


Behavioural and fitness effects of translocation to a novel environment: Whole-lake experiments in two aquatic top predators

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Abstract

1. Translocation into a novel environment through common fisheries management practices, such as fish stocking, provides opportunities to study behavioural and fitness impacts of translocations at realistic ecological scales. The process of stocking, as well as the unfamiliarity with novel ecological conditions and the interactions with resident fish may affect translocated individuals, leading to alterations of behaviours and causing fitness impacts.
2. Our objectives were to investigate how aquatic top predators behaviourally establish themselves and compete with resident individuals following introduction in a novel lake environment and to investigate the resulting fitness consequences.
3. Using high-resolution acoustic telemetry, we conducted whole-lake experiments and compared the activity, activity-space size and fate of translocated and resident individuals in two model top predators, the northern pike *Esox lucius* ($n = 160$) and European catfish *Silurus glanis* ($n = 33$). Additionally, we compared the reproductive success of translocated and resident northern pike. The experiment was conducted with large (adult) individuals of different origins, resilient to predation, but subject to agonistic interactions and competition with resident fish.
4. Over a period of several months, the translocated catfish exhibited consistently larger activity-space sizes than resident catfish, but did not differ from residents in activity and survival. The pike from one of the two translocated origins we tested also showed elevated space-use, and both translocated origins revealed higher mortality rates than their resident conspecifics, indicating maladjustment to their novel environment. When non-resident pike reproduced, they overwhelmingly produced hybrid offspring with resident fish, indicating that introductions fostered gene flow of non-native genes.
5. Our study indicates that fish introductions result in behavioural and fitness impacts even in large-bodied top predators that experience low levels of natural predation risk.

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acoustic telemetry, European catfish, fish behaviour, northern pike, reality mining, species introductions, stocking

1 | INTRODUCTION

Mobile animals frequently encounter novel environments via dispersal, migration or rapid environmental change (Holt, 2003; Thomas et al., 2001). Upon encountering a novel environment, to permanently establish itself an individual must overcome a number of challenges, including physiological barriers (Comte & Olden, 2017b; Pihl, Baden, & Diaz, 1991), finding food (Bachman, 1984) and shelter (Fjellheim, Raddum, & Barlaup, 1995; Stone, Ford, & Holtzmann, 2000), avoiding predation (Lima & Dill, 1990) and finding future mates (Magnhagen, 1991). An individual's immediate response after introduction to a novel environment is first physiological, followed by behavioural reactions (Sih, Ferrari, & Harris, 2011; Wong & Candolin, 2015). However, how newly translocated individuals behaviourally establish themselves in non-local, novel environments is largely unknown for aquatic species because it is challenging to observe what animals continuously do in the wild at whole ecosystem scales (Atwell, Cardoso, Whittaker, Price, & Ketterson, 2014; Krause et al., 2013). Yet, measuring individual behavioural responses following introduction to a novel environment is contemporarily important as wide-scale range expansions are expected to occur in response to climate change (Kelly & Goulden, 2008; Perry, Low, Ellis, & Reynolds, 2005), in particular for freshwater fish species (Comte & Olden, 2017a; Ficke, Myrick, & Hansen, 2007; Jarić, Lennox, Kalinkat, Cvijanović, & Radinger, 2018). Furthermore, anthropogenically mediated introductions through popular fisheries management actions such as fish stocking and introductions are particularly widespread in aquatic systems (George et al., 2009; Thomas, 2011). Anthropogenically mediated introductions occur in many forms, such as building migration corridors (e.g. through canals connecting river catchments; Galil, Nehring, & Panov, 2008), unintentional transport (Ricciardi, 2006) or intentional releases via introductions of non-local species or populations (Camp, Lorenzen, Ahrens, & Allen, 2014; Knapp, Corn, & Schindler, 2001; Lorenzen, 2008).

Introductions and stocking have a long history in fisheries management (Lorenzen, Beveridge, & Mangel, 2012). Fish stocking presents an opportunity to address questions regarding behavioural establishment in novel environments (Lorenzen, 2014). The potential ecological impacts from stocking have seen abundant research (Allendorf, 1991; Cowx, 1994; Lorenzen et al., 2012), but most investigations have focused on the impacts of interspecific and intraspecific predation and competitive interactions among stocked and resident fish (Einum & Fleming, 2001; Hearn, 1987) as well as genetic mixing and hybridization (Fraser, Cook, Eddington, Bentzen, & Hutchings, 2008; Gharrett & Smoker, 1991; Huff, Miller, Chizinski, & Vondracek, 2011). Yet, most of this previous work has overlooked the behavioural basis of the establishment process. Meta-analyses have shown that the natural mortality of stocked fishes frequently

exceeds the natural mortality of resident fishes (Lorenzen, 2006), indicating maladjustment to the new environment is common. This maladjustment should be reflected in systematic behavioural differences and in turn fitness differences between stocked and resident wild fishes (Barton, 2002; Schreck, Olla, & Davis, 1997). For example eel-tailed catfish *Tandanus tandanus* translocated from a reservoir to a river habitat selected fewer undercut bank and root mass habitat structures than their resident riverine counterparts as shown by fine-scale telemetry (Carpenter-Bundhoo et al., 2020).

A range of mechanisms can lead to maladjusted behaviour, including lack of experience with local ecological conditions (Malavasi, Georgalas, Lugli, Torricelli, & Mainardi, 2004; Olla, Davis, & Ryer, 1998), competitive exclusion by resident fish ('prior residence effect', O'Connor, Metcalfe, & Taylor, 2000; Weber & Fausch, 2003), genetic deficiencies (Mehner, Pohlmann, Elkin, Monaghan, & Freyhof, 2009), origin-specific vulnerability to diseases and parasites (Beacham & Evelyn, 1992) or transfer-induced physiological stress (Chandoo, Cooke, McKinley, & Moccia, 2005; O'Connor et al., 2010). With the exception of salmonids stocked in streams (Baer & Brinker, 2008; Bettinger & Bettoli, 2004; Kaspersson, Sundström, Bohlin, & Johnsson, 2013; Popoff & Neumann, 2005; Turek et al., 2010, 2018), few studies at whole ecosystem scales exist on this topic, constraining our understanding of which behavioural mechanisms could explain the larger mortality levels of stocked fishes relative to resident ones. In addition to survival costs of being novel in a given environment, a fitness reduction of translocated fishes may also result from reduced reproductive success as repeatedly shown in hatchery raised salmonids when compared with the per capita reproductive success of wild conspecifics under common garden conditions in the wild (Araki, Berejikian, Ford, & Blouin, 2008; Christie, Ford, & Blouin, 2014).

In the context of stocking, to understand the behavioural response to a novel environment, the behavioural changes in response to the stress of the novel environment must be experimentally isolated from the behavioural changes in response to stress from transportation and handling. When fish are stocked or translocated they are typically handled multiple times in the process of raising, sorting, catching and transport (Cowx, 1994; Lorenzen, Leber, & Blankenship, 2010). Such stocking-induced stressors (Mather & Wahl, 1989; Miles, Loehner, Michaud, & Salivar, 1974; Urbinati, de Abreu, da Silva Camargo, & Parra, 2004) can have large physiological impacts and are one cause for the high immediate release mortality in stocking programmes (Barton, Peter, & Paulencu, 1980; Hühn, Lübke, Skov, & Arlinghaus, 2014; Pitman & Gutreuter, 1993). Therefore, a robust introduction experiment designed to differentiate impacts of being non-local from stocking-induced stress effects must at least include the stocking of native fish with and without typical handling during stocking, in addition to the introduction of

non-local fish. After exposure to a stressor, such as handling, initial behavioural irregularities often appear to be short-term, where fish recover to normal behaviour within hours to days depending on species and context (Cooke, Raby, Hanson, & Clark, 2013; Ferter, Hartmann, Kleiven, Moland, & Olsen, 2015; Klefoth, Kobler, & Arlinghaus, 2008; Pullen et al., 2017). Therefore, in a stocking context one can expect particularly high behavioural impairments immediately after translocation to a novel environment, with the impacts diminishing over time. However, an experimental whole-lake study in largemouth bass *Micropterus salmoides*, showed carry-over impacts of one time stressor events many months after the event, causing not only hyperactivity but also quicker death in response to a natural challenge (hypoxia) in the wild (O'Connor et al., 2010). Long-term telemetry studies in the wild are therefore critical for understanding the behavioural legacy of an introduction to a novel environment and the possible associated fitness costs (Arlinghaus et al., 2007; Donaldson, Arlinghaus, Hanson, & Cooke, 2008; Krause et al., 2013).

We investigated the behavioural and fitness outcomes of introduction in two aquatic top predators, the northern pike *Esox lucius*, and the European catfish *Silurus glanis*. Both species, are important fisheries resources and are regularly stocked (Guillerault, Hühn, Cucherousset, Arlinghaus, & Skov, 2018). Pike are stocked widely across their range for both population enhancement (Guillerault et al., 2018) and to restore water quality in turbid, eutrophic lakes (Gulati, Pires, & Van Donk, 2008). European catfish are also (legally and illegally) stocked in some European countries for fisheries purposes, but stocking is more restricted than pike due to the species' invasive tendencies (Cucherousset et al., 2017). Both species are generally suitable models to study the behavioural adjustment and the fitness impact of being released in non-local environments. The circumpolar range, occupation of diverse aquatic habitats and common translocations and stocking of northern pike establish the relevance of the species as a model top predator for both ecology and fisheries management (Forsman et al., 2015). In its non-native range, the European catfish is considered invasive (Benejam, Carol, Benito, & García-Berthou, 2007; Castaldelli et al., 2013) and is one of the largest freshwater top predators in Europe (Copp et al., 2009; Cucherousset et al., 2017). The species is currently spreading naturally across Europe, also in its native range (e.g. throughout Germany), due to improved recruitment in a warming climate and due to introductions and stocking by anglers (Cucherousset et al., 2017). Understanding the behavioural response of the European catfish to novel environments therefore has special relevance for understanding current invasion dynamics and natural range expansion.

