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ARTICLE

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Using swim-up traps to assess Arctic charr (*Salvelinus alpinus*) spawning habitat and the phenology and density of emergent fry

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Abstract

The Arctic charr (*Salvelinus alpinus*) is a species of cultural, economic and conservation importance, but hitherto, investigations of critical early life stages have been few. Here, at a lake in the United Kingdom, we used swim-up traps to investigate the phenology of fry emergence and associations between fry density and habitat. The first emergence occurred on 4 or 5 March 2020 and 2021, with numbers peaking and remaining stable in the following 2 weeks. Emergence in 2021 had finished by 27 March but on the same date in 2020 emergence was ongoing when COVID-19 ended sampling. Substrate particle size ranged 31–94 mm and was negatively correlated with fry density. Likewise, density was negatively correlated with water depth and aquatic plant cover, but there was no relationship with flow velocity. Traps were effective and non-destructive for assessing the location and productivity of spawning sites for this locally threatened species.

KEYWORDS
conservation, depth, flow, monitoring, salmonids, substrate

1 | INTRODUCTION

Arctic charr (*Salvelinus alpinus*) populations near the species' southern range edge have declined at an alarming rate over recent decades (Igoe et al., 2003; Maitland et al., 2007), with low survival of early life stages (eggs and alevins) suspected to be one contributing factor (Kelly et al., 2020; Maitland et al., 2007; Miller et al., 2015; Winfield & Fletcher, 2009). Like most salmonids, Arctic charr lay their eggs in stony substrates clean from fine sediments that could cause anoxia in interstitial waters (Low et al., 2011; Riley et al., 2019; Smialek et al., 2021), meaning spawning areas are vulnerable to increased sedimentation that can follow from eutrophication (Miller et al., 2015). Temperature and anthropogenic climate change are critical for survival and phenology of early life stages, and winter spawning temperatures at the species' southern range edge often approach the upper thermal limit for egg survival (~8.5°C, Kelly et al., 2020). Other disturbances that threaten early life stages include acidification, heavy metal contamination, predation by non-native species, desiccation due to water abstraction and washout of eggs and alevins caused by flooding or hydropower operation (Crisp, 1990; Maitland et al., 2007; Setzer et al., 2011; Smith, 2022). However, despite concerns regarding reproductive success of Arctic charr, and recognition that early-life stage survival and ecology are critical to understanding salmonid population dynamics (Smialek et al., 2021), little attention has been directed toward studying early life stages in the wild or developing sampling methods (Winfield & Fletcher, 2009).

Because Arctic charr are locally threatened, and in some cases protected by law (Maitland et al., 2007), monitoring and research that has minimal impact on the population is important (Igoe & Ruane, 2012; Seymour & Smith, 2023). Researchers in Ireland identified snorkelling as a viable, non-destructive method for estimating the abundance of eggs at shallow littoral sites in lakes and successfully applied the technique to link egg density with habitat features such as depth, substrate particle size and interstitial space (Igoe & Ruane, 2012; Low et al., 2011). However, snorkelling in harsh conditions of winter is challenging, requires considerable manpower and skill and is very difficult in waters with even modest current (Smith, 2022). As an alternative to visual surveys by snorkelling, egg density can be measured with suction samplers that extract eggs from the gravel, but is destructive, and therefore not desirable for threatened populations (Butterworth, 1980; Stauffer, 1981). Redd counting from the bank or an aircraft, which is commonly used to assess spawning activity of salmonids (Groves et al., 2016), is unsuitable because Arctic charr rarely dig defined redds and may spawn in deeper waters (Frost, 1965; Low et al., 2011). Beyond the alevin stage, when fry first emerge from the gravel, proven methods of sampling are not described, so knowledge of phenology is extremely limited. In mild locations, such as the British Isles, fry emergence in autumn spawning populations (spawning in late November to December) occurs in spring, after which fry may quickly depart spawning grounds to feed in the pelagic or profundal zone (Baroudy & Elliott, 1994; Frost, 1965; Klemetsen et al., 1989).

A possible sampling method for fry widely used for closely related lake trout (*Salvelinus namaycush*), are swim-up fry traps (Casscles et al., 2016; Collins, 1975; Marsden et al., 2002). These traps exploit a behaviour of most salmonids, including Arctic charr, whereby fry emerging from the gravel must first surface to fill their swim bladder with air before becoming free-swimming fish (Collins, 1975; Wallace & Aasjord, 1984). Traps function by enclosing an area of substrate under a mesh cone that directs upward swimming fry into a collection vessel. Traps are suitable for a variety of habitats and water depths, which is an important requirement for Arctic charr that are highly variable in where they spawn (Frost, 1965; Klemetsen et al., 2003; Walker, 2007). A further advantage of swim-up traps is they sample a known area of substrate that enables investigating relationships between numbers of emergent fry and habitat beneath each trap and extrapolating catch across the whole spawning area to estimate total fry production.

Herein, we described a 2-year study of Arctic charr fry emergence using swim-up traps at Llyn Padarn in North Wales, United Kingdom. Objectives of the study were to (1) determine if swim-up traps could be effective for measuring the density of Arctic charr emergent fry; (2) assess phenological patterns in the numbers of emerging fry; and (3) investigate relationships between fry density and characteristics of spawning habitat. The design of swim-up traps featured a novel detachable collection vessel that was retrievable without removal of the main body of the trap from the water. This feature allowed rapid and frequent checking of traps by a lone field worker to generate fine-scale temporal measurements of the timing of fry emergence, thereby ensuring the precise location sampled by each trap remained consistent throughout the survey.

2 | METHODS

2.1 | Study site

Llyn Padarn is a mesotrophic glacial lake situated at low altitude (105 m) in the foothills of the Snowdonia Mountains in the United Kingdom. The lake is of moderate size (98 ha) and depth (27 m) and is near the southern limit of Arctic charr distribution (53.1301°N, 4.1382°W). The population spawns consistently in December, as confirmed by many years of monitoring by fyke netting and several DIDSON surveys (Butterworth, 1980; McCarthy, 2007; Smith, 2022). Prior to our study, the only confirmed spawning site was in the main inflowing river (Afon y Bala) ~ 300 m upstream of the lake (McCarthy, 2007; Smith, 2022). However, we identified a different spawning site at Penllyn, a short distance upstream of the lake's outflow (River Seiont), where swim-up traps were deployed.

