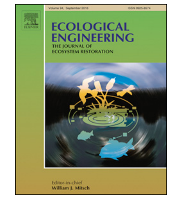
Ecological Engineering 155 (2020) 105956

Contents lists available at ScienceDirect

Ecological Engineering

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



Early fish colonization and community development in a shallow re-established lake

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ARTICLE INFO

Keywords:
Created lake
Fish assemblage
Northern pike
Perch
Roach
Regional species pool

ABSTRACT

The establishment of new lakes has gained momentum throughout Europe and North America as a way to remove nutrients, manage extreme rain events, establish recreational areas, and increase biodiversity. We compared freshwater fish colonization and community development of re-established Lake Fil, a 900-ha lake in Denmark, with fish communities in lakes in close proximity as well as those throughout the region. We found that fish migrated quickly into the lake from nearby refugia with fast initial colonization followed by saturation of the species pool. A total of 14 fish species migrated into the lake during the first five years. Over this period, the lake showed increasing similarity not only to the two directly connected lakes, but also to other lakes in the region. This could be seen in terms of species occurrence similarity, catch per unit of effort (CPUE) and biomass per unit of effort (BPUE). The first immigrant was the three-spined stickleback (*Gasterosteus aculeatus*), followed by roach (*Rutilus rutilus*) and pike (*Esox lucius*), which both came to dominate the fish biomass in the following years. However, the pike population showed no reproduction and perch (*Perca fluviatilis*) had low immigration and reproduction, pointing to a limited success, overall. One solution might be to stock Lake Fil and other new lakes with predatory fish, which might ensure a more balanced food web structure which positively influence the turbidity of the lake water and provide recreational value for anglers.

1. Introduction

Since 1990, Denmark alone has planned for the establishment of more than 2985 ha of shallow lakes (Hoffmann and Baattrup-Pedersen, 2007). The initiative is partial compensation for the removal of more than 200 larger Danish lakes during the preceding 200 years (Hansen, 2014), a historical development mirrored in North America (Dahl, 2011) and throughout Europe, where about 80% of wetland areas, including shallow lakes, were drained and reclaimed for agriculture (Revenga et al. 2000; Verhoeven, 2014). This is problematic for freshwater species, which show a high degree of endemism and are confined to naturally fragmented ecosystems (Dudgeon et al., 2006).

Faced with the historical loss of freshwater habitats and the decline of biodiversity, combined with a high potential for phosphorus retention and nitrogen removal in shallow lakes (Hoffmann and Baattrup-Pedersen, 2007; Hoffmann et al., 2011), initiatives have been taken to establish new lakes (Dahl, 2011; Hoffmann and Baattrup-Pedersen, 2007). However, very few comprehensive studies of colonization, biodiversity, and environmental conditions have been conducted in new and reconstructed lakes (Baastrup-Spohr et al., 2016; Kragh et al., 2017; Søndergaard et al., 2018), though some studies have shown that new lakes increase the occurrence of aquatic plants and birds (Møller et al., 2019; Sø et al., 2019; Søndergaard et al., 2018). This study follows fish colonization and community development in a large, re-established Danish lake, Lake Fil, which had been drained and claimed for intensive agriculture more than 60 years ago.

Fish species composition and community structure are of special interest in lake ecology because of their influence on the trophic structure and water clarity (Jeppesen et al., 2000). Despite this importance of the fish communities, little is known about freshwater fish colonization in new lakes. Recent evidence suggests that fish immigration into new lakes, as in old natural lakes, depends primarily on either hydrological connectivity to source populations or human interference, whereas fish dispersal by birds is very infrequent (Hirsch et al., 2018).

The structure of the fish community in natural lakes are highly influence by connectivity which is more important than environmental heterogeneity e.g. lake depth, nutrients, elevation, lake area in the

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https://doi.org/10.1016/j.ecoleng.2020.105956
Received 10 February 2020; Received in revised form 17 June 2020; Accepted 18 June 2020

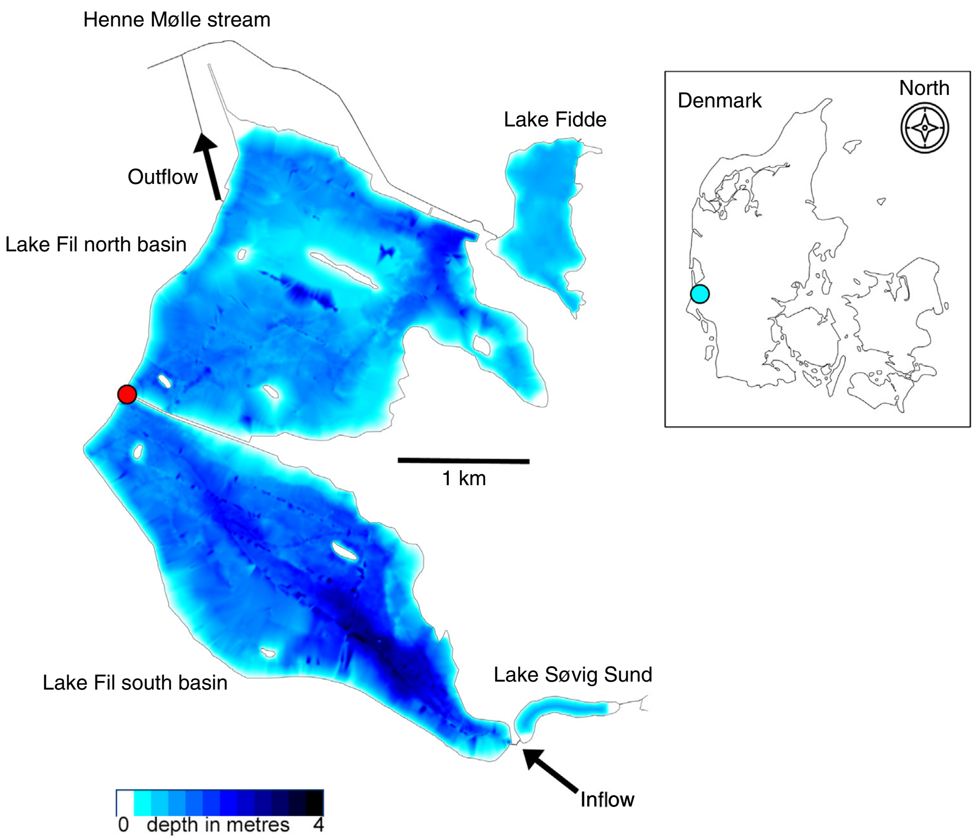

Fig. 1. Map of re-established Lake Fil, 55°42′02.1"N, 8°13′08.3″E, and the unaffected neighboring Lake Fidde and Lake Søvig Sund. Arrows indicate the inflow (bottom) and outflow (top) into Henne Mølle stream. The connection between the two basins is marked with a red dot. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

landscape, fragmentation, and landscape complexity (Drakou et al., 2009). The connectivity to streams and other lakes are thus structuring species richness and abundance of fish in new lakes (Bouvier et al., 2009). However, in re-established lakes and streams, it is important that relatively undisturbed water bodies are present in the catchment which are still housing species (i.e. species refugia) enabling recolonization (Lake et al., 2007). In agricultural landscapes, streams are often channelized, intensively managed or subterraneous, which may reduce the species pool of immediate immigrants to highly tolerant and generalist species (Lake et al., 2007). Without valuable species refugia, a new or re-established lake may never, or very slowly, attain the full species potential of its physical and chemical conditions (Sarr, 2002).