We expected the behaviour of northern pike and catfish to be symptomatic of competitive interactions following introduction. Both catfish and pike are known to show agonistic behavioural interactions towards conspecifics (Nilsson, 2006; Slavík, Horký, & Závorka, 2014) and should therefore experience interference competition with resident conspecifics. Although catfish has been described as temporarily social (Boulétreau et al., 2016), territoriality

is a well known phenomenon, resulting in confined home ranges that vary seasonally in dimension (Brevé et al., 2014; Carol, Zamora, & García-Berthou, 2007; Slavík & Horký, 2009; Slavík et al., 2014). Furthermore, catfish have been shown in a laboratory environment to strongly prefer sheltering with familiar over unfamiliar individuals (Slavík, Maciak, & Horký, 2012), suggesting that resident catfish might show interference with newcomers. Northern pike are strongly cannibalistic, size-structured ambush predators (Nilsson & Brönmark, 1999) that prefer to forage and shelter in structured habitats (Chapman & Mackay, 1984). Density dependence in pike has been shown to exert impacts through both competition for food (Haugen et al., 2006) and food-independent social stress, where crowding induces stress and reduces growth rates (Edeline et al., 2009). A stocking experiment with young-of-the-year pike in a natural lake showed that the smallest size classes have the largest displacement (Skov, Koed, Bastrup-Spohr, & Arlinghaus, 2011), suggesting behavioural interference and displacement by wild conspecifics, likely reflecting prior-residence effects abundantly reported from territorial salmonids in streams (Deverill, Adams, & Bean, 1999; O'Connor et al., 2000). Yet, an introduction experiment with another esocid, muskellunge *Esox masquinongy*, failed to find evidence of behavioural impacts of translocated fish when comparing three genetically distinct stocks introduced together in one study lake (Wagner & Wahl, 2011). However, Wagner and Wahl (2011) did not track resident fish and therefore the behaviour of translocated fish could not be compared to the typical behaviour of the resident fish. The behaviour of recently translocated European catfish relative to wild conspecifics has not been assessed in the wild.

The objective of our study was to assess potential behavioural maladjustment, survival costs and reproductive impairment (i.e. fitness consequences) from introduction into a novel environment where newly translocated fish are forced into competition with an established population in two top predators. To that end, we observed the behaviour of translocated and resident European catfish and northern pike of different origin using a whole-lake biotelemetry array. We focused our attention on swimming activity, and on the activity-space size as a surrogate for home ranges because it affects predator-prey interactions (Mitchell & Lima, 2002), density dependence (Efford, Dawson, Jhala, & Qureshi, 2016; Kramer & Chapman, 1999) and because space use can be a sensitive indicator of competition (Hansen & Closs, 2005). We assessed mortality via acoustic telemetry data, and reproductive success by assigning sampled juveniles to translocated and resident pike parents via microsatellites in the year following the introduction. We hypothesized that both translocated pike and catfish would show elevated swimming activity and larger activity-space sizes compared to wild conspecifics of the same length, as catfish and pike are expected to be at least partly agonistic towards conspecifics and may be displaced by competitively superior resident fish or show high activity in the search to establish themselves in the new environment. This prediction was derived from work in salmonids and pike (Skov et al., 2011) that have repeatedly shown that translocated fishes usually show

greater displacement compared to resident fish (Bachman, 1984; Baer & Brinker, 2008; Weber & Fausch, 2003). Furthermore, we hypothesized the behavioural impacts to be transient and be most strongly expressed after release and vanish over time at a temporal scale of weeks. Finally, we hypothesized that any behavioural impairments (judged relative to resident controls) would lead to reduced survival and reproductive success, e.g. due to growth impacts post-introduction affecting specifically the stressed newcomers (Klefoth, Kobler, & Arlinghaus, 2011).

2 | MATERIALS AND METHODS

2.1 | Study site

Kleiner Döllnsee (52°59'03.2"N, 13°34'04.6"E) is a 25 ha, shallow, summer-stratified weakly eutrophic natural research lake (mean depth 4.1 m, maximum depth 7.8 m) equipped with a high resolution acoustic telemetry system of 20 receivers (WHS 3050; 200 kHz; Lotek Wireless Inc.). The telemetry system receivers were distributed throughout the entire lake at fixed locations, allowing whole-lake tracking of fish equipped with ultrasonic transmitters (for a full lake description see: Baktoft, Zajicek, Klefoth, Svendsen, & Jacobsen, 2015; Klefoth et al., 2011; Kobler, Klefoth, Wolter, Fredrich, & Arlinghaus, 2008). Based on measuring precise arrival times of unique acoustic transmitter signals at the receivers throughout the lake, fish positions could be trilaterated. Fourteen fish species are found in the lake (see Table S1), most of which are naturally reproducing. The fish community is typical for mesotrophic to slightly eutrophic small natural lakes in the German lowlands (Eckmann, 1995). Common top predators are northern pike and large Eurasian perch *Perca fluviatilis*, both of which are native, naturally recruiting species. A further top predator is European catfish, which was introduced into the lake in the early 1990s for research purposes. European catfish is now naturally reproducing in Kleiner Döllnsee and is native to Germany and the catchments around Kleiner Döllnsee. The typical forage fish community encompasses several smaller-bodied cyprinids (e.g. roach, *Rutilus rutilus*) and small percids.

The lake is not connected to neighbouring lakes. It is closed to the public and is only accessible to research. The lake is currently classified as eutrophic as the TP concentration was 38 µg/L at spring overturn in 2015. The lake has undergone other limnological changes over time, such as an increase in water level (+1 m) due to altered water management in the catchment and a strong decline in submerged macrophytes from the beginning of the first tagging period in 2010 to the last tagging period in 2014. During our study period, the mean secchi depth was 3.28 ± 0.35 m (2.70–4.00 m) in 2010 and 2.38 ± 0.82 m (1.15–3.80 m) in 2014, also indicating increased eutrophication and reduced visibility, likely responsible for the decline in submerged macrophytes.

The population size of pike throughout the years 2007–2010 was estimated using a multi-year mark-recapture model (fish captured and tagged using intensive electrofishing of the shoreline and

angling) to be, on average, 1844 (95% CI: 1,601–2,061) pike \geq age 1 (M. Palmer, unpubl. data, pike in this study were \geq age 2). An adjusted Petersen estimate (Ricker, 1975) using mark-recapture data for catfish (sampled with gill-nets and hook and line) indicated that from 2009 to 2013 the population size of catfish between 70 and 166 cm was approximately 55 individuals (95% CI: 23–101).

2.2 | Study periods and fish tagging

A summary and timeline of our study outlining the treatments and their origins, and differences between the catfish and pike experiments can be found in Figure 1.

2.2.1 | Pike

We compared the behaviour of pike in four treatments (see Figure 1; Table S2 for detailed information), a resident control treatment ($n = 33$), a resident stocked treatment ($n = 43$), and two translocated treatments from nearby Lake Groß Vätersee ($n = 43$) and Lake Wuckersee ($n = 41$). The two translocated origins represented natural pike populations in direct vicinity to Kleiner Döllnsee only a few kilometres away in the same drainage region (Figure 1). In total, 160 pike were tracked through acoustic telemetry for 22 weeks from 17 October, through the fall and winter, until midnight of 14 March 2012. The resident control fish from Kleiner Döllnsee were sampled by angling and electrofishing (EFGI 4000, 4 KW, Bretschneider Spezialelektronik, anode ring: 45 cm) in spring 2011 (23 May to 16 June) and immediately released into the lake following sampling and acoustic transmitter implantation (described in Section 2.2.3).

