

INVITED REVIEW

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Six decades of ecohydrological research connecting landscapes and riverscapes in the Girnock Burn, Scotland: Atlantic salmon population and habitat dynamics in a changing world

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Abstract

Long-term data are crucial for understanding ecological responses to climate and land use change; they are also vital evidence for informing management. As a migratory fish, Atlantic salmon are sentinels of both global and local environmental change. This paper reviews the main insights from six decades of research in an upland Scottish stream (Girnock Burn) inhabited by a spring Atlantic salmon population dominated by multi-sea-winter fish. Research began in the 1960s providing a census of returning adults, juvenile emigrants and in-stream production of Atlantic salmon. Early research pioneered new monitoring techniques providing new insights into salmon ecology and population dynamics. These studies underlined the need for interdisciplinary approaches for understanding salmon interactions with physical, chemical and biological components of in-stream habitats at different life-stages. This highlighted variations in catchment-scale hydroclimate, hydrology, geomorphology and hydrochemistry as essential to understanding freshwater habitats in the wider landscape context. Evolution of research has resulted in a remarkable catalogue of novel findings underlining the value of long-term data that increases with time as modelling tools advance to leverage more insights from “big data”. Data are available on fish numbers, sizes and ages across multiple life stages, extending over many decades and covering a wide range of stock levels. Combined with an unusually detailed characterization of the environment, these data have enabled a unique process-based understanding of the controls and bottlenecks on salmon population dynamics across the entire lifecycle and the consequences of declining marine survival and ova deposition. Such powerful datasets, methodological enhancements and the resulting process understanding have informed and supported the development of fish population assessment tools which have been applied to aid management of threatened salmon stocks at large-catchment, regional and national scales. Many pioneering monitoring and modelling approaches developed have been applied internationally. This

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history shows the importance of integrating discovery science with monitoring for informing policy development and assessing efficacy of management options. It also demonstrates the need to continue to resource long-term sites, which act as a focus for inter-disciplinary research and innovation, and where the overall value of the research greatly exceeds the costs of individual component parts.

KEYWORDS

Atlantic salmon, catchment science, climate change, Girnock Burn, long term monitoring

1 | INTRODUCTION

In 1966, two fish traps were installed on the Girnock Burn (Figure 1); a tributary of the River Dee in northern Scotland draining a 31 km² catchment dominated by mountains and moorland (Figure 2). The traps were operated by the Freshwater Fisheries Laboratory (FFL) of the Department of Agriculture and Fisheries for Scotland, for monitoring as part of international efforts to understand and manage stocks of Atlantic salmon. The River Dee, like many large Scottish rivers, provides a renowned freshwater habitat for Atlantic salmon (*Salmo salar*): an iconic, keystone species both important for conservation and popular for angling, leading to financial significance to the rural economy (PACEC, 2017). The Girnock was identified as having an important population of “spring” salmon; fish that predominantly spend more than 1 year at sea (multi-sea winter fish (MSW)) and return to freshwater early in the year, spawning in the following autumn and early winter (Figure 3). One fish trap was designed to capture out-migrating juveniles leaving the freshwater habitat for the marine phase of their life cycle (Bacon et al., 2015). The other trap was designed to capture their later return as adult fish to spawn in their natal headwater stream. This initiated an ongoing unique time series of the annual out-migration of juvenile salmon and returning adults (Glover & Malcolm, 2015a, 2015b). Together with regular and pioneering electro-fishing, behavioural studies, stocking experiments and genetic analyses, this has resulted in a unique, globally important long-term record of an Atlantic salmon population. This data set has captured quantitative changes in the return rates, distribution, size, growth and age of salmon; giving a comprehensive picture of the demographic structure and population dynamics in the stream which is rivalled by very few other studies (Glover et al., 2020). Unfortunately, it also shows a worrying record of declining fish numbers (Figure 4) indicating the loss of salmon populations from some small sub-catchments such as the Girnock is not inconceivable in the coming decades if marine survival remains poor (Figure 4b).

These salmon studies stimulated a wider range of ecohydrological research aimed at better understanding the physico-chemical habitat used by salmon at different life stages and its temporal variability in relation to climate and other factors such as land use. Initially in-stream studies, encompassing hydrology, geomorphology and water quality, focused on the dynamics of in-channel habitat at the river-reach scale (e.g. Malcolm, Soulsby, et al., 2004). But to fully understand these complex interactions, investigations linking the river

network to the wider landscape have facilitated comprehensive catchment-scale, process-based understanding of the energy and water budgets that drive the fluctuations in streamflow and water quality that maintain salmon habitats (e.g. Fabris et al., 2018). These studies linking the landscape to the riverscape have increasingly relied on fusing high-resolution environmental observation data into spatially distributed models (e.g. Ala-Aho et al., 2017). These more extensive studies—which are unusual for a salmon research site—have begun to inform fish population analysis and brought about a much

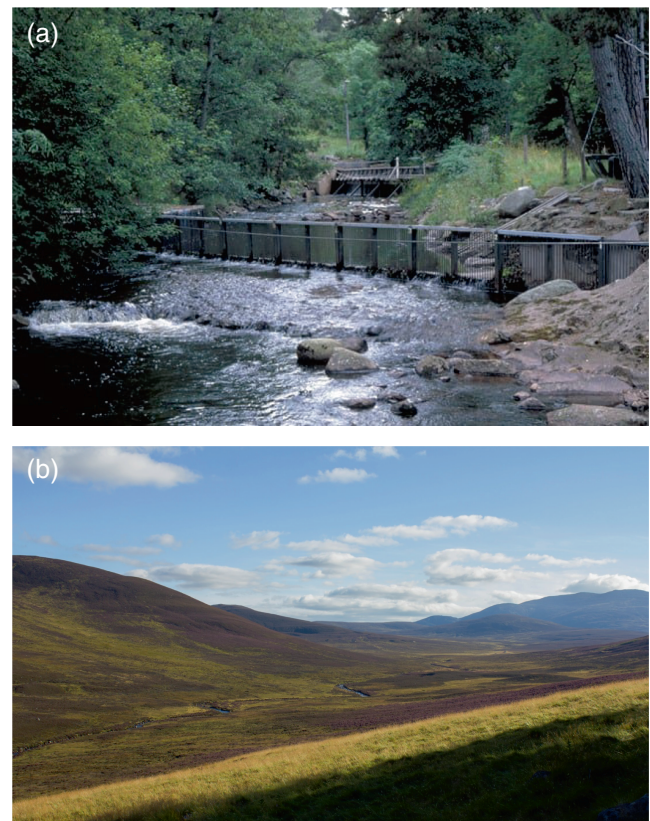


FIGURE 1 (a) The fish traps on the lower Girnock; these are located c.1 km upstream of the confluence with the River Dee. The lower trap intercepts immigrating adults; the upper trap emigrating smolts and parr. (b) Upper catchment some 5 km upstream of the traps where the channel provides juvenile and spawning habitat. Note the lack of riparian tree cover and montane nature of the upper catchment.

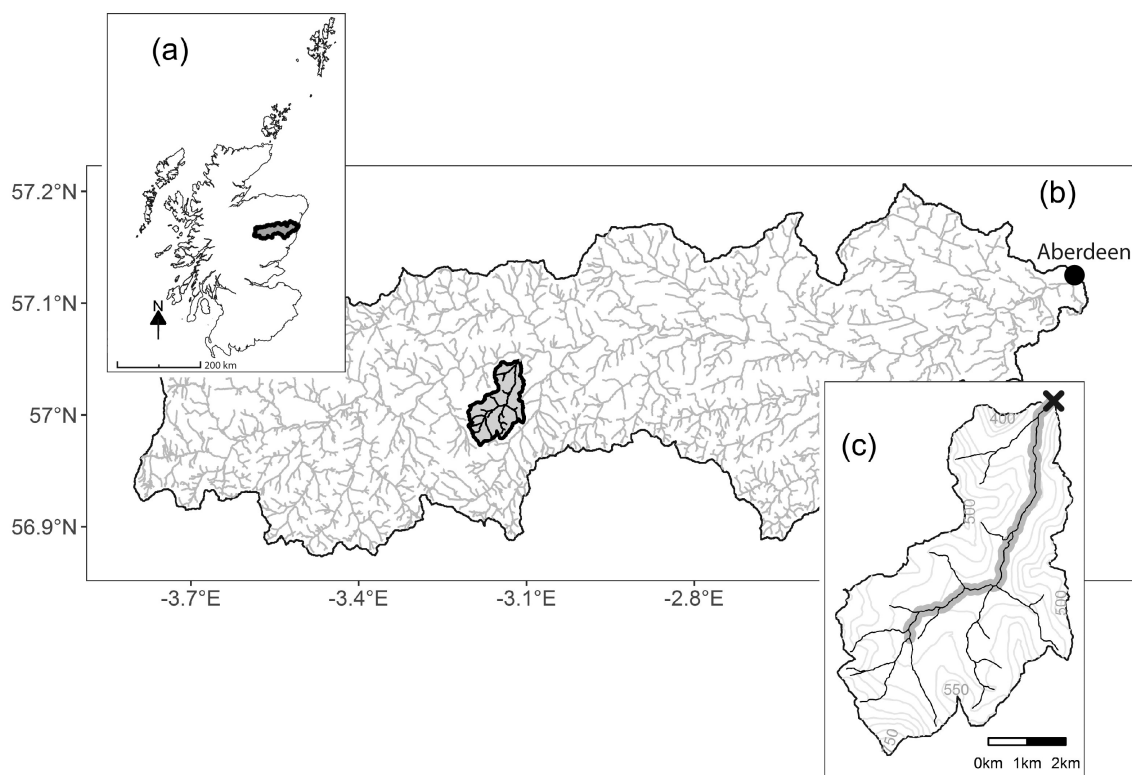
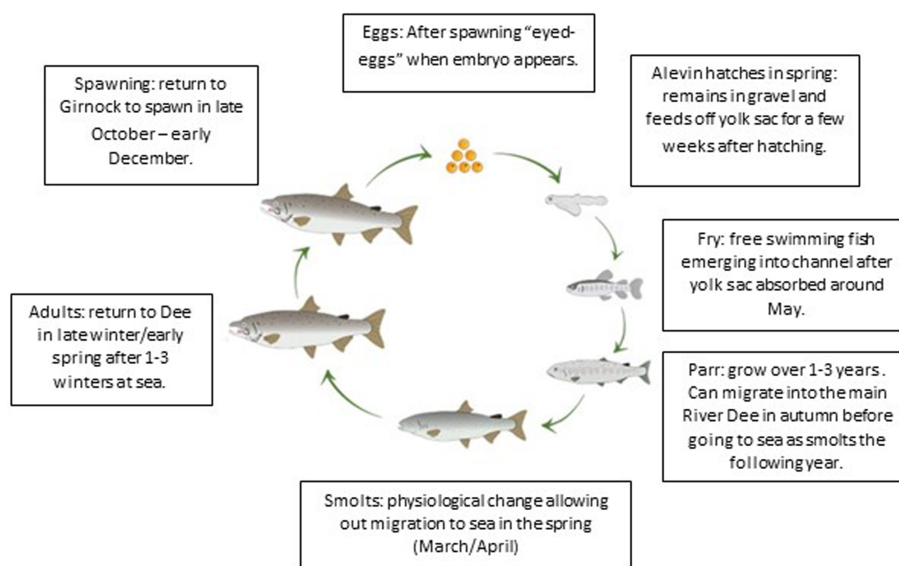


FIGURE 2 (a) Location of the River Dee catchment in Scotland. (b) Location of the Girnock sub-catchment within the Dee and the city of Aberdeen where the Dee enters the North sea and (c) the location of the fish traps (X) upstream of the Girnock's confluence with the Dee and the main area of salmon habitat (shaded) along the main stem of the stream.

