



Ecological Consequences of Animal Migration: Prey Partial Migration Affects Predator Ecology and Prey Communities

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ABSTRACT

Patterns of animal migration and the ecological forces that shape them have been studied for centuries. Yet ecological impacts caused by the migration, such as altered predator–prey interactions and effects on community structure, remain poorly understood. This is to a large extent due to the scarcity of naturally replicated migration systems with negative controls, that is, ecosystems without migration. In this study, we tested whether partial migration of certain species within the overall prey community affects foraging ecology of top predators and thereby alters energy pathways in food webs. We carried out the study in independent

replicated freshwater lake systems, four with and four without opportunity for prey migration. Specifically, we compared predator foraging mode in lakes where cyprinid prey fish perform seasonal partial migrations into connected streams with lakes lacking migratory opportunities for prey fish. We found clear seasonal bottom-up effects of prey migration on predators, including changes in size structure and total biomass of ingested prey, size-specific changes in littoral versus pelagic origin of diet, and a higher degree of feast-and-famine for predators in systems with migratory prey. Our analyses further showed that partially migratory prey species constitute a larger part of the prey community in systems that allow migration. Hence, prey migrations have important implications for predator foraging ecology and may cause seasonal shifts in the importance of their supporting energy pathways. We suggest that such bottom-up effects of partial migration may be a widespread phenomenon both in aquatic and in terrestrial ecosystems.

Key words: bottom-up effects; freshwater fish; movement ecology; predation; pike; *Esox lucius*.

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Author's Contribution JB conceived the ideas and designed the study with support from CS, CB, KH, LAH, BBC and PAN; JB and CS collected the data; JHH analysed the samples; JB and HB analysed the data (HB specifically CPUE and length–weight relationship); JB and JHH led the writing of the manuscript. All authors read and commented upon earlier versions of the manuscript and gave final approval for publication.

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INTRODUCTION

Migration is a widespread and important ecological phenomenon occurring across the entire animal kingdom and over a variety of geographic distances (for example, Alerstam and others 2003; Hays 2003; Dingle and Drake 2007; Hansson and Åkesson 2014; Brönmark and others 2014). Animals migrate between habitats for a variety of reasons, for example, to enhance foraging opportunities, improve reproductive success, or to avoid predators or parasites (Fryxell and Sinclair 1988; Bowler and Benton 2005; Altizer and others 2011). The term migration often evokes images of spectacular seasonal movements of animal populations, and research on migration has historically mainly focused on the causes and patterns of these large-scale animal movements. However, migratory animals also have the potential to affect the stability and dynamics of entire ecosystems, by altering energy and nutrient pathways within and between their alternative habitats (Bauer and Hoye 2014; Hansson and Åkesson 2014). When considering ecological effects associated with animal migrations, the arriving species has primarily been in focus. Yet, individuals arriving to one habitat are undeniably linked to departure from another. Hence, when migratory animals are dominant or keystone species in their respective ecosystems, both their arrival and departure may have potential impacts on food-web structure and trophic dynamics.

Several studies have demonstrated top-down effects of predator migration on lower trophic levels (Brodersen and others 2008a; Post and others 2008), but studies of ecological bottom-up effects caused by seasonal departure of migratory prey in natural systems are scarce (see, however, Brodersen and others 2015 for trophic diversification effects). Such effects should nevertheless be expected, especially since many predators do not follow migrating prey (Fryxell and Sinclair 1988; Sinclair 2003). This has previously been hypothesized to affect predator feeding rates (Fryxell and others 2007), but could potentially also affect energy pathways in ecosystems and prey community structure. However, a key challenge when studying the effects of migration in the wild is to achieve replication at the level of populations and ecosystems and to have negative controls, that is, similar systems without migration. Due to their distinct geographic borders and spatial replication, freshwater lakes and the predator-prey interactions occurring within their fish communities are ideal natural systems for replicated study designs. Sea-

sonal fish migrations from lake ecosystems to connected streams provide a particularly powerful opportunity for cross-population studies on the consequences of animal migration (Brönmark and others 2008).

Migrations of cyprinid fish have received considerable attention during the last decade (for example, Jepsen and Berg 2002; Brönmark and others 2008; Brodersen and others 2008b; Skov and others 2011). Certain species of cyprinids, especially roach (*Rutilus rutilus*) and smaller specimens of bream (*Abramis brama*) and white bream (*Blicca bjoerkna*), migrate from their natal lakes into connected streams to overwinter and then return to the lake habitat in spring (Jepsen and Berg 2002; Skov and others 2008). The migrations are driven by seasonal shifts in the trade-off between predator avoidance and growth opportunities in lakes and streams (Brönmark and others 2008). Cyprinids generally leave the lake when the ratio between predation risk and growth opportunity becomes lower in the streams than in lakes during autumn (Brönmark and others 2008; Brodersen and others 2008b; Skov and others 2014; Hulthén and others 2015). This is caused by substantial reductions in potential growth rate at low temperatures in combination with sustained predation from pike (*Esox lucius*), which does not follow the migratory prey into the streams over winter (Skov and others 2008, 2011). Migration in cyprinid fishes is commonly partial (Chapman and others 2012), that is, not all individuals migrate due to intra-population differences in predation vulnerability (Skov and others 2011), personality (Chapman and others 2011) and size and energetic status (Brodersen and others 2008b). Despite this variation, a significant proportion of prey fish migrates from shallow lakes during winter, which would be predicted to have powerful implications for predators that remain resident in the lake habitat. This has yet to be empirically demonstrated and is a major focus of the present study.

The two other main objectives of this study are to examine how partial migration of prey affects (1) prey fish community structure, potentially as a consequence of species-specific ability to escape predation risk during winter, and (2) possible alterations of the relative reliance on the littoral and pelagic food chains in the energy flow from primary producers to top predators. We explore these objectives using a replicated design, where we compare the foraging ecology of piscivorous pike between four lakes with opportunity for seasonal partial migration for prey fish and four lakes without migration opportunity, that is, where all

prey fish remain resident in the lake throughout the year. Overall, we predict that predators in systems where prey can migrate which will have different feeding patterns over seasons compared to predators in systems where prey migration is not possible, with consequences for energy pathways from primary producers to top predators and prey community structure.

