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Christian Skov^a, Anders Koed^a, Lars Baastrup-Spohr^b & Robert Arlinghaus^{c d}

^a National Institute of Aquatic Resources, Technical University of Denmark, Vejløvej 39, 8600, Silkeborg, Denmark

^b Freshwater Biological Section, University of Copenhagen, Helsingørsgade 51, 3400, Hillerød, Denmark

^c Department of Biology and Ecology of Fishes, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587, Berlin, Germany

^d Inland Fisheries Laboratory, Department of Crop and Animal Sciences, Faculty of Agriculture and Horticulture, Humboldt University of Berlin, Philippsstrasse 13, Haus 7, 10155, Berlin, Germany

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ARTICLE

Dispersal, Growth, and Diet of Stocked and Wild Northern Pike Fry in a Shallow Natural Lake, with Implications for the Management of Stocking Programs

Christian Skov* and Anders Koed

National Institute of Aquatic Resources, Technical University of Denmark, Vejløvej 39,
8600 Silkeborg, Denmark

Lars Baastrup-Spøhr

Freshwater Biological Section, University of Copenhagen, Helsingørsgade 51, 3400 Hillerød, Denmark

Robert Arlinghaus

Department of Biology and Ecology of Fishes,
Leibniz Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310,
12587 Berlin, Germany; and Inland Fisheries Laboratory, Department of Crop and Animal Sciences,
Faculty of Agriculture and Horticulture, Humboldt University of Berlin, Philippstrasse 13, Haus 7,
10155 Berlin, Germany

Abstract

Increasing evidence suggests that stocking northern pike *Esox lucius* has had limited success, especially when age-0 fish are stocked into water bodies where the recruitment of northern pike already occurs. To better understand the ecology of wild and stocked fry, we investigated the dispersal, growth, and food composition of advanced pike fry (~30 mm) stocked at a high density at a common release site in a shallow natural lake that contained wild young-of-the-year (age-0) pike. The stocked pike fry colonized the entire lake shoreline within just a few days. Dispersal was inversely related to size at stocking, suggesting that smaller fish were displaced by competitively superior larger individuals. While the stocked pike were initially larger than the wild age-0 pike, suboptimal growth was evident among the stocked pike and they were smaller than the wild ones at the end of the growing season. Stomach analyses revealed that the stocked pike ingested less diverse prey items and had higher fractions of empty stomachs throughout the study period. Overall, the fraction of stocked pike in samples rapidly declined over the season, which may have been caused by differential survival or immigration into or emigration out of the study system. Our study adds to the existing literature suggesting that the stocking of age-0 northern pike into waters with naturally reproducing pike populations will result in limited success. We propose two potentially complementary explanations for the apparent low fitness of stocked individuals in competition with wild conspecifics: (1) genetic-based local maladaptation among the stocked fish and (2) carryover effects from the hatchery. The latter may be less likely because the fry stocked were the offspring of wild fish and only spent a few weeks in the hatchery.

The northern pike *Esox lucius* is a phytophagic, top-predatory fish that is native to most slow-flowing and stagnant water bodies in the Northern Hemisphere (Raaf 1988; Craig 1996). It is fast growing, early maturing, cannibalistic, and heavily de-

pendent on structured littoral habitat that provides shelter and foraging areas (Grimm 1983; Grimm and Klinge 1996; Pierce and Tomcko 2005). The association with structured habitat is size specific, with smaller fish and younger age-classes being

*Corresponding author: ck@aqua.dtu.dk

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particularly bound to vegetation (Grimm 1983; Chapman and Mackay 1984; Grimm and Klinge 1996). Loss of vegetation through human-induced eutrophication and habitat loss, coupled with the high vulnerability of pike to recreational fishing (e.g., Pierce et al. 1995; Paukert et al. 2001), has prompted attempts to maintain and enhance pike stocks through stocking in their native range in Europe and North America (Raat 1988; Mann 1996; Diana and Smith 2008; Margenau et al. 2008). Pike have also been used in stocking-based biomanipulation projects to increase the predation pressure on zooplanktivorous fish, so as to release herbivorous zooplankton from predation pressure and thereby increase water clarity (Skov 2002; Mehner et al. 2004).

Although northern pike have been stocked extensively throughout and beyond their native range, there are few thorough assessments of the outcomes of stocking programs and most of the available studies concern the stocking of fry or juvenile fish (e.g., Grimm 1983; Sutela et al. 2004; Skov and Nilsson 2007). Many studies report that pike stocking programs are unsuccessful when the stocking occurs on top of a naturally recruiting population (Margenau et al. 2008), possibly because wild pike cannibalize stocked pike and outcompete them for usually scarce vegetated habitats (Grimm 1983; Grimm and Klinge 1996). This is particularly to be expected if the stocking is not timed to the natural production of prey and the stocked fish are smaller than the naturally recruited young-of-the-year (age-0) pike (Skov et al. 2003; Grønkjær et al. 2004). The inferiority of stocked pike to wild conspecifics could be aggravated by the stocked fish's having less ability to cope with natural challenges, as has been found in various salmonids held in hatcheries for only brief periods of time (Hansen 2002; Ruzzante et al. 2004; Araki et al. 2007). Any hatchery-induced carryover effects may be reflected in the increased mortality and reduced growth and body condition of stocked individuals.