FIGURE 3 Salmon life cycle with approximate timings for Girnock fish.



richer understanding of the ecological functioning of the stream. Such broader advances have enabled a multitude of more local, site-specific studies over the monitoring period to be better contextualized and understood in an integrated way. To facilitate this, advances in statistics and ecological modelling have been used to overcome the limitations in, and increase the value of, historic data (Glover et al., 2019).

Here, we provide a review of this integration of salmon and associated ecohydrological catchment research at the Girnock. We highlight notable inflection points in this trajectory, major shifts of focus and significant research breakthroughs. Imposing a narrative on what has been an organic process of scientific exploration (see Soulsby et al., 2019) is inevitably somewhat artificial, but for convenience,

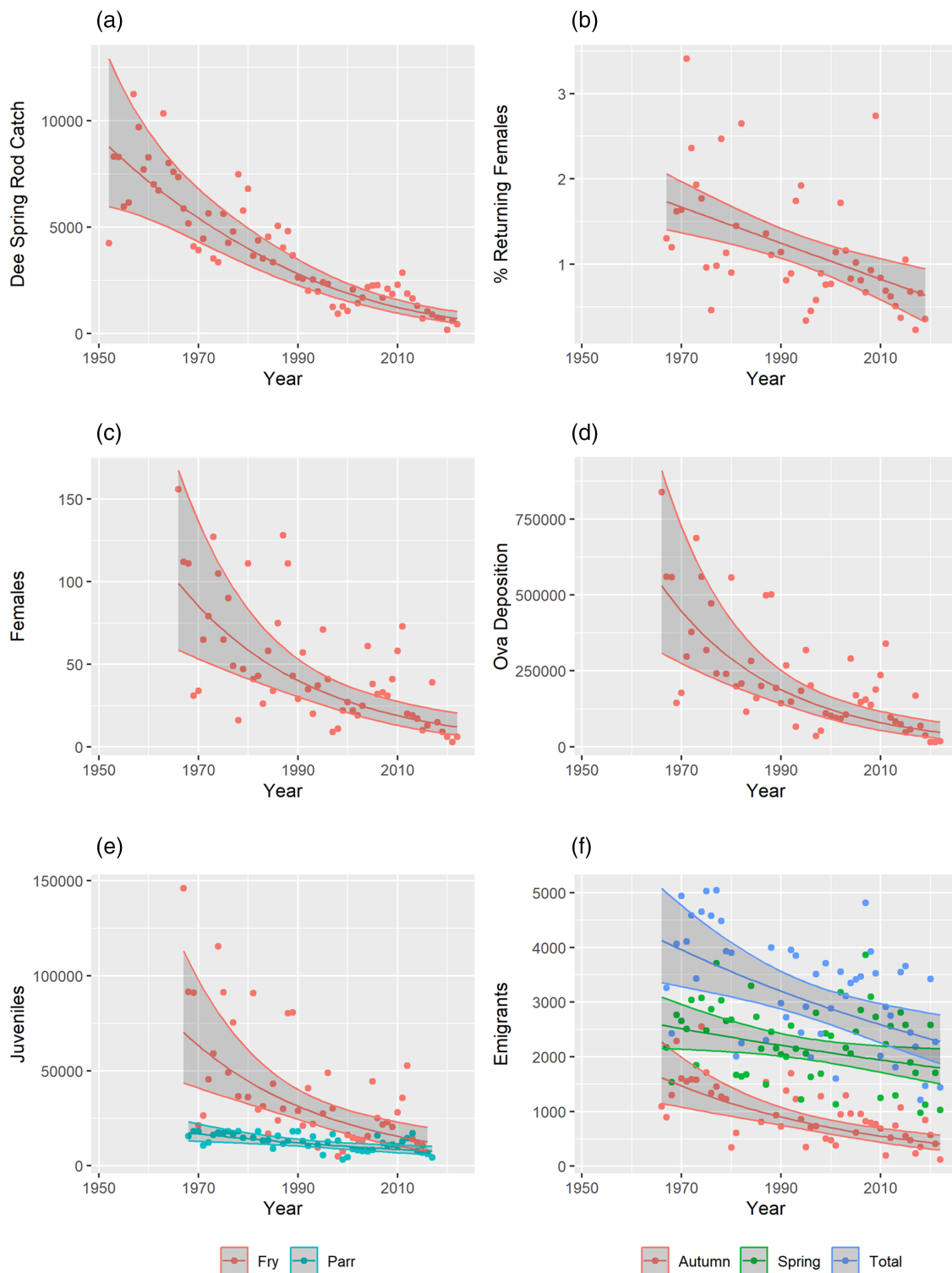


FIGURE 4 Long-term trends in the River Dee spring (February–May) rod catch (Scottish Government, 2023) (a), Girnock Burn percentage female return rates (Glover & Malcolm, 2015a) (b), female numbers (Glover & Malcolm, 2015b) (c), Ova deposition (d), Fry (0+) and Parr (>0+) production (e), and production of emigrants (Glover & Malcolm, 2015c) (f). Fry and Parr production estimates are for day of the year 240, following Glover et al., 2018.

after a brief description of the River Dee spring, we sub-divide the research review into three parts; (i) early fisheries research in the first 30 years, followed by (ii) the increased focus on environmental

context in second half of study period, and then (iii) consideration of how this has informed a more integrated understanding of salmon–environment interactions. We finally consider the lessons learned

from this near-60 year journey which may contribute a wider reflection on the future goals and value of the increasing number of long-term studies in environmental science (e.g. Holmes & Likens, 2016; Rosi et al., 2023; Tetzlaff et al., 2017) that are perpetually threatened by reduced funding and constrained resources (Laudon et al., 2017; Rosi et al., 2023). We do this from the perspective that we are in unchartered waters with regards to the declining status of Atlantic salmon, associated climate change and the biodiversity crises (Scottish Government, Marine Scotland, 2023). This recognizes the urgent need to develop and assess appropriate management responses (Scottish Government, 2023), but also strongly advocates that robust data-driven science is essential to provide an evidence base to inform rational policy and management decisions that do more good than harm (Oreskes, 2019).

2 | THE GIRNOCK CATCHMENT AND ITS SALMON POPULATION

The Girnock's topography reflects the underlying geology (Figure 5a,c) was set ~400 million years ago as the granite pluton that formed Scotland's Cairngorm mountains was emplaced and metamorphosed the pre-existing sedimentary rocks (Goodman, 2007). Subsequent erosion exposed granite in the higher elevations of the catchment (>400 m), whilst the lower slopes comprise metamorphosed schists, some of which are calcareous (Soulsby et al., 2007). The now-subdued landscape has been subject to many erosion cycles, including successive glaciations, resulting in a river network occupying over-widened valleys, extensively covered by glacial and post glacial deposits (Hall, 2007).

These deposits control the distribution of soils and vegetation (Figure 5d) (Tetzlaff et al., 2007). Waterlogged peaty soils lie above poorly drained drifts in the valley bottom (Soulsby et al., 2016b). On steeper slopes, more freely draining podzols form on coarser drift deposits, whilst poorly developed rankers form along exposed interfluvies and steeper scree slopes. On the wetter valley-bottom peats with *Sphagnum* mosses dominate, along with grasses such as *Molinia* where minerogenic groundwater drainage occurs. On the podzols and rankers, Scots Pine (*Pinus sylvestris*) is the dominant natural forest vegetation, though this has been extensively cleared in the past, with re-generation inhibited by grazing Red Deer (*Cervus elaphus*). Forest now only remains over <10% of the catchment (Figure 5b). About half of this comprises semi-natural patches of Scots Pine and birch (*Betula* spp.) on steeper, more inaccessible slopes and half is fenced plantations mainly of Scot pine and exotic conifers (Neill et al., 2021). Where the forest has been cleared, *Calluna* and *Ericaceae* heather shrubs are the dominant land cover. These have been sustained by a burning cycle – typical on Scottish Highland estates – which further suppresses forest regeneration to promote feeding habitat for grouse (*Lagopus lagopus*) and red deer as game species with sports shooting the main land use. Sheep grazing is limited to small fenced pasture in the lower catchment and there is no peat cutting.

The glacial legacy has a profound effect on river channel morphology and salmon habitats in the Girnock. The gradient is relatively gentle and the stream bed is well-armoured by coarse glacial lag deposits, creating high channel roughness (Moir et al., 1998). This provides hydraulically complex conditions typical of mountain streams (Fabris et al., 2017) that contain extensive areas ideal for juvenile salmon (Glover et al., 2018, 2020). In some places, moraine deposits constrict the river channel; with short reaches of alluvial channel forming upstream where the valley gradient is lower. These areas with less coarse sediments are favoured for salmon spawning, where female fish lay their eggs in open gravel structures called “redds”, excavated in the river bed (Figure 3) (Malcolm et al., 2005).

Climate in the Girnock is at the temperate/boreal transition, with ~1000 mm annual precipitation; evapotranspiration accounts for 30%–40%, the remainder becomes streamflow. Precipitation is distributed throughout the year, though winter months (Nov–Jan) tend to be wettest and spring (May) driest (Figure 6). Most rain occurs in small low intensity events (<10 mm), with larger daily totals (>25 mm) only occurring 3–4 times per year. Snow usually accounts for <10% of inputs and snowpack accumulation below 700 m generally lasts only a few weeks. Winter temperatures are cold (Jan mean ~0°C), and summer is mild (July mean = ~14°C).

The climate, topography and soil cover result in the Girnock having a “flashy” hydrological regime (Figure 6); with low baseflows during periods of dry weather sustained by groundwater stored in the drift, interspersed by rapid rainfall-runoff responses generated as a result of saturation overland flow from the wet peats in the valley bottom (Figure 7; Tetzlaff et al., 2007). Dominant low intensity frontal rainfall dictates that large runoff events are relatively rare and restricted to high rainfall events (>25 mm) with wet antecedent conditions which drives non-linear connectivity between the hillslopes and saturated areas influencing large surface and near surface water fluxes (e.g. Soulsby, Dick, et al., 2017).

This ecohydrological context has sustained an Atlantic salmon population that probably colonized the Dee catchment soon after deglaciation c.10000 years ago (Cauwelier et al., 2018). Salmon have a complex life cycle that is adapted to their environment which begins in the freshwater where fish spawn and lay their eggs in redds in well-oxygenated river gravels, usually between late October and early December in the Girnock (Figure 3). These eggs hatch between late March and early April the following year where the small fish (alevins) remain within the gravels until their yolk sac is absorbed. Upon emergence into the stream in May and June the young, free-swimming salmon become known as fry, or 0 year old fish as they are spending their first year in freshwater. In the second year, the fish become known as parr and spend 1–3 years feeding on invertebrates and growing before migrating to sea. There are two distinct emigrations from the Girnock, in the autumn and spring (Youngson et al., 1983). Tagging studies show that those emigrating in spring go straight to sea, whilst those leaving in the autumn remain in freshwater over winter and migrate to sea the following spring (Youngson et al., 1994). As the emigrants migrate from natal rivers towards the sea they undergo a physiological change known as smolting which allows them to