2.2 | Swim-up trap design

Swim-up fry traps shared three components with other published designs: a circular rim that rests on the substrate and provides ballast, a mesh cone attached to the rim and a collection vessel at the top of the cone to trap fry (Figure 1). A relatively heavy trap was required because Arctic charr at Llyn Padarn spawn in flowing water. The rim of the trap was therefore constructed from a 2 m length of large diameter corrugated hose (ø59 mm), filled with sand and joined into a circle using a short section of 58-mm-diameter wooden dowel. The cone was made from uncoated aluminium insect screen (1.36 mm mesh size), cut into a circle with a triangular sector removed and sides stapled together to form a cone. To create a hole to direct fry into the collection vessel, a small incision was cut at the apex of the cone and a 96-mm-diameter plastic funnel was inserted so that the funnel neck (70 mm long, ø 5 mm) through which fry would swim protruded from the top of the cone. The funnel neck was cut in half along the vertical axis, down to its base, to reduce the distance fry needed to swim upwards through a narrow tube. Leaving the height of the neck in place, rather than removing it, added stability to the collection vessel when anchored to the top of the trap. The funnel was secured to the mesh by bolting a second plastic funnel, with neck removed, over the outside of the cone top. The completed mesh cone was then attached to the hose rim using cable ties.

The removable fry collection vessel was made from a 130-mm-length of 68-mm-diameter drainage pipe. A machine-cut disc of clear acrylic (5 mm thickness) was inserted into the base of the pipe, with a hole that fitted a 90-mm-length by 38-mm-diameter section of pipe. This internal pipe was slotted over the aforementioned plastic funnel to direct fry into the vessel. The lid of the capture vessel was made in the same manner as the base. Small holes

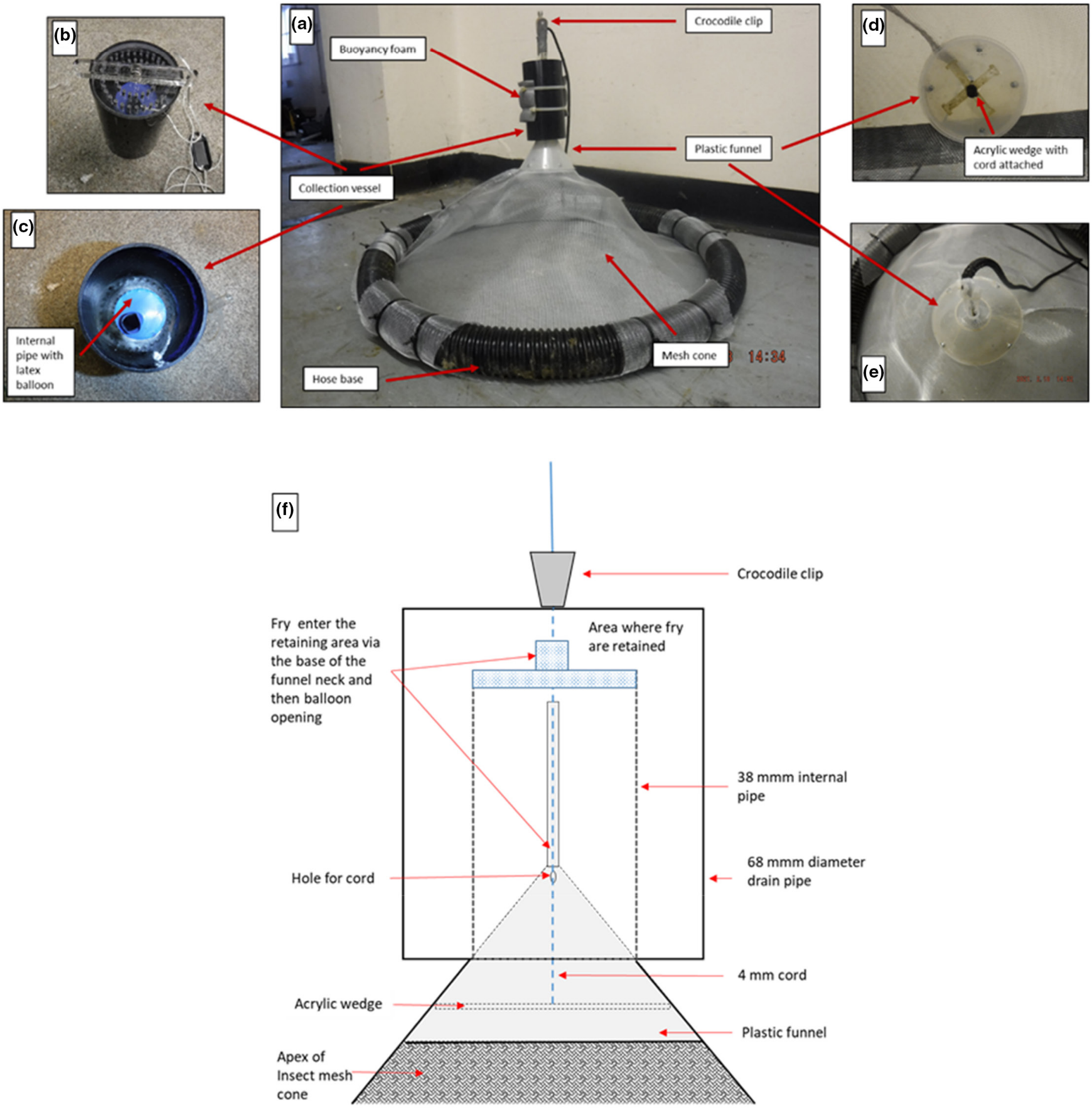

FIGURE 1 Swim-up trap design used to sample Arctic charr fry at Llyn Padarn in North Wales, United Kingdom in spring 2020 and 2021: (a) the completed trap; (b) the fry collection vessel with lid in place; (c) the internal pipe with latex balloon; (d) the acrylic wedge inside the funnel that secured the chord for attaching the fry collection vessel; (e) the funnel at the top of the mesh cone that directed fry into the collection vessel; and (f) a diagram showing how the fry collection vessel fitted onto the trap.