Previous studies have shown that the carrying capacity of an ecosystem for age-0 northern pike is determined by the amount of vegetated or otherwise structured habitats, such that any increase in the population above its carrying capacity that results from stocking should be quickly removed by cannibalism or displacement (Grimm and Klinge 1996; Schreckenbach 2006). Therefore, minimizing the risk of poststocking cannibalism is particularly important when stocking small-sized pike (e.g., fry or fingerlings). It has been suggested that age-0 pike should be evenly distributed in the littoral zone to minimize cannibalism among stocked fish or predation on stocked fish by wild ones (Klupp 1978; Jacobsen et al. 2004; Schreckenbach 2006). Furthermore, the stationary behavior of small pike in vegetation (Grimm and Klinge 1996 and references therein) may result in a high concentration of individuals at the stocking site, further increasing the risk of density-dependent interactions such as cannibalism. However, stationary behavior is not necessarily to be expected. First, laboratory experiments have shown that high densities of pike increase social stress, which increases energetic costs and induces growth depression (Edeline et al.

2010). Although that study was conducted with large pike, social stress resulting from high densities after stocking may also cause free-swimming age-0 pike (>15 mm; Bry and Davigny 2010) to disperse to increase survival. Thus, rapid dispersal after stocking might be more common than assumed a priori even in the early life stages.

To address the issue of poststocking dispersal and the subsequent fate of advanced northern pike in a natural lake, we designed a study to examine the distributional patterns of pike fry stocked at high densities at a common release site. We also investigated the growth of stocked and wild age-0 pike to better understand the performance of stocked pike in natural water bodies. Our objectives were to determine (1) whether stocked pike disperse from a single stocking point and (2) whether growth and diet vary between stocked and wild pike.

METHODS

Study site.—This study was conducted in a shallow natural lake named Lake Halle (55.986557°N, 9.477413°E) from May to August 2003. The lake is 31 ha in size and has a mean depth of 2.3 m and a maximum depth of 3.8 m. A small stream (Mattrup Stream) runs through the lake. In 2002, the concentration of total phosphorus was 81 ± 40 µg/L (mean \pm SD) and the chlorophyll-*a* concentration was 66 ± 64 µg/L (DME 2010), revealing that the lake is eutrophic. Consequently, in 2002 the Secchi depth was low (1.2 ± 1.0 m; DME 2010). The vegetation in the lake was dominated by common reed *Phragmites australis*, with cattails *Typha* spp., sedges *Carex* spp., water knotweed *Polygonum amphibium*, common rush *Juncus effusus*, lakeshore bulrush *Schoenoplectus lacustris*, and paleyellow iris *Iris pseudacorus* as subdominant species. Branches of trees were also present in the littoral zone. There was no submergent vegetation in the lake. In 1995, when the most recent fish surveys took place, the lake contained natural populations of roach *Rutilus rutilus*, Eurasian perch *Perca fluviatilis*, northern pike, European eel *Anguilla anguilla*, threespine stickleback *Gasterosteus aculeatus*, and ruffe *Gymnocephalus cernuus*, with roach being the dominant species (Skårup and Møller 1996). Pike represented the dominant top predator in the lake.

Pike breeding.—The northern pike used for stocking were purchased from a local hatchery that at the time of the study produced more than 100,000 age-0 pike annually for stocking in Danish lakes. According to Danish law, the age-0 pike used in Danish stocking programs are to be the progeny of wild parents captured in lakes within the geographical vicinity (<200 km) of the target lake, a total of 25 males and 25 females are to be used, and care is to be taken to ensure that all males and females are crossed to maintain genetic diversity. In our case, adult pike were caught in Lake Vandet (57.013709°N, 8.557342°E; about 130 km from Lake Halle) and brought to the hatchery, stripped for eggs and sperm, and released back into Lake Vandet. The fertilized eggs were then transferred to Zuger glasses until hatching, whereafter the pike were transferred to