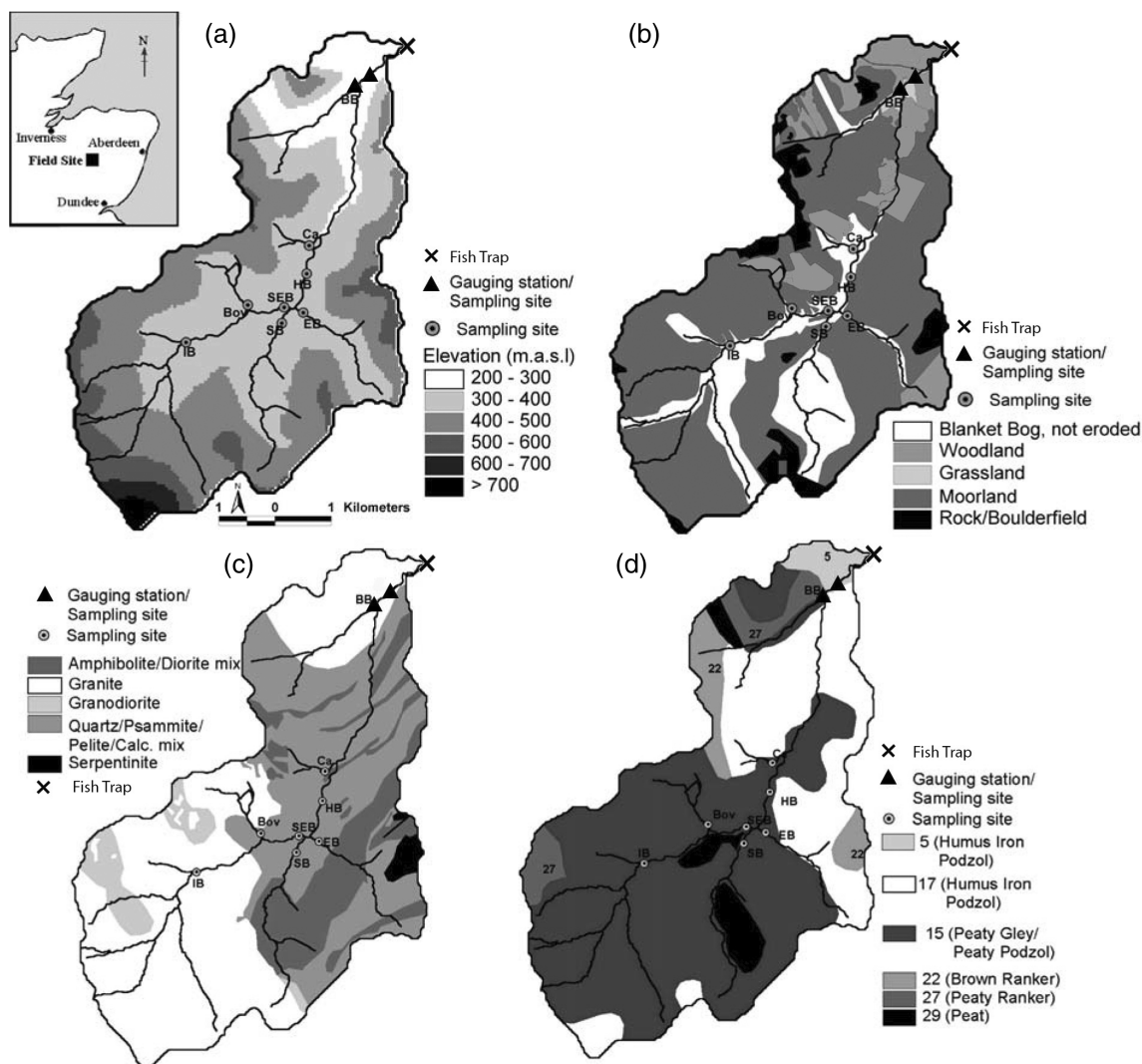


FIGURE 5 Characteristics of the Gironck catchment upstream of the fish traps (X): (a) topography, (b) land use, (c) geology and (d) soil cover. Main stream flow gauging sites (black triangles) on the Gironck and Bruntland Burn (BB) sub-catchment are also shown. Important sampling sites and tributaries are also shown (Bov, Bovaglie; Ca, Camlet; EB, East Burn; HB, Hampshire's bridge; IB, Iron Bridge; SB, South/ East Burn).

osmoregulate as they move between freshwater and marine environments. They then spend 1–3 years at sea on a long migratory path to the north Atlantic where they feed and grow into adult fish (Gilbey et al., 2021; Malcolm et al., 2010). They then typically return to their native river system, many to their natal stream to spawn (Youngson et al., 1994) for the life cycle to start over again. A notable feature of the Gironck salmon is that they are prized “spring” MSW fish that spend two or more winters at sea, before returning to freshwater early in the year. This forms an important economic component of the fishery in terms of angling in the early fishing season, an ecological characteristic that is restricted more to the northern part of the range of Atlantic salmon (Youngson et al., 2002).

With this complex lifecycle, salmon are truly “citizens of the world” with a lifecycle spanning a large part of the northern hemisphere. As such they are sentinels of both global and local environmental change. Our ever-increasing understanding of this, and how

salmon populations might be sustained in the future is informed by trans-Atlantic monitoring sites collecting similar data to the Gironck (Gurney et al., 2010; Prévost et al., 2003); although with a few exceptions these rarely include both detailed long-term multi-life stage census data and supporting ecohydrological characterization and understanding.

3 | EARLY SALMON RESEARCH

The first decade of research at Gironck focused on building a basic understanding of salmon biology and taking steps towards population assessment with an annual census of returning adults and emigrating juveniles at the fish traps. Size, and sex (for adults) were also recorded, and scale samples taken to determine ages via scale reading (Buck, 1976; Youngson & Hay, 1996; Figure 4). Sex was determined

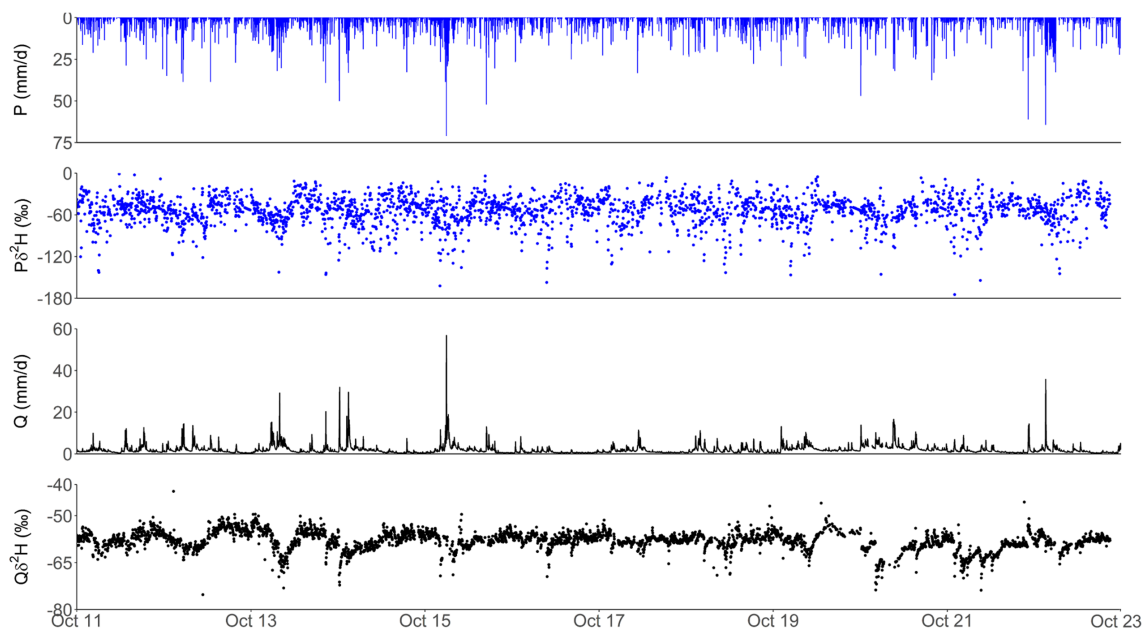


FIGURE 6 Rainfall (P) –runoff (Q) in the Bruntland Burn tributary of the Girnock and daily isotope variations for deuterium in precipitation and stream water in hydrological years 2011/12–2022/23.

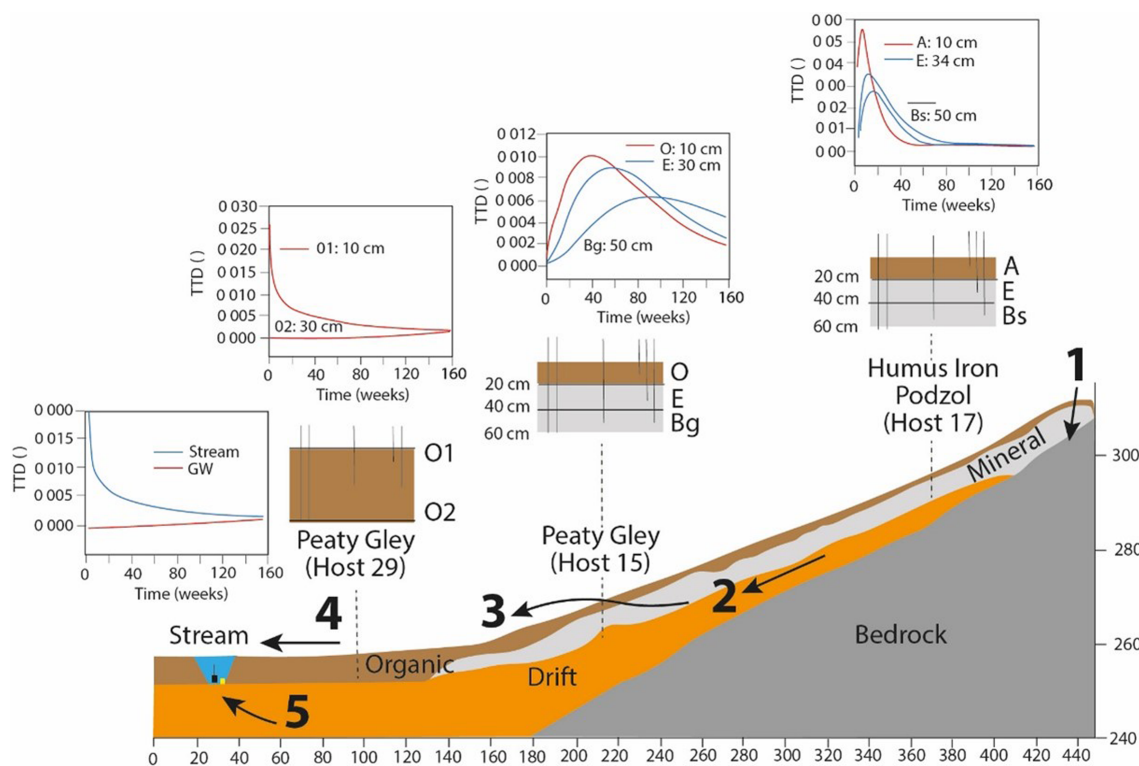


FIGURE 7 Dominant hydrological pathways in typical Girnock hillslope: 1: vertical percolation through podzolic soils, 2: lateral flow at permeability boundaries, 3: exfiltration of hillslope groundwater in saturated valley bottom areas with gley soils, and 4: saturation overland flow on peat and 5: deeper groundwater flow. Insets show profiles of dominant soils and travel time distributions as probability density functions for major soil horizons, groundwater and the stream channel.

based on morphological appearance which was reliable as adult fish only entered the traps within a few weeks of spawning. This early work necessitated pioneering development of electrofishing and

tagging techniques as fisheries science evolved. Emigrating smolts were tagged to assess return rates (Youngson et al., 1994), as well as to track marine migratory routes and determine rates of exploitation

when captured by commercial and recreational fisheries. This identified the areas around West Greenland and Faroe islands as important feeding grounds during their marine migration (Malcolm et al., 2010). However, it also highlighted the prevalence of Gironck salmon in the rod fisheries on the river Dee with peak numbers caught in February, particularly in the lower and mid-Dee, and declining catches through the spring and summer.