If refugia are present, the rates by which species colonize a new lake are controlled by the number of individuals, their behavior, and their survival rate (Anderson, 2007). That is, the gain rate of species is first governed by the dispersal rate, while later survival is determined by environmental conditions, food availability and interspecific relations. The species loss from the lake will be related to the biotic interactions within the system (Anderson, 2007). Thus, the fish community in a new lake is largely determined by colonizers present in the connecting waterways, which also sets the time scale of immigration.

For streams, species recovery has been reported to occur within 5 to 25 years if colonizers have been removed, while stream sections with colonizers present upstream or downstream experience rapid recovery, within 90–400 days (Gore and Milner, 1990). Direct fish movement between lakes has been documented in a few studies. For example, Daniels et al. (2009) found that only 0.9% of tagged fish moved to another lake in an interconnected system and that the species present near the inlet and outlet were similar to those within the lakes and in the streams between the lakes.

Recently, seasonal fish migration between streams and lakes has been observed for many species, including roach (*Rutilus rutilus*, Brodersen et al., 2008), white bream (*Blicca bjoerkna*), perch (*Perca fluviatilis*), and pike (*Esox lucius*, Skov et al., 2008). These seasonal migrations have been linked to parameters such as individual fitness (Brodersen et al., 2008), boldness (Chapman et al., 2011), and predator avoidance (Brönmark et al., 2008). In a particular lake-stream system, Skov et al. (2008) found that 40% of tagged roach individuals and 55% of white bream individuals migrated out of the lake and into the stream during winter, whereas only 0.9% of perch and 2.1% of pike migrated. The development of fish biomass and composition in new lakes could thus be influenced by these migrations; zooplantivorus species migrating much more than others, but it is unknown whether they migrate back to their native lake or into the new lake.

In temperate northern lakes, roach and bream have a negative impact on water quality by predating on zooplankton or stirring up the nutrient-rich bottom sediment as they search for macroinvertebrates (Breukelaar et al., 1994). In foraging on zooplankton, roach is competitively superior to young perch, which inevitably reduce predation by perch as fewer grow large (Estlander et al., 2010; Persson, 1987). This is problematic for the ecosystem because poor water clarity in eutrophic lakes reduces spawning sites and juvenile habitat quality for piscivorous species such as pike and perch (Grimm, 1981) further reducing the predation on roach and bream. In contrast, high biomass of perch and pike can, especially in shallow lakes, enhance predation on roach and bream and exert top-down control on fish community composition (Jeppesen et al., 1997). Hence, it is important to follow the piscivores and zooplantivores fish colonization and community development in newly established lakes.

Our overall objective was to evaluate the initial colonization and development of the fish community in a re-established lake. We further wanted to evaluate species-specific colonization and development to facilitate better management of re-established lakes. Given the generally high dispersal potential of freshwater fish from connected waterways, we hypothesized that: 1) species from nearby and hydrologically connected refugia will rapidly colonize the newly established lake, 2) piscivorous species, like pike and perch, will colonize the lake to a lesser degree than zooplantivorus species, and 3) populations will develop towards similarity to lakes in the region on a longer time scale.

2. Methods

2.1. Study area

Lake Fil used to be the third-largest lake in Denmark (2185 ha). However, draining of the lake began in 1852 and proceeded in stages until 1952 were only two small separated lake fragments remained, namely Lake Søvig Sund at 20 ha and Lake Fidde at 45 ha. For 60 years, the area was used for agriculture and was kept dry by a large pumping station. The area was since bought by Aage V. Jensen Nature Foundation with the aim of re-establishing the lake on the agricultural soils. During the construction, topsoil was scraped in eight areas to form small islands as bird refuges. However, the major part of the area was left undisturbed. In the autumn-winter of 2012, the pumps were shut off and Lake Fil was re-established to a size of 900 ha. The lake is divided into two basins, south and north, which are connected via a six-meter-wide culvert through a ten-meter-wide dike (Fig. 1). The main inlet is a short canal that connects the south-eastern corner of the south basin to Lake Søvig Sund. The outlet is located in the north-western corner of the north basin and continues for 2 km as Henne Mølle stream to the North Sea (Fig. 1). Lake Fidde is located immediately north of Lake Fil, and Henne Mølle stream serves as their common outlet.

Lake Fil is located in the sandy western part of the country within a 104 km^2 catchment primarily (71%) consisting of agriculture (Kragh et al., 2020). The lake receives 87% (approximately 1.4 $m^3 s^{-1}$) of its water from the main inlet and the rest from groundwater inflow (Kragh et al., 2020). The mean annual precipitation is 792 mm, lowest in April with 30 mm and highest in August with 99 mm (no rainy season) and the mean temperature is 8.9 °C (measured from 2006 to 2015, DMI, 2020). The lake is shallow (mean depth of 1.05 m, maximum depth of 3.4 m) and the water volume is 8.6 million m^3. Detailed monitoring after re-establishment showed that Lake Fil has a short water retention time of 20–183 days (average 70 days). Strong winds and a long fetch across the lake surface often causes resuspension of sediment particles, while high gas exchange across the air-water surface results in oxygen concentrations usually close to air saturation (Kragh et al., 2017).

The total phosphorus concentration ranged from 25 to 150 μg P L^{-1} and Secchi-transparency averaged at 0.81 m in 2014 and 0.87 m in 2015 (Baastrup-Spohr et al., 2016), with mean dissolved organic carbon concentrations of 1530 μmol L^{-1} and mean colored dissolved organic absorbance of 1.3 m^{-1} (400–700 nm). Suspended particles and colored dissolved organic matter accounted for 96% of the light attenuation (Kragh et al., 2017; Baastrup-Spohr et al., 2016, and unpublished data).

2.2. Species colonization

To follow species colonization, we sampled the basins using bait fish traps and cast nets from 2013 to 2018 (Table 1). Sampling both basins separately can point to whether the colonizers originate from either Lake Fidde or Lake Søvig Sund. Cast nets were used on all occasions where fish were visually observed. They were cast either from a boat or by wading in shallow water. In the boat, a side-scan sonar (Lowrance HDS Gen 3, Structurescan 3D module, Airmar P66 transducer) was used to locate both schools and individual fish, which were then caught with the net. The cast nets were either 7′ wide with a mesh size of 1/4″ or 12′ wide with 3/8″ mesh. Net casting was done for approximately two hours in each basin using the two mesh sizes equally frequently. On all occasions, 8–10 bait fish traps were deployed 24 h in advance, and they were distributed from the middle of each basin to the shore (Table 1). These point-sampling methods enabled sampling in areas where gillnets could not be placed, e.g. the littoral zones, small adjacent streams, and canals, and thus supplemented the species recordings from the gillnet catches during the main fishing campaigns (described below). Graphic representations in this paper are limited to samplings that revealed new species in one or both of the basins.

Table 1
Sampling intensity with castnet, gillnet and fishtraps in Lake Fil. Castnetting was done for approximately 2 h in each basin with 18–21 yearly samplings, gillnets were used 1–2 times yearly with a total of 2–48 placed each year (2–24 net each sampling), fishtraps were placed 8–10 times yearly with 8–10 traps used each sampling resulting in 80–100 nets yearly.

