

LIFE-HISTORY STRATEGIES OF PIKE IN A HIGH-ALTITUDE LOCH IN SCOTLAND

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Introduction

The pike, *Esox lucius*, a top piscivore of fish communities in north temperate fresh waters (Raat 1988; Craig 1996), is common in many lowland waters in the British Isles and is normally found in diverse fish assemblages which may include cyprinids, percids and salmonids. However, in Scotland where fish species diversity is restricted following the last glaciation, ca. 10,000 years ago (Maitland 1977), the pike is mainly found in simple fish assemblages and may become the dominant species by suppressing salmonid stocks. The pike is also a major predator of duck chicks and can restrict the distribution of certain species of waterfowl in highland lochs (R. N. Campbell, personal communication; Treasurer 1980; Maitland & Campbell 1992). In northern and eastern Scotland, pike are frequently present in simple predator-prey associations with perch (Treasurer et al. 1992). In these lochs, pike numbers (5.4 per ha), biomass (range 3.9-5.9 kg per ha) and growth rate are typical of pike in other waters in the British Isles (cf. Raat 1988).

Although pike inhabit a wide climatic range and their distribution in Eurasia extends to the Arctic, being found at temperatures as low as 0.1 °C, they are best adapted to shallow, moderately productive mesotrophic-eutrophic fresh waters (Casselman 1996). The present study examines the life history strategies of pike in a high-altitude loch, Loch Callater, and compares growth and reproduction with pike in other locations in the British Isles. The potential impact of pike in pristine salmonid-dominated communities, following the end of the last glaciation, will be discussed. Although not an extreme environment in terms of the temperate zone, Loch Callater, at 495 m, is the highest lake in the British Isles containing a population of pike and has a subarctic environment with low water temperatures, falling to below 2°C, for up to six months of the year. The loch is 85 km from the sea and is situated in the most continental part of Scotland.

Study area

Loch Callater is located in the Cairngorm mountains in the River Dee catchment, 6 km south of Braemar. The loch (Fig. 1), 1.35 km long and 320 m



FIG. 1. (*Opposite page*) Two views of Loch Callater, looking southeast into the hills surrounding the head of the loch.

Table 1. Water chemistry of Loch Callater and the afferent stream Allt An Loch Burn. Concentrations of determinands are given in mg per litre above the line, and in μg per litre below the line.

Determinands	Loch Callater 22 August 1983	Allt An Loch Burn 22 August 1983	Allt An Loch Burn Jan-Dec 1996
Conductivity (μS per cm)	37	42	48
pH	6.6	6.6	7.0
Alkalinity (as CaCO_3)	14	14	13
Calcium	3.55	3.58	4.41
Magnesium	0.70	0.92	0.85
Sodium	3.13	3.32	2.72
Potassium	0.58	0.65	0.49
Sulphate	3.4	4.6	3.6
Chloride	2	3	3
Orthosilicate-Si	1.25	2.07	2.07
Total organic carbon	4.1	4.5	2.6
Ammonia-N	12	8	28
Total oxidised-N	0	130	220
Nitrite-N	4	7	4
Orthophosphate-P	0	4	10
Dissolved aluminium	28	54	47
Total iron	326	225	56
Total zinc	6.7	4.5	3.7
Total manganese	189	77	5

wide, was surveyed in 1906 by Murray & Pullar (1908) who recorded a mean depth of 3.7 m, and a maximum of 9.1 m. The loch is fed by the Allt na Loch Burn which has a catchment area of 19.8 km². Glacial action produced the steep and rocky hillsides surrounding the loch and deposited a gravel ridge across the glen, creating Loch Callater. It is a typical nutrient-poor highland loch (Table 1) with an annual mean nitrate level of 0.22 mg per litre and 0.01 mg per litre of phosphate. The pH is higher than expected and increased from 6.6 in 1983 to 7.0 in 1996 (R. Owen, personal communication). Other fish caught in the loch in this survey were salmon *Salmo salar*, brown trout *Salmo trutta* and eel *Anguilla anguilla*. Pike were present in the River Dee catchment in 1790 (Maitland 1977), but there is no record of the introduction of pike to Callater and it is probable that pike were introduced by humans.

