

Natural recruitment, density-dependent juvenile survival, and the potential for additive effects of stock enhancement: an experimental evaluation of stocking northern pike (*Esox lucius*) fry

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Abstract: Density-dependent mortality in young life stages should strongly limit the potential for additive effects caused by stocking of fish sizes that are smaller than size at recruitment into the fishery. Indeed, stocking models have suggested that stocking of fry should not elevate year class strength in self-sustaining stocks. However, limited data based on replicated and controlled experiments are available to support this prediction. We performed a pond experiment ($N = 4$ per treatment) to compare the stock enhancing outcome of stocking hatchery-reared northern pike (*Esox lucius*) fry and the natural production of young in self-recruiting pike populations. We also added a treatment where pike fry were stocked into ponds that otherwise did not have pike to mimic the absence of natural recruitment. Fry stocking into self-reproducing stocks did not elevate year class strength over unstocked controls. However, in the absence of competition, year class strength of juveniles in late summer emerging from fry stocking was similar to the production of natural recruits. Overall, we demonstrated the competitive disadvantage of hatchery-reared fry when released into waters already containing natural recruits, the partial replacement of natural recruits by hatchery-reared fry, and the lack of additive effects of stock enhancement in naturally reproducing stocks. A stock-enhancing effect of pike fry stocking may only be expected in the absence of natural recruitment.

Résumé : La mortalité dépendante de la densité durant les premières étapes du cycle de vie devrait fortement limiter la possibilité d'effets additifs causés par l'empoissonnement avec des poissons de tailles plus petites que la taille au moment du recrutement dans la pêche. De fait, des modèles d'empoissonnement donnent à penser que l'empoissonnement avec des alevins ne devrait pas accroître la force des classes d'âge dans les stocks dont le maintien est assuré par la reproduction naturelle. Cependant, il y a peu de données issues d'expériences répétées et contrôlées disponibles pour appuyer cette prédiction. Nous avons réalisé une expérience en étang ($N = 4$ par traitement) pour comparer les résultats de la valorisation du stock par empoissonnement avec des alevins d'élevage de grand brochet (*Esox lucius*) à la production naturelle de juvéniles dans des populations de brochets maintenues par autocrutement. Nous avons également inclus un traitement dans lequel des alevins de brochet étaient empoissonnés dans des étangs par ailleurs exempts de brochets afin de reproduire l'absence de recrutement naturel. L'empoissonnement d'alevins dans des stocks autoproducteurs n'a pas rehaussé la force des classes d'âge par rapport à celle de populations témoins non empoissonnées. Cependant, en l'absence de concurrence, la force des classes d'âge à la fin de l'été de juvéniles issus de l'empoissonnement avec des alevins était semblable à celle découlant de la production de recrues naturelles. En général, nous démontrons le désavantage concurrentiel des alevins d'élevage relâchés dans des eaux qui renferment déjà des recrues naturelles, le remplacement partiel de recrues naturelles par des alevins d'élevage et l'absence d'effets additifs de la valorisation du stock dans des stocks se reproduisant de manière naturelle. Un effet de valorisation du stock par l'empoissonnement avec des alevins de brochet ne serait à prévoir qu'en l'absence de recrutement naturel. [Traduit par la Rédaction]

Introduction

Stocking is conducted for multiple reasons, ranging from conservation of threatened fish species to enhancement of fisheries quality (Lorenzen et al. 2012). One common fisheries objective is the enhancement of stocks to sustain and improve catches. In this context, stocking of fish into self-reproducing stocks — so-called compensatory stocking (Cowx 1994) or stock enhancement when the aim is to elevate fisheries yield (Lorenzen et al. 2012) — is frequently conducted across the globe (Welcomme and Bartley 1998). Its aim is the generation of additive effects in relation to existing natural recruitment, meaning an increase of abundance or bio-

mass, and hence catch rate or biomass yield, of the target stock above its naturally achieved levels (Hilborn 1999). Because many fish stocks are recruitment-limited (Walters and Juanes 1993), for example owing to habitat bottlenecks, recruitment overfishing or life stage-specific mortality stemming from intra- or interspecific interactions (reviewed in de Roos and Persson 2013), there is the potential that stock enhancement may elevate stock sizes even in situations where natural recruitment occurs (Lorenzen 2005; Rogers et al. 2010; Lorenzen et al. 2012).

Substantial scientific and heated public debate surrounds the question of whether stocking fish into self-sustaining stocks indeed

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produces additive effects or simply replaces wild recruitment (e.g., Leber et al. 1995; Walters and Martell 2004; Young 2013). The controversy is further aggravated because of a range of usually undesirable ecological and genetic effects that are conceivable as results of enhancements (e.g., Araki et al. 2007; Lewin et al. 2008; Laikre et al. 2010). Additive effects of experimental stock enhancement have been documented in several situations (Leber et al. 1995; Brennan et al. 2008), but there are equally many studies that reported failed stocking success, particularly when natural recruitment of the stock-enhanced species was present in the recipient water body (Li et al. 1996; Skov et al. 2011; Young 2013). Stocking models support the assumption that additive effects are unlikely when stocking programs are conducted with larval fish or other early life stages in naturally reproducing stocks (e.g., Lorenzen 2005; Rogers et al. 2010). This is because juveniles are usually too small to have surpassed density-dependent mortality bottlenecks and in addition suffer from high density-independent mortality (Lorenzen 2000, 2005). Irrespective of these findings, many practical guidelines for fish stocking recommend stocking fry or juvenile fish over older life stages (e.g., Baer et al. 2007). Early life stages are recommended over older for stocking because these life stages are assumed to readily adapt to new environments, are exposed only for short durations to artificial environments and thus suffer from reduced domestication selection, and for cost-effectiveness reasons. There is also the assumption that relying on juvenile fish prevents practitioners from overstocking, which is more likely when adults are released. This is because adults constitute a life stage that is mainly regulated by density-dependent growth and no longer suffers from high mortality after stocking (Lorenzen 2005).

Lack of nonstocked controls, insufficient replication, poor contrast, inappropriate experimental design, and poor assessments based on single-fishery case studies limit the inference space as to the potential for additive effects caused by stocking (Walters and Martell 2004). Indeed, there are few replicated field studies that have analyzed the potential additive effects of fry stocking across a gradient of natural recruitment (e.g., Li et al. 1996; Brennan et al. 2008). Given the billions of fish that are released annually into the wild, there is a need for better studies to understand the density-dependent processes governing enhancement dynamics and the consequences of releasing hatchery-reared fish into natural ecosystems (Lorenzen et al. 2012).

Many fish species targeted by recreational fisheries are top predators (Donaldson et al. 2011), where cannibalism contributes strongly to size- and density-dependent population regulation (Polis 1981; Claessen et al. 2000; Ohlberger et al. 2012). Northern pike (*Esox lucius*, hereinafter referred to as pike) is an example of such a strongly cannibalistic predatory fish species (Grimm 1983; Bry et al. 1992; Persson et al. 2006) whose population dynamics are characterized by comparatively stable conditions relative to other top predators with a narrower gape size (Claessen et al. 2004; van Kooten et al. 2010). Pike is in heavy demand by recreational and commercial fisheries in North America and Eurasia (Paukert et al. 2001; Arlinghaus and Mehner 2004; Arlinghaus et al. 2008). As a consequence of perceived recruitment impacts caused by loss of spawning habitat, the species is regularly stocked in North America and Europe (Raat 1988; Mann 1996; Pierce 2012). Pike has also been regularly used in biomanipulation projects to improve water quality through top-down control of zooplanktivores (e.g., Prejs et al. 1994; Benndorf 1995; Skov et al. 2003a). The heavy degree of self-regulation of pike populations through cannibalism may strongly limit the possibility to generate additive effects by pike stocking unless natural recruitment is strongly impaired (e.g., Vuorinen et al. 1998; Sutela et al. 2004; Schreckenbach 2006).