	Castnet	Gillnet		Fishtrap	
	Number of samplings (2 h each basin)	Number of net used	Number of sampling events	Number of traps used	Number of sampling events
2013	18	2	1	80	8
2014	21	42	2	80	8
2015	21	48	2	100	10
2016	17	28	1	80	8
2017	17	12	1	80	8
2018	19	12	1	100	10

2.3. Abundance and biomass indicator

Catch and biomass per unit of effort (CPUE and BPUE) data were collected using multi-mesh gillnets with EU-standardized dimensions, 30 × 1.5 m with 2.5 m sections of different mesh sizes (CEN, 2005). Three main fishing events were conducted in May 2014, September 2014, and May 2015 using 14–24 gillnets. In addition to the main fishing events, a single pioneer gillnet was placed in each basin in June 2013 before the intensive sampling began. Gillnets were set by boat at 18:00 h and pulled the following morning after an average of 18 h of exposure. Previous studies found no effect of the direction of the nets in low-transparency lakes, either parallel or perpendicular to the coast (Menezes et al., 2013). The nets used in the present study were usually placed parallel with the wind. All fish specimens caught in gillnets were identified by species and weight measurement for each individual were recorded (rounded to nearest gram using a field balance). The species-specific catch and biomass data from the gillnets were expressed as CPUE and BPUE by dividing the summarized species-specific number or weight of fish by the number of gillnets used.

In late March 2015, just before the expected spawning, a population of large perch (> 15 cm long and with a combined weight of 250 kg) was caught in Lake Fidde and released into Lake Fil (corresponding to 0.27 kg perch ha^{-1} added to Lake Fil). Standardized gillnet CPUE and BPUE from 2013 and 2014 indicated that natural immigration of perch had been low, so the release was conducted in order to establish a spawning perch population in the lake. Due to the very low introduced biomass per lake area, and aware that perch fry from that year's spawn would be too small to be caught in the gillnets, the release is not expected to influence data collected one month later, in May 2015. Furthermore, we observed no clear differences In BPUE of perch between May 2014 vs May 2015 (Fig. 4) indicating that the addition of perch had little effect on the total biomass in 2015. The perch release was shown to have influenced the biomass distribution in the later gillnet samplings, but did not influence species diversity in the lake. Thus, while biomass distributions were not usable after May 2015, yearly gillnet samplings in August or September continued until 2018 and were used to track the appearance or loss of species in the system, together with other sampling methods described in Table 1.

2.4. Regional fish community

To identify the origins of the fish populations in Lake Fil, data on neighboring Lake Søvig Sund and Lake Fidde from August 2010, the most recent sampling before Lake Fil's re-establishment, were extracted

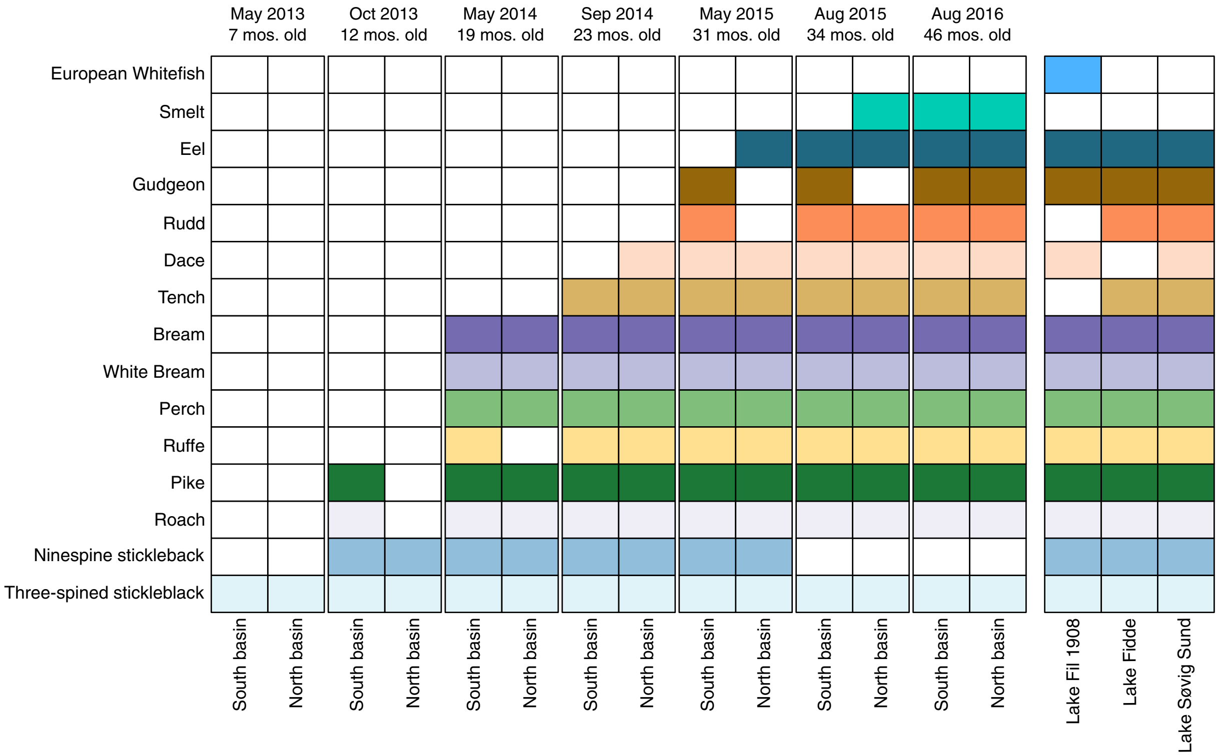

Fig. 2. Cumulative list of species caught in samplings in the south basin and north basin of Lake Fil from May 2013 to August 2016, when the latest new species was observed in both basins. No new species, or disappearance of species, were observed between August 2016 and August 2018. Filled boxes illustrate that the species was found while white boxes show that the species was not found. Colors are consistent with those used in Fig. 4. The species pool in neighboring Lake Søvig Sund, Lake Fidde and species observed in Lake Fil in the year 1908 (Lake Fil 1908) are also shown.

from the Danish national environmental monitoring program (NOVANA, 2017). This data had been collected using the same European standardized gillnet sampling method as described above for Lake Fil, together with supplementary fish traps. Data from Lake Fil before reclamation was collected from historical records published between 1830 and 1908 (Carl 2012; personal communication with H. Carl, University of Copenhagen, 2018). The hybrid roach-bream, found in gillnet samplings, and the rainbow trout (*Oncorhynchus mykiss*) reported in the historical records as having been introduced, are not sexually viable species (under Danish conditions) and were not included in the analyses. Furthermore, data from investigated lakes in the region within 80 km of Lake Fil was collected from reports and the Danish national environmental monitoring program (NOVANA, 2017) for a regional comparison with Lake Fil.

2.5. Data analysis

To test if the variable number of nets influenced the results, we used a bootstrap analysis where individual net biomass and number of fish at the given fishing event was randomly combined in groups of between three and 24 nets. This was done one hundred times, providing the basis for calculating the mean and 95% confidence interval of each randomly combined group.