(ø1.5 mm) were drilled into the lid, base and sides of the collection vessel to ensure adequate oxygen supply. The vessel was attached to the body of the trap by a 4-mm-diameter piece of cord tied to a cross-shaped piece of acrylic that wedged inside the plastic funnel of the mesh cone. The vessel slid down the cord via the internal pipe and a 6-mm-diameter hole in the lid to rest on top of the external plastic funnel, where it was anchored using a heavy-duty crocodile clip. Before attaching the vessel, a latex balloon was stretched over the opening of the internal pipe and cut near the base to inhibit fry from returning into the internal pipe, where they would be lost when retrieving the vessel from the trap. The completed trap was ~43 cm high at the top of the collection vessel, weighed ~6 kg in air and covered an area of 0.32 m^2. Fry collection vessels were deployed and retrieved by wading, while wearing a membrane dry suit at depths up to chest high. Great care was taken while wading to avoid disturbing spawning substrate and fry. After deployment, organic sediment and filamentous algae that accumulated on the mesh were periodically removed using a brush attached to a long handle.

2.3 | Sampling of emergent fry

Traps were positioned at the Penllyn spawning site in areas where eggs had been observed by snorkelling during the prior egg incubation period (see Smith, 2022). Traps were deployed in transects of three or four traps running parallel to the direction of water flow (Figure 2). Traps on the same transect were tethered together and anchored to a concrete block to ensure they would not move during high-flow events. The distance between traps was ~1.0–1.5 m.

Surveys in 2020 began on 28 February, when eight traps were set (Transects 1 and 2, Figure 2), followed by seven traps (Transects 3 and 4, Figure 2) on 2 March. Fry collection vessels were initially examined every 3–4 days, decreasing to ~2 days after fry were first captured ($\mu = 2.08$ days between sampling, range = 1–3 days). The survey continued until 27 March, when sampling was ended prematurely by the COVID-19 outbreak. Fry in each collection vessel were counted and catch per unit effort (CPUE) was calculated as the number of fry divided by nights fished. Nights were used because salmonid fry swim up during darkness (Brüning et al., 2011), so variation in the number of daylight hours fished (generally small) was not expected to affect capture numbers. The distribution of CPUE was strongly left skewed, so the geometric mean and 95% confidence intervals were used for summary statistics. To account for zero catches when calculating the geometric mean, one was added to all trap lifts and then subtracted from the geometric mean (de la Cruz & Kreft, 2019).

Traps in spring 2021 were deployed on 1 March, when seven traps (Transects 3 and 4, Figure 2) were deployed at Penllyn, and other traps were deployed at the spawning site in the main inflowing river (Afon y Bala). Surveys at Afon y Bala were not successful because flooding caused traps to be buried under gravel and prevented access. Flooding in 2021 slightly reduced the frequency of sampling at Penllyn compared to 2020 ($\mu = 2.37$ days between sampling, range = 2–4 days). Based on survey results for 2020, the 2021 survey was continued until the end of March, or until no fry were captured for 1 week.

2.4 | Habitat characteristics at trap locations

Spearman rank correlation (R Base Package, R Core Team, 2022) was used to test relationships between habitat at each trap and the number of emergent fry captured. Flow velocity at 5 cm above the substrate was measured adjacent to each trap using a Geopacks Advanced Flowmeter, calibrated by the manufacturer under laboratory conditions to an accuracy of ± 0.05 m/s. Water depth was measured using a tape measure fixed to a pole. Substrate particle size was measured from photographs of the substrate beneath each trap taken with a Fuji Finepix XP130 waterproof camera mounted 48 cm above a 0.16 m^2 quadrat. A uniform grid of 25 stratified points was generated for each image and the length of the longest visible dimension of the substrate particle beneath each point was measured (PhotoQuad, Trygonis & Sini, 2012). The geometric mean was used to summarize average particle size in each image. Points covered by aquatic plants were recorded as such, and substrate particles covered by >1 point were measured only once. Points where size could not be measured because the substrate particle was not distinguishable (e.g., covered by aquatic plants, too small or out of focus) were recorded as missing. Due to cessation of research activity in 2020 because of the COVID-19 outbreak, measurements of habitat characteristics at trap locations originally planned for the end of fry sampling were delayed until August 2020. In 2021, depth and velocity were measured on 2 April and substrate images were taken when sampling ended on 6 April. When depth of traps was

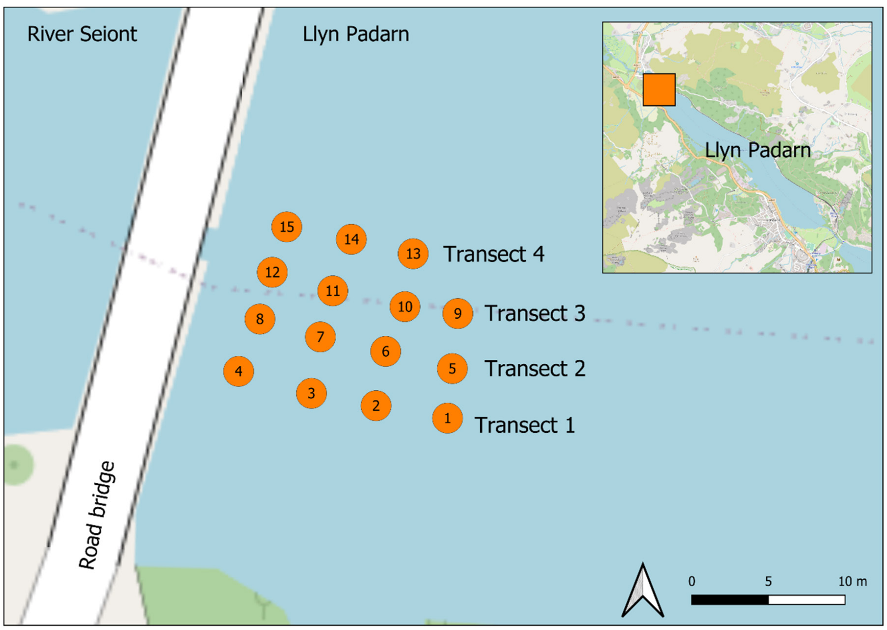

FIGURE 2 The location of swim-up traps used to sample Arctic charr fry at the Penllyn spawning site at Llyn Padarn in North Wales, United Kingdom, in spring 2020 and 2021.