Translocated pike from Lakes Wuckersee and Großer Vätersee served as two independent replicates of translocated fish that were stocked into Kleiner Döllnsee in autumn 2011. Großer Vätersee (53°00'16"N, 13°33'09"E) is a 12-ha, mesotrophic to slightly eutrophic (TP 27 µg/L) natural lake with a mean depth of 5.2 m, a maximum depth of 11.5 m and secchi depth of 2.7 m. Großer Vätersee is located approximately 2 km northwest of Kleiner Döllnsee (Figure 1). Lake Wuckersee (53°0'28"N, 13°38'33"E) is a small (23 ha), mesotrophic (TP 12 µg/L) natural lake with a mean depth of 8 m, maximum depth of 16 m and secchi depth of 4.2 m. Wuckersee is located approximately 4 km northeast of Kleiner Döllnsee (Figure 1). Fish from both lakes were sampled by angling and electrofishing in September 2011 and underwent a surgery for transmitter implantation (see Section 2.2.3). The fish were then exposed to a simulated stocking experience as they were transported for 60–90 min in a hatchery vehicle equipped with a 1,000 L tank to $13 \times 6 \times 1$ m earthen ponds where the fish were maintained for 2–32 days. On 17 October 2011, fish were transported back to Kleiner Döllnsee and released. Because the stocking of fish from Großer Vätersee und Wuckersee increased the density of the unexploited pike stock (which was supposed to be at carrying capacity), between May and June 2011, 84 pike

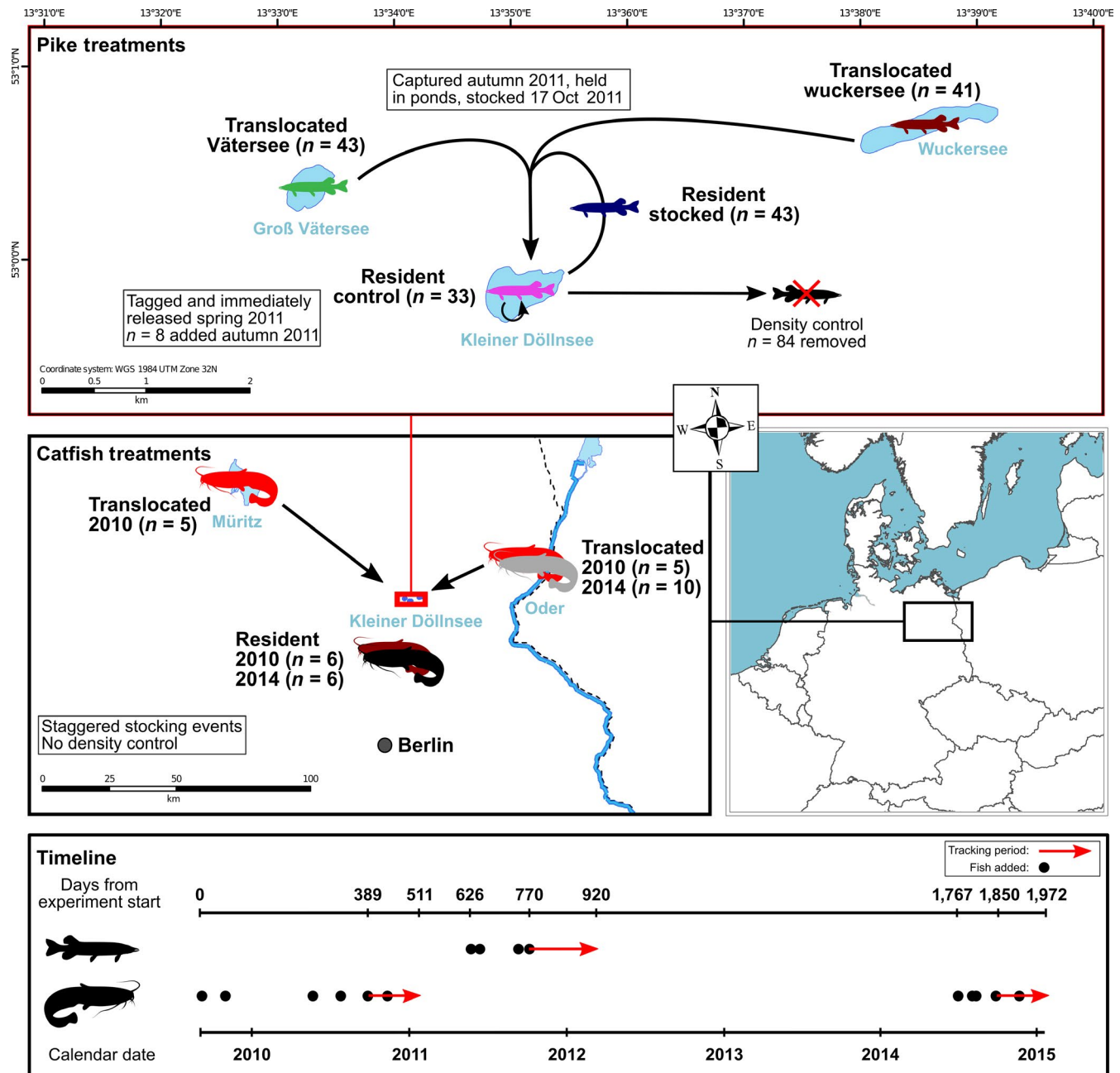


FIGURE 1 An overview of our experimental treatments, their origins and sample sizes and differences between pike and catfish experiments. We used four treatments of pike consisting of a resident control to gather data on natural behaviour in the study lake from which translocated behaviour can be compared, two translocated treatments to evaluate behaviour after translocation and a resident stocked treatment to separate the effects of stocking and handling from introduction to a novel environment. The resident control treatment was sampled and tagged earlier (spring) than the other three treatments to ensure recovery from tagging. Eight control fish were added in autumn to supplement for control fish mortality and to evaluate stocking mortality against natural mortality. Furthermore, 84 pike were removed in autumn to maintain the same population density in the study lake after the introduction of the two translocated treatments. Our assessment of catfish also consisted of resident and translocated treatments, but had no control for stocking and handling stress. Furthermore, two independent groups of catfish were studied in 2010 and 2014 respectively, and in both cases the tagging and stocking of both residents and translocated fish were staggered rather than conducted in batches. No catfish were removed to control for density. The bottom panel of the figure shows a timeline of stocking and tracking periods for both pike and catfish

(TL = 529 ± 123 mm, $M \pm SD$) were removed from Kleiner Döllensee prior to translocation by angling.

To establish a control for stocking-induced stress and to differentiate this effect of being non-local, a resident 'stocked' treatment

from Kleiner Döllensee was established. To that end, a further sample of pike from Kleiner Döllensee was acquired by angling and electrofishing in autumn 2011 (14 September to 10 October). This group also underwent a simulated stocking experience following the same

procedure as described above for fish from Wuckersee und Großer Vätersee. On 17 October 2011, the resident stocked fish were transported back to Kleiner Döllensee, along with the translocated Vätersee and translocated Wuckersee treatments, and released.

Eight of the resident control fish were added from 13–16 September 2011, to supplement the sample size and assess tagging mortality. We assessed tagging mortality to better separate the contribution of handling and translocation to mortality in the translocated treatments. Specifically, the mortality of eight newly tagged resident control fish in autumn 2011 was assessed against the mortality of the surviving resident control fish stocked previously in spring 2011, because by autumn 2011, the effects of sampling stress in the control treatment stocked in spring 2011 were assumed to be gone and any mortality of the spring stocked resident control fish after autumn 2011 would be due to natural causes.

2.2.2 | Catfish

We tracked daily behaviours of resident and translocated catfish simultaneously on two separate study years; July 2010 to February 2011 and July 2014 to February 2015 (see Figure 1; Table S3 for detailed information). In winter 2010, 16 fish were tracked, though one catfish did not produce data because of mortality or tag loss, reducing the sample size to 15. Of the 16 fish, six were resident catfish, five were translocated (29 September 2010) from the nearby river Oder and five were translocated (15 November 2010) from a commercial fishery pond in the Müritz region about 150 km north of the study lake (53°30'58.9"N, 12°40'55.7"E). In 2014, 18 catfish were tracked. Of the 18 fish, six were resident catfish and 12 were translocated from the river Oder (Figure 1). One resident catfish in the 2014 tracking period was a recapture of a translocated catfish from the 2010 tracking period, but was considered resident as it had been living in the lake for approximately 4 years. The resident catfish were sampled by gillnets, electrofishing and hook-and-line baited with squid, while the catfish translocated from the river Oder were captured by fyke nets, and the catfish translocated from a fishery pond were removed after draining. We restricted our behavioural analysis to the months of October through January in both 2010/2011 and 2014/2015, to maintain comparability with the pike dataset. Because we had two origins of catfish only in one of the two study years and sample size was lower relative to pike, the non-local catfish were modelled as one translocated treatment.

2.2.3 | Transmitter implantation

Acoustic transmitters were surgically implanted into fish body cavities by a skilled surgeon according to procedures described in previous studies by our group (Hühn, Klefoth, Pagel, Zajicek, & Arlinghaus, 2014; Kobler, Klefoth, Mehner, & Arlinghaus, 2009). Fish were anaesthetized by submersion in a 9:1 95% EtOH–clove oil

solution (Carl Roth) added to water at 1 ml/L and tags and surgical tools were sterilized with a 7.5% povidone-iodine solution (Braunol, R.B. Braun) added to tap water. We used adsorbable PDS-II monofilament sutures and FS-1 3-0 needles (Ethicon) to close the incision following tag implantation.

Several tag models that were used were dependent on availability from the manufacturer, fish size, desired burst rate frequency and battery life (see Tables S2 and S3 for individual tagging data and per cent body weight of the tags). The per cent body weight taken by the tag was on average 1.18% (range: 0.37%–2.37%) for pike, and was on average 0.39% (range: 0.13%–1.77%) for catfish. All transmitters were equipped with a pressure sensor to transmit depth or once per minute temperature (not considered in this study) instead of depth. All pike received MM-M-11-28 TP transmitters (Lotek Wireless Inc.), with a transmission burst interval of 25 s. Catfish sampled in 2010 received dual acoustic and radio tags, CH-TP-16-33 ($n = 11$; Lotek Wireless Inc.) or CH-TP-16-25 ($n = 5$; Lotek Wireless Inc.), with a transmission burst interval of 9 s, and catfish sampled in 2014 received MM-M-16-50 TP (Lotek Wireless Inc.) transmitters with a transmission burst interval of 7.5 s.