Specifically, we predict that (1) prey availability will be reduced during the migration period in lakes where prey are able to migrate, (2) predators in lakes with prey migration will have lower fish prey biomass in their stomachs during the migration period, (3) the diet of predators in systems with prey migration will be dominated by smaller prey during the migration period since migratory propensity in the main prey fish, roach, increases with size (Brodersen and others 2008b), (4) predators from systems with migrating prey will have a higher dependence on littoral food resources during the migration period, as migratory prey species generally inhabit open water while non-migratory prey species are more littoral (Skov and others 2008), leading to a change in energy pathways in the lakes with partial prey migration, (5) the predicted decrease in prey availability during the migration period in lake systems where prey have migration opportunity will lead to reduced predator somatic condition and, finally, (6) migratory prey species will be relatively more abundant, measured as the proportion of the total prey fish community (including both migratory and resident individuals), in lakes where they have the ability to migrate during winter.

MATERIALS AND METHODS

Study System

We evaluated seasonal changes in the feeding patterns of predatory pike in a total of eight shallow, eutrophic lakes in Denmark and Sweden (Table 1). All focal lakes contain populations of cyprinid prey fish, primarily roach (*Rutilus rutilus*) along with other prey fish species, predominantly perch (*Perca fluviatilis*). Pike is the dominant top predator in all lakes. Four of the lakes have connected in- and outlet streams to which cyprinid fish populations partially migrate during winter. These lakes are hereafter referred to as *open lakes*. The remaining four lakes have no connected inlet or outlet streams, ruling out migration from these systems, and these lakes are hereafter referred to as *closed lakes*. Partial migration has been reported in all of the open lakes (Jepsen and Berg 2002; Skov

and others 2008, 2010, 2014; Brodersen and others 2014). In lakes Loldrup Sø, Søgård Sø, and Krankejön, seasonal patterns of prey migration have been closely monitored for the last 11–14 years, including the year of the current study.

We sampled each lake on five occasions from August 2011 to May 2012, covering both the migratory and the residence period. We here define the migratory period as the time period covering the entire duration of the migratory cycle, from when the prey fish migrate out of the lake, across the winter stay in streams, until the fish have returned to the lake. Based on previous data on the migratory patterns of the cyprinid prey fish species (that is, Skov and others 2008, 2010, 2014; Brodersen and others 2014), we further classified the time of the five sampling events as *pre-migration* and *post-migration* (both in the residence period), and *early migration*, *mid-migration*, and *late migration* (all in the migratory period; Table S1, supplementary material).

Sampling of Predators

A total of 627 pike (total length range: 335–1017 mm) were caught by electrofishing in the littoral zone of the lakes during the study (Table S1). We excluded smaller pike, since they may not be fully piscivorous (Skov and others 2003). Size differed between individual lakes (mean length range: 489–656 mm), but not between lake types (Nested ANOVA; Lake type: $F = 0.22$; $p = 0.64$; Lake: $F = 16.0$; $p < 0.01$). Upon capture, pike were individually weighed (± 1 g), measured (nearest mm, total length), the stomach contents were collected by gastric lavage (Light and others 1983), and a muscle biopsy of white muscle tissue for isotope analyses was taken anterior to the dorsal fin (Schielke and Post 2010), after which pike were released at the capture location. Stomach content and muscle samples were frozen for later analyses upon return to the laboratory.

Prey Availability

On each sampling occasion, five randomly chosen transects, generally along edges of emergent or submerged aquatic vegetation in the littoral zone of each study lake, were electrofished for 5 min each. Each transect covered approximately 50–100 m. All potential prey fish (see below) caught in each transect were frozen and stored for later analysis in the laboratory, where individual prey fish were identified to species, and individually weighed and measured (to nearest mm). Prey availability was

Table 1. Area (km²), Depth (m), Mean Summer Secchi Depth (m), and Type of Lake (Migration Opportunities (Open) and Non-migration Opportunities (closed)) of the Eight Study Lakes

Lake	Lake type	Position	Area (km ²)	Depth (m)		Mean secchi depth (m)	Additional fish species present
				Max	Mean		
Fjällfotasjön	Closed	55°31'N, 13°18'E	1.55	2.5	1.4	0.4	Se; Ab; Bb; Ga; Tt (Aa; Sl; Ld)
Halesø	Closed	56°36'N, 9°35'E	0.10	1.1	0.8	Bottom	
Havgårdssjön	Closed	55°29'N, 13°21'E	0.54	5.8	3.1	1.1	Tt; Bb; Ab; Gc; Se (An; Ld; Cy)
Udbyover Sø	Closed	56°39'N, 10°12'E	0.21	2.6	1.1	0.8	Ca
Krankejön	Open	55°42'N, 13°28'E	3.38	3.0	1.0	1.6	Bb; Se; Tt; Ab; Gc (Ca; Aa)
Loldrup Sø	Open	56°29'N, 9°26'E	0.39	3.3	1.2	1.1	Ab; Gc; Ga (Se; Sl)
Stigsholm	Open	55°58'N, 9°29'E	0.21	1.2	0.8	0.9	Tt; Ga; Gc; An
Søgård Sø	Open	55°25'N, 9°19'E	0.27	2.7	1.6	0.6	Tt; Pp; Gg; Ab; An (Se; Bb; Cy)

Additional fish species present refer to other species than roach, pike and perch, which were present in all lakes (Ab: *Abramis brama*; Se: *Scardinius erythrophthalmus*; Tt: *Tinca tinca*; Gc: *Gymnocephalus cernua*; Ca: *Carassius carassius*; Aa: *Alburnus alburnus*; Sl: *Sander lucioperca*; Bb: *Blicca bjoerkna*; Ld: *Leucaspis delineates*; Cy: *Cyprinus carpio*; Ga: *Gasterosteus aculeatus*; An: *Anguilla anguilla*; Gg: *Gobio gobio*; Pp: *Phoxinus phoxinus*). Species are listed according to their abundance in the transects and subsequently according to their presence in pike stomachs (if not caught in transects). Species in brackets were neither caught in transects, nor observed in pike stomachs, but are known from the lakes either from survey fishing or from observations during electrofishing for pike in this study.

then estimated for each lake and each of the five time periods by calculating the mean catch for the five electrofished transects per minute. Only fish with body depths below the gape-size limit (Nilsson and Brönmark 2000) of the average size of pike (574 mm) were included in the calculation of littoral prey availability.

Based on previous observations of species-specific migration patterns (Skov and others 2008, 2011), prey fish were categorized as either potentially migratory, that is, species that exhibit partial migration in open lakes (roach (*Rutilus rutilus*), bream (*Abramis brama* \leq 30 cm), white bream (*Blicca bjoerkna* \leq 30 cm), cyprinid hybrids), or as non-migratory prey fish species (eel (*Anguilla anguilla*), gudgeon (*Gobio gobio*), crucian carp (*Carassius carassius*), minnow (*Phoxinus phoxinus*), perch (*Perca fluviatilis*), pike (*Esox lucius*), rudd (*Scardinius erythrophthalmus*), ruffe (*Gymnocephalus cernua*), tench (*Tinca tinca*), three-spined stickleback (*Gasterosteus aculeatus*)). These groups of fish species are henceforth referred to as 'potentially migratory' and 'non-migratory' prey species, respectively, for both open and closed lakes.