All fish caught, regardless of fishing method, were used to establish species incidence data (presence-absence) for each sampling event. Using incidence data, gain rate and loss rate of species in the lake basins were calculated as described in Anderson (2007) using eqs. 1 and 2,

$$G_P = \frac{G}{(1/2)\,[S(t_1) + S(t_2)]} \text{ and } L_P = \frac{L}{(1/2)\,[S(t_1) + S(t_2)]} \qquad (1,2)$$

where G_P (Gain rate, e.g. the colonization rate) and L_P (Loss rate, e.g. the loss of species) are the proportion of the average number of species present during the sampling period, $S(t_1)$ and $S(t_2)$ are the species richness at the beginning and end of a sampling period, and G or L are the numbers of new or lost species in the sampling period (Anderson, 2007). Species that were missing in a single sampling but found in earlier and later samplings were included as still being present in the system; their absence is presumed to be an artifact of sampling or population stochasticity. An F-test in GraphPad Prism 7.0 enabled us to determine whether the slope of G_P and L_P followed a linear or exponential decay. A *t*-test were used to compare the fish biomass between the two basins.

Using incidence data, we evaluated how the species composition in the entire Lake Fil resembled that of the neighboring lakes (with a hydrological connection) and with Lake Fil's historical fish community by calculating the Sørensen similarity (Sørensen, 1948) between the communities. Further, we evaluated the temporal development of the fish communities of each lake basin, in comparison to neighboring and regional lakes (environmental data shown in Table S1), using ordination analysis (Non-Metric Multidimensional Scaling, NMDS). NMDS was used because of its flexibility to base the ordination on different dissimilarity measures (Borcard et al., 2011). Temporal development was evaluated using both incidence, BPUE and CPUE data. In the NMDS analysis of temporal incidence data, we used Sørensen similarity as the dissimilarity measure. In the quantitative BPUE and CPUE NMDS analyses of the development of species dominance patterns, we used Bray-Curtis similarity of relative abundance data and not the total biomass or number of caught fish. The relative abundances were square-root transformed before analysis to down weigh the influence of very dominant species (Clarke and Warwick, 2001). The ordination analyses were conducted using Primer-E (v6.0, Clarke and Ainsworth, 1993).

3. Results

3.1. Species colonization

Three-spined stickleback (*Gasterosteus aculeatus*) was the first species observed, in May 2013 in both basins of Lake Fil, seven months after re-flooding of the lake had started (Fig. 2). Five months later, roach was dominant, and pike and nine-spined stickleback (*Pungitius pungitius*) were also found in the south basin. During the next 24 months, nine additional species were observed: ruffe (*Gymnocephalus cernua*), perch, bream (*Abramis brama*), white bream, dace (*Leucicus leuciscus*), tench (*Tinca tinca*), gudgeon (*Gobio gobio*), rudd (*Scardinius erythrophthalmus*), and European eel (*Anguilla anguilla*) (Fig. 2). Between August 2015 and the end of the study in 2018, no nine-spined stickleback was caught in the lake. In August 2015, smelt (*Osmerus eperlanus*) was observed and it persisted throughout the rest of the study period (Fig. 2). Fish species were caught with a variety of fishing gear during the sampling period. Most species were observed first in cast nets, although tench, rudd and European eel were first caught in fish traps and smelt in gillnets.

The temporal gain rates of species in the north and south basins were initially high and subsequently declined according to an exponential decay function (F-test: north basin $p = .0017$ and south basin $p = .001$), with high coefficients of determination (Fig. 3, R^2: 0.86 for the north basin and 0.87 for the south basin). The loss rate was low and constant over time and did not deviate significantly from zero ($p = .92$ for both basins, Fig. 3).

During the first five years of its existence, a total of 14 species migrated into the new lake (Fig. 2). Combining records from both lake basins, the observed species composition of the fish communities in 2018 (no species changes observed after 2016) showed a similarity of 80% to the one found in the lake before it had been fully drained. Compared to the original species reported in historical records in 1830 and 1908 from Lake Fil, only European whitefish (*Coregonus lavaretus*)

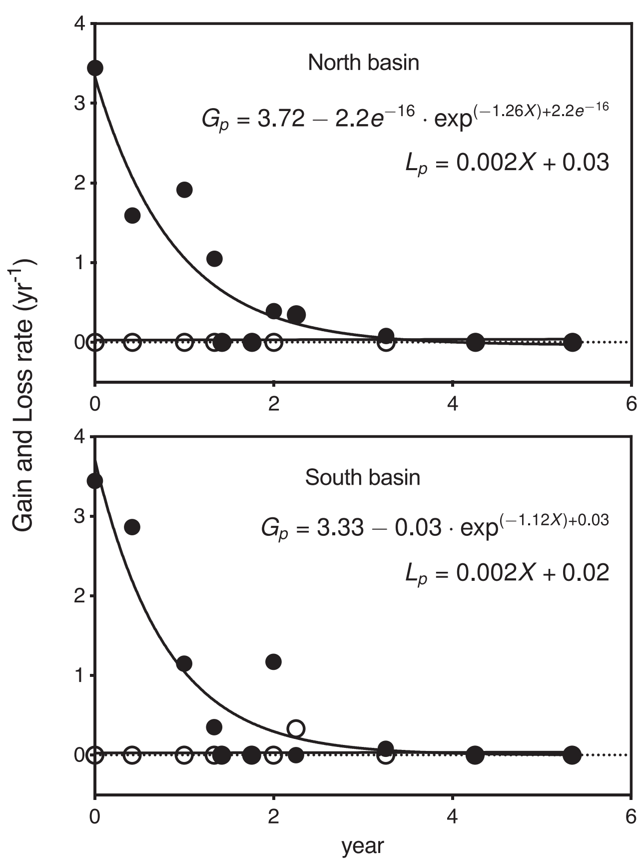

Fig. 3. Yearly species gain (filled circles) and loss rates (open circles) in the northern and southern basins of Lake Fil. While loss rates were low and constant over time, gain rates declined exponentially over time.