2.3 | Measuring behaviour

Prior to any calculation of behavioural metrics of fish behaviour, the raw acoustic telemetry data was processed first by a proprietary software from the manufacturer of the system (Alps v 2.30). Afterwards, a Hidden Markov Model was applied for further smoothing (for details, see Baktoft et al., 2015) to reduce the impact of outliers without removing datapoints. Hence, error in positioning was strongly minimized (median system error was 3.1 m, Baktoft et al., 2015). Earlier performance studies showed that the performance of the tracking system varies across habitats, and within the reed habitat, very few detections occur (Baktoft et al., 2015). Therefore, activity (i.e. distance travelled) and activity-space size (i.e. the area covered by swimming) calculations represent activity and activity-space size within the sublittoral and pelagic habitats only. Previous work has shown that pike move very little (only a few metres at most) within the dense reed habitat (Zajicek, 2012), and therefore, the activity and activity-space size behaviour of pike measured in the sublittoral and pelagic habitats can be considered representative of spatial pike behaviour.

We extracted measures of activity and activity-space size from the processed positions. Summarized behaviours were extracted on a weekly basis for pike and on a daily basis for catfish. We used a species-specific temporal partitioning, because pike were hiding in the reed belt during many days generating a greater numbers of daily data gaps than was the case for catfish. Therefore, we needed to aggregate over a longer (weekly) time-scale to estimate activity and activity-space sizes in pike. Furthermore, pike showed weak diurnal activity patterns in the study lake (Kobler et al., 2008), while the catfish, known to be nocturnal (Slavík, Horký, Bartoš, Kolářová, & Randák, 2007), showed pronounced diurnal behavioural patterns,

and therefore analysis at a daily scale was more appropriate to represent catfish behaviour.

For both pike and catfish, swimming activity was summarized as the sum of the Euclidean distances between consecutive positions in two-dimensional space as in previous studies (Laskowski et al., 2016). To avoid the accumulation of tracking error when fish were stationary, we did not include consecutive positions that were indistinguishable from error (i.e. positions less than the average error of the telemetry system). Moreover, we did not consider distances between positions that suggested swimming speeds above the theoretical maximum swimming speed of the individual (Wolter & Arlinghaus, 2003). We calculated activity-space sizes using 95% volume contour of the kernel density utilization for each fish using the `ADEHABITATHR` package (Calenge, 2011) in R (version 3.5), considering a 200 by 104 cell grid, with a cell size of 5.78, 10 m smoothing parameter and the lake shoreline as a boundary. Activity-spaces were not calculated if fewer than 1,000 pike positions were collected over a weekly period or if fewer than 500 catfish positions were collected over a daily period, as a subsampling exercise (see Figures S2 and S3) indicated that activity-space size may be underestimated with fewer positions. For both pike and catfish, the first 7 days of behaviour were excluded from the analysis to avoid confounding adverse effects from surgical tag implantation with stocking effects.

2.4 | Measuring survival

We assessed pike and catfish mortality for two reasons. Firstly, to assess the impacts of stocking stress and translocation on a fitness component and secondly to be sure that the telemetry data used in the behavioural analysis were generated from live fish. The determination of mortality was based on examining the telemetry data visually by plotting two-dimensional trajectories. The challenge in identifying when a fish has died is that error (jitter) from the positioning can sometimes appear like a live fish. Therefore, we considered multiple metrics to decide if a fish had perished. We calculated the daily SD in latitude and longitude for each fish along with a daily range in depth use and average distance from the bottom by comparing the transmitter depth to the lake depth at the transmitter position using a previously estimated depth contour map (Baktoft et al., 2015). When an individual showed a decline in space use and depth use, and consistent positions with no increase later in the tracking period, it was considered dead. All positions of individual fish were also visually inspected by plotting the positions within the shoreline of the lake (see Figure S1 for examples). Visually, a transmitter constantly present in one place can be distinguished from positions from live fish which show directed trajectories in their movement. Fish were considered to have died on the first day when the hallmark characteristics of a dead fish (low variation in space use and time near the bottom of the lake) were observed. However, tag failure or loss may still occur, which cannot be reliably differentiated from death, and therefore our estimates of mortality are biased upward. We have no possibility to differentiate tag failure from natural

mortality based on tracking data, but we have evidence that tag failure existed by recapturing a few tagged fish that were no longer transmitting data. Furthermore, 13 individual fish appeared to have died based on tracking data, but were later found to have produced offspring in spring 2012. We considered these fish as alive in our survival analysis. Hence, overall our mortality estimates likely represent an overestimate of mortality rates, but we assume the error is systematic across treatments and therefore does not affect our relative fitness measures.

With respect to pike, our aim was to compare the impacts of translocation to natural mortality rate in the lake from the moment the translocated treatments were introduced into the study lake. Therefore, we excluded 16 control fish from our survival analysis that died (or had tag failures) between the spring stocking of the resident control treatment and the autumn stocking of the three other treatments.

To assess tagging mortality, we compared the mortality rate over 1 month of eight resident control fish tagged between 13 and 16 September to the resident control fish tagged in Spring 2011 that were still alive by 13–16 September, assuming any mortality from fish stocked in Spring was due to natural causes. We compared estimated 95% CIs of the mortality rates to assess for a significant tagging mortality relative to control mortality according to Wilde, Pope, and Strauss (2004). All eight resident control pike, tagged and released between 13 and 16 September survived. During a 1-month period following their release, one control fish added in Spring 2011 died. Therefore, we found no significant impact of transmitter implantation on mortality, and most pike mortality was likely from other causes.

2.5 | Measuring reproductive success

The reproductive success was only measured in pike because there is no opportunity to sample sufficient catfish offspring with reasonable effort in our study lake as their recruitment is very low and sporadic. To sample the young-of-the-year offspring (YOY) of pike, we randomly sampled the shoreline (the main location of structure in our study lake to provide shelter for YOY pike; Craig, 2008; Skov & Berg, 1999) by electrofishing from May to October 2012 along 50 m transects covering the whole shoreline per day (in total 40.8 hr of electrofishing, electrofishing gear as above). Over the course of 49 sampling days, 304 YOY were caught. Fin clips were taken from these YOY upon capture, and from adults during implantation of the acoustic transmitters. From the fin-clips, DNA was extracted with a genomic DNA isolation kit for tissue and cells (Nexttec). Multiplex polymerase chain reactions (PCRs) from a total of 13 microsatellites (see Table S6) were performed with the Multiplex PCR kit (Qiagen). Fragment analysis was done via capillary electrophoresis using an 'Applied Biosystem 3500 xL' machine (Applied Biosystems) and 'Gene Mapper 4.1' software (Life Technologies).

Parentage assignment was performed with Cervus 3.0 (Kalinowski, Taper, & Marshall, 2007). The aim was to assign

304 YOY pike caught and genotyped in 2012 to the telemetry pike stocked/tagged in 2011. To that end, the adults sampled in 2012 were supplemented by additional 1,039 pike caught and genotyped in lake Kleiner Döllensee from 2007 to 2010 obtained through the study of Pagel, Bekkevold, Pohlmeier, Wolter, and Arlinghaus (2015), because these fish could have survived to 2012 and been in the spawning population. Genotyping errors were set to 1% and CIs were initially tested from 95% to <60% to maximize assignment of all YOY genotypes to parents. To assess assignment efficiencies at lower than 95% CIs, internal standards were employed created *in silico* with Hybridlab 1.0 (Nilsson, 2006) from defined crossings of known parental genotypes. Of the 600 randomly selected genotypes from all possible crossings, 98.8% were correctly assigned to at least one parental pike. This result was used as an indicator of highly probable assignment of YOY to unknown parental pike of the 2012 spawning season even at CIs >60% during the actual assignments.

2.6 | Environmental variables

Our objective was to investigate the behavioural effects of translocation after accounting for behavioural variation due to environmental change, which will also influence behaviour. To that end, we used data from a weather station installed in Kleiner Döllensee, which records air temperature (°C), air pressure (hPa) and wind velocity (m/s) at 10-min intervals. Data from an in-lake water quality sensor (YSI 6600, YSI Inc.), situated 2 m deep in the epilimnion in the pelagic zone of Kleiner Döllensee, additionally provided water temperature (°C), turbidity (ntu), conductivity ($\mu\text{S}/\text{cm}$), dissolved oxygen concentration (mg/L) and chlorophyll a concentration ($\mu\text{g}/\text{L}$) at 15-min intervals.

2.7 | Data analysis

We used a principal component analysis (PCA) to understand collinearity among the scaled and centred environmental variables. As our analyses for pike and catfish were based on different time periods with different temporal resolution, we conducted separate PCAs for catfish based on daily environmental averages, and pike based on weekly averages. Based on the respective loadings of the PCAs (Tables S4 and S5) we narrowed down several variables, which explained the most environmental variation to be included in our statistical analysis in their original, untransformed form. We only selected one variable with a high loading value per PC axis to avoid collinearity and we used original scalings of key indicator variables rather than PCA scores to improve interpretability.

We ran four separate models in which we predicted log-transformed distance travelled for pike and catfish, and log-transformed activity-space size for pike and catfish. Linear mixed effects models (Bolker et al., 2009) were used to account for the repeated measures of multiple individual fish over time, and the ability to account

for temporal autocorrelation in behavioural measures. Our models included the environmental variables, fish size (total length), day (or week for pike) and treatment as fixed effects. Environmental variables were centred for each catfish ID to measure the effect of relative environmental change (Van De Pol & Verhulst, 2006), as catfish were added to the sample throughout the tracking period. We were interested in the coefficient estimate of the treatment effect as a test of our hypotheses. Random slopes based on individual ID were included in the model. If assumptions of heteroscedasticity were violated (checked by visual inspection of residuals), we added variance weights to the fixed effects causing the violation (for details, see Zuur, Ieno, Walker, Saveliev, & Smith, 2009), and we accounted for temporal autocorrelation across the day or week. Models were implemented using the NLME package (Pinheiro, Bates, DebRoy, & Sarkar, 2018) in R (version 3.5).