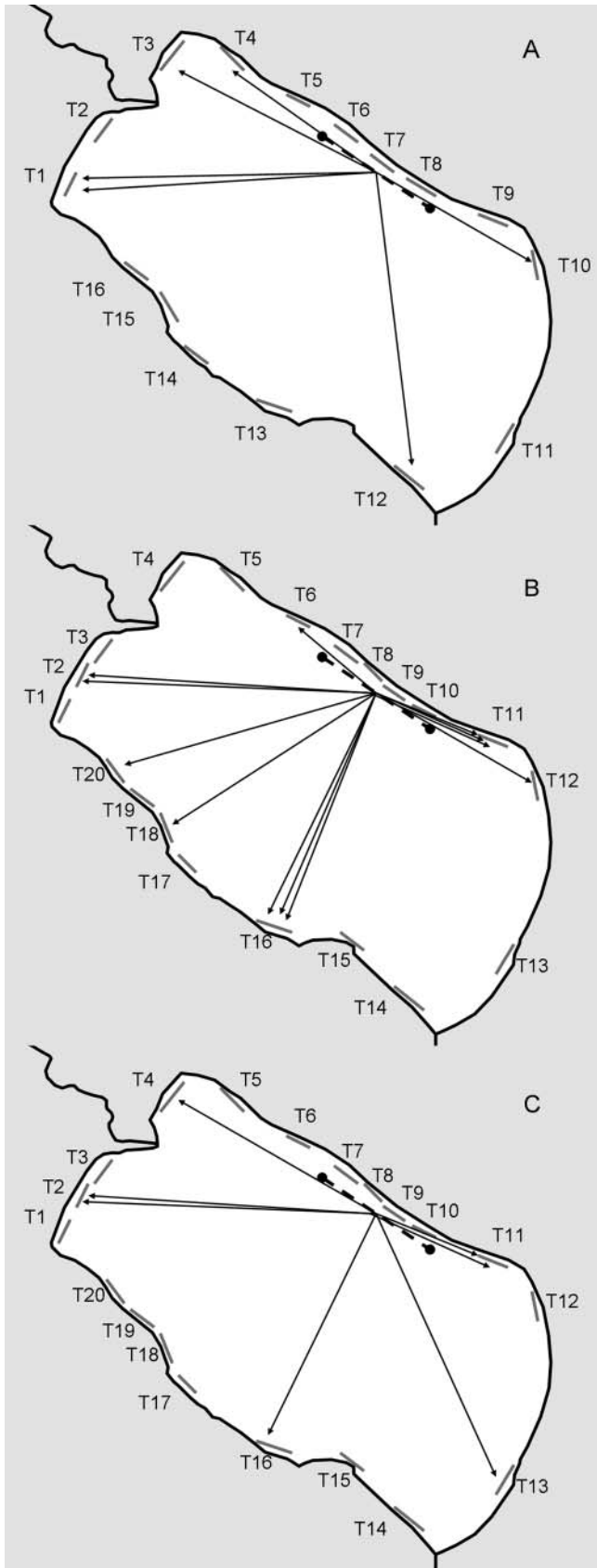


TABLE 1. Number of stocked and wild age-0 northern pike captured on seven sampling dates in 2003 and their total lengths (mm [means \pm SDs]).

Date	Event	Stocked pike		Wild pike	
		N	Total length	N	Total length
15 May	Stocking (random sample)	28	32 \pm 4		
23 May	Sampling	6	37 \pm 0.79	3	34 \pm 2.01
28 May	Sampling	15	42 \pm 1.17	10	39 \pm 2.16
3 Jun	Sampling	7	52 \pm 1.54	11	49 \pm 2.16
19 Jun	Sampling	5	72 \pm 3.85	11	75 \pm 3.00
7 Jul	Sampling	4	85 \pm 9.85	15	105 \pm 2.99
30 Jul	Sampling	1	134	8	136 \pm 5.63
22 Aug	Sampling	2	136 \pm 40.50	14	176 \pm 5.84

2-m \times 2-m indoor fiberglass breeding pools. Here the small pike were kept at high density on a diet of excess zooplankton for about 15 d until the time of release. The ecological conditions differ between Lake Halle and Lake Vandet, with the latter being deeper (mean depth, 9.5 m) and larger (5 km²) and having clearer water (Secchi depth, 4.3 m [2002]) and dense submerged vegetation.

Marking of stocked fish.—To distinguish between stocked and wild northern pike (referring to those hatched in the lake), stocked fish with a total length of 32 \pm 4 mm (mean \pm SD) were chemically marked with alizarin complexone (ALC) the day before stocking. We marked about 5,500 age-0 pike in 100-L plastic tanks on 13–14 May 2003. Immersing the pike into an ALC solution (100 mg/L) for 23 h resulted in a distinct fluorescent mark on the otoliths that was detectable for several months. Alizarin has been used routinely to mark age-0 pike in Denmark, and the mortality related to the marking procedure was negligible, as only a few dead individuals (<50) were observed between the time of marking and that of stocking about 48 h later. See Skov et al. (2001) for details and an evaluation of the marking method.

On 15 May 2003, northern pike were stocked into a 245-m stretch on the north side of Lake Halle that was dominated by a 3–4-m-wide band of common reed (Figure 1; Table 1). The pike were distributed haphazardly throughout the entire stocking stretch using small jars, resulting in an average density of about 6.3 pike/m² in the stocking area. A sample of 30 stocked fish was checked for the quality of the ALC marking. Lapillar

FIGURE 1. Map of recaptures of stocked age-0 northern pike in Lake Halle. The dotted line in bold shows the area where stocking occurred, and the marks along the shoreline with numbers beginning with the letter "T" represent the various sampling transects. Arrows point to the transects in which pike were recaptured and the lengths of the lines indicate the calculated minimum traveled distances (A) 8 d, (B) 13 d, and (C) 19 d after stocking.

otoliths were removed by dissection, individually mounted in thermoplastic glue (Crystal Bond), and examined for the presence of ALC marks using a (100 × microscope magnification) equipped with a mercury lamp that produced UV light and appropriate filters (excitation wavelength, 450–490 nm; emission wavelength, >515 nm). All 30 pike had clearly visible marks.