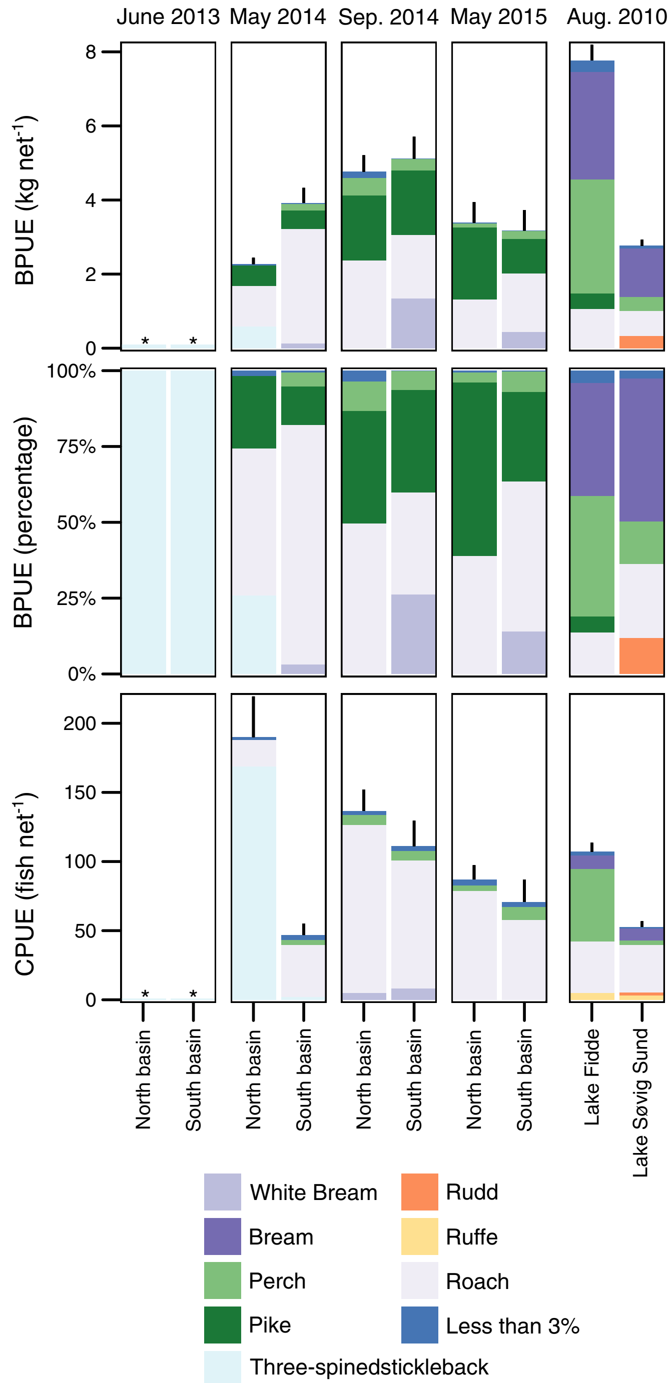

Fig. 4. Biomass catch per unit effort (BPUE, kg net^{-1}), biomass distribution among species (percentage) and catch per unit effort (CPUE, fish net^{-1}) in the southern and northern basins of Lake Fil, and in Lake Søvig Sund and Lake Fidde. Samplings are from gillnet surveys from June 2013 to May 2015. Data from Lake Søvig Sund and Lake Fidde is from the latest sampling before the establishment of Lake Fil. Different species are marked with colors and species contributing to less than 3% of the total weight or number of fish are pooled (Less than 3%). In the first BPUE and CPUE sampling (*) we do not have a biomass or number estimate. Whiskers show the standard error for the total CPUE or BPUE. Gillnet data is presented as the percentwise distributions of BPUE and CPUE from June 2013 to May 2015.

did not reappear. The species similarity of the combined basins in the current Lake Fil to neighboring Lake Fidde (76%) and Lake Søvig Sund (76%) was in the same range.

3.2. Biomass and abundance

Total fish biomass quickly increased in the basins of Lake Fil after the re-establishment in 2012. Already in May 2014, biomass reached levels comparable to levels in neighboring lakes (Fig. 4). At the end of the investigation, in May 2015, there was no significant difference between the biomass in the two basins (*t*-test, $p = .79$). Roach dominated by weight in both basins (1.1–3.1 kg net^{-1}), although pike also comprised a large proportion of the total biomass (0.5–1.7 kg net^{-1}). In comparison, bream dominated in neighboring lakes, with a BPUE of 2.77 kg in Lake Søvig Sund and 7.77 kg in Lake Fidde. While CPUE in May 2014 was dominated by three-spined stickleback, with 169 fish net^{-1} in the north basin, they were far scarcer in the southern basin, with just 47 fish net^{-1} (Fig. 4). In later samplings, roach dominated the number of fish caught, with 19–122 fish net^{-1}, while perch was much less common (0.3–9.5 fish net^{-1}, Fig. 4). In June 2013, three-spined stickleback was the only abundant species. The gillnets were full, which effectively inhibited further catch, so the actual biomass of three-spined stickleback is not known. To obtain an estimate of its population size, fry net fishing was applied in August 2013. Using this method, 3.7 fish m^{-2} were caught in shallow water (< 1 m) and 1.5 fish m^{-2} in water deeper water (> 1 m) in both basins.

A large biomass of bream and perch distinguishes neighboring Lake Søvig Sund and Lake Fidde from Lake Fil. Also, rudd was very common in Lake Søvig Sund (Fig. 4). Despite these observed differences with neighboring lakes, the fish communities in both basins developed towards a composition that resembles those of neighboring and regional lakes (Fig. 5). As observed in the species-specific analyses, the community in the south basin developed more quickly after the lake was established, as compared with the north basin.

3.3. Regional perspective

The NMDS ordination had a low stress value of 0.06 indicating a good representation of the structure in the data. The obtained pattern showed a directional development over time of the fish communities in each of the two basins moving towards those found in neighboring and regional lakes (Fig. 5). Both incidence data (presence-absence) and quantitative data (CPUE and BPUE), indicate that not only the species found but also their relative abundances developed towards those of natural lakes. Also, it was evident that compared to the north basin, the communities of the south basin, located closest and downstream to a neighboring lake, initially developed faster (Fig. 5).

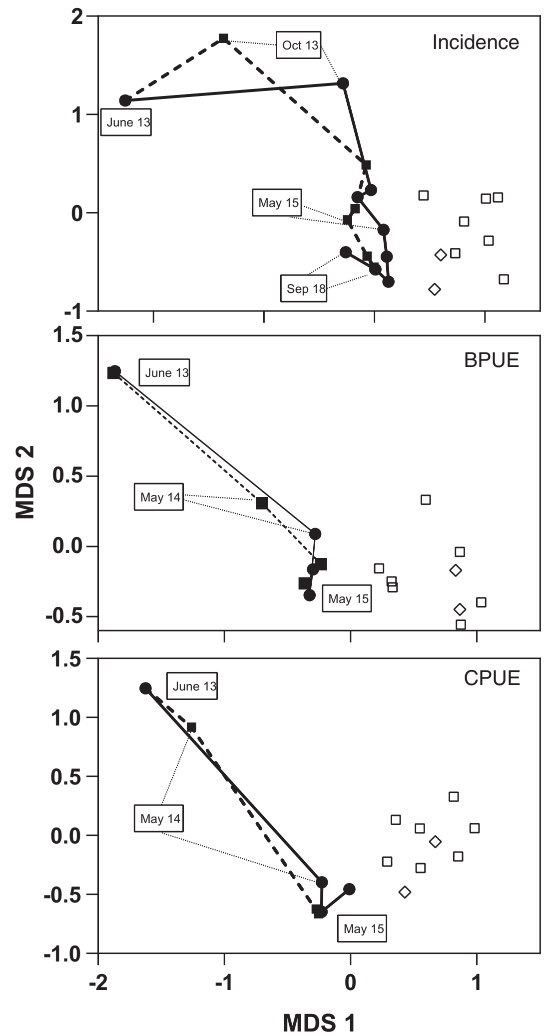

Fig. 5. NMDS plot of incidence, BPUE, and CPUE of fish species in the south basin (filled circle and solid line) and the north basin (filled square and dotted line) from samplings between June 2013 and September 2018. The community composition in the two basins in Lake Fil followed each other closely over four years and, at the same time, moved closer to those in neighboring lakes (rotated square) and other shallow lakes in the region (square). Basic information for the regional and connected lakes is available in Table S1.

4. Discussion

4.1. Species richness

Within just three years following the re-establishment of Lake Fil, 14 fish species had migrated into the lake. This species composition closely resembles that of the neighboring lakes and other lakes in the region, as well as in the original lake as reported in historical records before 1908. Tench, smelt, and rudd were the only new species compared with the historical community. In new ecosystems, colonization rate is mostly controlled by dispersal (Anderson, 2007) as food resources often remain high during the first years of establishment and carrying capacity of species tend not to be limited by food availability. Our results show that the gain rate starts at a high initial level and then rapidly decreases as time progresses. This time course is very common, especially in plant communities (Anderson, 2007). In addition, a small second wave of colonization was observed during the second winter (between Oct. 2013 and May 2014, Fig. 2). This might have been driven by winter migration of species, which is a prominent phenomenon in the region (Brodersen et al., 2008; Brönmark et al., 2010; Skov et al., 2008). Only one species disappeared during our samplings: the nine-spined stickleback. Whether its disappearance is due to competition or predation is not known, but both three- and nine-spined sticklebacks are highly vulnerable to predation (Byström et al., 2007; Patankar et al., 2006).