We assessed statistical differences in mortality by fitting a Cox proportional-hazards model fit to Kaplan–Meier curves, where data were right censored after the last day of tracking. We applied a firth correction and assessed *p*-values and CIs by the Wald method (Firth, 1993), using the R package COXPHF (Ploner & Heinze, 2015), to deal with quasi-separation of data as the resident control treatment did not show any mortality after autumn 2011. We included total length as a covariate in the Cox proportional-hazards model to control for size-dependent mortality.

Reproductive success expressed as number of offspring was calculated by applying Hurdle Regression (Zeileis, Kleiber, & Jackman, 2008) using the R package PSCL (Zeileis et al., 2008) to account for zero inflation (Martin et al., 2005) in the dataset resulting from pike without offspring. The hurdle model specifically assesses whether individuals differed among treatments in their probability of reproducing at all, and the differences among treatments in the number of offspring for individuals that had at least one offspring. We included total length as a covariate in the hurdle regression to control for size-related differences in reproductive success and included all living fish at the time of stocking in September 2011 in our analysis.

3 | RESULTS

3.1 | Description of fish behaviour

The pike ($n = 114$ individuals generating data throughout the tracking period) swam on an average 6.37 km (range: 0–50.24 km) per week (Figure 2), and had an average weekly activity-space size of 3.12 ha (range: 0.22–14.96 ha) over 22 weeks from 17 October to 14 March (Figure 3). The pike of all treatments showed clear peaks in activity in early spring, between 23 January and 12 March, which likely coincided with pre-spawning behaviour.

Between 1 October and 31 January, the catfish swam on an average 1.66 km (range: 0.003–10.05 km) per day during the first measurement period (2010/2011) and swam on an average 3.88 km (range: 0.003–13.00 km) per day during the second measurement

FIGURE 2 A comparison of weekly activity levels of four pike treatments across the entire 22-week tracking period from October 17 to March 14. The top panel shows a direct comparison of the four treatments, while the bottom four panels show each time series separately where the shaded errors show the SD of the distance travelled for each week

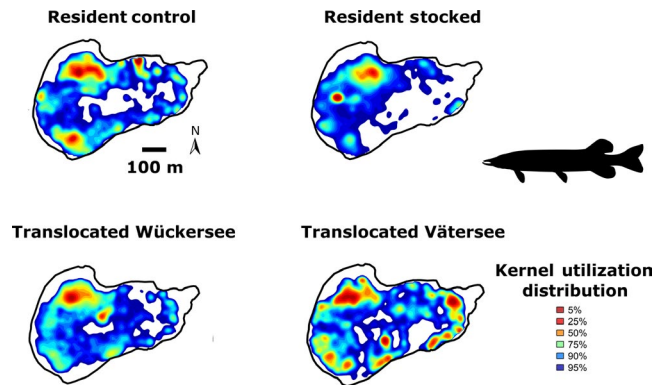
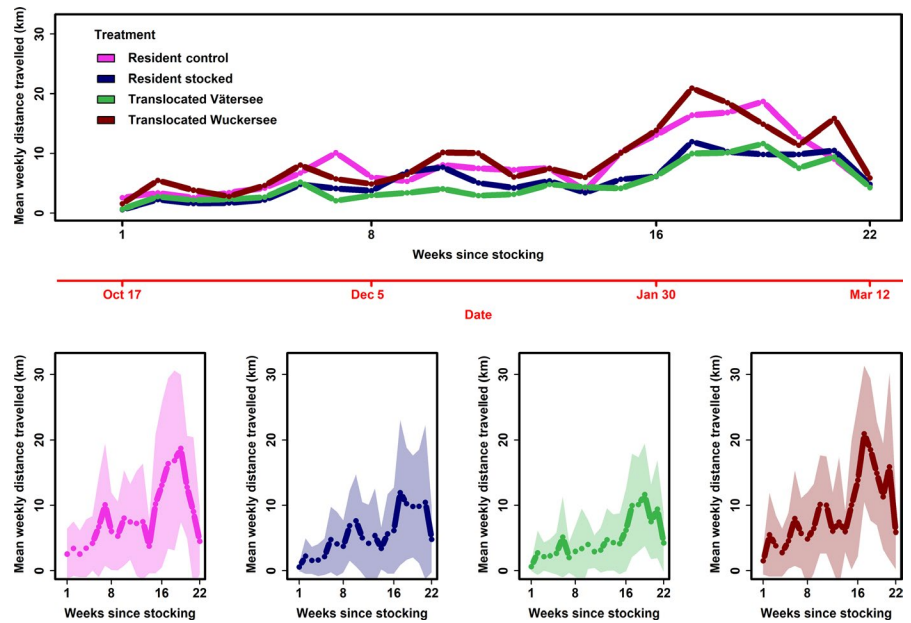


FIGURE 3 A comparison of activity-space size estimated by kernel utilization density for four treatments of pike tracked over the entire 22-week study period from 17 October to 14 March. The black outline represents the shoreline of the study lake, Kleiner Döllensee, and the heat maps indicate the pike hotspots

period (2014/2015; Figure 4). Relative to pike, the catfish had a more stable activity pattern over time. There was no obvious activity peak in the 2010/2011 tracking period, but activity peaked in December in the 2014/2015 season (Figure 4). The catfish had an average daily activity-space size of 1.35 ha (range: 0.19–12.27 ha) per day in the first measurement period and an average daily activity-space size of 2.40 ha (range: 0.19–11.47 ha) in the second experimental phase (Figure 5), suggesting among year variability in average behaviours.

3.2 | Translocation and fish behaviour

3.2.1 | Pike

Pike activity was unrelated to stocking treatment (Figure 2), but the pike's activity increased with pike total length and calendar week

(Table 1). The activity-space sizes of the resident stocked fish were not different from controls. By contrast, the two translocated origins revealed a higher activity-space size than the resident controls over 22 weeks tracking period from 17 October to 14 March, but this was statistically significant only for one of the two translocated treatments (Wuckersee; Figure 3). The elevated activity-space use of the translocated Wuckersee treatment was consistent over the 22-week experimental period as there was no detectable interaction between the measurement week and any of the treatment groups (Table 2). The activity-space size of the pike was positively related to the pike's total length. There were no detectable relationships of environmental variables (temperature, oxygen) and pike behaviour, but there was a trend for increasing oxygen increasing activity-space size ($p = 0.06$) and increasing air pressure reducing activity ($p = 0.08$; Tables 1 and 2).

3.2.2 | Catfish

The activity of the catfish did not differ among the stocking treatment (Figure 4; Table 3), but there was a trend for catfish becoming less active with increasing dissolved oxygen levels ($p = 0.06$). Moreover, there was a difference in activity between years independent of origin, where activity was higher in the second tagging year than in the first (Figure 4; Table 3). Both catfish activity and activity-space size were unrelated to catfish size (Tables 3 and 4). Translocated catfish had a higher activity-space size than their resident conspecifics (Figure 5; Table 4). The activity-space size was also positively related to water temperature, and there was a negative relationship between activity-space size and dissolved oxygen ($p = 0.06$, Table 4), which was close to significance. Finally, the activity-space size was larger overall in the 2014 stocking period relative to the 2010 stocking period and November relative to October (Table 4).

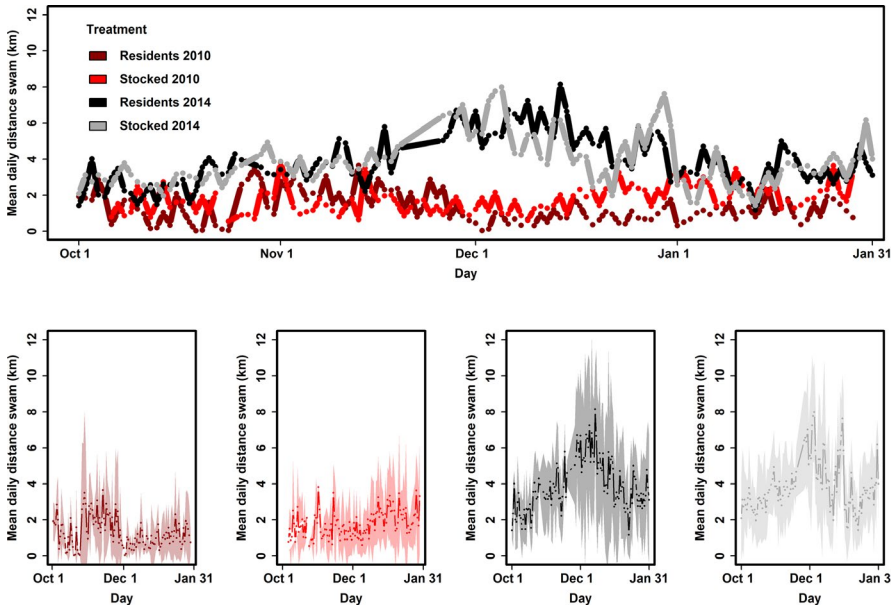


FIGURE 4 A comparison of daily activity levels of resident and translocated catfish in two tracking periods (2010 and 2014) over 4 months of tracking. The top panel shows a direct comparison of the mean daily activity of the four groups, while the bottom four panels show each mean time series separately where the shaded errors show the SD of the distance travelled for each day