Prey Biomass and Size

Pike stomach content samples were thawed in the laboratory and prey fish were identified to the

lowest recognizable taxonomic level. Individual prey length (nearest mm, standard length) was measured or estimated (if the prey fish was partly digested) using species-specific relationship between caudal fin length and standard length (Table S2). These species-specific relationships were obtained from our electrofishing samples of fish used to estimate prey availability. Individual weights of prey fish at the time of predation were estimated from species-specific length-weight relationships, also obtained from the prey availability study (Table S2). Based on these, we estimated total prey biomass as well as potentially migratory prey biomass per individual pike stomach. In addition, we calculated the mean prey biomass for each stomach to evaluate lake-type variations in prey size in relation to migration period as we expected smaller mean prey sizes in lakes with partially migratory prey during the migration period.

Stable Isotope Analyses

Pike samples were prepared from white muscle tissue (216 ± 94 mg wet weight, mean \pm SD) taken anterior to the dorsal fin. All samples were dried at 55°C for 48 h and homogenized using a TissueLyser II (QIAGEN®) grinder. For each individual, 0.47 ± 0.03 mg (mean dry mass \pm SD) of

sample was weighed into pre-weighed tin capsules (5×9 mm). Stable carbon isotope analyses were performed at the Swiss Federal Institute of Aquatic Science and Technology (Eawag), Center for Ecology, Evolution, and Biogeochemistry (CEEB), Switzerland. Samples were combusted in a Flash 2000 elemental analyser coupled to a Delta V Advantage isotope ratio mass spectrometer via a ConFlo IV interface. Standards for $\delta^{13}\text{C}$ were calibrated against Vienna Peedee Belemnite (VPDB).

We sampled mussels and pulmonate snails in each lake at the first and last sampling event. These samples, however, provided unreliable baselines over all sampling events. Specifically, the pike were often outside the $\delta^{13}\text{C}$ range of the baseline organisms, where both snails and mussels were generally more depleted in $\delta^{13}\text{C}$ than the pike (Figure S1). Mussels were in the far majority of cases more depleted in $\delta^{13}\text{C}$ than the pike, which is in accordance with isotope theory (for example, Post 2002), suggesting that it was the snails that provided the unrealistic results. We were therefore not able to test for an absolute shift in relative dependence on the littoral food chain, but only whether pike of different sizes differed in their relative dependence of the littoral food chain in the different lake types after the prey fish started migrating (see below).

Statistical Analyses

Statistical analyses of prey availability and somatic condition were carried out in R (R Development Core Team 2016) and analyses of biomass and size of ingested prey and energy pathways in SPSS, v. 23.0. (SPSS Inc., Chicago, IL, USA). For detailed information on statistical analyses, see supplementary material.

RESULTS

Prey Fish Availability and Community Structure

The biomass of potentially migratory prey present in the lake was significantly lower during the migration period in open lakes ($p < 0.001$; Figure 1, Table 2), whereas in closed lakes, the abundance of potentially migratory prey species did not differ with season ($p = 0.96$; Figure 1, Table 2). Likewise, the abundance of non-migratory prey did not decrease significantly during the migration period; no significant difference in biomass was found between periods in either of the two lake types ($p > 0.10$; Figure 1, Table 3). Visual inspec-

tion of model residuals indicated that model assumptions were met.

During the residence period, we found a significantly higher abundance of potentially migratory prey species in the open lakes than in the closed lakes (Est. Diff. (s.e.) = 1.59 (0.63), $p = 0.0145$). For non-migratory prey species, no such difference was found (Est. Diff. (s.e.) = 0.14 (0.47), p value=0.76).

Diet: Relative Contribution of Potentially Migratory Prey Species

The diet of pike, all lakes combined, was as expected numerically dominated by fish (93%), whereas small invertebrates (6%) and plant material (1%) only made up a minor proportion of the diet. Of the prey identified to species level ($n = 879$), there was a strong dominance of roach (71.3%), followed by perch (9.4%) and bream (8.4%). During the entire sampling period, potentially migratory prey species were more abundant in the diet than non-migratory prey and accounted numerically for 85% of the prey fish in the diet. Overall, there was a significant effect of both pike size (binomial logistic regression; $\chi^2_{1,288} = 11.2$; $p < 0.001$) and time period (migratory vs. residence period; binomial logistic regression; $\chi^2_{1,288} = 23.2$; $p < 0.001$) on the dominance of potentially migratory prey species in the pike diet. Specifically, potentially migratory prey species were more frequent in the diet of larger pike and during the winter migration period (Figure 2). Additionally, there was an effect of individual lake identity (binomial logistic regression; $\chi^2_{7,288} = 19.8$; $p = 0.006$). Lake type did not affect the dominance of potentially migratory prey in the diet and, hence, pike switched to feeding more on potentially migratory prey species even in lakes with prey fish migration.

Diet: Total Biomass of Ingested Prey

During the migration period, the total estimated biomass (log transformed) of fish in the stomachs increased with pike size and differed significantly between lake types, with pike in closed lakes generally having a higher biomass of fish in the stomachs (Table S3; Figure 3B). During the residence period, there was only a significant effect of size, but not of lake type (Table S4; Figure 3A). There was no effect of lake identity for neither the migration nor the residence period (Tables S3 and S4).

