp, E.V., 2019. Density-dependence in the life history of fishes: when is a fish recruited? Fish. Res. 217, 5–10.

Lorenzen, K., Enberg, K., 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proc. R. Soc. B 269, 49–54.

Maday, A., Matern, S., Monk, C.T., Klefoth, T., Wolter, C., Arlinghaus, R., 2023. Seasonal and diurnal patterns of littoral microhabitat use by fish in gravel pit lakes, with special reference to supplemented deadwood brush piles. Hydrobiologia 850, 1557–1581.

Matern, S., Klefoth, T., Wolter, C., Arlinghaus, R., 2021. Environmental determinants of fish abundance in the littoral zone of gravel pit lakes. Hydrobiologia 848, 2449–2471.

Mittelbach, G.G., Persson, L., 1998. The ontogeny of piscivory and its ecological consequences. Can. J. Fish. Aquat. Sci. 55, 1454–1465.

Monk, C.T., Chéret, B., Czapla, P., Hühn, D., Klefoth, T., Eschbach, E., Hagemann, R., Arlinghaus, R., 2020. Behavioural and fitness effects of translocation to a novel environment: whole-lake experiments in two aquatic top predators. J. Anim. Ecol. 89, 2325–2344.

Myers, R.A., 2002. Recruitment: understanding density-dependence in fish populations, in: Hart, P.J.B., Reynolds, J.D. (Eds.), Handbook of fish biology and fisheries, Vol 1. Fish biology. Blackwell Science, Oxford, pp. 123–148.

Nilsson, P.A., 2006. Avoid your neighbours: size-determined spatial distribution patterns among northern pike individuals. Oikos 113, 251–258.

Nilsson, P.A., Brönmark, C., 2000. Prey vulnerability to a gape-size limited predator: behavioural andmorphological impacts on northern pike piscivory. Oikos 88, 539–546.

Nilsson, K.A., Persson, L., 2013. Refuge availability and within-species differences in cannibalism determine population variability and dynamics. Ecosphere. 4, 100.

Olla, B.L., Davis, M.W., Ryer, C.H., 1998. Understanding how the hatchery environment represses or promotes the development of behavioral survival skills. Bull. Mar. Sci. 62, 531–550.

Pagel, T., Bekkevold, D., Pohlmeier, S., Wolter, C., Arlinghaus, R., 2015. Thermal and maternal environments shape the value of early hatching in a natural population of a strongly cannibalistic freshwater fish. Oecologia 178, 951–965.

Persson, L., de Roos, A.M., Bertolo, A., 2004. Predicting shifts in dynamics of cannibalistic field populations using individual-based models. Proc. R. Soc. B 271, 2489–2493.

Persson, L., de Roos, A.M., Claessen, D., Byström, P., Lövgren, J., Sjögren, S., Svanbäck, R., Wahlström, W., Westman, E., 2003. Gigantic cannibals driving a whole-lake trophic cascade. Proc. Natl. Acad. Sci. 100, 4035–4039.

Persson, L., Amundsen, P.A., de Roos, A.M., Klemetsen, A., Knudsen, A.R., Primicerio, R., 2007. Culling prey promotes predator recovery—alternative states in a whole-lake experiment. Science 316, 1743–1746.

Persson, L., Bertolo, A., de Roos, A.M., 2006. Temporal stability in size distributions and growth rates of three *Esox lucius* L. populations. A result of cannibalism? J. Fish. Biol. 69, 461–472.

Plummer, M., 2003. JAGS: a program for analysis of bayesian graphical models using gibbs sampling, in: Leisch, F., Zeileis, A. (Eds.), Proceedings of the 3rd international workshop on distributed statistical computing, Vol. 124. Technische University at Wien, Austria, pp. 1–10.

Post, J.R., Sullivan, M., Cox, S., Lester, N.P., Walters, C.J., Parkinson, E.A., Paul, A.J., Jackson, L., Shuter, B.J., 2002. Canada's recreational fisheries: the invisible collapse? Fisheries 27, 6–17.