measured, the lake level was recorded from a permanent datum board to standardize measurements in 2020 and 2021. Midday temperature at <2 m depth was recorded by an automated monitoring buoy at the centre of the lake to summarize water temperature at Penllyn between spawning (December) and fry emergence. Because of the low numbers of fry captured in 2021 and fewer traps being deployed, relationships between CPUE and habitat characteristics at trap locations were only analysed for 2020.

[Correction added on 29 July 2023, after first online publication: minor tweaks have been applied to this paragraph to support clarity.]

2.5 | DNA barcoding of fry

Atlantic salmon (*Salmo salar*) and trout (*Salmo trutta*) spawned at or near the Penllyn site, so one fry captured on each sampling day in 2020 was euthanized using clove oil and preserved in ethanol for species confirmation by DNA barcoding. The QIAGEN DNeasy blood tissue kit was used for DNA extractions using PCR conditions and primers (COI-3 primer set) selected from Ivanova et al. (2007). A BLAST search was used to match sequencing data to reference libraries for salmonid species. Fry not returned to the laboratory were released at suitable habitat ~100 m from the sampling site.

3 | RESULTS

3.1 | Swim-up fry density and phenology

Of 260 fry captured at the Penllyn site in 2020, all were alive and active when removed from collection vessels. DNA barcoding confirmed that fry returned to the laboratory ($n = 11$) were Arctic charr, so we assumed all fry captured were Arctic charr.

The first fry was caught on 5 March (Figure 3), although only eight traps were deployed on 2 March, and those traps generally caught the fewest fry during the survey period (19% of total CPUE). Geometric mean CPUE increased steeply from 7 March to a peak (0.63 fry/trap-night) on 12 March (Figure 3). After 12 March, geometric mean CPUE ranged 0.43–0.55 fry/trap-night until the end of sampling period, although confidence intervals widened as more fry were captured in fewer traps (Figure 3). From 9 to 19 March, 122 fry were caught in 14 traps, compared to 138 fry caught in 9 traps from 19 to 27 March. Geometric mean CPUE over the entire period of fry emergence averaged 0.41 fry/trap-night (95% CI = 0.16–0.71 fry/trap-night).

A Wilcoxon test (R Base Package, R Core Team, 2022) showed geometric mean CPUE during the emergence period in 2021 (0.06 fry/trap-night; 95% CI = 0.00–0.13 fry/trap-night) was significantly lower than in 2020 (N traps = 15 and 7 in 2020 and 2021, respectively, $p < 0.05$). Moreover, of 16 fry captured in 2021, 10 were dead in collection vessels and 1 live individual showed symptoms of swim-up syndrome (poor buoyancy control and swimming capability; Fitzsimons, 1995; Wolgamood et al., 2005). The highest CPUE (0.12 fry/trap-night) in 2021 was on 3 sampling days (9–18 March), and all fry were captured between 4 and 27 March (Figure 3). Fry were only caught in four of seven traps, all near the lake outflow.

3.2 | Habitat characteristics

Habitat beneath swim-up traps was characterized by a substrate particle size of 31.7–104.9 cm, a depth of 55.3–79.7 cm, a velocity of 0.04–0.41 m/s and aquatic plant coverage of 0%–60% (Table 1; Figure 4). Water temperature during the egg incubation period to the end of swim-up (December to end of March) averaged 6.71°C ± 0.27 (range = 6.35–7.61°C) in 2020 and 6.69°C ± 1.01 (range = 4.07–8.85°C) in 2021. During 2019–2020, the automated monitoring buoy only recorded data on 34 days.

A Kruskall–Wallis test (R Base Package, R Core Team, 2022) showed geometric mean CPUE of fry differed significantly among traps in 2020 (df = 14, $p < 0.001$). Traps closest to the lake outflow captured the most fry, particularly traps 11 (14% of total CPUE), 12 (28%) and 15 (21%). The number of fry captured in 2020 was negatively correlated with substrate particle size ($R_S = -0.83$, df = 13, $p < 0.001$), depth ($R_S = -0.94$, df = 13, $p < 0.001$) and aquatic plant coverage ($R_S = -0.65$, df = 13, $p < 0.01$). Fry catch was not monotonically related to flow velocity ($R_S = -0.19$, df = 12, $p = 0.49$).

4 | DISCUSSION

Reproductive ecology and success are critical to understanding population dynamics of fish (Smialek et al., 2021), yet studies in the wild of Arctic charr early life stages have been fewer than many other salmonids. For the first time, we demonstrated suitability of swim-up traps for measuring Arctic charr fry density and our novel trap design allowed high-frequency temporal sampling without moving the trap, which facilitated insights into phenology and habitat. Our findings add important new information to sparse literature, including timing and duration of fry emergence, density of emergent fry and associations between fry density and spawning habitat characteristics.

We demonstrated that swim-up traps were useful for Arctic charr population assessment. Possible management applications include longitudinal monitoring of fry density to assess the efficacy of conservation interventions (e.g., habitat restoration, Kennedy et al., 2014) and measuring productivity of known or putative spawning sites within lakes to identify those of particular importance, and therefore worthy of protection (Butterworth, 1980; Miller et al., 2015; Milner, 1985). In Llyn Padarn, swim-up traps, combined with DNA barcoding, provided robust evidence of a new spawning site that was more productive and suitable than the only previously known site at the Afon y Bala (Smith, 2022). This finding was regarded by local stakeholders and managers as highly significant for future conservation of this imperilled population.