Additive effects of stocking cannibalistic species have been demonstrated in release experiments of age-1 common snook (*Centropomus undecimalis*) in coastal environments (Brennan et al. 2008). In contrast, the pike stocking literature contains few re-

ports of successful stock enhancement with pike fry or juveniles (Sutela et al. 2004; Skov and Nilsson 2007; Skov et al. 2011). However, most of the cited pike studies were observational single-fishery case studies in lakes, lacking appropriate replication and contrast of situations with and without natural recruitment. The objective of the present work was to evaluate the outcome of stock enhancement through the release of hatchery-reared fry into self-sustaining fish populations using pike as a model species. It was predicted that owing to density-dependent juvenile mortality, the abundance of age-0 pike would not be enhanced by stocking hatchery-reared fry into naturally recruiting populations (Skov and Nilsson 2007). By contrast, stocking pike fry or juveniles may be highly successful when fish are stocked in ecosystems without pike (Vuorinen et al. 1998; Sutela et al. 2004). In line with observational data from the wild (Skov et al. 2011), we also hypothesized that released fish would suffer from lower fitness compared with naturally recruited conspecifics. Accordingly, we expected lower growth and survival of hatchery-reared fish compared with naturally recruited fish under competitive situations. To test our hypotheses, we implemented a replicated pond experiment where we simulated stocking in the absence of natural recruitment compared with stock enhancement of naturally recruiting populations.

Methods

Experimental setup and artificial reproduction of pike fry

We conducted a controlled experiment in $N = 12$ earthen ponds to represent littoral zones in which pike are known to spawn and strive as juveniles (Bry 1996; Casselman and Lewis 1996; Pierce 2012). The pond surface areas ranged from 921 to 1409 m² (mean \pm SD, 1074 \pm 123 m²), and the maximum depth of ponds varied between 95 and 115 cm (mean \pm SD, 107 \pm 6 cm). The pond shorelines hosted common reed (*Phragmites australis*) that was scythed before experimentation to provide comparable conditions in each pond. Ponds were drained and left dry over winter and were flooded on 4 March 2012. Nets were installed at the inflow of each pond to prevent unintended immigration and subsequent emigration of fish during the experiments (2 mm \times 2 mm mesh size, replaced in June by 4 mm \times 4 mm mesh size nets). Pond outlets were closed over the entire study period and were not passable for fish. When experimentation commenced, the ponds were overgrown with submerged macrophytes (dominated by fennel pondweed, *Potamogeton pectinatus*), providing an optimal habitat for juvenile pike (Raat 1988).

Three treatment groups were established: (1) naturally recruiting pike populations without addition of hatchery-reared pike fry (referred to as natural recruitment, NR), which mimicked the situation of natural reproduction without stock enhancement; (2) naturally recruiting pike populations with addition of hatchery-reared pike fry of the same genetic background (referred to as natural recruitment and hatchery-reared fry, NRHF), which mimicked a stock enhancement program into self-sustaining stocks; and (3) populations that stocked hatchery-reared fry without natural recruitment of pike (referred to as HF), which mimicked the lack of a spawning stock due to recruitment overfishing or simply a lack of spawning habitat. Treatments were replicated four times and assigned randomly to the ponds.

To meet the requirements of simulating naturally reproducing pike stocks (treatment NR and NRHF), we stocked mature pike spawners into the ponds at a density that resembled natural unexploited pike stocks at carrying capacity in suitable vegetated habitat. Wild spawners were caught with trap nets in a connected water system consisting of several natural lakes, between 8 and 16 March 2012. Fish were externally sexed (Casselman 1974) and directly transferred to the experimental ponds. We released four to five female pike (total length (TL) range 512–760 mm) and eight to ten males (TL range 402–673 mm) into each pond to achieve a

Table 1. Pond surface area and composition of fish communities prespawning (adult pike as broodstock to allow for natural recruitment) and postspawning, and after stocking of hatchery-reared fry in the three treatment groups.

Treatment	Pond No.	Pond surface area (m ²)	Prespawning pike stock ^a (brood stock)				Postspawning fish community		
			No. of female pike	Female pike biomass (kg·ha ⁻¹)	Estimated egg deposition (eggs·m ⁻²)	No. of male pike	Male pike biomass (kg·ha ⁻¹)	Age-1 and older pike biomass ^b (kg·ha ⁻¹)	Cyprinid biomass ^c (kg·ha ⁻¹)
NR	2	1004	4	75	202	8	107	81	352.6+99.6
	4	1409	5	75	202	10	78	91	350.2+100.0
	8	1038	4	75	202	8	78	111	350.2+100.1
	10	1158	4	74	199	8	57	68	350.2+100.1
NRHF	5	1019	5	75	203	10	126	71	349.9+100.0
	7	1080	4	75	202	8	67	69	350.9+100.0
	9	990	4	73	196	8	67	71	354.0+100.0
	11	1143	4	75	203	8	77	79	339.0+99.7
HF	1	921	0	0	0	0	0	64	350.2+99.9
	3	1049	0	0	0	0	0	65	350.3+100.0
	6	1026	0	0	0	0	0	65	350.4+100.3
	12	1050	0	0	0	0	0	63	353.8+100.0

Note: Naturally recruiting pike populations without (NR) and with (NRHF) addition of hatchery-reared pike fry and hatchery-reared fry only without natural recruitment of pike (HF). Each treatment was replicated in four ponds. Potential egg deposition was calculated based on an average fecundity of 27 eggs·(g female body mass)⁻¹ (Frost and Kipling 1967).

^aPike brood stock population to simulate spawning of self-sustaining pike populations.

^bTo simulate a natural pike population, we removed some pike from the NR and NRHF ponds and stocked them in the HF ponds; in addition, age-1 pike were stocked to generate a nature-orientated population structure.

^cStocked cyprinid biomass composed of two-thirds roach (*Rutilus rutilus*) and one-third common bream (*Abramis brama*); to compensate for some losses, we additionally stocked 100 kg·ha⁻¹ of cyprinids.

sex ratio of two males per female, similar to reports from the wild on spawning sites (Raaf 1988; Billard 1996). We used a narrow and similar size range of spawners to avoid size-related maternal effects on egg quality and early survival of larvae (Arlinghaus et al. 2010; Kotakorpi et al. 2013). Mean pike density (±SD) in the various ponds was 116 ± 14 pike·ha⁻¹ (range 104–147 pike·ha⁻¹). This numerical abundance represented a mean pike stock biomass ± SD of 157 ± 23 kg·ha⁻¹ (range 131–201 kg·ha⁻¹; Table 1). Such values are at the upper end of natural pike biomasses reported in the literature (Raaf 1988; Grimm 1989) and should safeguard sufficient egg deposition. Potential egg deposition in the ponds was approximated based on a mean fecundity of female pike of 27 eggs·(g female body mass)⁻¹ following Frost and Kipling (1967; Table 1). Assuming egg to fry survival of 3%–6% (Wright and Shoemith 1988), the estimated fry density in the naturally reproducing ponds was expected to range between 6 and 12 fry·m⁻².

Simultaneous to the release of wild spawners, the ponds were stocked with adult cyprinids of various species to provide food for the adult pike and to provide newly produced larval fish after reproduction as prey fish for age-0 pike. We released a total cyprinid biomass of 350 kg·ha⁻¹ into the ponds (Table 1), representing a common fish biomass of eutrophied water bodies (Grimm and Blackx 1990). The species mix was approximately two-thirds roach (*Rutilus rutilus*; TL range 10–25 cm), one-third common bream (*Abramis brama*; TL range 10–45 cm), and some sporadic rudd (*Scardinius erythrophthalmus*; Table 1).

After pike spawning was completed (documented by visual census and observation of spawning fish and fry in the ponds), a comparable adult pike density was established in each of the 12 ponds by reducing the number of adult pike in the eight ponds of the NR and NRHF treatments and adding at least four adult postspawned pike into the four ponds that were previously devoid of pike during spawning time (HF treatment). In addition, four to six age-1 pike were released into each of the ponds in early May to provide a more natural size structure. The final pike stock biomass ranged from 63 to 111 kg·ha⁻¹, which is typical for eutrophied natural ecosystems (Raaf 1988; Grimm 1989; Grimm and Blackx 1990). To compensate for early losses of prey fish by piscivorous birds (e.g., cormorant (*Phalacrocorax carbo*) and grey heron (*Ardea cinerea*)), we additionally stocked roach (100 kg·ha⁻¹) on 4 May 2012

into each of the ponds prior to the commencement of spawning by the cyprinid fishes.