Sampling.—After being stocked, the northern pike were sampled from the lake by repeated electrofishing using high-frequency pulsed DC (800 Hz, 3/4 pulse width, rectangular wave at 300 V with a variable duty cycle of 0–50%; Electra-catch WFC12; Table 1). The first sampling event took place 8 d after stocking on 23 May 2003, and altogether seven samplings were conducted. The sampling period ended on 22 August 2003. Since we expected dispersal to be highest in the first period after stocking, we scheduled a higher number of sampling occasions in May and June than in July and August (Table 1). A total of 20 sampling areas distributed throughout the lake were electrofished on each sampling occasion except for 23 May, when only 16 sampling areas were electrofished. Electrofishing was done by wading. The electrofishing equipment was in a boat situated about 10 m behind the person who was fishing in order to minimize disturbance. At each sampling area we fished continuously for 5 min from a fixed starting point. The length of the electrofished stretch was normally between 10 and 25 m. We sampled fixed areas as opposed to conducting random point abundance sampling (Skov and Berg 1999) so that we could calculate the minimum distances traveled by stocked pike from the stocked area on subsequent sampling dates. Point sampling would have required us to stop and record a Global Positioning System (GPS) location for each sampled pike and individually store it, such that it would have been impossible to conduct the sampling in a single day. Electrofishing was always carried out in the proximity of vegetation or other structures. In some transects vegetation was present across different depths. When that was the case, we sampled in shallow water at the beginning of the season and then gradually included deeper water in the sampling area. After finishing a transect, we estimated the average sampling depth. Sampled pike were measured for total length (TL; mm), euthanized by a swift cut through the backbone of the fish just behind the head, and conserved in 80% ethanol for further analysis. With fish longer than 50 mm, the abdomen was cut open before preservation to facilitate the immersion of ethanol into the stomach, thereby ensuring more efficient preservation.

Lapillar otoliths were removed by dissection in the laboratory to assess the origin of the sampled northern pike as well as their size at stocking. Otoliths from fish longer than 90 mm were ground and polished using successively finer grades of sandpaper. Polished and unpolished otoliths were examined for the presence of ALC marks (see above for a description of the macroscoping process). A video camera connected to a PC with the software Olylite (Olympus; Ballerup, Denmark) was used to trace the outline of the ALC mark and subsequently calculate the area of the mark to assess the size of the pike at stocking (Grønkjær et al. 2004). The relationship between size at stocking

and alizarin mark size was estimated from a random sample of pike captured on the day of stocking: $TL \text{ (mm)} = 0.0007 \times \text{area of mark } (\mu\text{m}^2) + 6.7523$ ($R^2 = 0.7275$, $F = 65.97$, $P < 0.001$). To prevent overestimation of the ALC area in larger otoliths, a drop of immersion oil and a cover glass was placed on top of the glue (Grønkjær et al. 2004).

Assessment of dispersal.—Latitude and longitude were recorded with a GPS unit (Garmin) at the stocking location at the beginning and end of each sampling transect. The movements of the stocked northern pike were estimated from these GPS positions using Map Source (Garmin). When measuring the distance between the stocking area and the transect at which a pike was recaptured, we used the most direct (i.e., the shortest) distance so that the minimum traveled distance (MTD) was calculated. The proportions of stocked fish inside the stocking area and at each sampling point were calculated on seven occasions from 23 May to 22 August 2003. To investigate whether the movement of pike was related to size at stocking and to test for seasonal differences in the distances moved (i.e., whether the pike colonized the lake progressively over the season), we conducted a two-way analysis of covariance (ANCOVA) with the individual MTDs as the dependent variable and time after stocking (May, June, or July [a categorical variable]) and size at stocking (a continuous variable) as the independent variables. August was excluded from this analysis because only two stocked pike were recaptured. The decision probability (α) was 0.05.

Assessment of growth and proportion of stocked pike in the catch.—The growth of stocked and wild northern pike over the season was compared using two-way analysis of variance (ANOVA) with length at capture as the dependent variable and sampling date and origin (stocked versus wild) as independent categorical variables. The proportions of stocked and wild age-0 pike were compared across the sampling season using a chi-square test. If the proportions of the two groups were constant throughout the season (i.e., there were no differences in mortality and migration into or out of the lake), the relative frequencies of stocked and wild pike on each sample date would also be constant.

Stomach analysis.—The stomach contents of all recaptured stocked and wild age-0 northern pike were analyzed using frequency-of-occurrence methodology (Hyslop 1980). Hence, all food items were removed from the stomachs, identified to the lowest possible taxonomic level, and counted, and prey items were classified into five different groups (Insecta, Malacostraca, fish, Entomostraca, and miscellaneous). Frequencies of occurrence were calculated for all five prey groups as well as for empty stomachs. We analyzed this data using a full factorial logistic regression for each of the five prey groups with prey group as the dependent variable, pike origin (stocked versus wild) as a fixed factor, and pike TL as a covariate using a backward-elimination approach. The level of significance was Bonferroni-corrected according to Sokal and Rohlf (1995). Differences in the number of different prey groups between individual stocked and wild