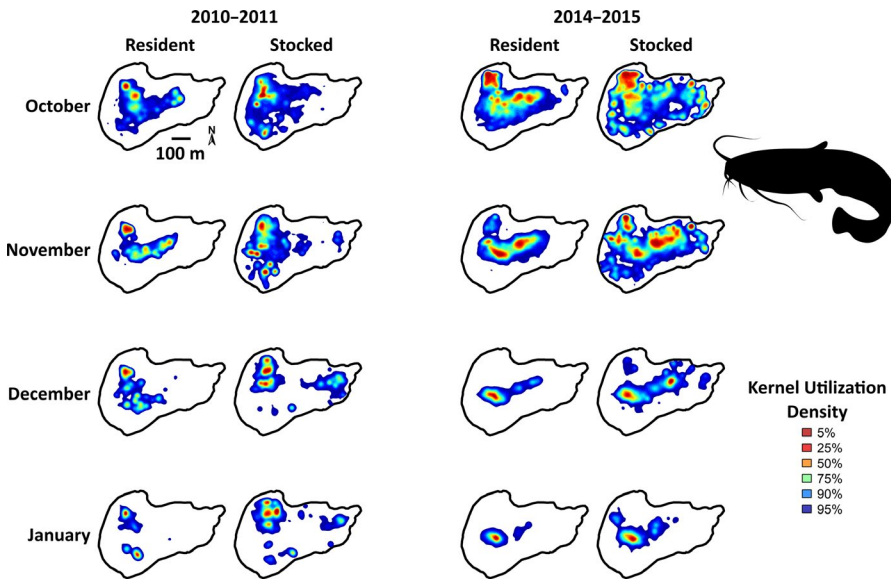


FIGURE 5 Comparison of resident and stocked European catfish monthly activity-space sizes estimated with kernel utilization density methods for two different stocking periods. The black outline represents the shoreline of the study lake, Kleiner Döllnsee, and the heat maps indicate the catfish hotspots. Translocated catfish had consistently larger activity-space sizes than resident catfish

3.3 | Translocation and mortality

With respect to pike, at the moment where the three other treatments were added to the lake in October 2011, including eight newly tagged resident fish, 17 resident control fish tagged in spring were still transmitting positions. During the next 22 weeks, zero of the 24 resident control pike (0–3.3% 95% CI) died, while 6 of 43 resident stocked (2.8–11.7% 95% CI), 14 of 43 translocated Vätersee (8.8–20.4% 95% CI) and 11 of 41 translocated Wuckersee fish (6.4–17.2% 95% CI) died.

The mortality of the translocated pike was distributed across the 22-week tracking period until March with no clear moment of high mortality (Figure 6). The survival analysis indicated a higher mortality rate in the translocated Vätersee treatment relative to the resident control treatment, and strong indications of a higher

mortality rate of the translocated Wuckersee treatment relative to the resident control treatment ($p = 0.06$, Figure 6; Table 5). In terms of mortality, the stocked resident pike were in between the stocked pike and the mortality of the resident fish as predicted, but with no differences to the resident control fish that were not subjected to stocking stress. A Cox proportional hazard model comparing only the two translocated treatments to the resident stocked treatment showed detectable differences between the translocated Vätersee treatment and the resident stocked treatment, but not between the translocated Wuckersee treatment and the resident stocked treatment (Table S7). No size-related differences in mortality were observed. The assumption of proportional hazards was met (Table S8).

We observed no catfish mortality and thus no differences in mortality among resident and translocated fish.

TABLE 1 Coefficients, SEs, statistics and *p*-values from a linear mixed effects model predicting log transformed pike weekly activity, where all coefficients are relative to the resident control treatment. An asterisk indicates statistical significance

Predictor	Coefficient	SE	df	t-value	p-value
Intercept	4.82	1.36	1,486	3.55	<0.001*
Resident stocked	0.23	0.33	109	0.52	0.61
Translocated Vätersee	-0.44	0.39	109	-1.14	0.26
Translocated Wuckersee	0.14	0.37	109	0.37	0.70
Week	0.08	0.03	1,486	2.67	0.007*
Total length	0.004	0.001	109	3.48	<0.001*
Water temperature	0.0002	0.002	1,486	0.01	0.92
Dissolved oxygen	-0.028	0.02	1,486	-1.14	0.26
Air pressure	-0.084	0.05	1,486	-1.75	0.08
Week × resident stocked	-0.015	0.03	1,486	0.47	0.64
Week × translocated Vätersee	0.02	0.03	1,486	0.70	0.49
Week × translocated Wuckersee	0.01	0.03	1,486	0.50	0.62

TABLE 2 Coefficients, SEs, statistics and *p*-values from a linear mixed effects model predicting log transformed pike weekly 95% activity-space size, where all coefficients are relative to the resident control treatment. An asterisk indicates statistical significance

Predictor	Coefficient	SE	df	t-value	p-value
Intercept	7.062	0.750	750	9.410	<0.001*
Resident stocked	0.044	0.25	96	0.17	0.86
Translocated Vätersee	0.165	0.240	96	0.69	0.49
Translocated Wuckersee	0.58	0.21	96	2.701	0.008
Week	0.023	0.016	750	1.44	0.15
Total length	0.005	0.001	96	6.75	<0.001*
Water temperature	0.0004	0.001	750	-0.32	0.75
Dissolved oxygen	0.024	0.013	750	1.89	0.06
Air pressure	0.040	0.025	750	1.58	0.12
Week × resident stocked	-0.004	0.017	750	-0.24	0.81
Week × translocated Vätersee	-0.002	0.016	750	-0.12	0.91
Week × translocated Wuckersee	-0.022	0.015	750	-1.48	0.14

TABLE 3 Coefficients, SEs, statistics and *p*-values from a linear mixed effects model predicting log transformed catfish daily activity. Month 2, Month 3 and Month 4 represent November, December and January respectively, where all coefficients are comparisons to Month 1, October. An asterisk indicates statistical significance

	Coefficient	SE	df	t-value	p-value
Intercept	5.81	0.86	2,011	6.72	<0.001*
Translocation	0.65	0.40	26	1.64	0.11
Month 2	1.10	0.33	2,011	3.34	0.001*
Month 3	0.74	0.45	2,011	1.65	0.099
Month 4	0.57	0.48	2,011	1.20	0.23
Total length	-0.0003	0.001	26	-0.49	0.64
Year 2	1.50	0.35	26	4.30	<0.001*
Water temperature	-0.016	0.042	2,011	-0.39	0.69
Air pressure	0.006	0.004	2,011	1.56	0.12
Dissolved oxygen	-0.086	0.05	2,011	-1.87	0.062
Translocation:Month 2	-0.56	0.39	2,011	-1.42	0.15
Translocation:Month 3	-0.032	0.39	2,011	-0.08	0.94
Translocation:Month 4	-0.13	0.41	2,011	-0.32	0.75

	Coefficient	SE	df	t-value	p-value
Intercept	8.55	0.35	2,024	24.74	<0.001*
Translocation	0.44	0.19	26	2.31	0.03*
Month 2	0.54	0.22	2,024	2.50	0.01*
Month 3	0.46	0.29	2,024	1.61	0.11
Month 4	0.33	0.30	2,024	1.11	0.27
Total length	-0.0001	0.0002	26	-0.37	0.71
Year 2	0.50	0.17	26	2.90	0.01*
Water temperature	0.08	0.03	2,024	3.05	0.002*
Air pressure	0.002	0.0002	2,024	1.01	0.31
Dissolved oxygen	-0.05	0.03	2,024	-1.83	0.07
Translocation:Month 2	-0.16	0.25	2,024	-0.65	0.52
Translocation:Month 3	-0.20	0.22	2,024	-0.91	0.37
Translocation:Month 4	-0.13	0.23	2,024	-0.56	0.58

TABLE 4 Coefficients, SEs, statistics and p-values from a linear mixed effects model predicting log transformed catfish daily 95% activity-space size. Month 2, Month 3 and Month 4 represent November, December and January respectively, where all coefficients are comparisons to Month 1, October. An asterisk indicates statistical significance

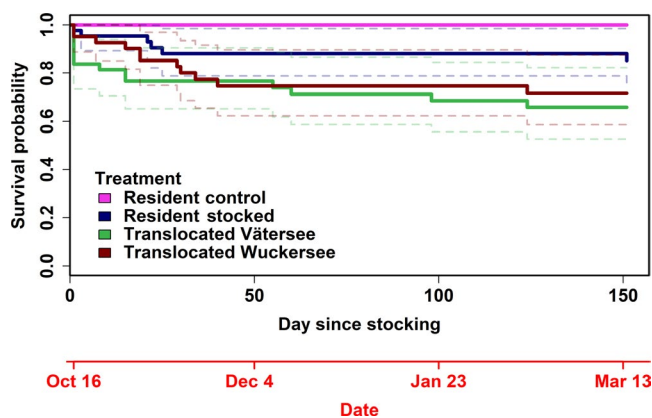


FIGURE 6 The survival probability after stocking for four treatments of pike represented by Kaplan–Meier survival curves. Dotted lines indicate upper and lower 95% CIs. Day 0 on the x-axis refers to the first day of stocking for the resident stocked, translocated Vätersee and translocated Wuckersee treatments in Fall 2011. The resident control treatment, was stocked earlier in Spring 2011, and therefore the resident control curve represents natural mortality without mortality impacts from stocking and handling stress