Because of population variation in Arctic charr spawning habitat, it is desirable that a sampling technique is suitable for different habitats. Arctic charr spawn in lakes and rivers (Walker, 2007), and to our knowledge, our study was the first to deploy swim-up traps in flowing water. Flow velocities at Penllyn (<0.41 m/s) did not appear to affect trap function, but if fabric mesh had been used, rather than more rigid aluminium insect mesh, the mesh cone would likely have been compressed or flattened. Sampling at the Afon y Bala, a generally slow-flowing river but subject to significant floods, demonstrated the design would require modification if deployed into this type of environment. The primary issue was that traps were covered by sediment and collapsed, sometimes causing minor damage to the mesh. Other designs of swim-up traps use sheet metal mesh and appear considerably more robust (Collins, 1975), but could still be buried under sediment.

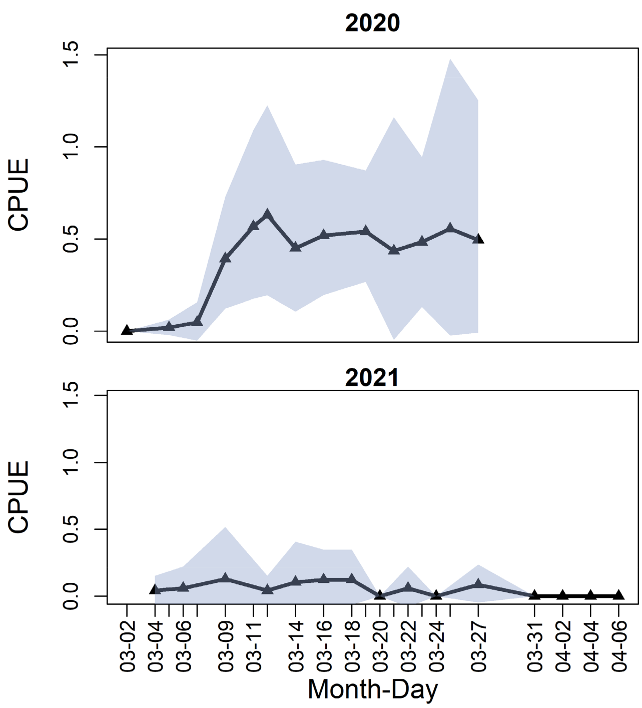

FIGURE 3 Geometric mean CPUE (fry/trap-night) of Arctic charr fry (solid line and triangles) caught in 15 swim-up traps in 2020 and 7 traps in 2021 at the Penllyn spawning site at Llyn Padarn in North Wales, United Kingdom, in spring 2020 and 2021. Blue-shaded areas depict 95% confidence intervals.

Peak emergence of Arctic charr fry on 12 March 2020 occurred 88 days after spawning, assuming peak spawning was on 15 December 2019 (Arctic charr typically spawn at Llyn Padarn during the 2nd and 3rd weeks of December; Butterworth, 1980; Smith, 2022). This was earlier than expected, given that 50% hatching was 78–86 days for the autumn-spawning population at climatically similar Lake Windermere (Baroudy & Elliott, 1994), leaving an unrealistic 2–10 days for alevins to reach the swim-up stage at Llyn Padarn. Thus, the duration of egg development at Llyn Padarn in both 2020 and 2021 was likely shorter than at Windermere (Baroudy & Elliott, 1994), which is supported by in situ studies of egg survival at the Afon y Bala spawning site during winter 2019–2020 (Smith, 2022). Temperature is the principal environmental variable regulating the rate of early life stage development, and Crisp (1988) showed the relationship between temperature and development is independent of species within salmonids, although *Salvelinus* spp. were not included. The approximate value of 88 days between fertilization and swim-up for Arctic charr at Llyn Padarn is at the lower end of values measured for other salmonids (Crisp, 1988). Our findings suggest future monitoring of emergent fry at Llyn Padarn and other climatically similar lakes with December spawning populations should be between the 2nd and 4th weeks in March. Temporal stability of CPUE during these weeks may reduce the need to survey for the full duration of the swim-up period to estimate fry density. Timing of surveys may need to be adjusted in unusually warm or cold winters, which could alter the timing of spawning and development of eggs and alevins.

Our study was the first to use swim-up traps for estimating density of Arctic charr emergent fry, so we cannot know if densities we measured are useful thresholds for classifying population status for conservation and management. Nonetheless, swim-up trap densities we measured for Arctic charr fry at Penllyn in 2020 were near the upper end of the reported range for lake trout in North America, but near the lower end in 2021 (Table 2). Different sampling strategies, trap designs, habitat and species vulnerability limit comparisons among studies (Collins, 1975). Fewer fry captured in 2021 than in 2020 was possibly caused by variation in egg, alevin or emergent fry survival (Kelly et al., 2020; Mari et al., 2016). Warm temperatures at the incubation stage are a primary cause of elevated egg mortality (Kelly et al., 2020; Mari et al., 2016), and maximum temperatures in

TABLE 1 Substrate size, depth, velocity and occurrence of aquatic plants at 15 swim-up traps in 2020 and 7 traps in 2021 set for Arctic charr fry at the Penllyn spawning site at Llyn Padarn in North Wales, United Kingdom, in spring 2020 and 2021.

Habitat variable	Penllyn 2020 (*n* = 15)	Penllyn 2021 (*n* = 7)
Substrate size (mm)	53.8, 32.9–94.3 (31.7–104.9)	60.3, 31.5–71.7 (27.9–72.9)
Depth (cm)	69, 55.3–81.6 (55–82)	69, 57.3–79.7 (57–80)
Velocity (m/s)	0.096, 0.04–0.41 (0.04–0.41)[a]	0.12, 0.05–0.16 (0.05–0.17)
Occurrence of aquatic plants (%)	0, 0–48.8 (0–60)	0, 0–19.4 (0–20)

Note: Values are the median and 95% confidence intervals (CI), except for substrate size, which is geometric mean and 95% CI (range in parentheses).