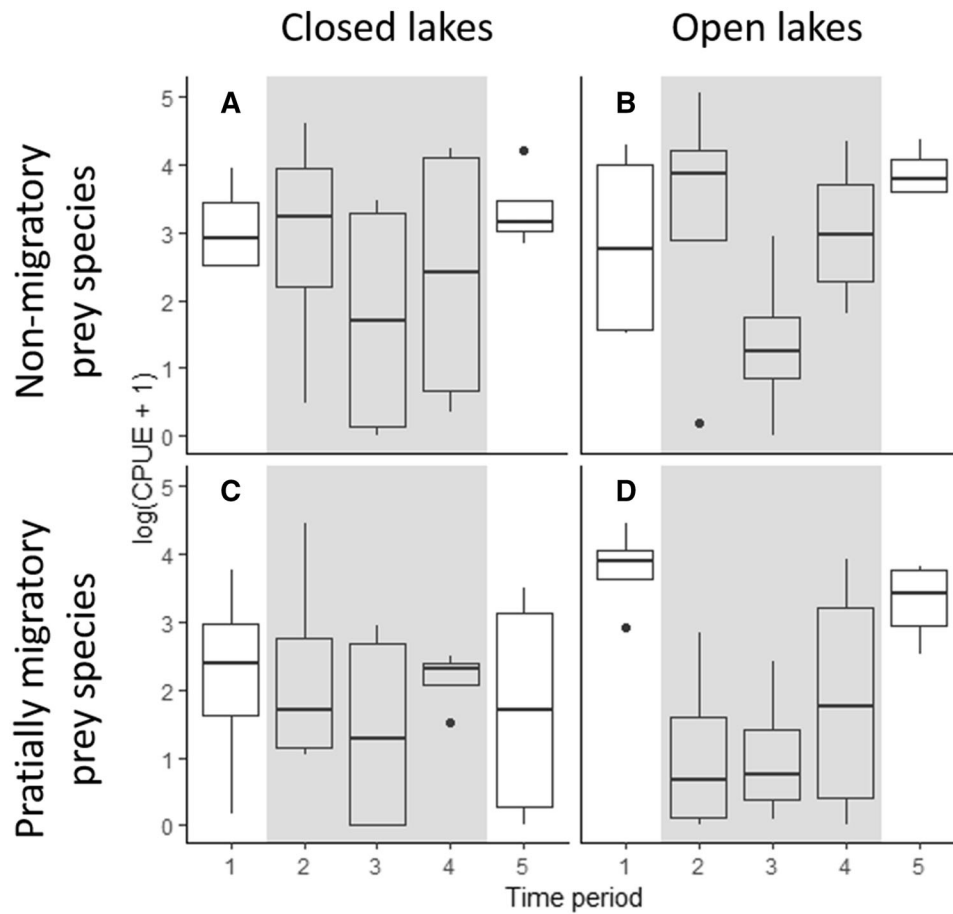


Figure 1. Prey availability measured as $\log(\text{CPUE} + 1)$ in the four combinations of lake type and prey type. Top row (**A** and **B**) represent resident prey type, bottom row (**C** and **D**) migratory prey type, while left and right columns represent closed (**A** and **C**) and open (**B** and **D**) lake types, respectively (compare with Table 2). *Shaded areas* represent the migration periods. There was significantly higher prey availability outside than inside the migration period in migratory prey in open lakes ($p < 0.0001$, panel **D**); Table 2).

Table 2. Estimated Differences in Prey Availability Between Inside Versus Outside Migration Period for all Four Combinations of Lake Type and Prey Type Obtained from the Linear Mixed Effects Model (M1)

	Lake type	Prey type	Est. Diff. (s.e.)	p value
(a)	Closed	Resident	0.88 (0.55)	0.11
(b)	Open	Resident	0.81 (0.61)	0.19
(c)	Closed	Migratory	0.03 (0.65)	0.96
(d)	Open	Migratory	2.23 (0.45)	< 0.0001

Only the combination of open lake type and migratory prey (d) had significantly different prey availability between seasons. Compare with Figure 1.

We found the same pattern when only considering potentially migratory prey species, that is, a positive effect of pike size and a higher biomass in the stomachs in closed lakes during the migration

period (Table S5; Figure S2B) and only an effect of pike size, but not of lake type during the residence period (Table S6; Figure S2A). Here, however, there was a lake identity effect for both the migration and the residence period (Tables S5 and S6, respectively). For total biomass of non-migratory prey species in the stomachs of pike, there were no effects of neither pike length, nor lake type (Tables S7 and S8; Figure S2C and S2D). Here, there was a lake identity effect only in the migratory period (Table S7 and S8).

Diet: Size of Ingested Prey Fish

Generally, over the whole year and across lake types, the average biomass of individual prey fish found in the stomachs of pike increased with pike size (Figure 4). After taking this into consideration, pike in open lakes had significantly smaller prey in

Table 3. Summary of Fitted Models Modelling Log(Body Weight) as a Function of Common Intercept (α), Time Period (TP), Lake Type (LT), Log-Transformed Length (log(L)) of Pike (i) from Lake (j), and Relevant Two-Way Interactions

Model	Fixed part	DIC	Δ DIC
M2a	$\alpha + TP_{ij} + LT_{ij} + \log(L_{ij}) + TP_{ij} * \log(L_{ij}) + LT_{ij} * \log(L_{ij}) + TP_{ij}*LT_{ij}$	- 1051.3	-
M2b	$\alpha + TP_{ij} + LT_{ij} + \log(L_{ij}) + LT_{ij} * \log(L_{ij}) + TP_{ij}*LT_{ij}$	- 1036.7	14.6
M2c	$\alpha + TP_{ij} + LT_{ij} + \log(L_{ij}) + TP_{ij} * \log(L_{ij}) + TP_{ij}*LT_{ij}$	- 1052.1	- 0.8
M2d	$\alpha + TP_{ij} + LT_{ij} + \log(L_{ij}) + TP_{ij} * \log(L_{ij}) + LT_{ij} * \log(L_{ij})$	- 1047.0	4.3

The random component was identical in all models, namely $a_j + b_j * \log(L_{ij})$. Blank spaces indicate which two-way interaction was taken out of models M2b, M2c, and M2d. Model M2c provided the parsimonious best fit and was used for subsequent analyses.