As these core datasets increased in duration and variability, an understanding of population dynamics began to emerge. Of particular interest were the relationships between stock levels (e.g. number of females or ova deposition) and subsequent recruitment of offspring. These relationships can be modelled in a number of ways using different lifestage combinations, providing information on the carrying capacity of habitats, population regulation and bottlenecks to production. The relationships between returning adult numbers (and ova deposition) and subsequent production of emigrants was of particular interest in the early years (Buck, 1976; Buck & Hay, 1984). Stock-recruitment (S-R) curves are an important step in fisheries management (Prévost et al., 2003) and the Gironck is one of the very few places with accurate S-R data in Scotland, and one of only two places with detailed ova-emigrant estimates over a large range of stock levels. These data are considered to be of particular value because they exclude the noisy (and trending) density independent marine phase of the lifecycle that is incorporated when working with adult-adult or ova-ova stock recruitment relationships (Gurney et al., 2010).

Gironck S-R data (particularly ova-ova, for consistency with a wider range of rivers) have been used to try and scale production estimates and develop management tools for salmon across the UK and Europe (e.g. Prévost et al., 2003), and continue to be used in support of adult based assessment methods to manage exploitation of salmon in Scottish rivers. Gironck stock-recruitment data have also been used to provide an important independent check to “benchmark” juvenile densities used to assess the status of juvenile salmon stocks in Scotland (Malcolm et al., 2019) through the National Electrofishing Programme for Scotland: NEPS (Malcolm et al., 2023).

Aside from the core focus on the development of assessment data, other aspects of basic salmon ecology became apparent as studies progressed. For example, the number and spatial distribution of salmon redds was related to interannual differences in female numbers (Hay, 1987). It was initially assumed that one female salmon produced one redd, where she laid her eggs. The story was shown to be much more complex, with females often producing multiple redds, that may extend pre-existing structures, and where the eggs of individual females were commonly being fertilized by more than one male. This included small precocious parr that sexually mature early in freshwater occasion (Buck & Youngson, 1982; Taggart et al., 2001) and may contribute to the population on more than one occasion.

Wider salmon-environment interactions also became apparent. Application of novel radio-tracking to adult salmon showed the inter-relationships between hydrology and spawning, as fish movements into the Gironck from the Dee related to periods of increased flows following rainfall events, as indeed were many subsequent

movements of fish upstream to spawning sites in the Gironck's headwaters (Webb & Hawkins, 1989). Environmental cues for the outmigration of juvenile fish were also investigated by Youngson et al. (1983) who found complex interactions between stream temperatures, flows, phases of the moon, cloudiness and the timing of smolting in springtime runs that were difficult to disentangle. The outmigration of parr occurring in autumn was also discovered and subsequently found to form an important component of the Gironck's returning adult population (Youngson et al., 1994).

Observational studies also contributed to an understanding of the behaviour of both adult and juvenile salmon. Radio-tracking of spawning salmon was accompanied by 3 years when the river network was walked daily during the spawning season to map spawning locations and the timing of spawning events (Webb et al., 2001). Further work on spawning sites used emerging genetic techniques to better understand the role of sexually mature male parr in the fertilization of eggs (Jordan & Youngson, 1992). There was also a suggestion that Gironck salmon may represent a distinct breeding population within the Dee system (Jordan & Youngson, 1991). This assertion was supported by a high proportion of returning adults known to have migrated from the catchment as juveniles, (Youngson et al., 1994) increasing the likelihood of distinct local breeding populations.

For juvenile fish, behavioural studies were carried out in an artificial channel near the Gironck traps. This channel was historically constructed to take water from the stream to power a now-disused sawmill, but was later used for experiments to assess fish responses to habitat manipulation (e.g. changing flows and substrate etc.). Behavioural studies using both direct observations and pit-tagged fish showed strong organizational patterns of juvenile salmon for foraging space, with larger fish able to compete better for areas where food resources (invertebrates carried by the in-stream current) were delivered (Armstrong et al., 1999). These studies also showed that fish may only have limited knowledge of total habitat availability and may therefore be unable to respond to changing conditions (e.g. decreasing streamflows or food sources) (Armstrong et al., 1997, 1998).

The early studies in the Gironck provided the basis for intercomparison of fish population performance with other sites. This has included an examination of the broader context of salmon in other tributaries of the river Dee (Shackley & Donaghy, 1992). Importantly, the annual Gironck adult numbers (Glover et al., 2018, Figure 4c) are strongly and significantly correlated with spring rod catches in the Dee (Youngson et al., 2002 and Figure 4a), showing that population trends in Gironck salmon are highly likely to be more generally representative of those experienced in the upper tributaries of the Dee and other rivers where spring stocks dominate. Further, the Gironck acts as a key index monitoring site for comparison with salmon populations elsewhere in Europe and North America (Friedland et al., 2009).

The development of the Gironck as a more inter-disciplinary research site was initiated in the early 1990s, when FFL senior scientist Alan Youngson looked to involve scientists from other disciplines to develop more integrated research agendas aimed at an improved understanding of complex salmon-environment interactions. This

coincided with growing concern from the government, fishery owners and anglers, over declining salmon catches generally and those of spring fish in particular (see Section 5). Such concern focused minds towards developing stronger evidence-based, inter-disciplinary approaches for sustainable management of salmon. These in turn fed into government policy at a national level through the Scottish Salmon Task Force (e.g. Scottish Office, 1997) and more locally with a Salmon Action Plan for the river Dee, launched at a scientific meeting about enhancing the Dee's stocks (Youngson, 1995). As part of this knowledge transfer, salmon research from the Girnock was summarized in *The Lives of Salmon* (Youngson & Hay, 1996) book which targeted a non-specialist audience.

4 | ECOHYDROLOGICAL RESEARCH: FROM CHARACTERIZING SALMON HABITATS TO CATCHMENT SCIENCE

Since the second half of the 1990s, the much broader research focus on salmon and their habitats not only led to better understanding of the ecology of the species, but also a greater appreciation of the physical and chemical processes that linked the landscape of the Girnock's valley (Figure 1b) to the riverscape of its channel network (cf. Hynes, 1975).

4.1 | Salmon spawning habitat

The first involvement of a wider network of environmental scientists at the Girnock sought to understand why salmon spawn in particular places (Soulsby et al., 2019). Both redd counts and behavioural studies showed spawning distributions clustered around a small number of relatively discrete locations, with about 50% of spawning occurring in just five reaches of the river (Figure 8). Moir et al. (2004) showed this related to the distribution of gravel-cobble sized sediments, and a specific combination of river depths and velocities to provide suitable hydraulic conditions to assist females with redd excavation and construction. Such favoured locations were restricted to areas upstream of valley constrictions or lower gradients. Other smaller spawning sites were more randomly distributed and related to patches of suitably sized gravels where hydraulic conditions at the time of spawning were appropriate. In one particular reach, integration of field observations with hydraulic models showed that spawning locations under different flow conditions could have a reasonable degree of predictability (Moir et al., 2005; Webb et al., 2001).

Nevertheless, inter-annual spatial patterns were time-variant likely due to both physical and biological controls. In general, high flows allow fish to access the river earlier (Tetzlaff et al., 2005) and in greater numbers (Lazzaro et al., 2017) and penetrate further into the river system, with redds observed up to 8 km upstream of the fish trap (Moir et al., 1998; Webb et al., 2001). However, it is likely not just

an issue of flow, as high numbers of spawning females probably create density dependent dispersive pressures that result in the use of increasingly suboptimal hydraulic and sedimentary habitats further upstream.

4.2 | Groundwater-surface water interactions

Excavation of spawning areas to recover and transplant ova formed part of experimental work in the 1990s to test whether transplanting ova from areas of high to low spawner density might increase juvenile production through reductions in density dependent mortality (Youngson & McLaren, 1998). Indeed, some have advocated for similar approaches more recently, with a focus on moving wild salmon fry rather than ova (Young, 2017).

Surprisingly high ova mortality was found at some of the most heavily used, and apparently suitable, spawning sites on the Girnock (Malcolm et al., 2005). It was initially hypothesised by fisheries researchers that fine sediment infiltration was causing anoxic conditions through low interstitial velocity in redds. However, the "fine" sediment fraction in the Girnock was found to be comprised mainly of sand (Moir et al., 2002). Furthermore, interstitial velocities were often high and not clearly correlated with oxygen concentrations (Malcolm et al., 2011). Subsequent process-based investigations, including the first use of continuous optical dissolved oxygen sensors capable of being deployed in the hyporheic zone (the streambed interface between surface water and groundwater), showed that some spawning sites were vulnerable to anoxic conditions where chemically reduced groundwater discharges occurred through the stream bed (Malcolm et al., 2006; Malcolm, Soulsby, et al., 2004). These areas of groundwater discharge coincided with valley constrictions that forced upwelling of reduced groundwater into reaches of the stream where sedimentary conditions were good for spawning but provided sub-optimum habitat in terms of sufficient oxygen levels to sustain ova (Malcolm et al., 2005). Such conditions were shown to be worse in wetter winters, when groundwater fluxes were higher, and less prevalent in drier winters when well-oxygenated stream water dominated the hyporheic zone (Soulsby et al., 2009). Therefore, it seems spawning site selection in the Girnock represents a trade-off between optimal sedimentary conditions and the risk of de-oxygenation in some years.

These local investigations into the hydrology of specific spawning reaches were subsequently placed in a catchment-scale context through characterization of deeper groundwater flow paths (Figure 7) as part of hillslope hydrology research in the catchment. This has used a combination of synoptic surveys of environmental tracers in springs and streams (Blumstock et al., 2015; Scheliga et al., 2017; Soulsby et al., 2007); sampling deeper and shallower wells (Blumstock et al., 2016; Scheliga et al., 2018, 2019), geophysical mapping (Soulsby, Bradford, et al., 2016b) and modelling (Ala-Aho et al., 2017). Much of this work focused in the smaller, more accessible 3.2 km² Bruntland

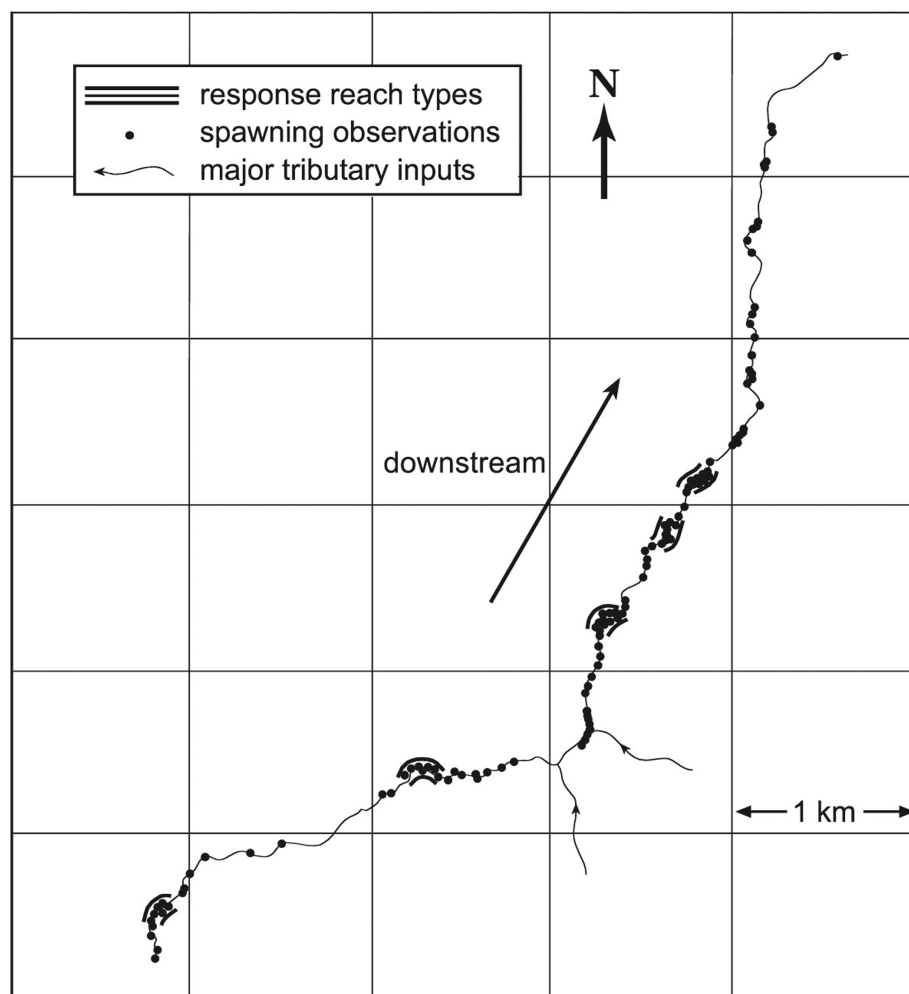


FIGURE 8 Spawning distributions in the Girnock (after Moir et al., 2004).