Chlorophyll *a* and total phosphorus concentration were analyzed once a month between April and June 2012. The study ponds did not differ in chlorophyll *a* (mean ± SD, 38.8 ± 45.1 µg·L⁻¹; ANOVA: $F_{[2,33]} = 0.66, P = 0.55$), total phosphorous (mean ± SD, 187.5 ± 54.2 µg·L⁻¹; ANOVA: $F_{[2,33]} = 0.25, P = 0.78$), and Secchi depth (mean ± SD, 0.5 ± 0.2 m; ANOVA: $F_{[2,33]} = 0.47, P = 0.63$). Oxygen concentration was measured daily in March and April and later twice a week using a Horiba U-10 Multiparameter meter (Horiba Ltd., Japan) and was also not different among treatment ponds (mean ± SD, 9.5 ± 0.4 mg·L⁻¹; ANOVA: $F_{[2,33]} = 0.735, P = 0.51$) over the study period (Table 2). Studies by Skov et al. (2002, 2003b) and Skov and Koed (2004) demonstrated that pike are able to hunt well in turbid water, and we thus assumed that low visibility within the ponds did not constrain the development of juvenile pike. Water temperature was recorded in each pond using automated data loggers (HOBO Pendant, type 64K-UA-001-64, accuracy ±0.53 °C) that were programmed to measure the temperature once every hour. Mean water temperature ± SD during the study was 13.4 ± 4.3 °C, and mean minimum and maximum temperature ± SD over all ponds were 3.7 ± 1.0 and 22.7 ± 1.0 °C, respectively. There were no differences in mean water temperatures among the treatment groups (ANOVA: $F_{[2,57]} = 0.028, P = 0.97$). Using water temperature information, we calculated the growing degree-days (GDD; McMaster and Wilhelm 1997) after draining the ponds, with 5 °C as the base temperature (Casselman 1996; Table 2). Mean cumulative GDD between stocking of fry in April 2012 and draining of ponds in July 2012 was not different among treatment groups (Table 2; ANOVA: $F_{[2,9]} = 0.55, P = 0.60$). Mean ± SD treatment GDD ($N = 4$ per treatment) were 1031 ± 30 °C, 1030 ± 6 °C, and 1050 ± 40 °C for HF, NR, and NRHF ponds, respectively. Therefore, environmental conditions were essentially identical among ponds and treatments over the study period.

To produce hatchery-reared pike fry for HF and NRHF treatments, adult pike were caught between 18 and 23 March 2012 with trap nets from the same water system from which the wild spawners had been obtained. We used fish from the same genetic origin for both artificial reproduction and as natural spawners in the ponds to control for any stock-specific effects.

Table 2. Growing degree-days (GDD) and environmental conditions (total phosphorus concentration (TP), Secchi depth, chlorophyll *a* concentration, and oxygen concentration) in the experimental ponds ($N = 12$).

Treatment	Pond No.	GDD (days)	TP ($\mu\text{g}\cdot\text{L}^{-1}$)	Secchi depth (m)	Chlorophyll <i>a</i> concentration ($\mu\text{g}\cdot\text{L}^{-1}$)	Oxygen concentration ($\text{mg}\cdot\text{L}^{-1}$)
NR	2	1033	135 \pm 33	0.69 \pm 0.21	22.23 \pm 30.45	7.11 \pm 0.96
	4	1032	174 \pm 19	0.44 \pm 0.13	43.15 \pm 63.74	8.65 \pm 0.89
	8	1022	242 \pm 26	0.52 \pm 0.23	61.11 \pm 64.54	9.37 \pm 1.04
	10	1035	179 \pm 51	0.54 \pm 0.21	38.13 \pm 56.08	8.99 \pm 2.26
NRHF	5	1001	188 \pm 17	0.57 \pm 0.17	42.55 \pm 63.46	7.89 \pm 1.22
	7	1041	211 \pm 29	0.35 \pm 0.18	57.65 \pm 58.01	8.10 \pm 2.19
	9	1098	208 \pm 63	0.53 \pm 0.15	31.98 \pm 50.24	8.99 \pm 0.93
	11	1058	180 \pm 53	0.48 \pm 0.13	59.02 \pm 55.21	8.45 \pm 1.03
HF	1	1026	124 \pm 23	0.69 \pm 0.20	9.77 \pm 12.85	7.64 \pm 1.40
	3	1046	169 \pm 25	0.44 \pm 0.16	26.41 \pm 33.46	8.21 \pm 1.02
	6	991	259 \pm 112	0.63 \pm 0.21	37.22 \pm 43.90	7.61 \pm 1.06
	12	1061	181 \pm 14	0.52 \pm 0.17	37.28 \pm 56.91	8.05 \pm 0.96

Note: Data of environmental condition represent mean \pm SD values over the whole study period from 12 April to 22 July 2012. Treatment NR refers to naturally recruiting pike populations, NRHF is naturally recruiting pike populations with addition of hatchery-reared pike fry of the same genetic background, and HF is stocked hatchery-reared fry without natural recruitment of pike.

Artificial reproduction was conducted on 23 March 2012. Eggs from six female pike (TL range 466–759 mm) were mixed with milt stripped from 17 male pike (TL range 482–602 mm), before water was added for insemination using the dry method (Schäperclaus and von Lukowicz 1997). Fertilized eggs were reared in Zuger jars until hatching. Hatched yolk-sac larvae were transferred to incubators until the end of the yolk-sac absorption. Mean \pm SD water temperatures during incubation were 10.8 \pm 0.6 °C (range 8–13 °C). The hatchery was fed with water from an artificial channel that also fed the experimental ponds.

Marking and release of hatchery-reared fish

To distinguish between hatchery-reared and naturally recruited age-0 fish, we batch-marked hatchery-reared fry. The fluorescent dye Alizarin Red S was used to mass-mark free-swimming fry at the end of yolk-sac absorption, the day before they were released into the experimental ponds (13 April 2012). Fry were bathed for 14 h in an aerated solution of 100 $\text{mg}\cdot\text{L}^{-1}$ Alizarin Red S following Beckman and Schulz (1996). We estimated the potential marking-induced mortality of fry by observing the mortality of marked and unmarked fry for 48 and 96 h after marking, respectively, in replicated ($N = 4$) small net cages (200 mm in height \times 250 mm in length \times 200 mm in depth), each stocked with 100 fry. Nets were installed in an indoor tank in the hatchery. Mortality of fry was not significantly different between marked and unmarked fry either at 48 h (t test: $t_{[1,6]} = 0.375$, $P = 0.72$) or 96 h (t test: $t_{[1,6]} = 0.063$, $P = 0.95$) after stocking. Therefore, marking did not seem to affect the initial performance of the hatchery fish.

Marked pike fry were stocked on 14 April 2012 in ponds assigned to treatment HF and NRFH in a density of 6 fry $\cdot\text{m}^{-2}$ following typical fry stocking densities reported in the literature (Bry and Souchon 1982; Wright and Giles 1987; Bry et al. 1991; Skov et al. 2011). Water temperature was 10.5 °C in the hatchery and ranged between 9.8 and 11.4 °C in the ponds at stocking. Water temperature in the transport bags was allowed to adapt to the pond water temperature for about 30 min before fry were randomly distributed along the shoreline of the ponds. The release of hatchery-reared fry in the NRHF treatment in addition to natural recruitment created an increase in fry density from theoretically 6–12 to 12–18 fry $\cdot\text{m}^{-2}$, more or less doubling the fry densities in each of the four ponds. Thus, theoretical pike fry densities after stocking hatchery-reared fry were 6 fry $\cdot\text{m}^{-2}$ in the HF ponds, 6–12 fry $\cdot\text{m}^{-2}$ in the NR ponds, and 12–18 fry $\cdot\text{m}^{-2}$ in the NRHF ponds.