Growth

Pike were captured with multifilament gill nets (mesh sizes ranging from 49 to 240 mm when stretched) set overnight in April 1989 and 1990. April was

chosen because it was planned to sample fish prior to spawning, in order to examine reproductive investment - for example fecundity, but the numbers of fish captured were low (5 pike, 2 brown trout). Therefore samples were also taken in May and August 1992 (4 pike, 1 brown trout) and July 1995 (7 pike, 2 brown trout and 4 salmon). Pike were measured to fork length (mm) and wet weight (g). Opercular bones and the cleithra (large paired bones forming the pectoral girdle) were removed, immersed in cedarwood oil and examined on a dark background with reflected light. Annual growth rings were easily distinguished in cleithra as a translucent zone followed by an opaque zone of high intensity, but in opercula the inner annulus was obscured. Therefore cleithra were solely used for back-calculation of length at previous ages. The distance from bone origin to each annulus was measured on the dorsal carina of cleithra under a low power (x40) microscope with an eyepiece micrometer (Casselman 1978). No "plus" growth (+) was observed on the outer edge of cleithra from pike captured on 18 April 1989 when water temperature was 0.5°C at 50 cm depth, indicating that somatic growth had not commenced, although additional growth beyond the last annulus was identified from pike captured on 11 April 1990 when water temperature was 6.0°C. Total lengths of opercula were plotted against fish length to apply a correction for allometric growth of back-calculations at previous ages: $X = 1.0027$ (SE 0.0232) + 1.0013 (SE 0.0142), $n = 16$, with a highly significant correlation, $r = 0.993$ ($df = 14$). As the slope almost passed through the origin, the growth of cleithra relative to fish length was isometric, permitting back-calculations of length at previous age by the direct proportionality formula (Tesch 1971).

The range in body length (fork length) of captured pike was 205 to 701 mm, wet weights were 75 to 2905 g, and ages ranged from 2 to 11 years.

Unusually, from 4 to 7 years of age, males were slightly longer than females (f-test at each age, $p > 0.05$), although not significantly (Table 2). Length-at-age was low compared with Deeside lochs at lower altitude (Treasurer & Owen 1991): the mean length of pike in Callater was 231 to 236 mm at age 3 (Table 2) compared with 400 mm in Loch Davan and 320 mm in oligotrophic Loch Kinord. Length-at-age was also lower than in other highland lochs (Fig. 2), 97 to 106 mm at age 1, ca. half the length of pike in Loch Lomond (Shafi & Maitland 1971) and Windermere (Kipling 1983), and similar to pike in Loch Choin, a highland loch with poor pike growth (Munro 1957). In Callater, growth of pike was slower than in Loch Choin from age 2 years and similar to growth of pike in the dystrophic Dubh Lochan (Shafi & Maitland 1971). The slow growth of pike in Loch Callater may be due to the low availability of alternative prey and a short growing season, as water temperatures were as low as 2.0°C from November to mid-April, frequently with continuous ice-cover through winter.

Table 2. Mean length-at-age (mm \pm 95% confidence limits) of seven female and eight male pike from Loch Callater, back-calculated from cleithra bones.

Age (years)	Females (mm length)	Males (mm length)
1	106 \pm 9	97 \pm 4
2	171 \pm 8	179 \pm 6
3	231 \pm 10	236 \pm 8
4	286 \pm 12	302 \pm 17
5	335 \pm 16	366 \pm 23
6	395 \pm 24	405 \pm 5.3
7	431 \pm 48	474
8	485 \pm 73	—
9	592 \pm 59	—
10	637 \pm 51	—
11	639	—

Table 3. Reproductive statistics for four female pike from Loch Callater, captured in mid-April 1989 (fish 1–3) and 1990 (fish 4). Spg/sp indicates spawning/spent fish.

Measurement	18 April 1989			11 April 1990
	Fish 1	Fish 2	Fish 3	Fish 4
Length (mm)	388	413	356	442
Wet weight (g)	383	445	303	523
Maturity stage	Gravid	Spg/sp	Spg.sp	Gravid
Gonad weight (g)	21.03	—	—	29.54
GSI (%)	5.5	—	—	5.7
Total number of eggs	1802	—	—	3515
Relative fecundity	4.7	—	—	6.7
Egg diameter (mm)	—	2.2–2.8	2.1–2.2	2.1–2.7

Reproduction

In 1989, spawning commenced in mid-April at a water temperature of 6.0°C (Table 3). The gonadosomatic indexes (GSIs as [gonad wt ÷ fish wt] x 100) of two fish were 5.5 and 5.7%, with 1802 and 3515 eggs respectively and relative fecundities of 4.7 and 6.7, at the lower end of the ranges reported by Raat (1988), i.e. 3700 to 234,000 eggs and relative fecundities of 4 to 46. The range in egg diameter, from 2.1 to 2.8 mm (Table 3), was typical of pike in Eurasia and North America. All fish sampled were mature or had spawned previously, males at 2 to 7 years old and females at 6 to 10 years.