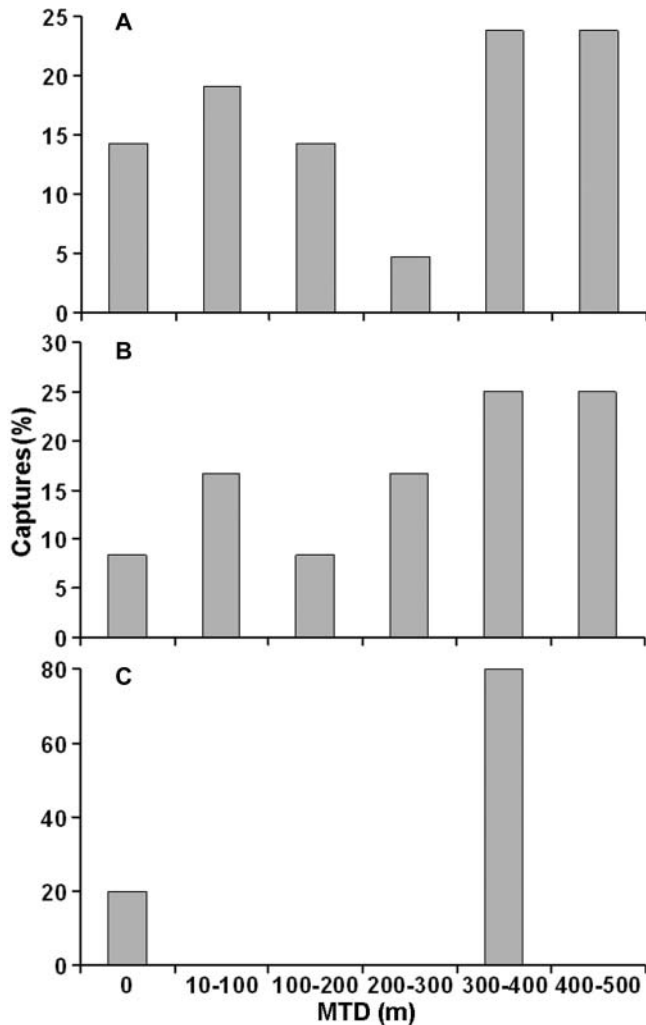


FIGURE 2. Distribution of minimum traveled distances (MTDs) by recaptured stocked northern pike in (A) May, (B) June, and (C) July.

pike were analyzed with logistic regression using number of prey groups (1 versus >1) as the dependent variable and pike TL and origin as the independent variables.

RESULTS

The depths of the sampling transects typically ranged from 20 to 40 cm and were rarely above 80 cm. A total of 110 age-0 northern pike were captured during the study period, and 40 of these (37%) had distinct ALC marks on their otoliths and hence originated from the stocking event in early May 2003 (Table 1).

Movement

Stocked northern pike were found throughout the lake within a few days of stocking, and the longest minimum distance traveled (467 m) was observed 8 d after stocking (Figure 1). On the first two sampling dates (8 and 13 d after stocking), 100% and 80% of the sampled stocked pike, respectively, were recaptured outside the stocking area (Figure 2). Consequently, there was no effect of time after stocking or the interaction between time after stocking and size on the patterns of distribution (two-way ANCOVA; time after stocking \times size: $F_{2,32} = 0.12$, $P = 0.883$; time after stocking: $F_{2,34} = 0.5$, $P = 0.620$; Figure 2), whereas size at stocking significantly influenced the distance traveled, with smaller individuals moving greater distances (Figure 3) (two-way ANCOVA; $F_{1,34} = 4.4$, $P = 0.043$).

Growth and Proportion of Stocked Fish in the Samples

Initially, the stocked northern pike were larger than the wild pike (42 ± 5 mm versus 39 ± 7 mm TL on 28 May 2003). However, toward the end of the season the wild pike were larger than the stocked pike (105 ± 12 mm versus 85 ± 20 mm on 8 July). The pattern of faster growth among the wild pike was confirmed by the significant interaction term between fish origin and time after stocking on TL at capture (two way-ANOVA;

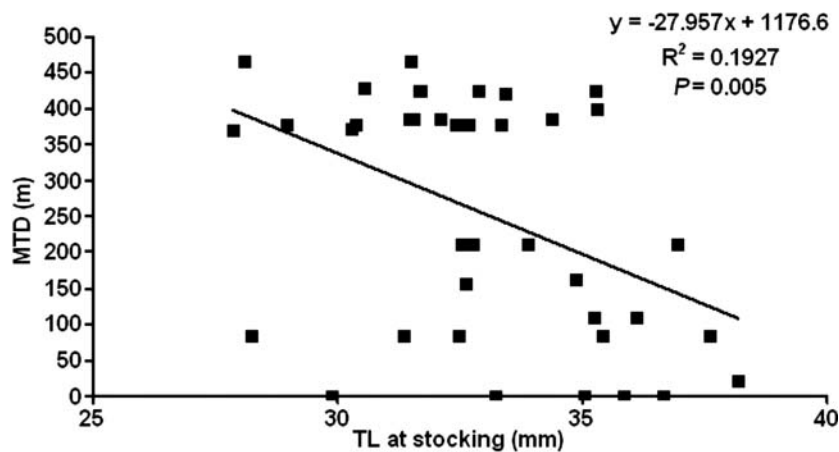


FIGURE 3. Relationship between the total length of northern pike at stocking and the minimum traveled distance (MTD) before being recaptured at sample transects.

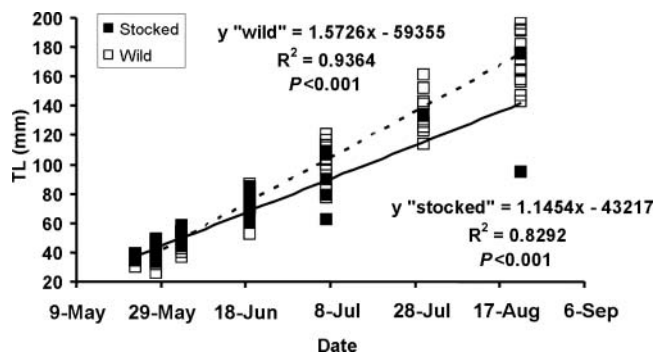


FIGURE 4. Total lengths of stocked and wild northern pike over the course of the study.