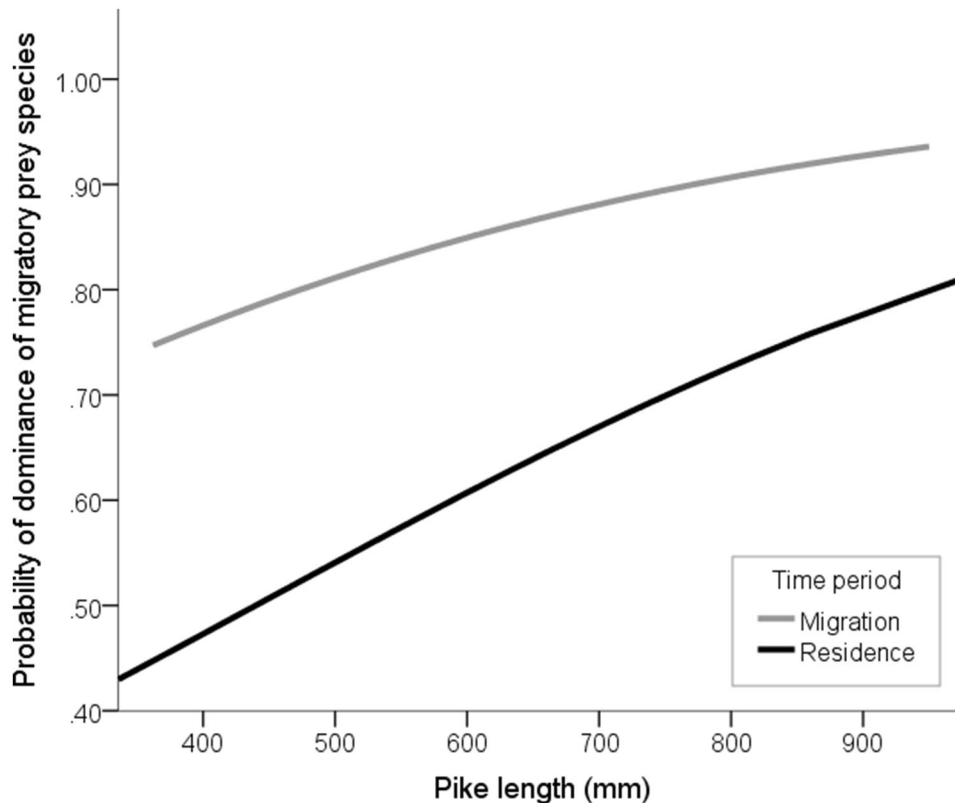


Figure 2. Estimated probabilities for dominance of potentially migratory prey species in the diet of pike as a function of pike length and time period (prey residence period: *black line*; prey migratory period: *grey line*). Potential migratory prey fish species include roach, bream (< 30 cm), white bream (< 30 cm), cyprinid) and non-migratory prey fish species include eel, crucian carp, perch, pike, rudd, ruffe, three-spined stickleback. The majority of the pike (87.5%) in the study had exclusively either potentially migratory or non-migratory prey species in their diet. We therefore translated proportion of potentially migratory prey in individual diets into a binary variable “dominance of potentially migratory prey species”.

their stomachs than pike in closed lakes during the migration period (Table S9, Figure 4B) and, in addition, there was a lake identity effect (Table S9). During the residence period, the effect of pike length was marginally significant, but there were no effects of lake type or lake identity on the average size of prey found in the individual pike stomachs (Table S10; Figure 4A).

Similar to total biomass in the stomachs, we found a highly significant effect of lake type on average size of prey during the migration period, when only considering potentially migratory prey species (Table S11; Figure S3B), with pike generally feeding on relatively smaller prey fish in open lakes. However, during the residence period, no such effect was found (Table S12; Figure S3A). For

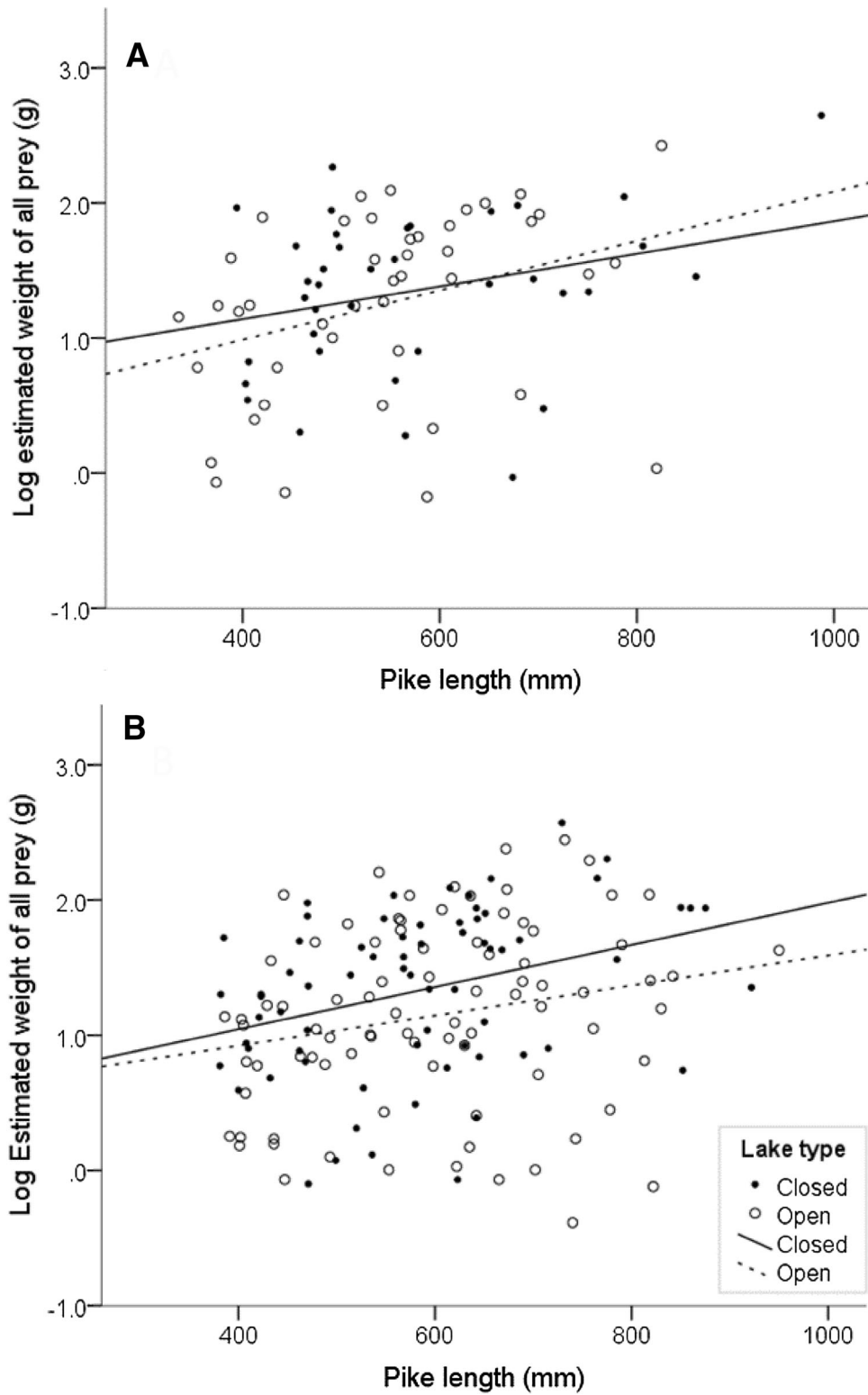


Figure 3. Total estimated weight of prey fish in pike stomachs in the residence (A) and migratory period (B) in open (open circles, broken line) and closed lakes (filled circles and full line) as a function of individual pike length.