We also estimated the initial mortality 24 h after stocking into the ponds. Three net cages (500 mm in height \times 600 mm in length \times 300 mm in depth) were used, each containing 120 marked pike fry. Nets were installed in three different experimental

ponds. Mortality 24 h after fry release was low (4.3% \pm 0.9%, mean \pm SE).

Sampling of pike fry

At the day of stocking (14 April 2012), all ponds stocked with spawners (NR and NRHF) were checked for naturally emerged pike fry using a fine-meshed dip net (0.5 mm mesh size). From standardized net hauls along the structured margins of the ponds, we calculated catch per unit effort (CPUE) (pike fry $\cdot(\text{net haul})^{-1}$) to compare the relative abundance of naturally recruited pike fry between ponds. All fry were measured to the nearest 0.1 mm using an electronic caliper. To test for size differences between naturally recruited (treatment NR and NRHF) and the stocking material, we compared TL of naturally recruited fry with a sample of hatchery-reared pike ($N = 100$) at the day of fry release.

The first sampling after release of hatchery-reared fry was conducted on 3 and 4 May 2012, using a battery-powered DC backpack electronic fishing device (Type EFGI 650, Bretschneider Spezialelektronik, Chemnitz, Germany) equipped with a 20 cm diameter anode. Each pond was sampled with 50 randomly assigned points while wading through the pond to estimate the density of pike fry (fry $\cdot\text{dip}^{-1}$). All sampled individuals were measured to the nearest 0.1 mm. We stored 40 randomly selected fry from each pond in ethanol (70%) for later determination of origin (hatchery-reared or naturally recruited) and analysis of stomach contents.

The second sampling was conducted on 7 June 2012 following the protocol described above. Unfortunately, these data could not be used for further analysis because sample sizes ranged between zero and seven fish per pond. Small sample size resulted from low catchability because of dense vegetation in the ponds.

All 12 ponds were terminally drained between 16 and 22 July 2012. To ensure that no pike were left in the ponds after draining, the ponds were reflooded and drained immediately a second time (Bry and Gillet 1980). All drained ponds were also visually investigated for remaining and stranded fish. All age-0 pike were counted. We randomly collected 100 age-0 pike from each pond to document body mass (Sartorius TE2101 with an accuracy of ± 0.1 g) and TL to the nearest millimetre. These fish were stored in ethanol (70%) for later analysis of stomach contents and assignment to origin based on the Alizarin Red S mark in the otoliths. All other pike were measured to the nearest millimetre TL to estimate the total biomass in each pond using length–mass relationships. Survival of stocked fry was estimated from the relative proportion of stocked pike in the subsample, based on the stocking density of 6 fry $\cdot\text{m}^{-2}$. Furthermore, the relative condition (Le Cren 1951) was estimated as $K_r = (W/W') \times 100$, where W is the individual fish mass and W' is the predicted standard length-specific mass estimated

based on a \log_{10} -transformed length–mass regression estimated from all naturally recruited pike.

In the laboratory, the lapillar otoliths were removed from the preserved heads to assess the origin of sampled pike. Otoliths were examined for the presence of Alizarin Red S marks using a fluorescence microscope (Olympus Vanox AHB T3; Skov et al. 2001). To control for the consistency of the marks, we determined the presence of Alizarin Red S marks of pike from the HF treatments in May ($N = 20$) and July ($N = 20$). In these samples, we found a mark present in 100% of all examined individuals and thus assumed full recovery of marked individuals in our samples.

Stomach analysis

All preserved stomachs were opened and all items were removed, identified to the lowest possible taxon, measured, and counted. The index of stomach fullness (K_f) was calculated as the ratio of the dry mass (μg) of stomach contents to the wet mass (mg) of fish (Hyslop 1980; Fox 1989). Dry mass of the stomach content was calculated based on TL information of prey items using length–dry mass regressions (see Lübke (2013) for a complete list of regression equations and references). Further, the index of relative importance (IRI) of prey species was calculated for each treatment and origin as follows: $\text{IRI} = (\%N_i + \%W_i) \times \%O_i$ (Chipps and Garvey 2007), where N_i was the percentage by number (numerical portion of i species in whole stomach content), W_i was the percentage by mass (portion of mass of i species in whole stomach content), and O_i was the frequency of prey occurrence (portion of stomachs containing prey i species) (Bowen 1996).

Statistical analysis

Comparisons of age-0 pike densities in May and July and age-0 biomass at draining between treatment groups were assessed by analyses of variances (one-way ANOVA). Multiple comparisons were conducted using Tukey's HSD post hoc test. Test for homogeneity of variances were conducted using Levene's tests (Levene 1960). Linear mixed models (LMM) were used to analyze differences in TL, number of ingested prey species, relative condition, and index of stomach fullness among the treatments. Linear mixed models allowed modeling the hierarchical nested structure of individual data from different ponds, using pond as a random factor. The fixed factors in the models were the origin of pike (hatchery-reared versus naturally recruited), presence or absence of a competitive situation, and the interaction term between origin and competition. Statistical analyses were performed using PASW (Predictive Analysis SoftWare) version 17 at a type 1 error probability of $\alpha = 0.05$.

Binary logistic regression was used to analyze the probability of occurrence of the different origins of pike fry at two distinct sampling dates (to assess differential survival over time), the probability of empty stomachs, and the probability of cannibalism as a function of pike origin, competition, and size. The pond was included as a random factor to represent the nested data structure. To run binary logistic regressions, the package lme4 in the software R (R Development Core Team 2013) version 3.0.1 was used.

Analysis of similarity (ANOSIM, $N = 999$ permutations; Clarke 1993) was used to test for significant differences in diet composition related to origin and competitive situation of pike. For R values between 0 and 1, $R > 0.75$ indicated well separated groups, $R > 0.5$ indicated overlapping but clearly different groups, and $R < 0.25$ indicated groups that were barely separable (Clarke and Gorley 2001). Subsequent similarity percentage analysis (SIMPER; Clarke 1993) identified species that contributed primarily to the differences in diet composition among origins in the competitive situation in case of significant ANOSIM test statistics. ANOSIM and SIMPER were calculated in PAST (paleontological statistics) version 2.17 (Hammer et al. 2012).

Results

Pond conditions at fry release

We detected naturally recruited pike at the day of release of hatchery-reared fry in all NRHF and NR ponds. There were no significant differences in initial mean densities of naturally recruited pike fry between the NR (mean \pm SE, 1.4 ± 0.7 fry·(dip net haul) $^{-1}$) and NRHF ponds (0.8 ± 0.3 fry·(dip net haul) $^{-1}$; t test: $t_{[1,6]} = -0.772$, $P = 0.469$). Also the mean TL \pm SE of natural recruits (NR treatment: 12.7 ± 0.1 mm; and NRHF treatment: 12.6 ± 0.1 mm) and hatchery-reared fry (12.6 ± 0.1 mm) were not significantly different at the moment of release of hatchery-reared fry into experimental ponds (LMM: $F_{[2,337]} = 0.22$, $P = 0.81$).

Early additive effects

Three weeks after stocking (May), mean pike densities achieved from stock enhancement in ponds lacking natural reproduction (HF; mean \pm SE, 0.55 ± 0.09 fry·dip $^{-1}$) was not significantly different from ponds with natural recruitment (NR; 0.67 ± 0.26 fry·dip $^{-1}$) (ANOVA: $F_{[2,9]} = 4.91$, $P = 0.036$; Tukey's HSD post hoc test: $P = 0.91$). Mean pike density was, however, significantly higher in the NRHF ponds (1.42 ± 0.25 fry·dip $^{-1}$) compared with HF ponds ($P = 0.043$), indicating an initial additive effect of stocking relative to ponds that lacked natural reproduction. Mean pike fry densities were doubled in NRHF ponds compared with NR ponds, but these differences were only significant at $P < 0.1$ ($P = 0.080$; Fig. 1). Therefore, despite clear trends, the statistical comparison revealed the absence of early additive effects of stocking into self-sustaining stocks when judged at the $P < 0.05$ level. Over all four ponds with natural recruitment and stocking combined, half (mean \pm SD, $49.7\% \pm 12.0\%$) of all fish were natural recruits in May (Fig. 2).