$F_{6,98} = 3.49$, $P = 0.004$; Figure 4). This analysis was repeated excluding the data from the last two sampling days to determine whether the small sample size of stocked fish had biased the result, but the interaction term was still significant ($F_{4,77} = 4.31$, $P = 0.003$).

The proportion of stocked northern pike in the samples differed significantly across the season ($\chi^2 = 20.5$; $df = 3$, 109; $P < 0.001$). In May, stocked fish represented 67.9% of all age-0 pike captured, but by August only 12.5% of the pike captured were stocked fish (Figure 5).

Stomach Analysis

The stomach contents of 107 northern pike were analyzed. The prey group Entomostraca consisted of copepods and Cladocera, the latter being dominated by *Daphnia* spp. Malacostraca consisted solely of waterlouse *Assellus aquaticus*, whereas Insecta was mainly represented by Ephemeroptera and Diptera larvae and, to much lesser extent, adult Heteroptera. The miscellaneous group was represented by annelids and mollusks, whereas the fish group was dominated by roach with a small number of Eurasian perch being represented as well.

The logistic regressions showed that the frequencies of occurrence of Entomostraca, Insecta, and fish changed with the length of the northern pike (Table 2). As expected, fish became a more frequent component of the diet as the pike got bigger; fish were found in fewer than 10% of the stomachs of pike less than 10 cm TL but in more than 95% of those of pike exceeding 15 cm. In contrast, Insecta became less frequent when the pike got bigger; Insecta were found in 50% of the stomachs of pike 7 cm long but in only 10% of the stomachs of those 17.5 cm long. Length did not influence the frequency of occurrence of empty stomachs or that of Malacostraca and miscellaneous and food items (Table 2).

The frequency of occurrence of Malacostraca (Figure 6a), Entomostraca (Figure 6c), and empty stomachs (Figure 6b) varied significantly between stocked and wild northern pike, with both Malacostraca and Entomostraca occurring less often in the stomachs of stocked pike and the frequency of empty stomachs also being higher among them (Figure 6; Table 2). By contrast, there were no differences in the frequencies of occurrence of Insecta, fish, and miscellaneous food items between stocked and wild pike (Table 2). There was no indication of intracohort cannibalism, as no pike were found in the stomachs of others. The number of different prey groups found in individual stomachs increased with length (logistic regression: $G = 13.03$, $P < 0.001$, Nagelkerke $R^2 = 0.16$), but overall there were more different prey groups in the stomachs of wild pike than in those of stocked pike ($G = 13.03$, $P = 0.051$, Nagelkerke $R^2 = 0.16$; length \times pike group, $P = 0.628$; Figure 6d).

DISCUSSION

The findings of our study support the notion that age-0 northern pike of about 30 mm TL at stocking (referred to as advanced fry) are highly mobile shortly after being introduced into the wild. Indeed, we found rapid dispersal and colonization of the entire lake after a few days, indicating rapid movement away from the stocking site.

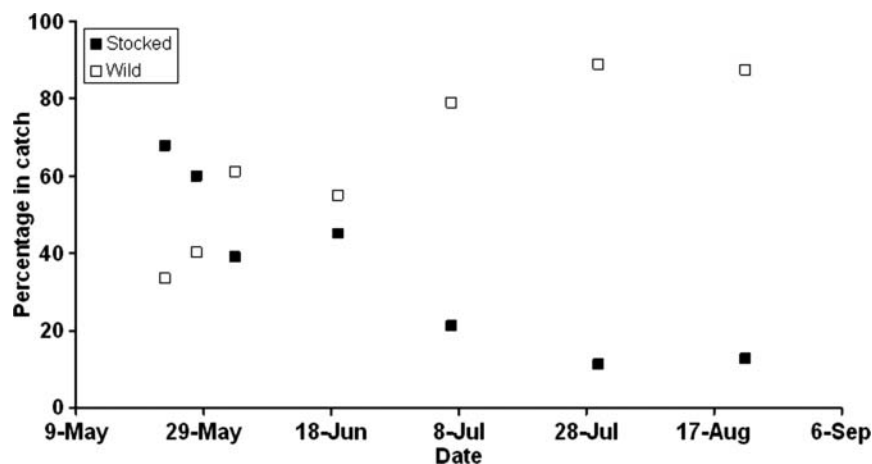


FIGURE 5. Percentages of stocked and wild northern pike on seven sampling dates in 2003. See Table 1 for sample sizes.