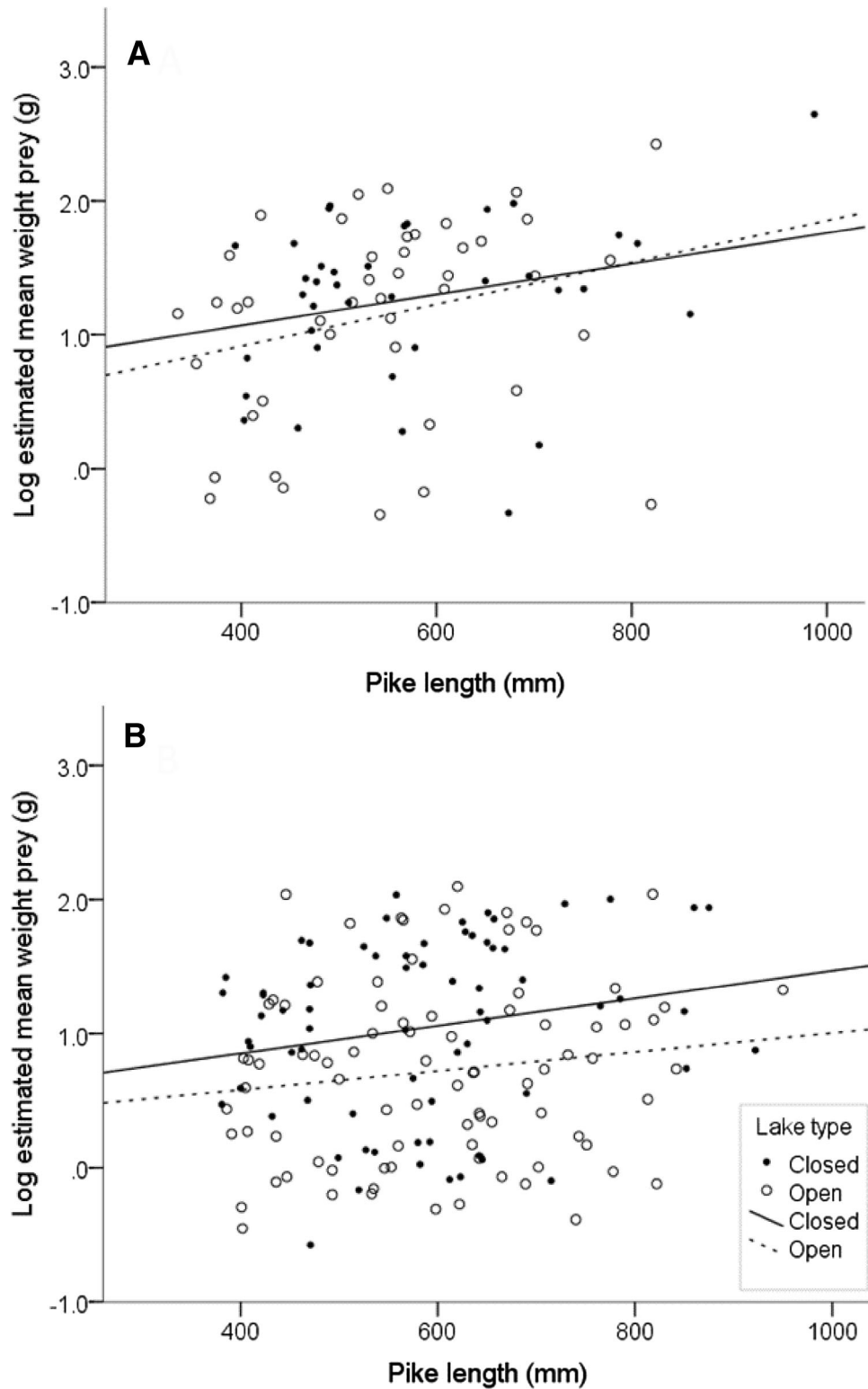


Figure 4. Mean estimated weight (log transformed) of individual prey fish in pike stomachs in the residence (A) and migratory period (B) in open (open circles, broken line) and closed lakes (filled circles and full line) as a function of individual pike length.

non-migratory prey species, there was no effect of lake type neither in the migration period (Table S13; Figure S3D), nor in the residence period (Table S14; Figure S3C).

When contrasting within lake types between time periods, we found a significant effect of time period on average size of prey in both open and closed lakes (Tables S15 and S16). Specifically, pike generally fed on smaller prey during winter, and this was more pronounced in open lakes. Similarly, we found a highly significant difference in size of potentially migratory prey species in the stomachs of pike between the residence and migration periods in open lakes (Table S17), but not in closed lakes (Table S18).

In the open lakes, there were no significant relationship between average weight of non-migratory prey species in the diet and time period and, further, no effect of size (Table S19). Here, however, we found a significant effect of individual lake identity (Table S19). In the closed lakes, the average weight of non-migratory prey species in the diet of the pike was significantly lower during the winter migration period, but we found no effect of either pike length or lake identity (Table S20).

Energy Pathways

The size-dependent use of littoral resources (Figure S4) was significantly influenced both by lake type and by time of sampling, with an additional effect of lake identity (Figure 5; Table S21). When analysing lake types separately, we found a significant effect of time period of sampling in open lakes (Table S22), but not in closed lakes (Table S23). Specifically, the positive effect of pike length on relative dependence on littoral resources became more pronounced in open lakes during the migration period.

Somatic Condition of Predators

The effect of time period on the weight-length relationship of pike varied with both pike length (Table 3 M2b; $\Delta\text{DIC} = 14.6$) and lake type (Table 3, M2d; $\Delta\text{DIC} = 4.3$). Conversely, the weight-length relationship was found to be practically identical in both lake types (Table 3, M2c: $\Delta\text{DIC} = -0.8$). Thus, model M2c provided the best parsimonious fit and was used for subsequent comparisons to elucidate the interplay between lake type and time period and associated effect on pike somatic con-