Burn (BB) sub-catchment of the Girnock (Figure 5), with broadly similar overall landscape properties (topography, soils, land use etc.) and hydrology where logistical challenges to monitoring are less severe (Birkel et al., 2014).

These studies have shown extensive groundwater storage in glacial deposits in the Girnock which in valley bottom areas can be ~40 m deep (Soulsby, Bradford, et al., 2016b). Generally, groundwater circulation here is slow due to the low permeability of these drifts and deeper groundwater is probably not well-connected to streams. Coarser, shallower drifts on the hillslopes have higher permeability and more dynamic groundwater responses. These appear to be fed by fracture networks in the granite and other rocks exposed on the catchment interfluvies which are activated in wetter periods (Scheliga et al., 2017, 2019). Groundwater chemistry is highly variable reflecting geology and residence times; but is mostly strongly alkaline from calcareous rocks in the drifts (Soulsby et al., 2007). Groundwater in granite is less alkaline (Soulsby et al., 1998). The spatial and temporal variability of groundwater inputs has a strong influence on the chemistry of the stream, and the chemistry of the hyporheic zone (and redd environment) depends on local hillslope-aquifer-stream connectivity (Malcolm et al., 2005; Soulsby et al., 2009).

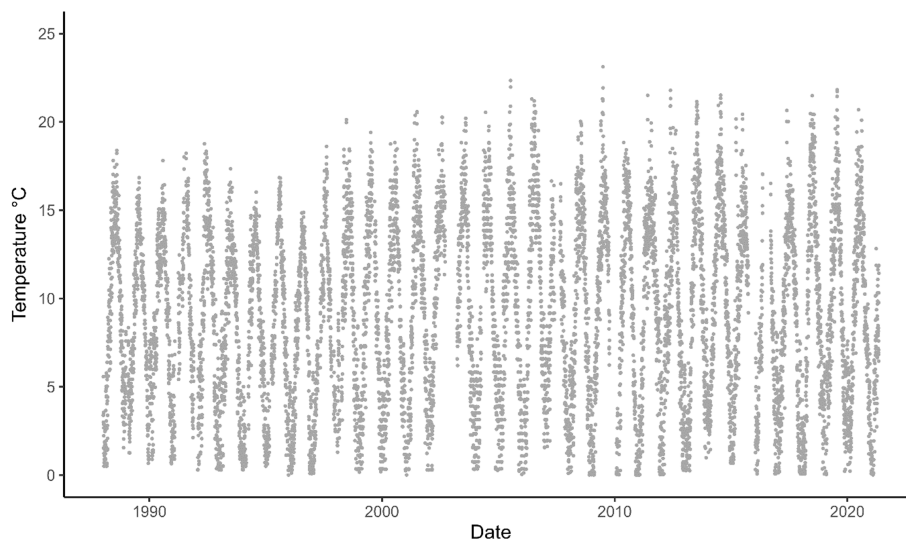
4.3 | Surface water quality

The Girnock is an ideal salmon stream in that it is a relatively cool mountain habitat that has the clean, well-oxygenated water that is fundamental to the species at all freshwater life stages. The stream is generally base-rich with a circum-neutral pH (Table 1). As many salmon life-traits are closely linked to phenology and seasonal temperature changes (e.g. ovulation, migration timing etc.) stream temperature was the first environmental variable measured to complement salmon data. The maintenance of the stream temperature monitoring has, coincidentally, resulted in the longest, continuous sub-daily river temperature record in Scotland (Figure 9). Early studies suggested that autumn and winter river temperatures decreased by ca. 0.76 and 0.57°C, respectively, between 1970 and 2000, but that spring and summer temperatures had increased by 1.46 and 1.04°C, respectively, over the same period (Gurney et al., 2008; Langan et al., 2001). Subsequent data collection and updated analysis has revealed a more complex picture of increase with seasonally varying trends and the need to correct for operational and instrument related temporal biases (Jackson et al., 2024).

Spatial patterns of stream temperatures have also been monitored by a distributed network of temperature sensors which evolved

TABLE 1 Chemical characteristics of the Girnock stream (2015–2022).

Determinand	Mean	Median	S.D.	Min	Max
pH (–)	7.19	7.23	0.35	6.01	7.82
Conduct. ($\mu\text{S}/\text{cm}$)	55.34	53	16.8	17	102.1
Alk. ($\mu\text{eq}/\text{L}$)	280.98	248.73	156.07	35	700.88
SiO_2 ($\mu\text{g}/\text{L}$)	8327.16	8300	2766.98	300	15 320
DOC (mg/L)	6.67	5.9	3.28	1.98	19.61
Na ($\mu\text{eq}/\text{L}$)	199.2	195.58	40.97	71	307.41
K ($\mu\text{eq}/\text{L}$)	15.15	14.2	4.66	3.53	32.01
Ca ($\mu\text{eq}/\text{L}$)	205.73	190.24	86.44	35	490.82
Mg ($\mu\text{eq}/\text{L}$)	127.09	120.15	46.2	27	262.59
Cl^- ($\mu\text{eq}/\text{L}$)	151.06	151.9	30.2	54	336.2
SO_4^{2-} ($\mu\text{eq}/\text{L}$)	57.93	57.37	17.34	2	128.89
NO_3^- ($\mu\text{eq}/\text{L}$)	1.76	1.77	1.04	0.5	8.08
NH_4^+ ($\mu\text{eq}/\text{L}$)	1.74	1.14	1.48	1	17
PO_4^{3-} ($\mu\text{g}/\text{L}$)	3.7	2	6.36	2	62
Total Al ($\mu\text{g}/\text{L}$)	18.78	15	14.12	3	98

FIGURE 9 Temporal variability in maximum daily stream temperature corrected for logger bias 1988–2021 (after Jackson et al., 2024).

to be consistent with the locations of long-term electrofishing sites (Malcolm, Hannah, et al., 2004). Mean daily stream temperatures show limited variability across the catchment, though extreme highs and lows can show substantial differences between the upper moorland catchment and the lower forested areas (Malcolm et al., 2008). Where riparian forest cover is present, day time temperatures are lower and night time temperatures remain higher than in more open areas upstream (Garner et al., 2014). Establishment of two automatic weather stations positioned over the river enabled ground-breaking process-based energy budgets to be modelled for forest and moorland stream reaches (Hannah et al., 2004, 2008). These showed that riparian tree cover reduces the rate of heating in the lower catchment by shading which, when combined with cooler water flowing from upstream overnight (advected heat), produces negative downstream gradients in observed water temperatures (Garner et al., 2014). Trees also reduce wind speeds and evaporative heat loss, and reduce net

losses of long wave at night, thereby reducing daily variability in temperature (Hannah et al., 2008).

Stream temperatures are also known to influence hyporheic temperatures and thus, the environment in which salmon eggs develop. However, this also varies with catchment wetness and local temporal dynamics in groundwater hydraulic gradients (Malcolm et al., 2002; Malcolm et al., 2008). In general, stream water ingress into the hyporheic zone is dominant in the upper 10 cm or so of the stream bed where permeability is highest, though temperature variability is moderated (i.e. decrease in summer and warm in winter) with depth (Birkel et al., 2016). Micro-habitat studies of spatial variations in temperatures in different morphological features (e.g. pools and riffles) provide little evidence of thermal refugia in the Girnock as the stream is generally well mixed and unstratified (Imholt et al., 2013).

Temperature monitoring and modelling at the Girnock proved prescient, given emerging concerns over climate change, highlighting

the importance of land use management and riparian woodland. Novel process-based modelling of the effects of riparian woodland (Fabris et al., 2018) combined with new remote sensing techniques (Dugdale et al., 2019) showed that riparian woodland could be an effective climate adaptation strategy, potentially mitigating lethal and sub-lethal effects of high temperatures. Such important insights provided the impetus for a national temperature monitoring network that developed large scale models to prioritize riparian woodland regeneration to locations where river temperatures and climate sensitivity are high (Jackson et al., 2018) and where woodland can have a substantial effect in reducing temperature extremes (Jackson et al., 2021).

Other important water quality parameters also relate to catchment characteristics and land use. The peaty soils of the Girnock generate high Dissolved Organic Carbon (DOC) concentrations during overland flow, especially during higher flows in the summer and autumn (stream DOC ~20 mg/l), where organic acids also reduce the alkalinity and pH of the stream (Dawson et al., 2011). Spatially distributed hydrological models (see below) have been used to simulate DOC production and transport in different landscape units and under varying degrees of catchment wetness and connectivity (Dick et al., 2015).

With a high population of Red Deer, as well as other riparian animals such as otters, water voles, sheep (in the lower catchment) etc., the potential for significant microbiological pollution of surface waters (indexed by Faecal Indicator Organisms (FIOs)) has been shown (Tetzlaff et al., 2010). Modelling has also used a hydrologically-based spatial framework and has gone some way to explaining the main drivers of FIO delivery in terms of temperatures, antecedent wetness and movements of red deer (Neill et al., 2019). The deer population has been implicated in other water quality issues; for example, detectable nitrate concentrations in parts of the Bruntland Burn corresponded to areas where larger numbers of deer congregate (Blumstock et al., 2015). This was unexpected in streams draining upland areas which are usually oligotrophic and any labile nutrients are usually taken up by aquatic plants. Though mostly N and P concentrations are low (Table 1).

4.4 | Primary production, invertebrates and drift

Continuous stream monitoring for dissolved oxygen (DO) has been carried out in conjunction with modelled estimates of net primary production from in-stream plants. Whilst the dominance of near surface runoff sources, rough channel topography and cool temperatures maintain relatively high dissolved oxygen concentrations in the Girnock; seasonal and diurnal variations reflect the balance of primary production and respiration from heterotrophic consumption in the stream (Dick et al., 2016). Algae and mosses on the stream bed drive the primary production through growth early in the year and later in summer, with primary production being highest in the upper, non-forested parts of the catchment where radiation inputs are highest (Birkel et al., 2013). Similarly, respiration is higher in the upper catchment, presumably reflecting the higher substrate for heterotrophs and warmer temperatures which make the stream heterotrophic overall.

The Girnock also has a diverse and abundant benthic invertebrate community in indicating high water quality, and dominated by stoneflies, mayflies and caddis flies (Gibbins et al., 2016; SEPA, 2024). This largely reflects the high alkalinity, high DO, and low nutrient levels in stream water and areas of gravel substrate. These animals graze on the primary producers, detritus and particulate organic carbon. Despite, strong groundwater influence in the hyporheic zone in some parts of the catchment, there are few anaerobic-tolerant invertebrates (Gibbins et al., 2016) implying that overall, strong well-oxygenated hyporheic flows dominant throughout most of the catchment for most of the time.

Invertebrates provide the main food for juvenile salmonids. Investigations into invertebrate drift in the Girnock have shown that it peaks early in the spring and drives the highest rapid seasonal growth rates in juvenile salmon. This complex interaction between food availability and temperature explains the strong disparity between juvenile growth rates predicted from laboratory-based temperature models with ad-lib rations (Elliott & Hurley, 1997) and those growth rates observed in the stream (Bacon et al., 2005). Later in the summer, reduced food availability and high metabolic costs associated with higher temperatures constrain growth potential (Jones et al., 2002). Furthermore, within the river channel, the highest availability of drift was correlated with areas of higher flow velocity linking hydraulic habitats with potential for growth, with most bio-energetic models assuming a trade-off between prey delivery and probability of capture which reduces at higher velocities. Nevertheless, optimal habitat utilization of such physical controls on food availability is also affected by fish behaviour and the density-dependent competition between juveniles.