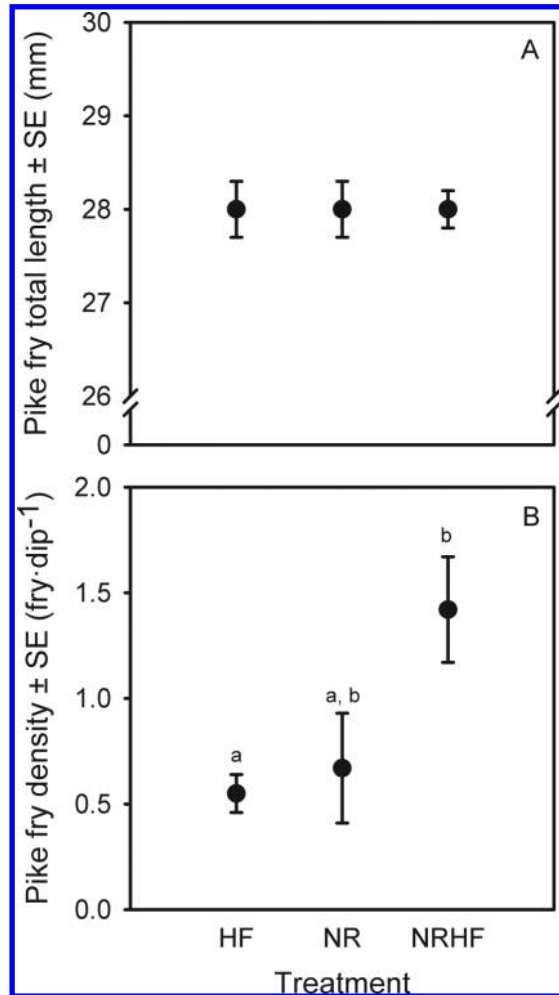
In May, TL of pike was 28 ± 0.3 mm (mean \pm SE) in HF ponds, 28 ± 0.3 mm in NR ponds, and 29 ± 0.4 mm of naturally emerged and 29 ± 0.3 mm of stocked pike in the NRHF ponds (Fig. 1). Length of pike juveniles was unrelated to origin (hatchery-reared versus naturally recruited; LMM: $F_{[1,411]} = 0.252$, $P = 0.62$), competitive situation (mixed versus not mixed; LMM: $F_{[1,411]} = 2.01$, $P = 0.16$), or their interaction term (origin \times competitive situation; LMM: $F_{[1,411]} = 0.66$, $P = 0.42$), indicating similar growth performance of stocked and wild recruits until May.

Stomach analysis in May revealed no empty stomachs. Moreover, we found no fish prey in the stomachs of the fry, which also suggested the absence of cannibalism in May. One-way ANOSIM suggested a significantly different yet somewhat overlapping composition of prey species between stocked and naturally recruited fry in the mixed ponds ($R = 0.502$, $P = 0.0001$). Copepods, cladocerans, and annelids accounted for 72.7% of the observed dissimilarity in the SIMPER analysis. Out of these prey items, copepods and cladocerans were the most important prey types according to IRI. Copepods represented 46.5% and 36.8%, and cladocerans 29.7% and 34.9%, of the prey items found in the stomachs of natural recruits and stocked fry, respectively. The number of prey species ingested by the fry of the two origins in the competitive situation was not significantly different (LMM: $F_{[1,166.5]} = 0.166$, $P = 0.68$; seven prey species in stocked and five prey species in naturally recruited fry). In the mixed ponds, mean dry mass of stomach contents was 0.402 ± 0.292 mg for naturally recruited and 0.310 ± 0.251 mg for stocked fry, but these differences were not significant (LMM: $F_{[1,167.9]} = 0.606$, $P = 0.44$).

Late additive effects

After draining the ponds in July 2012, numerical age-0 pike density (mean \pm SE) was highest in the HF ponds (5109 ± 1371 fry·ha $^{-1}$). The corresponding numerical densities were 3106 ± 555 fry·ha $^{-1}$ in the NR ponds and 2339 ± 362 fry·ha $^{-1}$ in the NRHF ponds. Differences in age-0 pike densities were not significant among treatments, although the P value was close to significant (ANOVA: $F_{[2,9]} = 2.64$, $P = 0.12$; Fig. 3), while biomass differences among treatments were

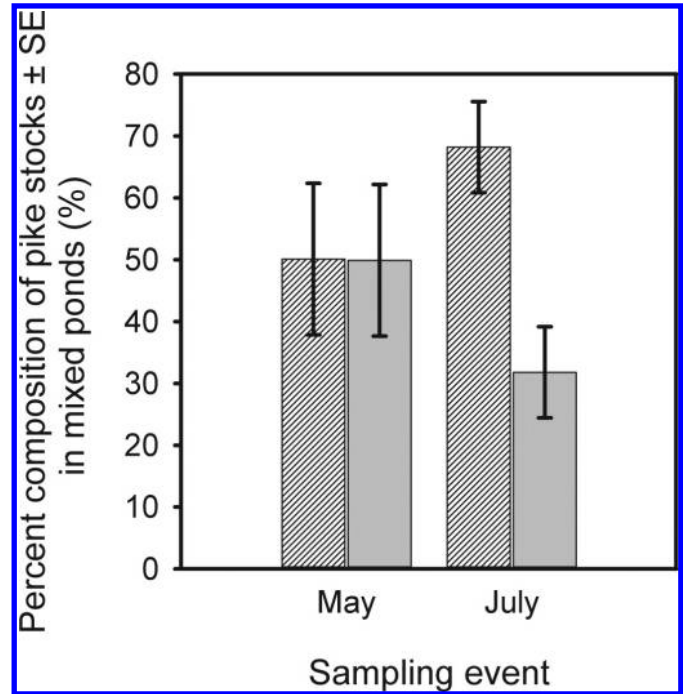
Fig. 1. Mean total length (mm) (A) and mean pike fry density (fry·(dip electrofishing unit)⁻¹) (B) in May 2012, 3 weeks after stocking of hatchery-reared pike fry. Treatment groups were naturally recruiting pike populations without addition of hatchery-reared pike fry (NR), naturally recruiting pike populations with addition of hatchery-reared pike fry (NRHF), and hatchery-reared fry only (HF). Differing letters symbolize significant differences at $\alpha \leq 0.05$. $N = 4$ ponds per treatment.



significant (ANOVA: $F_{[2,9]} = 4.57$, $P = 0.043$; Fig. 3). Young-of-the-year pike biomass was significantly higher in the HF ponds (mean \pm SE, 35.1 ± 4.8 kg·ha⁻¹) compared with NRHF ponds (21.9 ± 1.1 kg·ha⁻¹; Tukey's HSD post hoc test: $P = 0.046$). Mean biomass density in the NR ponds was 24.5 ± 2.8 kg·ha⁻¹, and there were no significant differences in biomass in comparisons with either the HF ponds ($P = 0.11$) or the NRHF ponds ($P = 0.85$). The lack of significant differences in the densities and biomasses of age-0 pike between NR and NRHF treatments indicated the absence of additive effects caused by pike fry stocking.

Survival of hatchery-reared pike released into ponds without natural recruitment (HF; mean \pm SE, $8.1\% \pm 4.6\%$) was significantly higher compared with the survival in the mixed ponds (NRHF; mean \pm SE, $1.3\% \pm 0.8\%$; t test: $t_{[1,6]} = 3.118$, $P = 0.021$). Estimated theoretical mean survival \pm SE of naturally recruited fry (assuming 6–12 fry·m⁻² based on potential egg deposition) was in a range of 1.3%–2.6% and 2.6%–5.2% in the NRHF and NR treatments, respectively. These data indicated lower survival of naturally recruited pike in the mixed ponds compared with survival in the natural recruitment treatment (NR). When comparing the survival of stocked and wild pike in mixed ponds, the probability to

Fig. 2. Percent composition of pike stocks in May and July 2012. Bars with hatch lines represent naturally emerged fry, and gray bars represent fry from hatchery origin.