While colonization was relatively fast in Lake Fil, it is nonetheless much faster in rivers. Gore and Milner (1990) found that species recovery lasted 90–400 days in rivers that contained close sources of colonizing species, while species recovery in Lake Fil from nearby lakes continued for about 1190 days, or almost three times longer than rivers, before the community could be described as stable. Species recovery in lakes can proceed more quickly than what was experienced in Lake Fil. In another shallow newly created Danish lake, Lake Årslev Eng (117 ha, mean depth 1 m, 550 m to nearest refugia), nine species were found after just six months (Bio/consult, 2003). In the same period, only the three-spined stickleback was found in Lake Fil. Lake Årslev Eng has a high input of stream water and a very short water retention time of only 3–20 days (Århus Amt Natur og Miljø, 2005), which could promote downstream drifting of fish.

Downstream drifting of fish is observed for many species (Reichard et al., 2002) and could be important for species colonization. Dozens of lakes have been recreated in Denmark, but species in the connected waterways are usually not examined, or are examined with such a low intensity that patterns remain unclear. Prior determination of species communities, as well as the physical and chemical conditions of the interconnected streams, would help us to understand which species colonize new lakes, and why. Moreover, temporal studies would help determine the order of immigration, which seems to be species-dependent and possibly influenced by species-specific differences in migration propensity and colonization potential.

4.2. Species abundance and biomass

The biomass composition of fish in the new Lake Fil was highly variable during the two first years after its re-establishment. Three-spined stickleback was the first species to arrive and rapidly occupied both basins. Three-spined stickleback is a generalist species whose multiple annual reproductions (Carl and Møller, 2012) enable it to quickly fill the open niches in a new system. It was likely present in the drainage ditches at the time of lake re-establishment, which enabled the fast colonization. Three-spined sticklebacks declined from a 100% dominance to complete disappearance in the south basin and from 100% of the biomass to 26% in the north basin during the following 19 months. After May 2014, when immigration of pike, perch, and roach had begun, very few (less than 3%) three-spined sticklebacks were caught in gillnets (Fig. 4).

Pike, a particularly efficient predator, poses a serious threat to three-spined sticklebacks (Patankar et al., 2006). In the re-established Lake Lovns, the introduction of 10,000 pike fry in 2003 reduced the contribution of sticklebacks to the total fish biomass from 8% in 2008 to 0% in 2011 (Hansen, 2014; NOVANA, 2017). The same pattern has been observed in lakes with nine-spined stickleback (Byström et al., 2007). Sticklebacks can be seen as a pioneer species that facilitate the development of slower-colonizing predator species in new lakes (Egler, 1954).

As sticklebacks were declining, the pike fry developed and supported a strong year class of pike in Lake Fil, with a length reaching approximately 40 cm during the first year (data not shown). Pike caught in November 2014 had produced milt and roe, which supported expectations of recruitment in 2015. Optimum conditions in Lake Fil, such as a large spawning stock (Walrath et al., 2015), presence of submerged vegetation, and winter flooding of terrestrial vegetation were expected to promote reproduction (Nilsson et al., 2014). Nonetheless, despite searching all possible habitats for the refuge-seeking juvenile pike, no fry were observed in May 2015.

While several mechanisms influence the survival of pike fry, the reasons for Lake Fil's several-year lack of fry has yet to be uncovered. Potentially, a higher risk of egg predation could exist in populations of newly established pike populations, where size differences between the sexes have not yet developed. During the spawning season, female pike often guard their eggs for a period (Frost and Kipling, 1967; Svärdson, 1947) and, when they are larger than the males hoping to mate, they refuse to move from the spot. However, personal observations suggest that when both female and male pike have the same size, female fish might experience mating pressure from the males, and thus may leave the eggs in littoral zones more quickly, which presents a higher risk of egg predation.

In autumn 2013, the first roach was observed in the lake and the population most likely spawned successfully in both lake basins in 2014. There was only a small difference in the biomass between basins after May 2014, which indicates that roach moved readily between them. Roach has previously been shown to be a frequent autumn and winter migrator (Brodersen et al., 2008), a behavior that has been linked to good condition, boldness (Chapman et al., 2011), and predator avoidance (Brönmark et al., 2008). If fast and successful establishment of a roach population is a common phenomenon in newly established lakes, as found in Lake Fil and constructed gravel pit lakes (Søndergaard et al., 2018), their abundance could, as emphasized, contribute to reducing water clarity by acting as efficient predators on zooplankton, especially in lakes with sparse plant cover (Jeppesen et al., 1997). During the sampling period, roach became the dominant planktivorous fish in Lake Fil. In natural lakes in Denmark, however, perch is often the most abundant species, closely followed by roach (Menezes et al., 2013).

Perch in Lake Fil did not attain the same high biomass as in neighboring Lake Fidde. The low perch BPUE in the north basin (0.46 kg) and the south basin (0.32 kg) in September 2014 compared to Lake Fidde (3.01 kg) points to restricted migration of individuals and low recruitment. Perch recruitment might be influenced by low vegetation cover (Persson and Greenberg, 1990), which has been observed in Lake Fil (< 8%; Baastrup-Spohr et al., 2016), and strong competition from young of the year (YOY) roach on YOY perch under the prevailing eutrophic, turbid conditions (Persson and Greenberg, 1990). In any event, roach migrated into Lake Fil more quickly and in greater numbers than perch.

Bream migration into Lake Fil was low compared to some other re-established lakes. Bream constituted half of the biomass in the re-established Lake Solbjerg Eng just two years after its establishment (Fiskeøkologisk Laboratorium, 1995). The bream population in Lake Solbjerg Eng resembled the cohort found in Lake Arre at that time and it was, therefore, believed to have migrated 6.9 km from the lake (Fiskeøkologisk Laboratorium, 1995). By contrast, very few bream were observed in Lake Fil, despite large populations in neighboring Lake Fidde and Lake Søvig Sund. Thus, showing an immigration pattern very different from that in Lake Solbjerg Eng. The bream migration pattern of individuals in another Danish system, where 1280 fish were followed for nine years, was found to be stochastic (Brodersen et al., 2019). If this stochastic behavior is common for many fish species, then the level of turbidity in newly established lakes, which is strongly affected by species-specific fish engagement with the food web (Jeppesen et al., 2000), becomes difficult to predict.

We know of only one other re-established Danish lake that was sampled during its first year. Lake Årslev Eng was established in March 2003 and sampled six months later, the main biomass consisted of roach 31%, perch 14%, pike 7%, and bream 41% (Bio/consult, 2003). Compared to Lake Fil, bream had colonized in larger numbers and roach was co-dominant. Pike spawned in Lake Årslev Eng, but also +2 pikes had migrated into the lake. The initial colonization by sticklebacks was not seen, likely either because it was rare in the interconnected streams or because it experienced high predation by pike and perch.

4.3. Regional comparison

Our analysis of the temporal development of fish communities in Lake Fil's two basins shows that community composition (incidence data) became increasingly consonant with not only neighboring lakes but also other lakes in the region. Generally, there was a high similarity to the fish communities of the natural lakes in the region (including the two neighboring lakes), which indicates the existence of a regional species pool. Temporal development of relative CPUE and BPUE of species in the basins also moved towards those found in regional natural lakes, indicating a small influence of being a newly re-established lake. The overall movement towards regional lakes is probably highly influenced by the distance to neighboring lakes with high hydrological connectivity, something that is commonly a main driver of species richness (Olden et al., 2001).