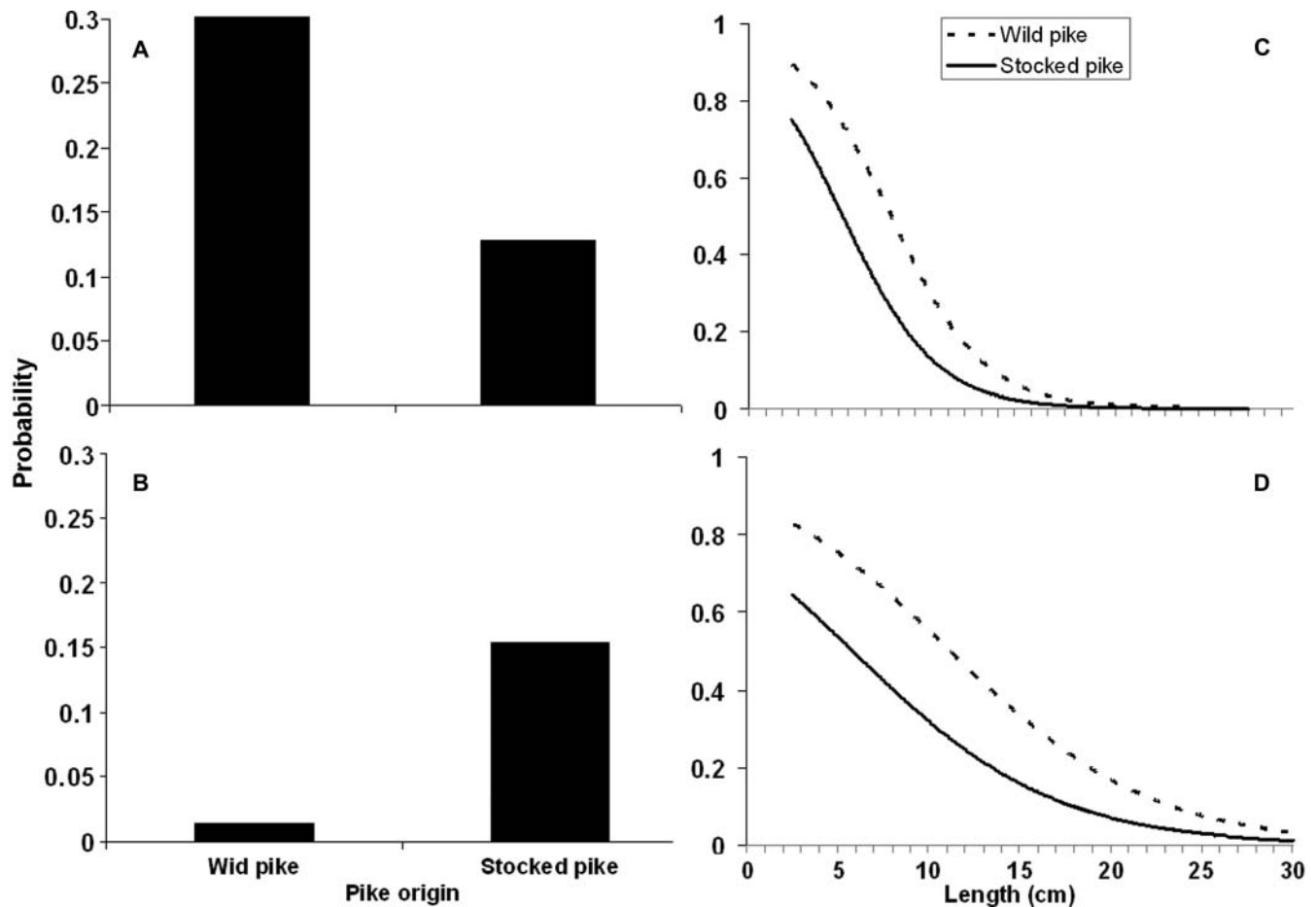


FIGURE 6. Panel (A) shows the probabilities of finding Malacostraca prey items in the stomachs of wild and stocked northern pike, and panel (C) shows the probabilities of finding Entomostraca prey items at different lengths at capture. Panel (B) shows the probabilities of finding empty stomachs and panel (D) the probabilities of finding two or more prey groups at different lengths at capture. For statistical results, see Table 2.

The density that we established in the stocking area (6.3 pike/m^2) was presumably high compared with that under natural conditions, but it was comparable to the densities obtained when stocking northern pike in shallow lakes for biomani- pulation purposes to control zooplanktivorous fish (Skov et al.

2003) and only slightly higher than the density of $5/\text{m}^2$ recommended by Wright and Giles (1987) for pike stocking programs. As we have no data on the dispersal of wild pike, we cannot rule out the possibility that high dispersal rates are common among age-0 pike in Lake Halle. Still, it is plausible that the high degree

TABLE 2. Results of logistic regression models of the differences in the frequencies of occurrence of different prey groups in stocked and wild northern pike in relation to fish total length. None of the interactions between length and origin (stocked or wild) were significant ($P > 0.1$).

Prey group	Model fitting information			Nagelkerke R^2	P -values	
	G	df	P -value		Pike origin	Total length
Entomostraca	38.02	2	<0.001	0.40	0.023	<0.001
Malacostraca	8.75	1	0.003	0.11	0.003	0.166
Insecta	21.01	1	<0.001	0.24	0.246	<0.001
Fish	80.37	1	<0.001	0.78	0.430	<0.001
Miscellaneous	2.38	3	0.482	0.04	0.121	0.160
Empty stomachs	7.80	1	0.005	0.18	0.005	0.180
Number of prey groups	13.03	2	<0.001	0.16	0.051	<0.001

of movement among the stocked individuals is the result of high density in the stocking area, with the dispersal of stocked fish being a reaction to reduce social stress (Edeline et al. 2010) and avoid or reduce the risk of cannibalistic attacks and intimidation interference by conspecifics (Nilsson 2006). This explanation is supported by the finding that individuals that were smaller at stocking moved greater distances than larger age-0 pike, possibly because they were displaced by larger and thus competitively superior fish (Kobler et al. 2009). These results are also in line with pond experiments showing that shortly after stocking the largest age-0 pike were found in the optimal vegetated habitats, whereas smaller individuals had moved to suboptimal habitats in open water (Skov and Koed 2004).