[a]*n* = 14.

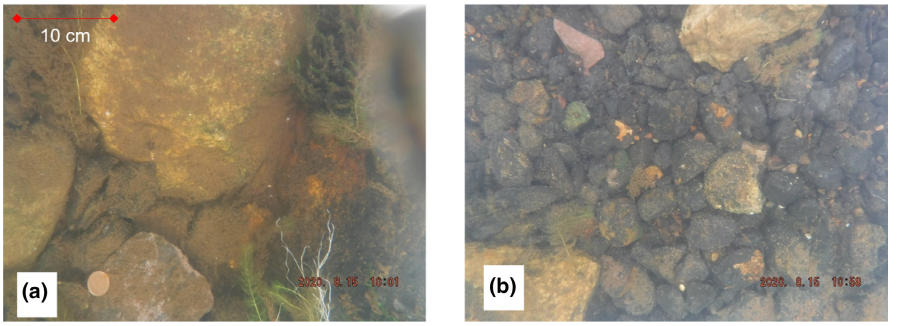

FIGURE 4 Substrate beneath the only trap not to capture fry in 2020 (a) and beneath the trap that captured the most fry in 2020 (b) at the Penllyn Arctic charr spawning site at Llyn Padarn in North Wales, United Kingdom. Both images are on the same scale.

TABLE 2 Density of emergent lake trout fry captured in swim-up traps compared to results from the present study.

Study site and year	CPUE[a]	Reference
Penllyn, March 2020	2.16	This study
Penllyn, March 2021	0.23	This study
Grande Isle, Lake Champlain, NY	2.65	Marsden et al. (2002)
Whallon Bay, Lake Champlain, NY	0.02	Marsden et al. (2002)
Bissel Point, Ostego Lake, NY, 2016	1.17	Winter et al. (n.d.)
Bissel Point, Ostego Lake, NY, 2013	0.07	Sawick and Foster (2014)
Bissel Point, Ostego Lake, NY, 2003	1.4	Tibbits (2007)
Bissel Point, Ostego Lake, NY, 2014	1.65	Lucykanish and Foster (2015)
Bissel Point, Ostego Lake, NY, 2015	1.28	Casscles et al. (2016)

[a]CPUE here is the number of fry per trap-day per m^2.

2021 (8.59°C) were substantially higher than in 2020 (7.71°C). Poor fry health in 2021 was indicated by a high proportion of dead fry in traps and one fry with symptoms of swim-up syndrome, a condition linked with thiamine deficiency in other *Salvelinus* spp. parents (Fisher et al., 1996; Fitzsimons, 1995; Wolgamood et al., 2005). Variation in spawning stock size and egg deposition could also explain lower fry catches (Solomon, 1985), but could not be investigated because attempts to quantify egg abundance by snorkelling were unsuccessful (Smith, 2022) and annual hydroacoustic surveys of adult abundance were not completed due to equipment failure in 2019 and COVID-19 restrictions in 2020.

The size of substrate particles at the Penllyn spawning site was similar to measurements by Low et al. (2011) at littoral sites in Ireland (geometric mean 59 mm; range 30–79 mm) and qualitative observations for other populations (Barbour, 1984; Frost, 1965; Milner, 1985). In salmonids, substrate particle size is strongly linked to body size because large fish have the strength to excavate redds in larger substrates than small fish (Riebe et al., 2014; Smialek et al., 2021). A rule of thumb is that salmonids will spawn in substrates which are ~10% of the fish body length (Crisp, 1993; Smialek et al., 2021). However, with an average fork length of ~270 mm (Smith, 2022), Arctic charr at Llyn Padarn do not fit this model, spawning in substrates ~20% of body length. The likely explanation is that Arctic charr do not dig redds as vigorously as most other salmonids (Frost, 1965), rather eggs are allowed to fall passively into the interstices (Low et al., 2011). The selection of the substrate is significant because it affects the oxygenation and stability of the spawning habitat. Substrate of the appropriate size allows for adequate water flow through the interstitial spaces, which helps oxygenate the eggs and remove waste products (Riebe et al., 2014; Smialek et al., 2021). Additionally, the gravel needs to be stable enough to protect the eggs from being buried or washed away by strong currents (Crisp, 1990; Riebe et al., 2014; Smialek et al., 2021). The larger particle sizes selected by Arctic charr may reflect lower flows in lakes compared to rivers where most other salmonid species spawn, meaning a substrate with larger interstices is required to ensure adequate water flow (Riley et al., 2019). In studies of river spawning Arctic charr, it is indicated that a finer substrate is selected and that redds may be dug (McCubbing et al., 1998), and in our study, which was undertaken in moderately flowing water at the lake outflow, substrates near the finer end of the sampled range produced a higher density of fry, although the analysis did not confirm an association with flow. The negative correlation between fry density and aquatic plant cover suggests fry numbers could be reduced by increased plant growth that can be caused by eutrophication, but to further investigate this hypothesis it would be necessary to control for other environmental variables that might be correlated with plant growth, such as depth, flow velocity and substrate.

Habitat could affect the efficiency of traps and may confound relationships between habitat and fry density. Traps might be more efficient on smaller substrates because they fit more tightly (Collins, 1975), although we feel this is unlikely to account for the very strong relationship between fry density and substrate particle size. Visual observation did not reveal any noticeable gaps between the substrate and the trap rim and to mitigate this potential issue our design featured a more flexible (corrugated hose) rim than some other designs. Given the very small size of fry and ability to move through interstitial spaces, it seems unlikely that the probability of sidewards escape would vary between traps because of minor differences in the gap between the trap rim and substrate surface. To further reduce fry escaping a weighted fine mesh skirt could be added to the outside of the rim, but fry could still escape via the interstitial spaces.