4.5 | Effects of flow on instream hydraulics and juvenile performance

Several studies have tried to better understand how instream hydraulics affect juvenile salmon habitat. At the catchment scale, higher flows at spawning and emergence time have been found to have a small positive effect on fry production; however, there is no evidence that flow variability has a substantial effect on parr numbers (Glover et al., 2020) or performance, even during extreme years like 2015 (when Storm Frank likely generated the highest flood on the River Dee for over 200 years). Early reach scale studies focused on using velocities as an index of spatio-temporal variations in useable habitat (Tetzlaff et al., 2005). These simplistically used the concept of critical displacement velocity (CDV) – i.e. velocity thresholds at which juvenile fish can no longer hold station, which varies with fish size and stream temperature (Fabris et al., 2017). However, CDVs are derived from flume experiments which may not translate to more complex stream environments. Further, the 3-dimensional hydraulics of the instream environment are complex, and the high channel roughness results in many boundary layer effects, that give fish more hydraulic shelter than simple velocity measurements infer (Höjesjö et al., 2016). Although extreme low flows and short periods of high flows during

larger storm events may temporarily affect the available habitat for salmon to forage for food, for most of the time juvenile habitat is not expected to be limited by hydraulic conditions in the Girnock (Fabris et al., 2017). In addition, while the spatial distribution of depths and velocities varies in relation to different types of river reach, as slope and bed roughness change, essentially there is little difference in terms of useable hydraulic habitat between reaches that have been studied.

4.6 | Isotope hydrology

To understand the influence of instream hydraulics on salmon under current and expected future climatic conditions, the role of catchment hydrology as the main driver of flow variability must be recognized. Short-term, seasonal and inter-annual flow variability depends on hydroclimate and its effect on the inputs of water as precipitation, how this water is stored in, and moves through the catchment, and how it exits as streamflow or evapotranspiration (Soulsby, Birkel, & Tetzlaff, 2016a).

Monitoring the hydrology of a large, complex and remote catchment like the Girnock is logistically challenging. Over a large heterogeneous area, it is unclear how the complexities of climate and landscape characteristics interact to govern the movement and storage of water as much depends on the subterranean landscape. In 2003, weekly samples of rainfall and streamflow were taken from several sites around the catchment over a year and analysed for stable water isotopes to gain a preliminary understanding of the integrated effects of these processes (Tetzlaff et al., 2007). This followed previous successful Scottish studies that used isotopes to understand streamflow generation processes in larger catchments (Soulsby et al., 2000, 2006). Isotopes of hydrogen and oxygen in rainfall vary seasonally and on a day-to-day basis, reflecting air mass sources and energy available to evaporate heavier isotopes (Figure 6). Isotopic variation in precipitation can be traced in the streamflow response and used to infer water travel times through the catchment and the ages of streamflow (Tetzlaff et al., 2007). This sampling evolved into a >12 year programme of daily sampling of isotopes in precipitation and streamflow which is internationally unique.

Resulting data show that isotopes in the stream follow the seasonality and short-term variations in precipitation inputs in a highly damped and lagged way (Figure 6). Spatial variation in the damping and lagging of the rainfall signal depends primarily on distribution of soil and drift which control the dominant streamflow generation processes (see travel time distributions in Figure 7) (Soulsby et al., 2007). A constant groundwater isotope signature dominates base flows, with groundwater discharging directly into the stream through the hyporheic zone or by exfiltration from hillslopes, via springs and seeps, around the edge of the peatlands in the valley bottoms (Scheliga et al., 2017). High flows are dominated by overland flow/shallow subsurface flow from peaty soils, though rainfall events largely displace water already stored in the catchment (Scheliga et al., 2019). The riparian peatlands act as “isostats” at high flows, damping the rainfall

isotope signal and the component of “new” rain water in storm runoff is usually <10% (Tetzlaff et al., 2014). The isotope studies have shown that the mean stream water age is around 1.5 years; ranging from a few weeks at high flows to over 3 years low flows (Benettin et al., 2017; Soulsby et al., 2015). However inter-annual variability in mean stream water age between drier and wetter years can be large, ranging between 2 years and <1 year, respectively (Birkel et al., 2015).

4.7 | Catchment hydrology

Initial isotope studies resulted in hypotheses about catchment hydrological function that were tested via direct monitoring of hillslope hydrology (Figure 7), also using tracers, to assess soil moisture dynamics in the catchment, groundwater responses and generation of overland flow in storm events (Tetzlaff et al., 2014). Most years, the Girnock catchment follows a clear annual water balance; in winter, higher precipitation inputs, coupled with low evapotranspiration, result in high runoff coefficients (>60%), whilst in drier summers the runoff coefficient is <40% and evapotranspiration is the dominant water flux out of the catchment (Kuppel et al., 2020).

Throughout the year, groundwater mostly stored in various glacial drift deposits sustains baseflows, and the Girnock and its major tributaries are perennial streams. This isotopic evidence shows the groundwater mainly recharges from winter precipitation, through the more freely draining podzolic soils. Monitoring isotopes in soils and groundwater along a hillslope transect showed that the hillslopes act as advective-dispersive flow systems (Tetzlaff et al., 2014). However, connectivity between hillslopes and riparian wetlands during rainfall events controls the non-linearity of the catchment's storm runoff response which is dominated by saturation overland flow (Ala-Aho et al., 2017; Birkel et al., 2010).

4.8 | Terrestrial ecohydrology and greenwater fluxes

Recent research has seen increased focus on the ecohydrology of the dominant vegetation communities in partitioning rainfall reaching the land surface (Soulsby, Braun, et al., 2017). This has involved direct monitoring of canopy-water interactions and transpiration, as well as coupling energy and water budgets in ecohydrological models (Wang et al., 2017). Evapotranspiration is the main loss of water from the catchment in most summers (between May and August) and contrasting vegetation communities have different effects on ecohydrological partitioning. Evapotranspiration losses are ~20–30% higher from Scots Pine than heather and Sphagnum covered areas, reflecting the combination of higher interception losses from the forest canopy, higher transpiration rates and higher soil evaporation (Kuppel et al., 2020; Wang et al., 2018). Isotopic ecohydrology studies also show the xylem isotopes in pine trees and heather stems, can be largely explained by the isotopic composition of water in the near surface soils, though internal storage and mixing in the trees appear to

contribute to a more complex picture (Tetzlaff et al., 2021). In contrast to streamflow, which tends to draw on older (>3 years) groundwater, evapotranspiration fluxes recycle much younger soil water. Soil evaporation is predominantly < a few weeks old and transpired waters tend to be a few months old (Kuppel et al., 2018). Transpired water is older from trees because water ages increase from ~weeks/months in shallow horizons to ~9 months at depth, with tree roots being able to access deeper water (Smith et al., 2020).

New insights into terrestrial ecohydrology have informed the evolution of catchment models used in the Girnock; which have uniquely also used isotopes and other tracers to improve model realism. These started with lumped conceptual models (Birkel et al., 2010, 2011b; Tetzlaff et al., 2008), which were then spatially distributed (van Huijgevoort et al., 2016a, 2016b) and have included complex physically-based models (Ala-Aho et al., 2017). Most recent has been the development of ECh_2O -iso, a new physically-based, spatially distributed ecohydrological model that includes an isotope mass balance module to help test and constrain process representation (Kuppel et al., 2018). Such robust tracer-aided models can then be used for predicting effects of environmental change in the Girnock, such as climate-driven changes where drier summers and warmer winters are likely to decrease and increase respective seasonal flows (Capell et al., 2013, 2014). Very recent work has examined the potential impacts of re-forestation on the catchment water balance, showing limited impacts on high flows, but potentially reduced groundwater recharge and diminished low flows (Neill et al., 2021). These effects are likely to be greatest in the first few decades of dense forest growth, with evapotranspiration likely declining as the forest matures. This is significant, given increased momentum behind re-forestation for re-wilding, nature-based solutions for flood management, carbon capture storage and biofuel production (Soulsby, Dick, et al., 2017).

Importantly, the tracer-aided modelling developed in the Girnock has been successfully applied in other studies in catchments as wide-spread as Germany (Smith et al., 2021), China (Zhang et al., 2019), Costa Rica (Correa et al., 2020), Sweden (Smith et al., 2019), USA (Ala-Aho et al., 2017) and Canada (Piovano et al., 2019). Again, this shows how high quality data and innovation at a long-term sites can leverage tools that can be applied elsewhere.

5 | TOWARDS MORE INTEGRATED, UPSCALED UNDERSTANDING OF SALMON POPULATION DYNAMICS

Ongoing salmon research, informed by the wider insights into physical and chemical variability in the catchment environment, has increasingly revealed more comprehensive and nuanced understanding of long-term spatio-temporal salmon population dynamics (Figures 10, 11) which coincides with increased evidence of the effects of climate change. With >50 years of age differentiated, multi-life stage data (Figure 4), we now know that return rates for adult females as a percentage of total emigrants are estimated to have declined from an average of ca. 1.7% in the 1960s to ca. 0.6% by 2020 (Figure 4b), a decline of ca. 63%

(Eagle et al., 2023; Glover & Malcolm, 2015a). Over the same time period the numbers of adult females declined from around 100 a year on average in the 1960s to ca. 12 fish by the early 2020s (Glover & Malcolm, 2015b, Figure 4c), a reduction of nearly 88%, the same reduction seen in the river Dee spring (February–May) rod catch (Figure 4a).

Reductions in both female numbers and sizes reduced ova deposition (Glover et al., 2018) from around 530 000 eggs in the 1966 to only 47 000 eggs by 2022, a reduction of ca. 91% (Figure 4d). Ova can be estimated on the basis of female size (indexed by tail fork length; Bacon et al., 2009). Because survival between ova and fry is density independent in the Girnock (Figure 11a), reductions in ova deposition (Figure 4d) have been approximately matched by changes in fry production (Figure 4e, Glover et al., 2018, 2020). Fortunately, downward trends in parr production (Figure 4f) have been buffered by reduced density dependent mortality (Figure 11b) with declines of ca. 56% between 1966 and 2015 (Glover et al., 2018).