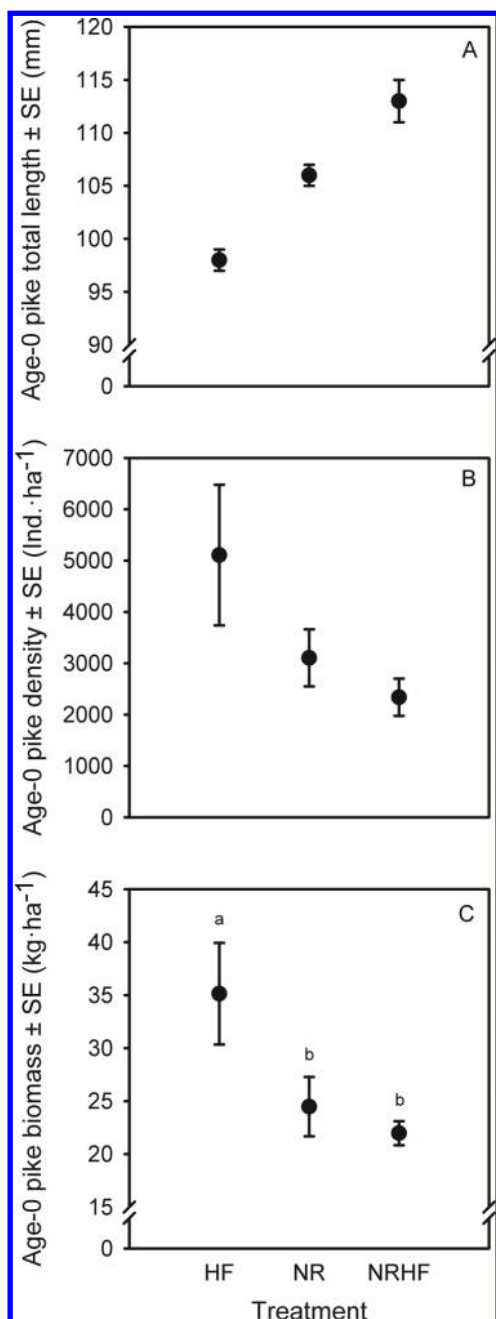
observe a naturally recruited pike in the mixed ponds was significantly greater in July compared with May (logistic regression: $z = -4.288$, $P < 0.001$; Fig. 2), suggesting greater mortality of stocked pike. In total, 68.6% ($N = 4$ ponds, range 48%–81%) of the pike were naturally recruited at the time of pond draining.

The mean TL of age-0 pike at draining was not significantly different among treatments (LMM: $F_{[2,10,9]} = 0.64$, $P = 0.54$; Fig. 3). The mean TL \pm SE was 97.9 ± 0.7 mm for the HF, 106.1 ± 0.8 mm for the NR, and 112.3 ± 1.6 mm for all age-0 pike in the NRHF treatments. However, hatchery-reared pike grew less in the competitive situation (NRHF) compared with naturally recruited age-0 pike, as indicated by a significant origin \times competitive situation interaction term (Table 3; Fig. 4). In fact, the mean TL \pm SE of hatchery-reared and naturally recruited age-0 pike sampled from NRHF ponds was 90.9 ± 1.9 and 121.3 ± 2.0 mm, respectively. In addition to origin, the LMM revealed a marginally significant influence of age-0 density on TL at draining ($P = 0.09$), but no effects of environmental variables such as temperature variation among ponds (Table 3).

Relative condition \pm SE of age-0 pike was 1.01 ± 0.006 for the HF, 1.03 ± 0.005 for the NR treatment, and 1.00 ± 0.007 and 1.00 ± 0.006 of hatchery-reared and naturally recruited age-0 pike in the NRHF treatment, respectively. LMM analysis revealed that the relative condition was not significantly affected by the origin of pike (hatchery-reared versus naturally recruited; $F_{[1,1182]} = 1.272$, $P = 0.51$), competitive situation (mixed versus not mixed; $F_{[1,1182]} = 0.408$, $P = 0.634$), or their interaction term (origin \times competitive situation; $F_{[1,1182]} = 0.091$, $P = 0.95$).

At the time of draining the ponds in July, the stomach content in all pike groups was dominated by dipterans (IRI range 17%–34%; Fig. A1). The stomachs also contained a considerable proportion of fish (IRI of fish up to 24%), especially pike. Age-0 cyprinids were observed in all experimental ponds, indicating a successful reproduction of cyprinids. Unfortunately, a quantitative assessment was not possible because of technical issues. However, age-0 cyprinids represented only a minor proportion of fish in the age-0 pike stomachs (IRI ranging from 0.4% to 2.4%). Despite the

Fig. 3. Mean \pm SE total length (A) (LMM: $F = 0.64$, $P = 0.54$), density (pike·ha⁻¹) (B) (ANOVA: $F = 2.64$, $P = 0.12$), and biomass (kg·ha⁻¹) (C) (Tukey's HSD post hoc test: $P = 0.046$) of age-0 pike in July at draining in three treatment groups ($N = 4$ per treatment group). Treatment groups were naturally recruiting pike populations without addition of hatchery-reared pike fry (NR), naturally recruiting pike populations with addition of hatchery-reared pike fry (NRHF), and hatchery-reared fry only (HF). Differing letters symbolize significant differences at $\alpha \leq 0.05$.



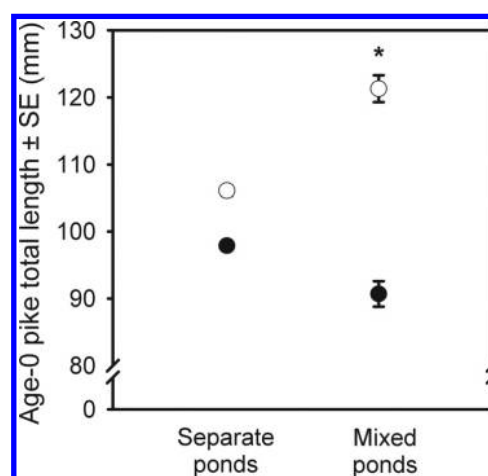
relatively high importance of cannibalism among the age-0 pike, only 5.9% of the sampled pike were assigned as cannibals. The mean \pm SD size of the prey fish was $53.3\% \pm 8.9\%$ and reached a maximum of 86.3% of the predator TL. However, logistic regression analysis revealed no origin-dependent difference in the occurrence of cannibalism (hatchery-reared versus naturally recruited; $z = 0.340$, $P = 0.73$) and no effects of competitive situation (mixed versus not mixed; $z = -1.209$, $P = 0.23$) or their inter-

Table 3. Linear mixed model to predict the effects of origin (naturally recruited versus hatchery-reared pike), competition (competitive situation between naturally recruited and hatchery-reared pike), their interaction, density, growing degree-days (GDD), and environmental factors (oxygen concentration, Secchi depth, and total phosphorus) on growth of pike fry until draining of ponds 94–99 days after stocking of hatchery-reared fry.

Factor	df	F	P
Intercept	1	0.010	0.927
Origin (naturally recruited versus hatchery-reared)	1	7.244	0.048
Competitive situation (yes versus no)	1	3.239	0.147
Origin \times competitive situation	1	10.445	0.026 ^a
Oxygen concentration	1	0.945	0.388
Secchi depth	1	0.173	0.699
GDD	1	0.987	0.378
Fry density (at draining)	1	5.168	0.087
Total phosphorus	1	2.360	0.203

^aP value significant at $\alpha \leq 0.05$.