4.4. Implications for the establishment of new lakes

Fish colonization of Lake Fil was remarkably rapid and all species found in the closely connected waterbodies appeared in the lake within five years after establishment. The species composition resembled that in the closely connected lakes and the trajectory moved towards the composition found in lakes throughout the region. The success and abundance, however, was not the same for all species. Three-spined stickleback was dominant during the first year, but then almost disappeared. Roach became established in large numbers, but perch was rare and only a single cohort of pike was observed; hence, planktivorous fish dominated the lake, relative to piscivorous.

For managers of newly established lakes, details of immigration patterns can be important, especially when lake characteristics like turbidity can vary dramatically as a result of otherwise apparently minor differences in immigration. The development in Lake Fil and other new lakes reveals both that natural immigration of piscivorous species can be low and that sustained recruitment can fail. Managers can respond to this situation simply by waiting and letting the fish community and food web structure develop without interference. Alternatively, they may decide to support a strong presence of piscivorous species be releasing them as fry or as larger individuals over two or three seasons, which is expected to enhance the establishment prospects of diverse cohorts that can exert predation on the planktivorous species that had swiftly migrated into the lake. This management practice would ensure that piscivorous species will contribute to a food web structure with less predation on zooplankton and stronger grazing on phytoplankton.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2020.105956.

Author contributions

Conceived and designed the investigation: TK, KSJ, MP, and JK. Performed field and/or laboratory work: TK, MP, JK, and EK. Analyzed the data: EK, TK, and LBS. Wrote the paper: EK, TK, KSJ, and LBS.

Data availability statement

The data that support the findings of this study are available from the corresponding author, EK, upon reasonable request.

Declaration of Competing Interest

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

Acknowledgment

We thank Aage V. Jensen Nature Foundation, Denmark, for grants to KSJ, TK, LBS, and EK by funding the monitoring program, the investigations of new lakes, and for offering housing during field visits.

References

Anderson, K.J., 2007. Temporal patterns in rates of Community Change during Succession. Am. Nat. 169, 780. https://doi.org/10.2307/4136997.
Århus Amt Natur og Miljø, 2005. Årslev Engsø.
Baastrup-Spohr, L., Kragh, T., Petersen, K., Moeslund, B., Schou, J.C., Sand-Jensen, K., 2016. Remarkable richness of aquatic macrophytes in 3-years old re-established Lake Fil, Denmark. Ecol. Eng. 95, 375–383. https://doi.org/10.1016/J.ECOLENG.2016.06.081.
Bio/consult, 2003. Fiskebestanden i Årslev Engsø 2003.
Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R, Numerical Ecology with R. Springer New York, New York, NY. https://doi.org/10.1007/978-1-4419-7976-6.
Bouvier, L.D., Cottenie, K., Doka, S.E., 2009. Aquatic connectivity and fish metacommunities in wetlands of the lower Great Lakes. Can. J. Fish. Aquat. Sci. 66, 933–948. https://doi.org/10.1139/f09-050.
Breukelaar, A.W., Lammens, E.H.R.R., Breteler, J.G.P.K., Tatrai, I., 1994. Effects of benthivorous bream (Abramis brama) and carp (Cyprinus carpio) on sediment resuspension and concentrations of nutrients and chlorophyll a. Freshw. Biol. 32, 113–121. https://doi.org/10.1111/j.1365-2427.1994.tb00871.x.
Brodersen, J., Nillson, A.P., Hannson, L.-A., Skov, C., Bronmark, C., 2008. Condition-dependent individual decision-makoing determines cyprinid prtial migration. Ecology 89, 1195–1200.
Brodersen, J., Hansen, J.H., Skov, C., 2019. Partial nomadism in large-bodied bream (Abramis brama). Ecol. Freshw. Fish eff., 12483. https://doi.org/10.1111/eff.12483.
Brönmark, C., Skov, C., Brodersen, J., Nilsson, P.A., Hansson, L.A., 2008. Seasonal migration determined by a trade-off between predator avoidance and growth. PLoS One 3. https://doi.org/10.1371/journal.pone.0001957.
Brönmark, C., Brodersen, J., Chapman, B.B., Nicolle, A., Nilsson, P.A., Skov, C., Hansson, L.A., 2010. Regime shifts in shallow lakes: the importance of seasonal fish migration. Hydrobiologia 646, 91–100. https://doi.org/10.1007/s10750-010-0165-3.
Byström, P., Karlsson, J., Nilsson, P., Van Kooten, T., Ask, J., Olofsson, F., 2007. Substitution of top predators: Effects of pike invasion in a subarctic lake. Freshw. Biol. 52, 1271–1280. https://doi.org/10.1111/j.1365-2427.2007.01763.x.
Carl, H., Møller, P.R., 2012. Atlas over danske ferskvandsfisk, 1. edt. Statens Naturhistoriske Museum. Københavns Universitet.
CEN, 2005. EN 14757: Water Quality – Sampling of Fish with Multi-Mesh Gill Nets.
Chapman, B.B., Hulthén, K., Blomqvist, D.R., Hansson, L.A., Nilsson, J.Å., Brodersen, J., Anders Nilsson, P., Skov, C., Brönmark, C., 2011. To boldly go: Individual differences in boldness influence migratory tendency. Ecol. Lett. 14, 871–876. https://doi.org/10.1111/j.1461-0248.2011.01648.x.
Clarke, K.R., Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. Mar. Ecol. Prog. Ser. 92, 205–219. https://doi.org/10.3354/meps092205.
Clarke, K., Warwick, R., 2001. Change in Marine Communities: An Approach to Statistical analySis and Interpretation. 2nd edition. Primer-E, Plymouth. Plymouth, United Kingsom Prim. 1–172. doi:1.
Dahl, T.E., 2011. Status and trends of wetlands in the conterminous United States 2004 to 2009. US Department of the Interior, US Fish and Wildlife Service, Fisheries and ….
Daniels, R.A., Morse, R.S., Sutherland, J.W., Bombard, R.T., Boylen, C.W., 2009. Fish movement among lakes: are lakes isolated. Northeast. Nat. 15, 577–588. https://doi.org/10.1656/1092-6194-15.4.577.
DMI, 2020. Klimanormaler Danmark [WWW Document]. URL. https://www.dmi.dk/vejrarkiv/normaler-danmark/ (accessed 5.14.20).
Drakou, E.G., Bobori, D.C., Kallimanis, A.S., Mazaris, A.D., Sgardelis, S.P., Pantis, J.D., 2009. Freshwater fish community structured more by dispersal limitation than by environmental heterogeneity. Ecol. Freshw. Fish 18, 369–379. https://doi.org/10.1111/j.1600-0633.2009.00354.x.
Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Stiassny, M.L.J., Sullivan, C.A., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biol. Rev. Camb. Philos. Soc. https://doi.org/10.1017/S1464793105006950.
Egler, F.E., 1954. Vegetation science concepts I. initial floristic composition, a factor in old-field vegetation development. Veg. Acta Geobot. 4, 412–417. https://doi.org/10.1007/BF00275587.
Estlander, S., Nurminen, L., Olin, M., Vinni, M., Immonen, S., Rask, M., Ruuhijärvi, J., Horppila, J., Lehtonen, H., 2010. Diet shifts and food selection of perch Perca fluviatilis and roach Rutilus rutilus in humic lakes of varying water colour. J. Fish Biol. 77, 241–256. https://doi.org/10.1111/j.1095-8649.2010.02682.x.
Frost, W.E., Kipling, C., 1967. A study of reproduction, early life, weight-length relationship and growth of Pike, Esox lucius L., in Windermere. J. Anim. Ecol. 36, 651. https://doi.org/10.2307/2820.
Gore, J.A., Milner, A.M., 1990. Island biogeographical theory: can it be used to predict lotic recovery rates? Environ. Manag. 14, 737–753. https://doi.org/10.1007/BF02394722.
Grimm, M.P., 1981. The composition of Northern Pike (Esox lucius L.) populations in four shallow waters in the Netherlands, with special reference to factors influencing 0+ Pike biomass. Aquac. Res. 12, 61–76. https://doi.org/10.1111/j.1365-2109.1981.tb00011.x.
Hansen, K., 2014. Folk og fortællinger fra det tabte land. In: Bind 1–2.
Hirsch, P.E., N'Guyen, A., Muller, R., Adrian-Kalchhauser, I., Burkhardt-Holm, P., 2018. Colonizing Islands of water on dry land-on the passive dispersal of fish eggs by birds. Fish Fish. https://doi.org/10.1111/faf.12270.
Hoffmann, C.C., Baattrup-Pedersen, A., 2007. Re-establishing freshwater wetlands in Denmark. Ecol. Eng. 30, 157–166. https://doi.org/10.1016/j.ecoleng.2006.09.022.
Hoffmann, C.C., Kronvang, B., Audet, J., 2011. Evaluation of nutrient retention in four restored Danish riparian wetlands. Hydrobiologia 674, 5–24. https://doi.org/10.1007/s10750-011-0734-0.
Jeppesen, E., Jensen, J.P., Søndergaard, M., Lauridsen, T., Pedersen, L.J., Jensen, L., 1997. Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. Hydrobiologia 342 (343), 151–164. https://doi.org/10.1023/A:1017046130329.
Jeppesen, E., Jensen, J.P., Sondergaard, M., Lauridsen, T., Landkildehus, F., 2000. Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. Freshw. Biol. 45, 201–218. https://doi.org/10.1046/j.1365-2427.2000.00675.x.
Kragh, T., Sand-Jensen, K., Petersen, K., Kristensen, E., 2017. Fast phosphorus loss by sediment resuspension in a re-established shallow lake on former agricultural fields. Ecol. Eng. 108, 2–9. https://doi.org/10.1016/j.ecoleng.2017.07.026.
Kragh, T., Martinsen, K.T., Kristensen, E., Sand-Jensen, K., 2020. From drought to flood:

Sudden carbon inflow causes whole-lake anoxia and massive fish kill in a large shallow lake. Sci. Total Environ. 739, 140072. https://doi.org/10.1016/j.scitotenv.2020.140072.
Laboratorium, Fiskeøkologisk, 1995. Notat vedrøremde fiskebestanden i Solbjerg Engsø.
Lake, P.S., Bond, N., Reich, P., 2007. Linking ecological theory with stream restoration. Freshw. Biol. https://doi.org/10.1111/j.1365-2427.2006.01709.x.
Menezes, R.F., Borchsenius, F., Svenning, J.-C., Søndergaard, M., Lauridsen, T.L., Landkildehus, F., Jeppesen, E., 2013. Variation in fish community structure, richness, and diversity in 56 Danish lakes with contrasting depth, size, and trophic state: does the method matter? Hydrobiologia 710, 47–59. https://doi.org/10.1007/s10750-012-1025-0.
Møller, M.J., Sand-Jensen, K., Baastrup-Spohr, L., 2019. Fuglenes biodiversitet i nye danske søer. Vand Jord 26 (2), 64–68.
Nilsson, J., Engstedt, O., Larsson, P., 2014. Wetlands for northern pike (Esox lucius L.) recruitment in the Baltic Sea. Hydrobiologia 721, 145–154. https://doi.org/10.1007/s10750-013-1656-9.
NOVANA, 2017. Det nationale overvågningsprogram for vandmiljø og natur. pp. 2017–2021.
Olden, J.D., Jackson, D.A., Peres-Neto, P.R., 2001. Spatial isolation and fish communities in drainage lakes. Oecologia 127 (4), 572–585. https://doi.org/10.1007/s004420000620.
Patankar, R., von Hippel, F.A., Bell, M.A., 2006. Extinction of a weakly armoured threespine stickleback (Gasterosteus aculeatus) population in Prator Lake, Alaska. Ecol. Freshw. Fish 15, 482–487. https://doi.org/10.1111/j.1600-0633.2006.00186.x.
Persson, L., 1987. Effects of habitat and season on competitive interactions between roach (Rutilus rutilus) and perch (Perca fluviatilis). Oecologia 73, 170–177. https://doi.org/10.1007/BF00377504.
Persson, L., Greenberg, L.A., 1990. Juvenile Competitive Bottlenecks: the Perch (Perca Fluviatilis)-Roach (Rutilus Rutilus) Interaction. Ecology 71, 44–56. https://doi.org/10.2307/1940246.
Reichard, M., Jurajda, P., Ondračková, M., 2002. Interannual variability in seasonal dynamics and species composition of drifting young-of-the-year fishes in two European lowland rivers. J. Fish Biol. 60, 87–101. https://doi.org/10.1006/jfbi.2001.1813.
Revenga, C., Brunner, J., Henninger, N., Kassem, K., Payne, R., 2000. Freshwater systems. World Resources Institute, Washington, DC.
Sarr, D.A., 2002. Riparian Livestock Exclosure Research in the Western United States: A Critique and Some Recommendations Origin and Types of Riparian Livestock Exclosures. https://doi.org/10.1007/s00267-002-2608-8.
Skov, C., Brodersen, J., Nilsson, P.A., Hansson, L.A., Brönmark, C., 2008. Inter- and size-specific patterns of fish seasonal migration between a shallow lake and its streams. Ecol. Freshw. Fish 17, 406–415. https://doi.org/10.1111/j.1600-0633.2008.00291.x.
Sø, J.S., Sand-Jensen, K., Baastrup-Spohr, L., 2019. Temporal development of biodiversity of submerged plants in newly established lakes. Freshw. Biol. https://doi.org/10.1111/fwb.13431.
Søndergaard, M., Lauridsen, T.L., Johansson, L.S., Jeppesen, E., 2018. Gravel pit lakes in Denmark: Chemical and biological state. Sci. Total Environ. 612, 9–17. https://doi.org/10.1016/j.scitotenv.2017.08.163.
Sørensen, T., 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons. K. Dan. Vidensk. Selsk. Biol. Skr. 5, 1–34.
Svärdson, F., 1947. Gaddlekstudier. Skr. söd. Sver. FiskFör 2, 34–59.
Verhoeven, J.T.A., 2014. Wetlands in Europe: Perspectives for restoration of a lost paradise. Ecol. Eng. 66, 6–9. https://doi.org/10.1016/j.ecoleng.2013.03.006.
Walrath, J.D., Quist, M.C., Firehammer, J.A., 2015. Population Structure and Dynamics of Northern Pike and Smallmouth Bass in Coeur d'Alene Lake, Idaho. Northwest Sci. 89. https://doi.org/10.3955/046.089.0308.