R Development Core Team, 2009. R: a language and environment for statistical computing. R. Found. Stat. Comput., Vienna, Austria (Available from). ⟨http://www.R-project.org/⟩.
Radinger, J., Matern, S., Klefoth, T., Wolter, C., Feldhege, F., Monk, C.T., Arlinghaus, R., 2023. Ecosystem-based management outperforms species-focused stocking for enhancing fish populations. Science 379, 946–951.
Rogers, M., Allen, M.S., Brown, P., Hunt, T., Fulton, W., Ingram, B.A., 2010. A simulation model to explore the relative value of stock enhancement versus harvest regulations for fishery sustainability. Ecol. Model. 221, 919–926.
Rose, K.A., Cowan Jr, J.H., Winemiller, K.O., Myers, R.A., Hilborn, R., 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish Fish. 2, 293–327.
Royle, J.A., Dorazio, R.M., 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Elsevier Academic Press, Oxford, UK.
Schnabel, Z.E., 1938. The estimation of total fish population of a lake. Am. Math. Mon. 45, 348–352.
Skov, C., Berg, S., Jacobsen, L., Jepsen, N., 2002. Habitat use and foraging success of 0+ pike (*Esox lucius* L.) in experimental ponds related to prey fish, water transparency and light intensity. Ecol. Feshw. Fish. 11, 65–73.
Skov, C., Jacobsen, L., Berg, S., 2003. Post-stocking survival of 0+ year pike in ponds as a function of water transparency, habitat complexity, prey availability and size heterogeneity. J. Fish. Biol. 62, 311–322.
Skov, C., Koed, A., 2004. Habitat use of 0+ year pike in experimental ponds in relation to cannibalism, zooplankton, water transparency and habitat complexity. J. Fish. Biol. 64, 448–459.
Skov, C., Koed, A., Baastrup-Spohr, L., Arlinghaus, R., 2011. Dispersal, growth, and diet of stocked and wild northern pike fry in a shallow natural lake, with implications for the management of stocking programs. N. Am. J. Fish. Manag. 31, 1177–1186.
Stewart-Oaten, A., Murdock, W.W., Parker, K.R., 1986. Environmental impact assessment: "pseudoreplication" in time? Ecology 67, 929–940. https://doi.org/10.2307/1939815.
Sugiura, N., 1978. Further analysis of the data by Akaike's Information Criterion and the finite corrections. Commun. Stat. Theory Methods A 7, 13–26.
Sutela, T., Korhonen, P., Nyberg, K., 2004. Stocking success of newly hatched pike evaluated by radioactive strontium (^{85}Sr) marking. J. Fish. Biol. 64, 653–664.
Szczepkowski, M., Zakęś, Z., Kapusta, A., Szczepkowska, B., Hopko, M., Jarmołowicz, S., Kowalska, A., Kozłowski, M., Partyka, K., Piotrowska, I., Wunderlich, K., 2012. Growth and survival in earthen ponds of different sizes of juvenile pike reared in recirculating aquaculture systems. Arch. Pol. Fish. 20, 267–274.
Szendrey, T.A., Wahl, D.H., 1996. Size-specific survival and growth of stocked muskellunge: effects of predation and prey availability. N. Am. J. Fish. Manag. 16, 395–402.
Terui, A., Urabe, H., Senzaki, M., Nishizawa, B., 2023. Intentional release of native species undermines ecological stability. Proc. Natl. Acad. Sci. 120, e2218044120.
Underwood, A.J., 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. Ecol. Appl. 4, 3–15.
van Kooten, T., Andersson, J., Byström, P., Persson, L., de Roos, A.M., 2010. Size at hatching determines population dynamics and response to harvesting in cannibalistic fish. Can. J. Fish. Aquat. Sci. 67, 401–416.
van Poorten, B.T., Arlinghaus, R., Daedlow, K., Haertel-Borer, S.S., 2011. Social-ecological interactions, management panaceas, and the future of wild fish populations. Proc. Natl. Acad. Sci. 108, 12554–12559.
Vuorinen, P.J., Nyberg, K., Lehtonen, H., 1998. Radioactive strontium (^{85}Sr) in marking newly hatched pike and success of stocking. J. Fish. Biol. 52, 268–280.
Wahl, D.H., 1999. An ecological context for evaluating the factors influencing muskellunge stocking success. N. Am. J. Fish. Manag. 19, 238–248.
Walters, C.J., Martell, S.J.D., 2004. Fisheries ecology and management. Princeton University Press, New York.
Wright, R.M., Giles, N., 1987. The survival, growth and diet of pike fry, *Esox lucius* L., stocked at different densities in experimental ponds. J. Fish. Biol. 30, 617–629.