TABLE 5 Coefficients, hazard ratios, SEs of the coefficients, statistics and p-values of a Cox proportional hazards model with a firth correction assessing survival after stocking, where all coefficients are relative to the resident control treatment. Confidence intervals and p-values were evaluated by Wald method. An asterisk indicates statistical significance

Treatment	Coefficient	Hazard ratio	SE (coef)	z-value	p-value
Resident stocked	2.10	8.17	1.52	1.91	0.16
Translocated Vätersee	3.05	21.19	1.49	4.20	0.04*
Translocated Wuckersee	2.81	16.60	1.50	3.53	0.06
Total length (mm)	-0.002	1.00	0.002	0.63	0.43

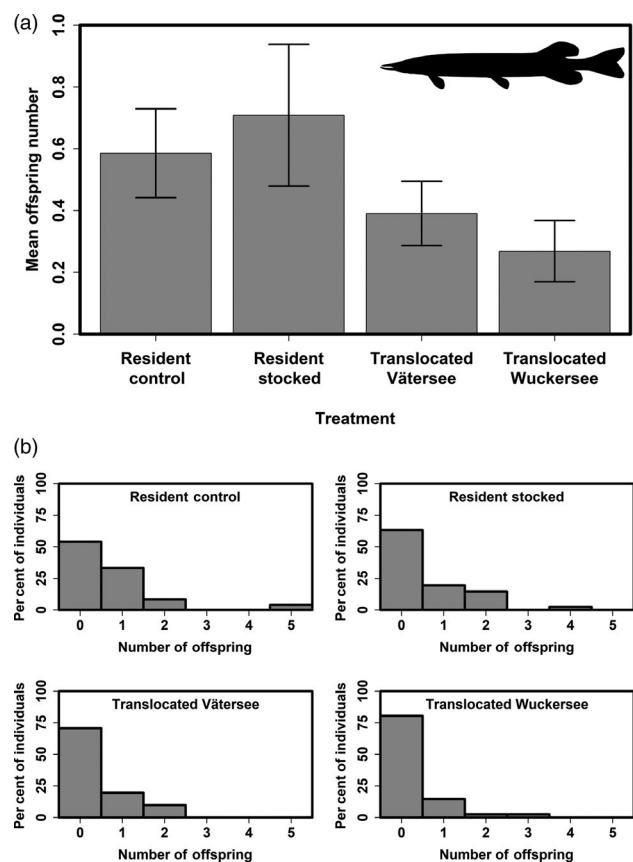


FIGURE 7 The mean number of offspring per treatment (panel a). Error bars represent standard error of the mean. There were no differences between the control and any other treatments as assessed by a hurdle model (Table 6). Panel b shows the percentages of individuals in each treatment contributing various numbers of offspring in the 2012 young-of-the-year sampling

3.4 | Translocation and pike reproductive success

The tagged pike contributed to 66 of the 304 sampled juvenile offspring. The majority, 104 (69%) of the tagged pike, did not contribute

TABLE 6 Coefficients, SEs, statistics and *p*-values from a hurdle model assessing differences in reproductive output among pike treatments in the year following translocation

	Count model coefficients				Zero hurdle model coefficients			
	Coefficient	SE	z-value	<i>p</i> -value	Coefficient	SE	z-value	<i>p</i> -value
Intercept	-2.61	1.51	-1.73	0.08	-0.55	1.21	-0.45	0.65
Resident stocked	-0.01	0.50	-0.02	0.98	0.42	0.52	0.81	0.42
Translocated Vätersee	-0.71	0.58	-1.22	0.22	-0.36	0.47	-0.77	0.44
Translocated Wuckersee	-0.34	0.63	-0.54	0.59	-0.83	0.51	-1.61	0.11
Total length (mm)	0.005	0.003	1.91	0.056	-0.00008	0.003	-0.03	0.97

to the sampled offspring, 30 (20%) of tagged pike had at least one offspring in the sample, and 16 (10%) pike had two or more offspring, with a maximum of five offspring per individual (Figure 7). The highest percentage of tagged pike with zero offspring in the sample was revealed in the two translocated origins (80.5% in translocated Wuckersee and 72.1% in translocated Vätersee compared to 64.3% in resident stocked and 54.2% in resident control; Figure 7b). On average, the resident fish of the two treatments (control or stocked) also had a higher mean number of offspring in the sample than the two translocated origins (Figure 7), but differences were not statistically different, both in terms of the probability of producing at least one offspring or none, and the number of offspring produced per capita from reproductively successful individuals (Table 6). We did not detect any relationship between total length and reproductive success, but there was a strong trend for larger, more fecund individuals to produce more offspring in the sample ($p = 0.056$, Table 6). All but one sampled offspring of translocated fish were the product of hybrids with the resident population, indicating substantial gene flow from the stocked non-native fishes into the wild stock (Table S9).

4 | DISCUSSION

Contrary to our predictions that the behavioural impacts from translocation would vanish over time, we found adult top predators of two species (pike and catfish) translocated to a novel environment to show persistent behavioural differences compared to resident conspecifics over a period of several months of post-translocation. Hence, we find that even large adult individuals of top predators may remain maladjusted to their new environment after introduction over the long term (months). Additionally, we only found behavioural impacts with respect to activity-space size, and not activity in disagreement to our prediction that both activity and activity-space size would be elevated in translocated individuals. In agreement with expectations, our results also showed that the impacts of translocation can have long-term fitness consequences in some species. In particular, we observed an increase in mortality rates for translocated pike. By contrast, despite altered activity-space size behaviour, translocated catfish did not show different mortalities relative to resident fish.

Maladjusted behaviour and elevated mortality in stocked hatchery fish has been documented in a range of species (Lorenzen, 2006; Lorenzen et al., 2012). These impacts are typically attributed to domestication effects stemming from hatcheries (Garlock, Monk, Lorenzen, Matthews, & St Mary, 2014; Lorenzen et al., 2012), relaxed natural selection in a hatchery (Araki et al., 2008), the release of a life stage with high density-dependent mortality (Hühn, Lübke, et al., 2014; Lorenzen, 2005) and a lack of life-skills training to cope with natural challenges (Brown, Ferrari, & Chivers, 2013; Olla et al., 1998; Sloychuk, Chivers, & Ferrari, 2016). In contrast to most stocking studies, we stocked wild fishes, which have had full life-skill training and full access to natural prey and predators in their original environment. Therefore, it is striking that even large, wild, experienced adult top predators also struggle to behaviourally adjust after introduction to a novel lake, and in the case of pike also show potential long-term fitness impairments in terms of mortality unrelated to stocking-induced transport stress.

It is unclear whether the behavioural effects that we observed in translocated catfish are because of social competition with resident individuals (similar to a study in pike, Edeline et al., 2009) leading translocated catfish to be consistently displaced from favourable habitat through prior-residence effects (Cutts, Brembs, Metcalfe, & Taylor, 1999; Deverill et al., 1999) or simply represent a struggle in finding food (leading to extended activity-space sizes). Our result may also be explained by lack of local adaptation (Carvalho, 1993; Cross, 2000). We are cautious to not overinterpret our findings as evidence of local adaptation because reaching such a conclusion would demand to test all genotypes for behaviour and fitness in both local and non-local environments through reciprocal transplant designs to rule out effects that may stem from among-ecosystem variation in habitat quality and ecosystem-specific expression of behavioural phenotypes (Kawecki & Ebert, 2004). A possible alternative non-evolutionary explanation for our findings may relate to prior-residence effects (Cutts et al., 1999; Kvingedal & Einum, 2011) and to intrinsic population-specific differences in behaviour and reproductive performance. Moreover, in the case of catfish also carry-over impacts of stocking-induced stress on behaviour are conceivable, which we cannot discount in this species due to the lack of an appropriate stocking-stress control. In the case of pike, however, the fact that the stocked resident fish were either performing in-between the resident controls and the two translocated origins

(e.g. in terms of survival) or similarly to resident fish (in terms of behaviour and reproductive success), is strongly suggestive that the differences in behaviour and fitness observed in the pike experiment are related to their foreign origin rather than being caused by stocking-induced stress. Also in pike, prior-residence effects of resident fish exploiting the most favourable habitats is a strong candidate explaining the behavioural responses (Skov et al., 2011). However, as the mortality rate of the translocated Wuckersee treatment was not different than the mortality rate of the resident stocked treatment, we cannot clearly conclude that the increased mortality of the translocated Wuckersee treatment was due to any factors beyond handling stress.