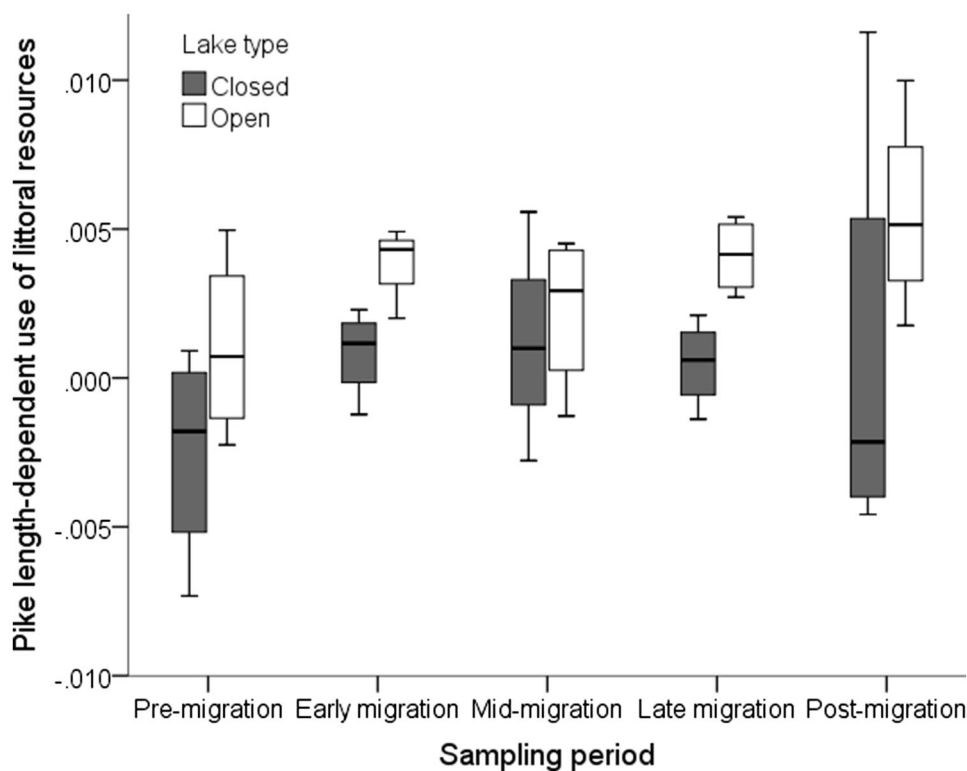


Figure 5. Difference in length-dependent use of littoral resources, obtained from regression slopes between pike $\delta^{13}\text{C}$ -isotope values and individual lengths, at different sampling periods for closed and open lakes. There is in general a higher size-dependent use of littoral resources in open lakes, and this increases with time after prey migration.

dition, that is, the important interaction between lake type and time period ($\Delta\text{DIC} = 4.3$). Mean somatic condition of the predators in lakes with partially migratory prey was higher before the migration period (pre-migration period), decreased during the migration period (early-, mid-, and late migration periods) and increased again after the migration period (post-migration period), as compared to somatic condition of pike in closed systems (Figure 6). Visual inspection of model residual indicated that model assumptions were met.

DISCUSSION

In recent years, there has been an increasing recognition that migration can have profound ecological consequences through changes in predator–prey interactions (Post and others 2008; Brodersen and others 2011a); yet empirical demonstrations in natural systems remain illusive. Previous studies on how migratory prey may influence resident predators have generally focused on how migration can lead to a temporary superabundance of food for resident predators upon arrival of migratory prey (Hilderbrand and others 1996; Samelius and others 2011; Bauer and Hoye

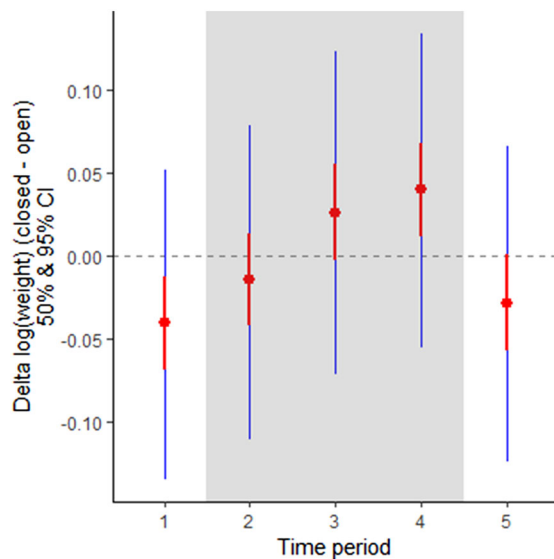


Figure 6. Mean somatic condition of pike in open lakes declined during the migration period and was 4% lower at the end of the migration period (period 4) compared to pike in closed lakes, that is, lakes without prey seasonal partial migration. Differences in population level mean (log) weight between pike in open and closed lakes and associated 50% and 90% credible intervals were obtained by sampling from the posterior distribution of model M2c.

2014 and references therein). In comparison, much less attention has been paid to the loss of potential foraging opportunities for resident predators when their prey leaves during the seasonal migrations. Our study reveals that seasonal partial migration of prey can have multiple effects on predator foraging ecology, including a higher degree of feast-and-famine, and seasonally change the relative importance of alternative energy pathways in lake ecosystems.

Due to the scarcity of systems that have either migratory or non-migratory prey populations of the same species and difficulties with replication at the ecosystem level, it is difficult to quantify and partition the effect of migration from those of seasonality. In the present study, we take advantage of a set of replicated ecosystems that allow or constrain seasonal migration in certain prey species, to quantify the effects of prey migration on the feeding ecology of a top predator. First, we find that overall prey availability in open-lake ecosystems is reduced during the migration period, as expected from present knowledge on prey fish migration patterns (for example, Skov and others 2008). Second, we find that mean size of prey ingested by pike is reduced during the migration period in open lakes and is lower than in the closed lakes during this period. This is likely caused by a general size-dependent propensity to migrate in roach, the main prey species, where smaller individuals generally have a lower migratory propensity than larger fish (Brodersen and others 2008b), resulting in small individuals being more abundant in the lake during the migratory period. Third, we find that total biomass of prey ingested by the pike is reduced during the migration period in open lakes and also lower than in closed lakes during this period. This difference is specifically driven by a lower biomass of potentially migratory prey species in the pike diet in the open as compared to the closed lakes during the winter migration period. However, potentially migratory prey species became more prevalent in the pike diet during the migratory period, and interestingly, this pattern was found also in open lakes with partially migratory prey, where the abundance of these species are lower during winter. This suggests that partially migratory species are particularly vulnerable to predation during the winter period as compared to the non-migratory prey species and may thus provide an explanation for why only certain prey species perform these winter migrations. The mechanisms underlying these species-specific differences are currently unknown, but may be related to species-specific differences in prey swimming performance

at very low temperatures (Temple and Johnston 1997).