In conclusion, our study generated new knowledge on the phenology of Arctic charr fry emergence and demonstrated that swim-up traps were an effective and non-destructive technique to assess the location and productivity of spawning sites for this locally threatened species. Swim-up traps could be used by fishery managers to assess trends in emergent fry densities in response to conservation interventions (e.g., spawning habitat restoration). Information on phenology will help managers target monitoring at the optimal time of year and avoid expending resources unnecessarily. Broader use of swim-up traps for estimating density of Arctic charr emergent fry would enable development of density thresholds for classifying population status (e.g., Bean, 2003). Additional applications could include collecting genetic samples from different spawning sites to resolve local population structure and longitudinal studies of emergence phenology to investigate relationships with climate. We hope our study will prompt and guide further research into the neglected topic of Arctic charr early life stage survivorship and ecology, which are critical for understanding population dynamics, and for conserving and managing fisheries.

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CONFLICTS OF INTERESTS STATEMENT

There are no confilict of interests to declare.

DATA AVAILABILITY STATEMENT

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

ETHICS STATEMENT

The refinement and reduction principles of the 3Rs were followed by designing sampling methods that caused little or no harm to animal subjects and by only sacrificing the absolute minimum number of individuals necessary to robustly confirm species identity. Arctic charr are a protected feature of the Llyn Padarn Site of Special Scientific Interest (SSSI) and all relevant permissions were obtained.

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REFERENCES

Barbour, S.E. (1984) *Variation in the life-history, ecology and resource utilization by Arctic char, Salvelinus alpinus, in Scotland University of Edinburg*. (PhD thesis).

Baroudy, E. & Elliott, J.M. (1994) Racial differences in eggs and juveniles of Windermere charr, Salvelinus alpinus. *Journal of Fish Biology*, 45, 407–415.

Bean, C. (2003) A standardised survey and monitoring protocol for the assessment of Arctic charr, Salvelinus alpinus L., populations in the UK. Scottish Natural Herritage.

Brüning, A., Hölker, F. & Wolter, C. (2011) Artificial light at night: implications for early life stages development in four temperate freshwater fish species. *Aquatic Sciences*, 73(1), 143–152.

Butterworth, A. (1980) *The biology of the Arctic char. Salvelinus alpinus L., of Llynnau Peris and Padarn; with special reference to the Dinorwic reservoir scheme. University of Liverpool*. (PhD thesis).

Casscles, J.B., Foster, J.R., Lucykanish, D.M. & Sawick, N.M. (2016) *Effects of zebra mussels (Dreissena polymorpha) on Lake trout (Salvelinus namaycush) fry recruitment in Otsego Lake. SUNY Oneonta BFS. Cooperstown, NY*. 48th Ann. Report (2014).

Collins, J.J. (1975) An emergent fry trap for Lake spawning Salmonines and Coregonines. *The Progressive Fish Culturist*, 37(3), 140–142.

Crisp, D.T. (1988) Prediction, from temperature, of eyeing, hatching and 'swim-up'times for salmonid embryos. *Freshwater biology*, 19(1), 41–48.

Crisp, D.T. (1990) Some effects of application of mechanical shock at varying stages of development upon the survival and hatching time of British salmonid eggs. *Hydrobiologia*, 194(1), 57–65.

Crisp, D.T. (1993) The environmental requirements of salmon and trout in fresh water. *Freshwater Forum*, 3, 176–202.

de la Cruz, R. & Kreft, J.-U. (2019) Geometric mean extension for data sets with zeros. Journal of LATEX Templates. [Preprint].

Fisher, J.P., Fitzsimons, J.D., Combs, G.F., Jr. & Spitsbergen, J.M. (1996) Naturally occurring thiamine deficiency causing reproductive failure in Finger Lakes Atlantic Salmon and Great Lakes Lake trout. *Transactions of the American Fisheries Society*, 125(2), 167–178.

Fitzsimons, J.D. (1995) The effect of B-vitamins on a swim-up syndrome in Lake Ontario Lake trout. *Journal of Great Lakes Research*, 21, 286–289.

Frost, W.E. (1965) Breeding habits of Windermere charr, Salvelinus Willughbii (Gunther), and their bearing on speciation of these fish. *Proceedings of the Royal Society B Biological Sciences*, 163(991), 232–284.

Groves, P.A., Alcorn, B., Wiest, M.M., Maselko, J.M. & Connor, W.P. (2016) Testing unmanned aircraft systems for salmon spawning surveys. *Facets*, 1, 187–204.

Igoe, F., O'Grady, M.F., Tierney, D. & Fitzmaurice, P. (2003) Arctic char salvelinus alpinus (L.) in Ireland: A millennium review of its distribution and status with conservation recommendations. *Biology and Environment: Proceedings of the Royal Irish Academy*, 103B(1), 9–22.

Igoe, F. & Ruane, N.M. (2012) Non-destructive techniques for the monitoring of Arctic char Salvelinus alpinus (L.) in Irish loughs II. Snorkelling to assess spawning success and incubation period. *Biology and Environment*, 112(3), 305–309.

Ivanova, N.V., Zemlak, T.S., Hanner, R.H. & Hebert, P.D.N. (2007) Universal primer cocktails for fish DNA barcoding. *Molecular Ecology Notes*, 7(4), 544–548.

Kelly, S., Moore, T.N., de Eyto, E., Dillane, M., Goulon, C., Guillard, J. et al. (2020) Warming winters threaten peripheral Arctic charr populations of Europe. *Climate Change*, 163, 599–618.

Kennedy, R.J., Johnston, P. & Allen, M. (2014) Assessment of a catchment wide salmon habitat rehabilitation scheme on a drained river system in Northern Ireland. *Fisheries Management and Ecology*, 21(4), 275–287.

Klemetsen, A., Amundsen, P.A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F. et al. (2003) Atlantic salmon Salmo salar L., brown trout Salmo trutta L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish*, 12(1), 1–59.