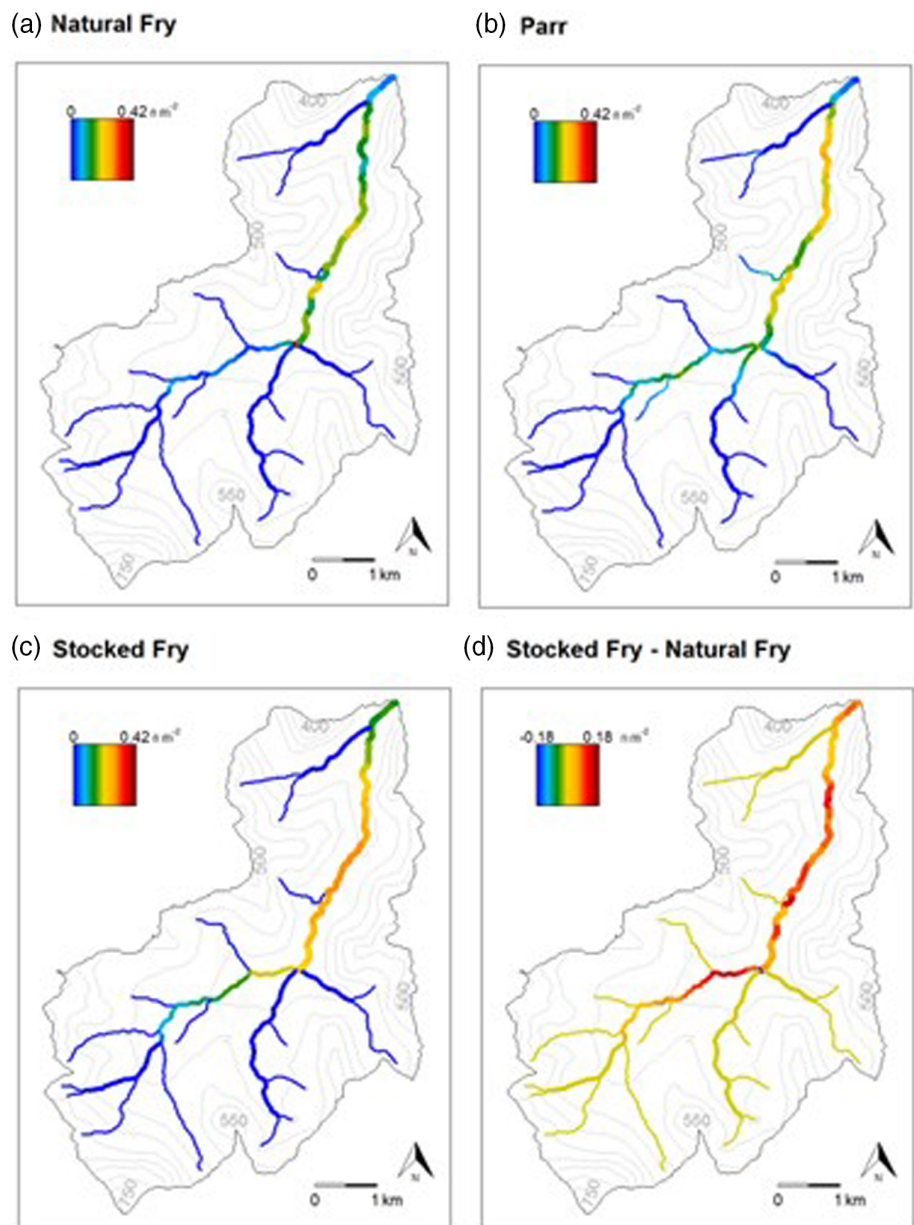
Changes in emigrant numbers have been further complicated by reductions in the age of fish at emigration and associated reductions in mortality. The modal age of smolts has changed from three-year old fish to two-year olds, driven by increased rates of growth due to reduced competition and warming temperatures (Gurney et al., 2008). These complex changes also appear to have altered the balance between autumn and spring migrants (Figure 4f), so while autumn migrant numbers have declined by ca. 75%, spring migrant numbers have only declined by ca. 30% with total migrant numbers now around 55% of their former levels from the 1960s. In the following sections the current understanding of the ecology, habitat requirements and controls on the production of each life stage is summarized and discussed in terms of any implications for management.

5.1 | Adult numbers and sizes

Rod catch can be a useful proxy for adult abundance (Thorley et al., 2005) and these data indicate that the numbers of spring salmon (defined as fish caught between February and May) returning to the river Dee have declined since records began in 1952 and are now at around 8% of their former levels (Figure 4a). Over the period 1966–2022 (over which the Girnock has operated) the Dee spring rod catch and number of females returning to the Girnock have both declined by ca. 88%, indicating that temporal trends and processes observed at Girnock are likely indicative of those across the upper Dee catchment where spring salmon are assumed to dominate. This makes the Girnock data especially valuable in understanding population bottlenecks, controlling processes and evidence-based management options at larger scales.

The relationship between emigrating juveniles and returning adult numbers is density independent (Figure 11d) so that greater emigrant numbers generally result in more returning adults (Gurney et al., 2010). However, there is also a strong downward trend in return rate, indicative of declining survival between emigration and adult return (Figure 4b). This is particularly concerning given the major

FIGURE 10 Spatial variability in the predicted densities of juvenile salmon populations in the Girnock (after Glover et al., 2018). Densities are illustrated for a median ova deposition level. (a,b) Densities of fry obtained from naturally spawned ova and densities of parr which were independent of stocking effects. (c) The more uniform spatial variability in fry densities resulting from uniform stocking. (d) The spatial differences in fry production between uniformly stocked and naturally stocked years.



reduction in distant water and domestic commercial exploitation over the same time period. Indeed, there are now no commercial distant water fisheries for salmon, local net fisheries have also been removed and catch and release is compulsory for anglers in spring (before the 1st of May) and applied almost universally (>99.5% in 2022) on the Dee regardless of the time of year.

The size of female salmon (and thus the number of eggs produced) has also declined nationally (Bacon et al., 2009) and locally (Glover et al., 2018). This combination of fewer and smaller females has had a substantial effect on egg deposition in the Girnock, although the effect is dominated by reductions in adult female numbers (Glover et al., 2018). In the last 10 years, it is estimated that ova deposition has only exceeded the number required to maximize emigrant production on a single occasion (2017), with major consequences for emigrant production and subsequent adult returns, particularly in recent

years. The factors driving these changes are multiple and complex. Poor marine survival and growth are thought to be key factors (Gilbey et al., 2021) resulting from declining food resources due to climate change (Nicola et al., 2018). However, commercial bycatch, and predators in both marine (e.g. seals and dolphins) and freshwater (piscivorous birds, otters and other fish including brown trout and pike) have been suggested as additional potential problems (Marine Scotland and Fisheries Management Scotland, 2023).

5.2 | Ova—alevin survival and performance

As the main spawning locations in the Girnock occur in geomorphologically stable lower gradient reaches where suitable gravel accumulates, there is no evidence to suggest winter wash-out of ova is a

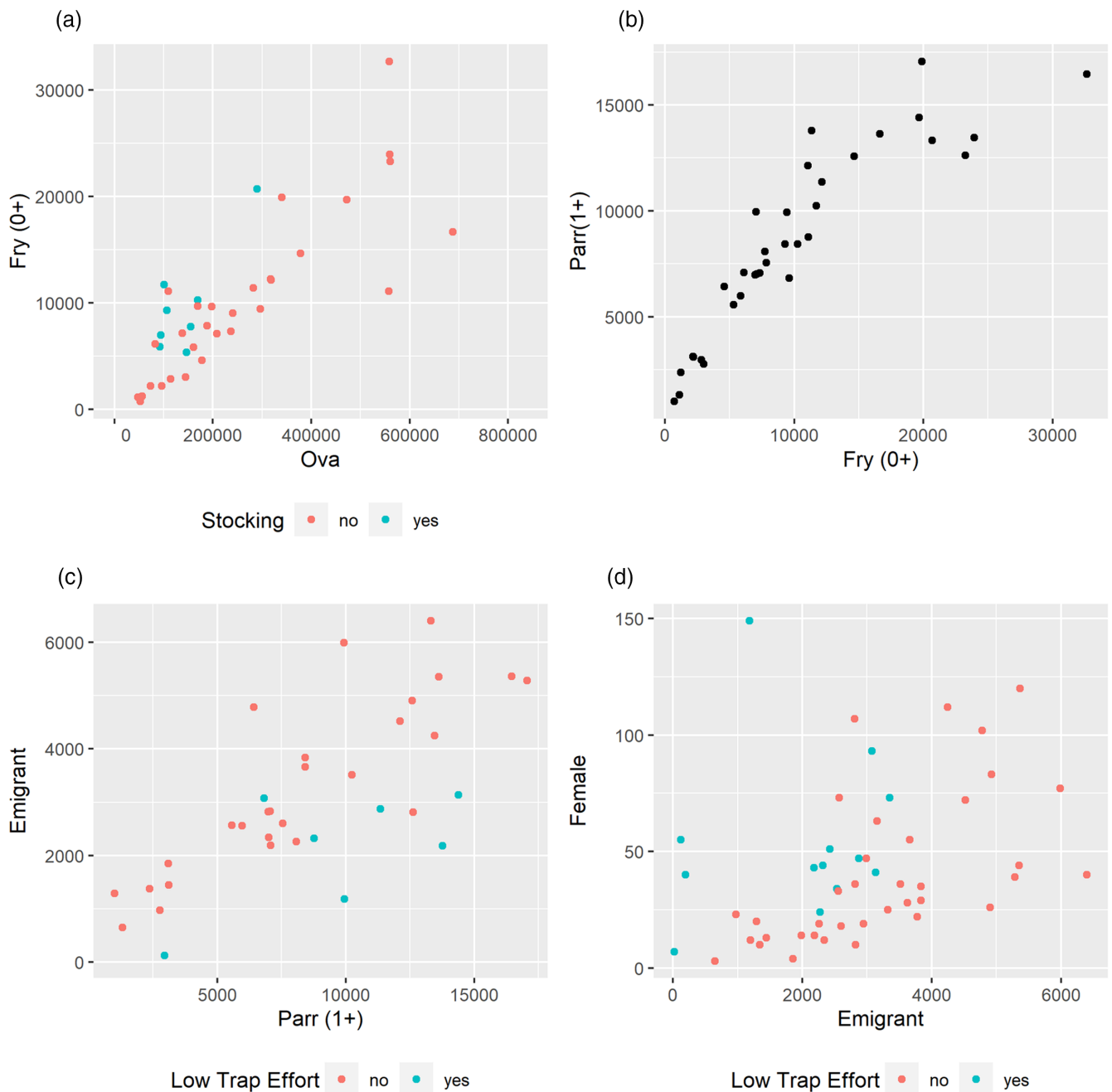


FIGURE 11 Gimnock stock recruitment relationships between Ova and Fry (0+) (a), Fry (0+) and Parr (1+) (b), Parr(1+) and total emigrants (autumn and spring) (c), and Emigrants and returning females. All data have been appropriately lagged using information on fish ages obtained from scale reading. Fry and Parr production estimates are for day of the year 291 and 241, for fry and parr respectively after Glover et al., 2020. Years affected by stocking (which enhanced fry production) and low trap effort (which reduces estimates of emigrant production) are indicated by varying point colour.

significant bottleneck on the salmon population even following extreme recent events such as Storm Frank (Glover et al., 2020).

As low DO concentrations can result in high ova mortality where spawning gravels coincide with areas of chemically-reduced groundwater discharge, conservation stocking has been shown effective at reducing ova mortality and increasing fry production. These stocking studies, which occurred over 8 years, are described in detail by Bacon et al. (2015). They involved artificial stocking of the river (at varying

densities and distributions) with eggs that were stripped and fertilized from adults caught at the trap, incubated overwinter and planted out in the spring. However, at least historically, the early benefits of stocking on fry production were offset at later life stages, not translating to substantial improvements in parr (Glover et al., 2018) or emigrant production (Bacon et al., 2015). While the reasons for this failure remain unclear, it emphasizes the challenges of trying to artificially manipulate and improve natural systems even where underlying processes

are extremely well understood. It is also consistent with the evidence from almost all stocking studies which show no benefits in terms of salmon production (McMillan et al., 2023), and in many cases report potential damage.

It has also been shown that low DO concentrations can result in delayed or prolonged hatch and smaller salmon fry. However, the potential for compensatory growth when emerging into high DO is also high and again appears to indicate a strong resilience to naturally encountered environmental challenges (Youngson et al., 2004).

5.3 | Fry (age: 0 salmon)

Densities of fry vary spatially, mainly with altitude in the Girnock (Glover et al., 2019 and Figure 10). Contrary to previous expectations (Nislow et al., 2011) they have been shown to occupy a wide range of habitats (Höjesjö et al., 2016) that were generally only constrained by proximity to suitable spawning substrate and the ability of fry to disperse after emergence (Webb et al., 2001). At the catchment scale, ova to fry survival in the Girnock was found to be density independent with ova and fry numbers linearly related (Figure 11). This was surprising as the ova to fry stage is usually assumed to be a major bottle neck to production in salmonid populations, including Atlantic salmon (Nislow et al., 2004) and anadromous brown trout (Elliott, 1987). The contrasting findings at the Girnock likely reflect the varying scales of observation and analysis, with a whole riverscape assessment of production at Girnock in contrast to more traditional studies focussed on the scale of individual electrofishing sites where emigration and mortality are strongly confounded. Of course local density-dependent mortality could still occur near individual redds, or groups of redds within the Girnock, and not be detected at the catchment scale (Einum & Nislow, 2005).