The above suggests that partial prey migration causes a substantial reduction in prey availability, leading to a reduction in prey biomass and mean size of prey ingested by the predators in the lakes during winter. Similarly, in terrestrial ecosystems resident predators may display seasonal changes in foraging patterns as a response to prey migration (for example, Owen-Smith 2008; Sand and others 2008; Metz and others 2012; Elbroch and others 2013). For example, Fryxell and others (2007) estimated that wildebeest (*Connochaetes taurinus*) migration out of lion (*Panthera leo*) territories reduces lion daily average feeding rates on wildebeest by 82%. Further, predators show different degrees of prey switching depending on system. Similar to pike, Patagonian pumas (*Puma concolor*) increases their relative consumption of partially migratory guanacos (*Lama guanicoe*) during the migratory period, despite lower relative abundance (Gelin and others 2017). In contrast, Yellowstone pumas switch their diet towards more non-migratory prey species during the ungulate migratory period (Elbroch and others 2013). However, evidence from terrestrial systems are generally based on comparisons of migratory and resident periods and do not include replication and negative controls, which makes conclusions about mechanisms more difficult.

Migration-induced seasonal changes in relative density of different types of prey have the potential to alter energy pathways within lakes between seasons. We find support for a predator size-dependent response in reliance on littoral resources during the migration period in lakes with prey migration, with larger pike having a relatively higher reliance on littoral energy pathways than smaller pike, specifically during the migration period and only in lakes with partially migratory prey. Several lines of evidence suggest that migratory and resident prey fish may differ in their position in the food web, that is, in their relative reliance on littoral vs. pelagic food chains. First, prey fish species associated with the open water habitat are generally more migratory than prey species associated with the structurally complex littoral habitat (Skov and others 2008). However, since pike in open lakes do not feed more on non-migratory prey species than in closed lakes during winter, this does not appear to cause the difference. Second, the primary prey species in this study, roach, generally has an ontogenetic niche shift from planktivory at smaller sizes towards an inclusion of a higher proportion of benthic

macroinvertebrates in larger individuals (Hjelm and others 2003). Also, this does not appear to cause the differences in size-dependent reliance on pelagic resources, because migratory propensity of roach increases with size in our study system (Brodersen and others 2008b). Lastly, roach populations consist of different phenotypes, with deep-bodied individuals being mainly resident and slender bodied individuals being migratory (Chapman and others 2015). These phenotypes are generally recognized as littoral and pelagic specialists, respectively (Faulks and others 2015). This suggests that individuals of potentially migratory prey fish remaining in the lakes during the migratory period could be more dependent on littoral resources than the migratory prey fish. It is likely that it is the presence of these individuals that causes larger pike to have a higher reliance on the littoral food chain only in open lakes during winter. Additionally, a seasonal decrease in available biomass of preferred prey may lead to increasing competition among different size classes of pike, with subsequent niche segregation. Top predators, here represented by pike, are important integrators of different energy pathways in ecosystems (Vander Zanden and Vadeboncoeur 2002). The observed lake-type-specific seasonal change in relative littoral dependence of the dominant top predator indicates a change in energy pathways in the lake food web caused by partial migration of prey. Hence, our study illustrates that migration of prey can change the relative importance of different energy pathways from primary producers to top predators, when the foraging ecology of resident prey differs from that of migratory prey. Still, the actual mechanisms involved deserve further attention in future studies.

Our results show that predator foraging regimes temporally change due to migration of a large fraction of especially larger individuals of the prey community. Aligned with our prediction, predators in open lakes have reduced somatic condition, especially towards the end of the migration period, potentially as a consequence of an overall lower food intake or foraging on smaller prey containing less energy per weight than larger prey, for example, due to relatively lower lipid content (for example, Thompson and others 1991). Since body condition integrates previous feeding conditions, it is not surprising that predator body condition differences become apparent at the end of the migration period, although tendencies towards a reduced body condition of pike in open lakes could be noted already during the mid-migration period. Interestingly, after the migration period has ended,

that is, when prey fish had returned from the streams to the lake habitat, the difference in somatic condition between the predators in the different lake types could no longer be detected. This is likely a result of compensatory feeding in the predators upon return of large numbers of migrating prey. Towards the end of the residence period, that is, at the pre-migration sampling point, pike in open lakes even had a higher condition than in closed lakes. Our results thus suggest that predators in systems with migratory prey, experience a higher degree of feast-and-famine (Armstrong and Schindler 2011), due to the higher temporal variation in prey availability. Feast-and-famine among resident predators experiencing migratory prey is well known from, for example, pacific salmon migration systems. Here, river resident bull trout (*Salvelinus confluentus*) obtains a large part of their yearly energy budget during the short period, when out-migrating sockeye salmon (*Oncorhynchus nerka*) smolts pass through their habitats (Furey and others 2016) and bears, when adult salmon return to their natal rivers to spawn (Schindler and others 2003). Interestingly, the seasonal migration of cyprinid fish differs from the salmon migration system in being partial and not adding significant amounts of nutrients acquired by prey in other habitats, than where the predators reside. It is therefore less of a pulsed enrichment compared to the pure resident environment, but a higher degree of temporal variation in prey availability caused by individual variation in life histories within prey.

In our study, prey fish migration induced temporal variation in prey abundances in open lakes and led to a higher somatic condition during the period of highest growth potential, but to lower condition shortly before reproduction, which may influence growth and reproductive output in different ways. Although a 4% reduction in condition may seem minor, it is important to consider that fish tend to compensate somatic energy loss with increased water content (for example, Brodersen and others 2011b), that is, somatic condition estimates based on wet weight are conservative estimates of reduced energy content. In general, the degree of feast-and famine in different types of migratory systems and its ultimate effects on the predator populations deserve more attention in future studies.

A crucial question in migration biology is whether prey migration affects overall population size and relative dominance in the community of the potentially migratory species. We here find that abundance of potentially migratory prey species during the lake residence period in summer is

higher in lakes where the prey can migrate as compared to lakes where prey are restricted to year-round residence. Hence, potentially migratory species appear to have a relative competitive advantage in systems where they are able to reduce their predation risk in winter, by migrating into refuges in streams. It is interesting in this regard that the effect of season on the relative contribution of potentially migratory prey species to the diet of predatory pike was more pronounced than the effect of migratory opportunity, suggesting that the potentially migratory prey species are particularly vulnerable during winter, which also may explain why some prey species are more migratory than others.

CONCLUSIONS

Previous studies have focused on top-down effects of migratory fish (Brodersen and others 2011a, Post and others 2008) or on bottom-up effects mediated by nutrient transfer between ecosystems by migratory animals (Holtgrieve and Schindler 2011; Subalusky and others 2017). However, we show here that partially migratory prey fish are also causing bottom-up effects on resident predators, leading to changes in energy pathways through the food web and, ultimately, alter community structure of prey. Moreover, our spatial replication of natural lake ecosystems offers a unique design with separate predator-prey systems as replicated experimental units. Such replication may be difficult to obtain in terrestrial or marine ecosystems, but multiple solitary observations from different terrestrial ecosystems suggest that such bottom-up trophic effects may be widespread.

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