Fig. 4. Mean \pm SE total length (mm) of naturally recruited (open circles) and hatchery-reared (solid circles) age-0 pike from ponds with naturally recruited pike without additional adding of hatchery-reared pike fry (separate ponds) and in ponds with hatchery-reared fry only (separate ponds) and of naturally recruited and hatchery-reared age-0 pike in the competitive situation from mixed ponds at draining in July. Significant difference ($P \leq 0.05$) is indicated by an asterisk (*).



action term (origin \times competitive situation; $z = 0.791$, $P = 0.43$) on cannibalism. By contrast, size (TL) at draining had a significant effect on cannibalism, with larger fish being more likely to be cannibalistic (logistic regression: $z = 10.42$, $\beta = 1.066$, $P < 0.001$). Overall, minor differences in diet composition existed relative to origin of pike (two-way ANOSIM: $R = 0.029$, $P = 0.005$) and the presence of competitive situation (two-way ANOSIM: $R = 0.073$, $P < 0.001$). Similarly, the frequency of empty stomachs of age-0 pike was not related to the origin of pike ($z = 1.047$, $P = 0.29$), competitive situation (mixed versus not mixed; $z = 0.653$, $P = 0.51$), or their interaction term (origin \times competitive situation; $z = -0.678$, $P = 0.49$). Instead, TL was most strongly related to the probability that a pike had eaten a prey item at the time of draining the ponds (logistic regression: $z = -5.510$, $P < 0.001$); the larger the pike the more likely an empty stomach was observed ($\beta = 0.986$).

The number of ingested prey item groups was not significantly related to origin of pike (hatchery-reared versus naturally recruited; LMM: $F_{[1,12,2]} = 0.29$, $P = 0.59$), competitive situation (mixed versus not mixed; LMM: $F_{[1,9,0]} = 1.054$, $P = 0.33$), or an interaction between origin and competitive situation (LMM: $F_{[1,12,1]} = 0.005$,

$P = 0.95$), but TL of pike was significant at $P < 0.1$ (LMM: $F_{[1,1176,4]} = 3.32$, $P = 0.069$). The number of ingested prey item groups tended to be lower among the larger age-0 pike ($\beta = -0.0023$). Further, the index of stomach fullness (K_f) was not significantly related to origin of pike (hatchery-reared versus naturally recruited; LMM: $F_{[1,29,4]} = 1.271$, $P = 0.27$), competitive situation (mixed versus not mixed; LMM: $F_{[1,9,7]} = 0.408$, $P = 0.54$), or their interaction term (origin \times competitive situation; LMM: $F_{[1,29,4]} = 0.091$, $P = 0.77$). Thus, the feeding habits of surviving pike were not found to be strongly affected by hatchery origin.

Discussion

We documented that stocking pike fry in the absence of natural recruitment resulted in a year class that was comparable to the year class emerging from natural recruitment in a similar pond environment. Conversely, we also demonstrated the inefficiency of stock enhancement if naturally recruited fry are already present. The data were consistent with strong density-dependent juvenile mortality regulation. Our results also supported the hypothesis that hatchery-reared pike suffered from lower growth and higher mortality compared with naturally recruited pike when forced into direct competition, indicating the competitive disadvantage of hatchery-origin fish of similar genetic origin to wild conspecifics. However, given the similar pike densities in the three treatments, we found stocking into self-sustaining stocks resulted in a replacement of about one-third (31.4%) of the natural recruits by hatchery fish. Our results cumulatively suggest that stock enhancement with young life stages in self-sustaining fish populations, with underlying strong density-dependent population regulation, is unlikely to generate additive effects. The outcomes of stock enhancement with young life stages that are forced through density- and size-dependent mortality thus seem to be strongly moderated by the presence of sufficient natural recruitment.

Observational studies of pike stocking in the wild align with the experimental evidence reported here. In particular, available data support the view that the release of fry leads to an increased abundance of age-0 pike only when natural recruitment is absent or severely limited (Vuorinen et al. 1998; Sutela et al. 2004; Jansen et al. 2013). A compensatory effect of stock enhancement when natural reproduction is lacking or low was also reported for other cannibalistic freshwater and marine species (Li et al. 1996; Brennan et al. 2008; Denson et al. 2012) and is also a common result of modeling studies (e.g., Lorenzen 2005; Rogers et al. 2010). Our empirical results fully support these conclusions.

In the very early phase of the experiment (May), the overall density of pike fry in the ponds was enhanced by the release of hatchery-reared fry, suggesting some initial additive effects of stocking. These were, however, quickly washed out over the course of the experiment. The ontogenetic shift from zooplanktivory to piscivory in pike commonly occurs at TL values of 50 to 100 mm within the first months of life (Fago 1977; Wright and Giles 1987; Skov et al. 2003b). The lack of cannibalism in May in the pike fry (TL \sim 30 mm) was confirmed by the stomach content analysis, and hence the ability of the pike fry to self-regulate density appeared to be limited in this period. Although Bry et al. (1992) reported that survival of pike fry stocked into ponds was density-dependent during the first 12 days after release even in the absence of cannibalism, our study indicated that stocking can be additive when pike fry are too small to cannibalize conspecifics. Contrary to our findings, Skov et al. (2003b) showed that cannibalism occurred in sizes comparable to the age-0 pike in our study in May. The availability of abundant alternative prey, such as zooplankton, can, however, reduce the occurrence of cannibalism in age-0 pike, and sufficient food can also remove density-dependent growth and substantially reduce density-dependent mortality in fish population regulation

(Skov et al. 2003b; Hazlerigg et al. 2012). We assumed that in our study food availability was sufficient owing to the fact that we found no empty stomachs in the sampled fry in May 2012 and because of the polytrophic states of the ponds. In line with the pond experiments by Wright and Giles (1987), our data therefore suggest the possibility of density-independent survival of pike fry under conditions when food availability is not a limiting factor. After juvenile pike have undergone the ontogenetic shift to piscivory (Hunt and Carbine 1951; McCarraher 1957; Skov et al. 2003a), however, strong population regulation through intracohort cannibalism regularly occurs in pike (Grimm 1983; Bry et al. 1992; Skov and Koed 2004). Not surprisingly, pike densities evened out and approached each pond's carrying capacity over the summer period, ultimately resulting in similar fry densities in the three treatments in July 2012. In this period, we also documented cannibalism as an important food source in selected pike individuals. Previous studies on pike reported intraspecific predation as an important cause of density-dependent mortality regulation in juvenile pike (Kipling and Frost 1970; Wright and Giles 1987; Skov et al. 2003b), and we suspect cannibalism was the major driver of population regulation in our study as well.

Strong density-dependent population regulation, which likely precluded additive effects of stocking fry or juveniles in our study, seems to be a general pattern in many stock-enhanced fish populations (Lorenzen 2005). The nonsignificant differences in the age-0 pike density in early summer among treatments with and without fry stocking on top of natural recruitment provides compelling evidence of rapid intracohort population regulation towards pond-specific carrying capacities. This is particularly noteworthy given that the pike fry densities were initially higher in the NRHF treatments. However, the equalization of densities across treatments at the end of the experiment indicated elevated juvenile mortality in the stock-enhanced pond as a regulatory response to the artificially elevated density. Evidence for the strong density-dependent population regulation was thus indicated by the lack of additive stocking effects as well as by the significantly lower survival of natural recruits in the enhanced treatment (NRHF) compared with the nonstocked treatment (NR). In line with our data, lack of stocking success in reproducing populations was reported in diverse piscivorous species (Li et al. 1996; Margenau 1999; Young 2013). The specific bottlenecks that have to be surpassed by the stock involve species- and ecosystem-specific habitat constraints, food limitation, or predation (Fielder 1992; Skov et al. 2003b; Sutela et al. 2004); elevated juvenile mortality in response to stocking-based elevation of densities seems to be widespread. Density regulation is the predominant force during the larval and juvenile life stages in fishes until recruitment, where the density dependence switches from mainly mortality regulation to predominantly growth regulation (Lorenzen 2005). Hence, additive effects of stocking in self-recruiting stocks are most likely to be achieved by stocking recruited fishes rather than fry or juveniles (Lorenzen 2005).