Our study indicates that stocked northern pike had slower growth than wild pike, suggesting that the former had reduced fitness prospects because fast early growth increases fitness in this species both in terms of survival and reproductive output (Edeline et al. 2007, 2009; Pagel 2009). We recognize that the differences in length at capture between the two groups of pike throughout the season could also be caused by size-selective mortality. However, this would imply that size-selective mortality differs between wild and stocked fish, and we see no immediate reasons for such a difference. Instead, we argue that the reduced growth among the stocked pike is the result of the high energy costs of moving or social stress (Edeline et al. 2010) or stems from lower overall energy intake due to impaired foraging. Support for the latter hypothesis comes from the stomach content analysis, which shows significant differences between natural and wild fish. The diet of age-0 pike usually follows specific ontogenetic shifts from Entomostraca to Insecta and from Malacostraca to fish (Hunt and Carbine 1951; McCarraher 1957; Skov et al. 2003). We found that the frequency of occurrence changed with length for some diet groups but that this was not the case for all prey groups (e.g., Malacostraca and miscellaneous food items). Interestingly, however, we found that for at least two of the prey groups examined (Entomostraca and Malacostraca) the frequency of occurrence was lower in the stocked pike. If the stocked pike compensated for the underrepresentation of these prey groups by consuming more of one or more of the other groups, one would expect higher frequencies of those groups; but this was not the case, as no differences were found in the frequencies of fish, Insecta, or miscellaneous food items. We thus interpret the differences in the frequencies of occurrence of specific prey items as a reflection of suboptimal foraging among the stocked pike.

Interestingly, the difference in foraging occurred among the prey groups preferred by the smaller pike, such as Entomostraca and Malacostraca, whereas there was no difference in the frequency of occurrence of fish, which is usually preferred by larger age-0 pike (Skov et al. 2003). This suggests that there is a critical initial period shortly after stocking and that reduced foraging might explain the smaller length at capture of stocked fish beginning in mid-June. The lack of differences in the frequencies of occurrence of energy-dense insects and fish could be the re-

sult of either increased adaptation to optimal foraging behavior among the stocked pike as the season progressed and their size increased or the low sample size of larger pike toward the end of the sampling period resulting in low statistical power in the logistic model. In support of the latter explanation, differences in foraging strategy among stocked and wild pike with regard to fish prey have previously been demonstrated (Skov 2002). No data on stomach fullness were available, but the stomachs of wild pike had a higher number of prey groups than the stocked pike, suggesting greater stomach fullness or more generalist foraging behavior. In addition, the occurrence of empty stomachs was highest among the stocked pike. Consequently, we argue that suboptimal foraging probably caused the reduced growth of stocked pike.

We found that the proportion of stocked age-0 northern pike decreased significantly over the season relative to that of wild pike. This could have resulted from the immigration of wild pike from downstream or upstream areas into the study lake, the emigration of stocked pike out of the lake, or higher mortality among stocked fish. If extensive movements occurred, they would further support our conclusion that age-0 pike are surprisingly mobile over large distances shortly after stocking. Alternatively, the divergent trends could have been caused by elevated mortality among the stocked pike. Although we cannot definitively conclude that differential migration or differential survival was the cause of the decrease in the proportion of stocked pike, we tentatively suggest that differential survival is the most likely explanation, as it fits well with the patterns of slower growth among the stocked individuals.

We see two potential explanations for the poor poststocking performance of the stocked pike in terms of growth and food composition and possibly survival as well. First, poor performance could stem from the stocked pike's being genetically maladapted to the environmental conditions in Lake Halle. Clearly, their lake of origin, Lake Vandet, was quite different ecologically, and genetically based local adaptations can lead to reduced fitness under alternative ecological conditions (Kawecki and Ebert 2004). Alternatively, the reduced fitness of the stocked age-0 fish in the wild could imply that certain early life experiences—even very brief ones—in a hatchery environment had carryover effects that caused suboptimal performance with respect to behavior, feeding, and food choice when they were released into the wild. Reduction in fitness by domestication selection and/or hatchery rearing of fry, even for brief periods of time, has been shown for salmonids (Hansen 2002; Ruzzante et al. 2004; Araki et al. 2007, 2009), but to the best of our knowledge this has not been reported in esocids. We can thus only speculate about the exact mechanism behind our findings, but we tentatively suggest that our results stemmed from the unnaturally high densities of pike fry in the Zuger glasses and hatchery tanks that are normally employed in the hatchery rearing of pike. Such unnaturally high densities during rearing have recently been shown to cause reduced growth and poststocking survival in brown trout *Salmo trutta* (Brockmark et al.

2010a), most likely because essential behavioral life skills were not properly developed (Brockmark et al. 2010b).

To conclude, we found that the stocked northern pike exhibited inversely size-dependent dispersal away from their release site. In addition, they experienced reduced fitness in terms of lower growth and possibly lower survival than wild fish. From a practical standpoint, our findings call into question the suitability of stocking pike on top of a naturally reproducing population by means of clumped stocking, but to substantiate this a controlled experiment involving replicate lakes with and without a wild population and clumped versus equal distribution of fish along the shoreline is needed. Also, it would be relevant to investigate whether wild pike show the same patterns of dispersal as stocked fish. Until such research is conducted, resource managers should assume that hatchery-reared fish will have poor performance relative to wild fish, especially when stocked into water bodies containing naturally reproducing populations.

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