Pike and catfish responded largely similar (with the exception of one translocated pike treatment where the statistical significance level of $p = 0.05$ was not reached) to introduction by elevating space use over extended periods of times (months). We translocated catfish on top of a naturally recruiting catfish population, without removing catfish prior to the introduction. By contrast, pike of two origins were translocated after first removing the same abundance of resident pike, keeping the natural population abundance at carrying capacity after the stocking intervention. As the catfish population has only been in the lake for a few generations since its introduction in the early 1990s, the population might not have reached carrying-capacity yet. Therefore, we cannot infer whether the degree of resource competition experienced by the translocated catfish and pike differed. However, because we did not remove resident catfish prior to the introduction it seems plausible that the translocated catfish experienced more density-dependent resource competition compared to pike, which could have increased the pressure on the newly translocated catfish to explore the environment intensively in the struggle to finding food. This in turn could explain why the activity-space size of the translocated catfish was consistently elevated relative to wild conspecifics—a pattern only seen conclusively (when judged based on statistical significance) in one foreign pike population. Previous catfish stocking experiments in Czech reservoirs have shown that catfish respond to conditions surpassing ecological carrying capacity with extended movements, declines in growth and high catchability to angling gear, indicating intensive foraging in their new environment (Vejřík et al., 2017, 2019). Also, in previous work catfish have been found to be stressed by social competition (Carol et al., 2007; Slavík & Horký, 2009; Slavík et al., 2014), and are also challenged by finding shelter among unfamiliar individuals (Slavík, Horký, Maciak, & Wackermannová, 2016). Alternatively, because the translocated catfish were relatively large-bodied, even the smallest catfish that we stocked unlikely experienced substantial risk of predation. This is indicated by the lack of size-dependent activity or activity-space size documented in catfish, while we found a positive relationship of pike size and both activity and activity-space size (in agreement with previous work in pike, Jepsen, Beck, Skov, & Koed, 2001; Kobler et al., 2008; Rosten, Gozlan, & Lucas, 2016), suggesting the smaller pike reduced swimming activity to reduce exposure to possible predation and minimize risk of predation (Chapman & Mackay, 1984; Grimm, 1983; Nilsson, 2006). The presence of a size

refuge in catfish could also have allowed the smaller catfish that were stocked to intensively explore the environment. By contrast, the smaller pike likely experienced significant risk of cannibalism from conspecifics or predation risk by other predators (including large catfish). The differential risk of predation experienced by pike and catfish in our study as well as potential differences in resource competition experienced by the stocking treatments could collectively explain why the behavioural reactions of the translocated pike treatments were not fully consistent over both treatments in statistical terms. We cannot rule out species-specific behavioural differences as also contributing to the explanation of our results.

The persistently elevated activity-space size of the translocated catfish is managerially relevant as the catfish invasion front is rapidly progressing due to climate change in many areas of the world (Copp et al., 2009; Cucherousset et al., 2017). Catfish encountering an invasion front, whether by anthropogenic introduction or natural dispersal, may increase their space use upon encountering a novel environment, which would thereby accelerate the dispersal rate (Chapple, Simmonds, & Wong, 2012; Sih, Cote, Fogarty, Weinersmith, & Brodin, 2010).

We only observed statistically different behaviour in one of our translocated pike treatments, which showed elevated space-use similar to the catfish. As noted before, the density of the pike population did not change through the experiment as the number of pike added to the study lake during the translocation was also removed before the translocation. Hence, the impacts we observed were not the result of enhanced competition for limited resources. Interestingly, substitutive stocking experiments (as in the case of pike in this study) with salmonids also did not lead to any differences in upstream or downstream movements between juvenile hatchery and wild brown trout *Salmo trutta* (Bohlin, Sundström, Johnsson, Höjesjö, & Pettersson, 2002). By contrast, stocking salmonids beyond carrying capacity has been found to show behavioural impacts similar to those we observed (Bachman, 1984; Baer & Brinker, 2008; Kaspersson et al., 2013; Weber & Fausch, 2003), where the intensity of interactions increased with density for some species (Ellis et al., 2002; Keeley, 2000). It is very likely that in our study, intensive agonistic social competition still played an important role in pike establishment. Pike growth has been shown in the past to be inhibited by social competition without any change in forage abundance (Edeline et al., 2009), and previous stocking experiments with young-of-the-year pike have revealed that stocked individuals are displaced at high rates by wild conspecifics (Skov et al., 2011). Therefore, we propose that translocated pike were displaced by conspecifics from forageable habitats through agonistic interactions (Nilsson, 2006), in turn increasing space use at no change in swimming activity.

We found an increased mortality rate for all the translocated pike individuals, with the stocked resident pike being in between the non-stocked wild fish and the two stocking origins. The increased mortality rate of the two translocated pike origins can most likely be attributed to the challenge of adjusting to a novel environment as the resident stocked treatment did not show increased mortality rates relative to the resident controls. Also the resident stocked

treatment showed a mortality pattern in between the resident control and the two translocated populations, suggesting a trend leading to a survival cost from stocking stress. Furthermore, we did not find a difference in mortality rates between the translocated Wuckersee treatment and the resident stocked treatment suggesting some mortality is also likely to be a result of handling stress. In earlier translocation experiments with smaller fish, the survival rate of wild reared pike was found to be higher than their hatchery reared counterparts (Franklin & Smith Jr., 1963; Hühn, Lübke, et al., 2014), agreeing with our work. We cannot exactly point to the mechanism that resulted in the elevated mortality of the translocated pike. It is possible that the translocated pike suffered from growth impairments (Hühn, Lübke, et al., 2014; Klefoth et al., 2011) or poor condition elevating mortality (Billard, 1996; Fabricius & Gustafson, 1958). It is also possible that the translocated pike experienced higher rates of infections and diseases (Snow, 1974) or cannibalism through elevated movement and thereby increased encounters with predators (Hulthén et al., 2017).

The translocated and resident pike showed differences in reproductive performance that followed the trajectory reported for survival, with the two translocated origins exhibiting lower reproductive success than the resident conspecifics. The treatment (Wuckersee) with the lowest reproductive success also demonstrated elevated space use. However, variation in reproductive performance among individuals was high and hence we did not find statistical support for a reproductive cost of being foreign in pike. The translocated pike overwhelmingly produced hybrids with resident pike, thereby adding to gene flow from the non-local genotypes into the resident population. The reproductive success of the translocated individuals may firstly be attributed to the absence of domestication effects typical of stocked fish (Lorenzen et al., 2012), which may fundamentally alter the life-history trajectories of the fish in a manner that might downplay reproductive allocation in favour of growth (Garlock et al., 2014; Lorenzen et al., 2012). Secondly, the translocated fish were introduced from nearby lakes with similar limnological characteristics, and therefore the spawning conditions and timing were probably similar to Kleiner Döllnsee. Perhaps if pike were translocated from a location several degrees in latitude away from the study lake, with a different set of local conditions, the translocated fish could be less fit as shown in salmonids (Fraser, Weir, Bernatchez, Hansen, & Taylor, 2011). More research is necessary to understand the fitness of wild stocked fish, as fish stocking practices have spread non-local genotypes widely across catchments (Bekkevold, Jacobsen, Hemmer-Hansen, Berg, & Skov, 2015; Eschbach et al., 2015), thereby interrupting local evolutionary processes and potentially creating situations of outbreeding depression (Lorenzen et al., 2012).

We did not observe any long-term adverse behavioural effects from handling and transport in adult resident pike relative to resident controls, though our analysis points towards a weak effect on natural mortality rate. We cannot draw conclusions about short-term effects of stocking stress as we deliberately excluded the first week of tracking post-stocking in our analysis to allow the fish to acclimate to their environment ensuring immediate stress from tag implantation, or stocking transport would not cloud our measure of long-term adjustment

to a novel environment. Typically, stress can be categorized into three stages, primary, secondary and tertiary, where the primary and secondary responses lead to the tertiary behavioural responses (Barton, 2002; Wendelaar Bonga, 1997). Tertiary stress can be shown in impaired growth rate, reduced immune responses and altered reproductive ability (Barton, 2002; Barton & Iwama, 1991; Einarsdóttir, Nilssen, & Iversen, 2000; Fries, 1986; Pickering & Pottinger, 1989), affecting the overall long-term condition of the fish and general competitive ability against more dominant resident fish (Edeline et al., 2008). As we did not observe changes in pike behaviour of the resident stocked relative to controls, it is unlikely that the pike were experiencing the effects of chronic stress from the stocking procedures. These findings agree with earlier studies showing that pike can recover from stressful catch-and-release events within a few hours (Arlinghaus, Klefoth, Cooke, Gingerich, & Suski, 2009; Arlinghaus, Klefoth, Kobler, & Cooke, 2008; Louison, Stein, Suski, Hasler, & Fenske, 2016; Pullen et al., 2017). However, Klefoth et al. (2011) reported long-term growth deficits in the from a single hooking and release event in the same study lake, suggesting that behavioural recovery does not necessarily mean that fitness remains unaffected even by a single stressor event under high food competition situations. By including a resident treatment that experienced stocking and transportation stress in our experimental design, we were able to test for impacts of stocking and transportation stress in isolation.

5 | CONCLUSIONS

We found that translocating large individuals to a nearby environment with a resident top predator population can cause long-term behavioural impairments symptomatic of elevated intraspecific competition and predation risk, leading to a challenge to establish. Furthermore, we found that releasing non-local wild fish into a natural ecosystem can lead to fitness impacts. Yet, despite being challenged, translocated fish hybridize with resident fish and contribute to gene flow, which can pollute and alter natural adaptations when stocking repeatedly happens in naturally recruiting stocks (Ayllon, Martinez, & Garcia-Vazquez, 2006; Perrier, Guyomard, Bagliniere, Nikolic, & Evanno, 2013). Many drawbacks to fish stocking are well known (Lorenzen et al., 2012); however, our study calls attention that even large individuals of top predators, which appear to be thriving could be performing poorly due to long-term stress from competitive interactions in their non-local environment. Our results suggest responses related to maladjustment to a non-local environment, but an ultimate test of local adaptation requires replicated local versus foreign study designs with reciprocal transplants (Kawecki & Ebert, 2004).

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AUTHORS' CONTRIBUTIONS

R.A., C.T.M., D.H. and T.K. conceived the ideas and developed methodology; C.T.M., D.H., E.E., R.H. and T.K. collected the data; C.T.M., B.C., P.C., E.E. and R.H. analysed the data; C.T.M. and R.A. led the writing and all authors contributed critically to the drafts and gave final approval to the data.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.95x69p8h1> (Monk et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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