The lower growth of hatchery-reared pike in competition with naturally recruited pike was likely a strong contributor to the lack of additive effects of stocking. Size-dependent cannibalism by larger wild recruits on smaller stocked fish also may explain the decreasing proportion of hatchery-reared pike over time in mixed ponds. However, at time of draining we did not observe any origin-dependent cannibalism, and hence other forms of size-dependent mortality may have been involved. For example, it is possible that hatchery-reared juveniles grew less because of social stress caused by competition with wild recruits (Edeline et al. 2010), potentially leading to increased movement and corresponding energy loss to reduce the risk of cannibalism by avoiding conspecifics (Nilsson 2006; Skov et al. 2011). Skov and Koed (2004) found that the larger juvenile pike are usually found in optimal habitats in vegetated areas, while smaller individuals are restricted to suboptimal habitats in open water with higher

risk of predation; therefore, it is possible that the competitively inferior stocked pike in mixed ponds were likely suffering elevated mortality by predators other than pike (e.g., by piscivorous insects). One possible reason why we found no origin-dependent cannibalism in our study might be that the age-0 pike cohorts were already regulated to carrying capacity when we drained the ponds.

Although feeding patterns of hatchery and wild fish were generally found to be similar, some difference in prey species use existed among hatchery-reared and naturally recruited juveniles. More pronounced differences in feeding and nutrition were reported by Skov et al. (2011) in a case study from a Danish natural lake where the frequency of occurrence of prey items differed strongly among wild and stocked juvenile pike. Possibly, the abundance of prey in the study ponds prevented feeding differences between stocked and wild fish to become pronounced in contrast with conditions in the wild. Similar to our study, Skov et al. (2011) also reported a decline in the proportion of released hatchery-reared pike fry over the season in a natural lake, indicating low fitness (i.e., lower survival) of stocked fish in the wild. However, in their study the stocked pike originated from a geographically distant lake, so a mismatch of genetically based local adaptation with conditions in the target lake may also have contributed to reduced fitness (Kawecki and Ebert 2004). In the present study, we controlled for genetic origin and assured that spawners released into the ponds and spawners stripped for artificial reproduction were of the same population origin. We can also exclude pond-specific temperature and productivity differences as well as elevated poststocking or marking mortality for having impacted the study results.

Which factors can be put forward as explaining the reduced growth of released fish compared with wild fish? One possible factor in addition to the stress-induced growth depression already mentioned includes carry-over effects resulting from rearing in a hatchery environment (Araki et al. 2007; Brockmark and Johnsson 2010), for example, impaired performance with respect to cognitive ability (Salvanes et al. 2013), feeding, food choice, and antipredation behavior (Hansen 2002; Ruzzante et al. 2004; Araki et al. 2009). Further, high densities in the artificial environment (in our study, Zuger jars and incubators) has been found to reduce growth and post-stocking survival in freshwater salmonids (Brockmark and Johnsson 2010; Hyvärinen and Rodewald 2013), most likely because essential life skills were not properly developed (Brockmark et al. 2010). We suspect similar mechanisms were at play in the present study.

Other forms of genetic or epigenetic impacts, beyond local adaptation, might still have been present in our study. In particular, the artificial reproduction circumvented sexual selection processes. Unconstrained mate choice determines offspring quality and survival in fishes (e.g., Barber et al. 2001; Wedekind et al. 2001; Rudolfson et al. 2005), and human-mediated disruption of mate choice in hatcheries has been demonstrated to reduce fitness of coho salmon (*Oncorhynchus kisutch*) when released into the wild (Thériault et al. 2011). Moreover, all fish in hatcheries are exposed to relaxed selection pressures, and hence many individuals hatch and survive that would otherwise die in the wild. Finally, an emerging literature on epigenetic effects suggests that early life environments may substantially alter the transcriptome and lead to protein expression that is adaptive in artificial environments (reviewed in Li and Leatherland 2013), but likely maladaptive in the wild. Therefore, although we can exclude population-specific genetic effects, a range of genetic impacts caused by artificial breeding and relaxed natural selection might still have been involved, reducing the fitness of the stocked fish when forced into competition with wild conspecifics. We attempted to exclude a set of detrimental factors that likely could bias the key results we presented (i.e., size-dependent maternal and genetic effects, marking and immediate stocking mortality, and size differences

between hatchery-reared and wild pike fry at stocking). Thus, the relaxation of natural selection pressures during the hatchery phase, the carry-over of hatchery effects into the wild, and the reduced competitive ability of hatchery fish when forced into competition with wild fish appear to be the most likely explanations for the lower survival and growth observed in hatchery-reared fish as compared with wild fish in our study.

We found stocking pike fry to be successful when natural recruitment is lacking. In contrast, when substantial natural recruitment is present, any additive effects of stocking pike fry are unlikely. Despite the lack of additive effects, important genetic risks of stock enhancement remain, namely introducing maladapted genotypes through replacement effects of natural recruits. Depending on the origin of the stocking material, stock enhancement will thus result in the establishment of some stocked individuals, which can then interbreed with wild conspecifics and lead to hybridization and loss of genetic diversity through genetic swamping (Laikre et al. 2010). Against this background, stocking pike fry into water bodies with natural reproduction should be discontinued for both economic and biodiversity conservation reasons. Stocking should only be continued in water bodies that clearly show signs of insufficient natural recruitment over prolonged periods of time. Further research is needed to understand the stock enhancing effect of older life stages where density-dependent mortality may be less expressed than in pike fry. It is also important to study whether additive effects of stock enhancement are possible in ecosystems with limited recruitment, because our study mimicked high natural reproduction based on an abundant spawning stock. The current study underscores the implication to be careful with pike fry stocking because it promises little to no fisheries benefits, while carrying substantial genetic risks.

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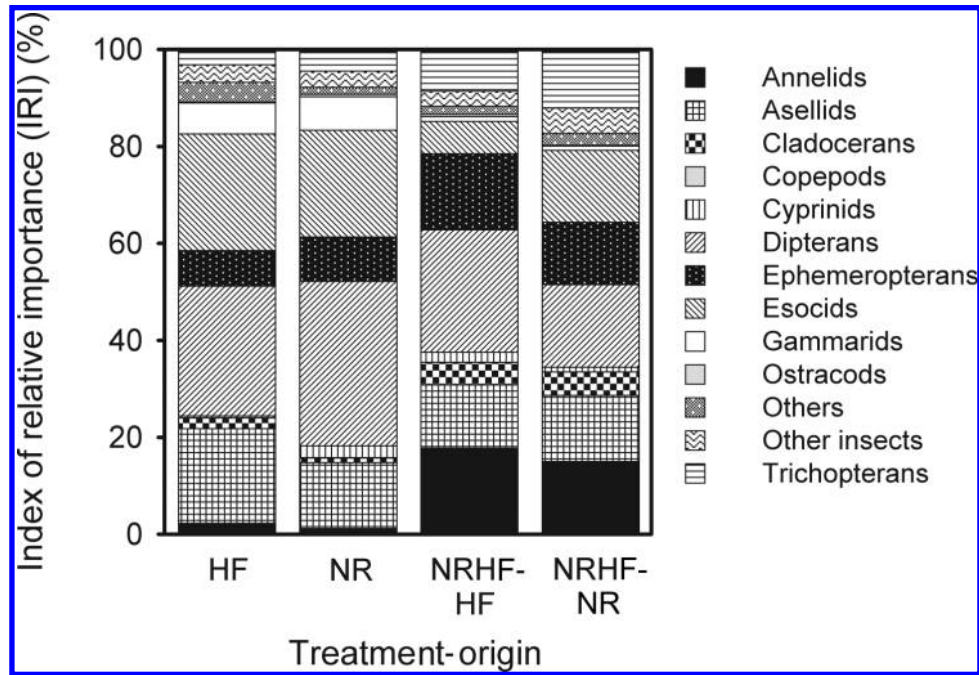
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Appendix A

Appendix Fig. A1 appears on the following page.

Fig. A1. Index of relative importance of different prey organisms in the diet of age-0 pike in the three treatment groups (HF, stocked hatchery fry; NR, naturally recruited fry; and NRHF mixed pond consisting of stocked (NRHF-HF) and naturally recruited fry (NRHF-NR)) at pond draining in July 2012.



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