Klemetsen, A., Amundsen, P.-A., Muladal, H., Rubach, S. & Solbakken, J.I. (1989) Habitat shifts in a dense, resident Arctic Charr *Salvelinus alpinus* population. *Physiology and Ecology Japan, Spec*, 1(1), 187–200.

Low, J., Igoe, F., Davenport, J. & Harrison, S.S.C. (2011) Littoral spawning habitats of three southern Arctic charr (*Salvelinus alpinus* L.) populations. *Ecology of Freshwater Fish*, 20(4), 537–547.

Lucykanish, D.M. & Foster, J.R. (2015) *Is lake trout recruitment impacted by zebra mussels in Otsego Lake, NY? SUNY Oneonta Biol. Fld. Sta. Oneonta*. 47th Ann. Rpt. (2014).

Maitland, P.S., Winfield, I.J., McCarthy, I.D. & Igoe, F. (2007) The status of Arctic charr *Salvelinus alpinus* in Britain and Ireland. *Ecology of Freshwater Fish*, 16(1), 6–19.

Mari, L., Garaud, L., Evanno, G. & Lasne, E. (2016) Higher temperature exacerbates the impact of sediments on embryo performances in a salmonid. *Biology Letters*, 12(12), 20160745.

Marsden, J.E., Chotkowski, M.A. & Ellrott, B.J. (2002) An inexpensive modified emergent-fry trap for Lake-spawning salmonids. *North American Journal of Fisheries Management*, 22, 1321–1324.

McCarthy, I.D. (2007) The welsh Torgoch (Salvelinus alpinus): a short review of its distribution and ecology. *Ecology of Freshwater Fish*, 16(1), 34–40.

McCubbing, D.J.F., Bayliss, B.D. & Locke, V.M. (1998) Spawning migration of radio tagged landlocked Arctic charr, *Salvelinus alpinus* L. in Ennerdale Lake, the English Lake District. Hydrobiologia. 371–372, pp. 173–180.

Miller, H., Winfield, I.J., Fletcher, J.M., Ben James, J., van Rijn, J., Bull, J.M. et al. (2015) Distribution, characteristics and condition of Arctic charr (Salvelinus alpinus) spawning grounds in a differentially eutrophicated twin-basin lake. *Ecology of Freshwater Fish*, 24(1), 32–43.

Milner, N.J. (1985) The use of divers to describe Charr and trout spawning areas in lakes. *Progress in Underwater Science*, 10, 117–128.

R Core Team. (2022) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Riebe, C.S., Sklar, L.S., Overstreet, B.T. & Wooster, J.K. (2014) Optimal reproduction in salmon spawning substrates linked to grain size and fish length. *Water Resources Research*, 50(2), 898–918.

Riley, S.C., Marsden, J.E., Ridgway, M.S., Konrad, C.P., Farha, S.A., Binder, T.R. et al. (2019) A conceptual framework for the identification and characterization of lacustrine spawning habitats for native lake charr Salvelinus namaycush. *Environmental Biology of Fishes*, 102(12), 1533–1557.

Sawick, N.M. & Foster, J.R. (2014) *Is Lake trout recruitment impacted by zebra mussels in Otsego Lake, NY? SUNY Oneonta Biol. Fld. Sta. Oneonta*. 46th Ann. Rpt.

Setzer, M., Norrgard, J.R. & Jonsson, T. (2011) An invasive crayfish affects egg survival and the potential recovery of an endangered population of Arctic charr. *Freshwater Biology*, 56(12), 2543–2553.

Seymour, M. & Smith, A. (2023) Arctic char occurrence and abundance using environmental DNA. *Freshwater Biology*, 68(5), 781–789.

Smialek, N., Pander, J. & Geist, J. (2021) Environmental threats and conservation implications for Atlantic salmon and brown trout during their critical freshwater phases of spawning, egg development and juvenile emergence. *Fisheries Management and Ecology*, 28(5), 437–467.

Smith, A. (2022) *The population dynamics and conservation of Arctic charr, Salvelinus alpinus; lessons from Llyn Padarn, North Wales. Bangor University*. (PhD thesis).

Solomon, D.J. (1985) Salmon stock and recruitment, and stock enhancement. *Journal of Fish Biology*, 27, 45–57.

Stauffer, T.M. (1981) Collecting gear for Lake trout eggs and fry collecting gear for Lake trout eggs and fry. *The Progressive Fish Culturist*, 43(4), 186–193.

Tibbits, W.T. (2007) The behaviour of Lake trout, Salvelinus namaycush (Walbum, 1792) in Ostego Lake: a Documention of the strains, movements and the natural reproduction of lake trout under present conditions. Occas. Pap. #42. SUNY Oneonta Biological Field Station, SUNY Oneonta.

Trygonis, V. & Sini, M. (2012) PhotoQuad: a dedicated seabed image processing software, and a comparative error analysis of four photoquadrat methods. *Journal of Experimental Marine Biology and Ecology*, 424–425, 99–108.

Walker, A.F. (2007) Stream spawning of Arctic charr in Scotland. *Ecology of Freshwater Fish*, 16(1), 47–53.

Wallace, J.C. & Aasjord, D. (1984) The initial feeding of Arctic charr (Salvelinus alpinus) alevins at different temperatures and under different feeding regimes. *Aquaculture*, 38(1), 19–33.

Winfield, I.J. & Fletcher, J.M. (2009) Feasibility study for the assessment of Arctic charr spawning grounds in Windermere. CEH Lancaster. CEH Project N0 C03569.

Winter, N.R., Winter, B.A. & Foster, J.R. (n.d.) The effectiveness of three fry emergence traps in measuring lake trout (*Salvelinus naymaycush*) recruitment in Otsego Lake, NY.

Wolgamood, M., Hnath, J.G., Brown, S.B., Moore, K., Marcquenski, S.V., Honeyfield, D.C. et al. (2005) Temporal and spatial variation of early mortality syndrome in salmonids from lakes Michigan and Huron. *Journal of Aquatic Animal Health*, 17(1), 65–76.

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