Recent work has demonstrated significant downward trends in fry abundance both at the catchment scale and at individual long-term electrofishing sites. However, it was only possible to reliably detect these downward trends where data were appropriately corrected for confounding trends in capture probability (Glover et al., 2019). This is because in such a long-term data set, the effects of varying staff and changes in equipment quality, as well as changes in fish density and size can introduce major biases in the time series (Glover et al., 2018). As with many novel aspects of research at the Girnock, the importance of these effects has been recognized more widely with similar patterns subsequently observed nationally (Malcolm et al., 2023) and in other countries (Dauphin et al., 2018).

5.4 | Parr (age: ≥ 1 salmon)

Parr densities exhibit complex spatial patterns of abundance over and above the effect of altitude that are thought to relate to substrate characteristics and over wintering habitat, though water quality and food availability are also likely secondary effects (Figure 10). Electrofishing data over five decades show significant downward trends once

the data are corrected for observation bias. The electrofishing data, combined with advanced population models, show that the survival of fry to 1 year old parr is strongly density dependent and this is where much of the natural population regulation has occurred historically at the Girnock (Figure 11b). In recent years low numbers of returning females mean that ova deposition is insufficient to fully stock the river resulting in salmon production that is well-below carrying capacity for fry, parr and emigrants. In these circumstances any management action aimed at increasing juvenile production would need to reduce density independent rates of mortality rather than increase the carrying capacity of habitat. In river systems such as the Girnock where there is ample cover from large boulders and plentiful available habitat, management actions making improvements to juvenile habitat quality without addressing poor adult returns and ova survival are unlikely to be successful. However, reducing early life stage mortality without adequate understanding of the constraints on parr survival will also likely be unsuccessful as shown through previous conservation stocking experiments (Glover et al., 2018).

5.5 | Emigrants (autumn parr and smolts)

There is increasing evidence that migrating juvenile salmon are leaving river systems earlier in the year (Malcolm et al., 2015). As with the younger age of smolts, this is likely related to an increase in stream temperature although the controls on emigration timing within years and season are hard to determine with confidence given available data (Buddendorf, 2018). The timing of migration is likely to be important to subsequent survival, matching arrival at sea with available food resources and potentially allowing migrants to avoid other pressures (Thorstad et al., 2012). The consequences of changing migration time from the Girnock are currently unknown, although the observed patterns are not unusual in the wider context (Otero et al., 2013).

The relationship between the production of 1-year old parr and emigrants is not obviously density dependent (Figure 11c). However, emigrant production is also affected by density dependent growth of juveniles (further modified by upward trends in river temperatures), changes in age at emigration and thus mortality. Although there are clear downward temporal trends in emigrant numbers, there are also complex temporal trends in the age composition of emigrants, and timing of migration (autumn vs. spring). Ignoring these important changes (e.g monitoring only spring migrants) could provide an extremely biased and misleading impression of the status of populations. Understanding these complex processes and their interactions calls for sophisticated numerical lifecycle models such as those deployed at Girnock previously (Gurney et al., 2008). Indeed, such lifecycle models are increasingly proposed for assessing and informing management action for salmon as populations decline and there is a need for careful consideration of resource expenditure (Bull et al., 2022). The Girnock remains one of the very few locations globally where such models can be realistically parameterised through detailed observational data collected across all relevant life stages and stock levels.

6 | LESSONS LEARNED OVER 60 YEARS

6.1 | Curiosity drives science

Whilst the initiation of monitoring in the Girnock catchment resulted from the need for scientific evidence to inform policy development for salmon fisheries management, much subsequent research evolved organically. The motivation for most of the research has been curiosity-driven science by individual investigators and has usually been galvanized by hypotheses arising from earlier observations at the Girnock itself, often informed by prevailing “hot” questions in the wider scientific community. The crucial importance of this motivation for discovery science is often overlooked, but as with other long-term sites (e.g. Peterken & Mountford, 2017; Rose, 2007), it is such motivation for interdisciplinary science that drives the commitment needed to procure funding, launch projects, manage research teams, analyse data and then communicate the research in the scientific literature or at national or international symposia (Burt & Thompson, 2020).

6.2 | Well-curated data are gold

A key lesson is that long-term meticulously collected field data has an inestimable value (Rosi et al., 2023). While ever more sophisticated models can integrate insights, enhance process-based understanding, test hypotheses and provide a basis for prediction; to be of most value, they need to be grounded in high quality data (Blair et al., 2019).

It follows that careful management, quality control, documentation and curation of data is crucial. Over long periods, staff, field methods, instruments, data storage capabilities and analytical tools all change. The accuracy and precision of data can therefore also change and there can almost never be enough documentation of meta-data to help later researchers utilize data effectively. Even where data are carefully quality controlled and archived, it is often only when time series are analysed in a robust manner that potential errors and biases become apparent (Glover et al., 2019). In some cases, in the Girnock study researchers have had to revert to original field notebooks to try and understand and correct data inconsistencies in very time-consuming data archaeology (Glover et al., 2020).

6.3 | Technology transforms

Since monitoring began in 1966, the technology available for data collection has inevitably been transformed, with environmental sensors becoming more accurate, reliable and inexpensive. Likewise, fisheries assessment tools, such as electrofishing and tagging have improved, leading to the need to compare methods and re-construct comparable time series. Fortunately, statistical and modelling tools for data evaluation are also continuously improving in the era of “big data” and often these can be used in model-data fusion to enhance the

maximum information content extractable from data, as well as quantify uncertainties associated with historic time series.

6.4 | Connecting local and global scales

The research questions prompting the initiation of the Girnock study were place-based, pertaining to the monitoring of a single site, even if the site was considered more broadly indicative of spring salmon habitats. Nevertheless, the process-based understanding is transferable and this has informed international scientific studies, as well as management. Likewise, the organic evolution of the research agenda has largely been driven by emerging local questions arising from observational science that have led to a more interdisciplinary approach linking salmon research to the wider environmental sciences. In other salmon streams around the world, local insights in understanding the salmon life cycle and its environmental controls have resulted in comparable time series, though very few have such a wide understanding of the catchment context. Likewise, environmental observatories without a specific salmon focus have been seeking similar functional understanding of catchment hydrology and biogeochemistry that the Girnock/Bruntland studies have, though in-stream the ecological implications are generally less well-covered. Thus, the Girnock occupies a unique position in a number of monitoring sites such as Burrishoole in Ireland (de Eyto et al., 2020, 2022; McGinnity et al., 2004, 2009) and Catamaran Brook in Canada (Cunjak et al., 2013) that allow intercomparison studies to leverage broader relevance to generic environmental and ecosystem conservation concerns that are truly global.

6.5 | Serendipity counts

Whilst carefully posed research questions are the main drivers of scientific progress, serendipity is often overlooked as part of research. In long-term environmental observation, this may include capturing extreme events (e.g. floods [Soulsby, Dick, et al., 2017] or droughts [Soulsby et al., 2021]) which offer new insights that would have been difficult to anticipate. Also, visitors to the site have brought fresh ideas, knowledge and experience that have resulted in collaborations and step changes in understanding. Even painful mistakes and errors provide opportunities where new ideas and conceptualisations emerge. There is inevitable danger when research programmes become too tightly constrained as budgets tighten and many benefits will be lost without the potential for serendipity and the ability to engage with other researchers.

6.6 | People are important

Environmental field research does not occur in isolation, it is people-orientated and invariably enhanced by teamwork, social interaction and endless discussion and conjecture involving many collaborators

with different roles. Over almost 60 years, changing personnel of key team members over successive generations also occurs. These include scientific “champions” of the research site who formulate key research questions, secure funding and are often imaginative thinkers with a long-term perspective. Equally, the intellectual gene pool needs to remain open, new cohorts of PhD students and post-doctoral researchers provide the tenacity and drive to make research happen, extend the boundaries of understanding of the site and disseminate research findings. Over 25 PhD theses have been based on work at the Girnock. However, the bedrock of successful scientific function are dedicated, skilled and determined technicians who year-after-year, day after day, and in all weathers operate the fish traps, do the electrofishing, download data loggers and empty samplers, in addition to many other essential services.

6.7 | Knowledge transfer and sustainable management for the future

Concerns about climate change and the risks to salmon populations, as well as other important issues, such as flood hazards, droughts and warming streams, are resulting in rapidly changing approaches to managing salmon streams that are increasingly catchment focussed and aimed at restoring natural processes and sustainability (e.g. FNLRT, 2021). Extensive riparian planting (to ameliorate stream temperatures), reintroduction of beavers, installation of large woody structures (to increase morphological diversity) and restoration of forests and peatlands are all being actively promoted as ameliorative measures in Scotland at present. In the right context, there may be much to be gained from such initiatives. But it is important that the goals of management are cognisant of the complex biotic and abiotic processes that sustain wild salmon populations, and in this regard are realistic about where changes can positively affect salmon production. Furthermore, management actions must certainly seek to avoid doing further harm and also avoid the allocation of constrained resources to actions that have a low likelihood of successful outcomes. In this context, the continued development of process-based understanding of salmon populations at low stock levels becomes increasingly important, as does understanding of the efficacy (or otherwise) of management actions. This includes sympatric relationships with brown trout and the consequences of changing interspecific competition as a consequence of declining salmon numbers and habitat change.

7 | CONCLUSIONS

The remarkable insights gained in 60 years of ecohydrological monitoring and research in the Girnock catchment underline the value of such interdisciplinary, long-term observatories. Of particular importance are: (1) The unrivalled value of the detailed process data for both scientific understanding and underpinning evidence for assessment and management tools. (2) The ability of such sites to provide a baseline against which to assess major management actions through

detailed process understanding. These have included previous stocking assessments and the potential to assess future management actions such as enhancing riparian woodlands. However, this work needs to be undertaken in a carefully controlled manner to ensure the integrity and interpretability of the long-term data for other purposes. (3) The need for detailed data and process understanding to parameterise models; both to integrate knowledge, and underpin assessment and management. These include adult and juvenile assessment methods and salmon life cycle models. (4) The need for very detailed monitoring sites where processes are understood so we can more reliably understand and predict the cumulative effects of future climate and land use change. Though these requirements and consequent benefits are widely recognized within the scientific community (e.g. Tetzlaff et al., 2017), maintenance of funding for such research sites is a constant and significant challenge. Academic funding agencies often prefer short term hypothesis-driven research and it is not uncommon for long-term place-based studies to be erroneously disparaged as “mindless monitoring” or “case studies” as noted by Burt (1994). Of course, the published track record of research at the Girnock shows obvious added value results from being able to contextualize short-term hypothesis-driven research at data-rich long-term sites. It is therefore to be hoped that central public funding continues to support the basic research infrastructure and core monitoring at the Girnock and elsewhere, as alternative funding sources are rare and Government is uniquely placed to sustain and curate such long-term data collection. Indeed, the exceptional knowledge generated from the Girnock emphasizes the value of collaboration between Government and research organizations which can bring contrasting but complimentary resources and perspectives with associated benefits for research and innovation. The commitment to maintaining such research will be crucial in creating process-based evidence for understanding how freshwater ecosystems evolve in response to looming climatic and other (e.g. land use) environmental change. This will help communicate issues to stakeholders and underpin the evolution of management strategies that might ameliorate adverse impacts and conserve important ecosystems that sustain iconic species such as Atlantic salmon.

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DATA AVAILABILITY STATEMENT

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

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