The mean maximum GSIs of pike in Callater were lower than in two other Deeside lochs, Davan (8%) and Kinord (9%) respectively, but were similar to the Loch of Skene (4 to 9%) in the lower Dee Valley (Treasurer 1990). GSIs were much lower than those found in southern lakes in the British Isles; for

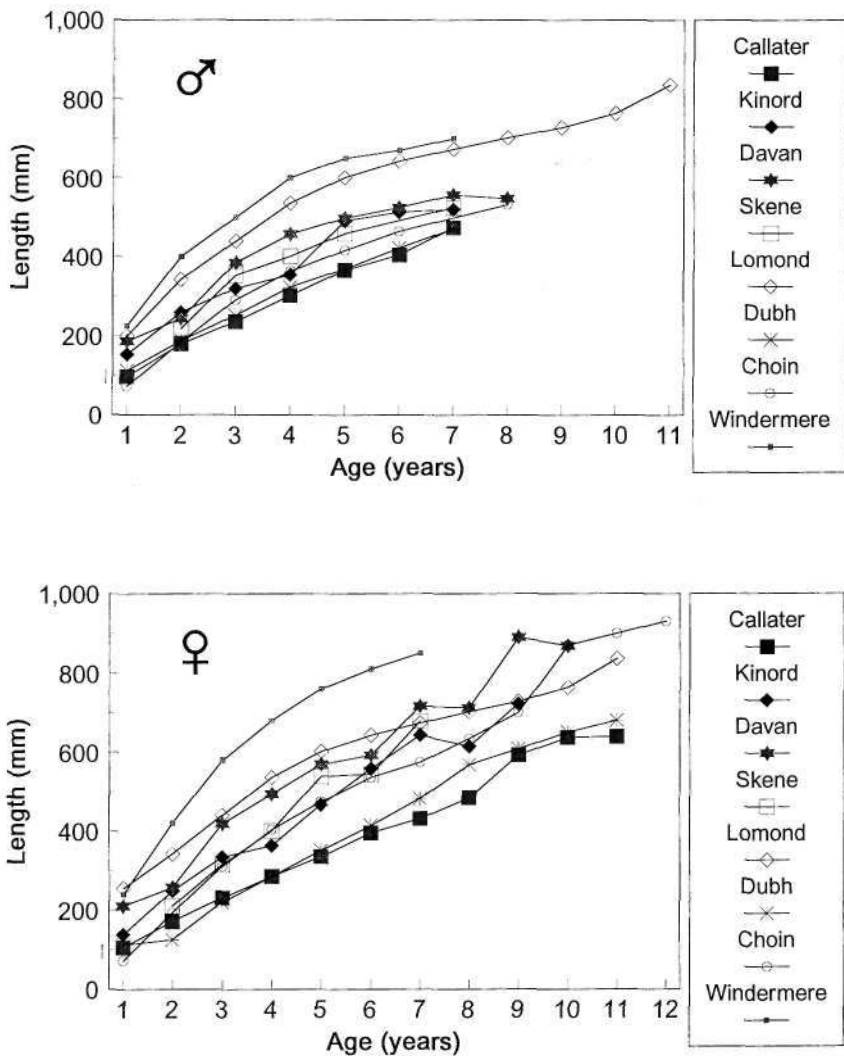


FIG. 2. The back-calculated fork-lengths (mm) at various ages of male pike (*above*) and female pike (*below*) in Loch Callater, compared with other locations in the River Dee Valley (Loch Kinord, Loch Davan and Loch Skene) (Treasurer & Owen 1991), with other highland lochs in Scotland, Loch Lomond and Dubh Lochan (Shah & Maidand 1971) and Loch Choin (Munro 1957), and with Windermere in northwest England (Kipling 1983).

example, mean maximum GSIs of 15 to 20% were reported from pike in Windermere (Kipling & Frost 1969) and 17% was reported from pike in Slapton Ley (Bregazzi & Kennedy 1980). Fecundity of pike is dependent on several factors, e.g. temperature and food availability (Billard 1996). Food is restricted in Callater by the limited number of prey species; there are no small prey such as sticklebacks, perch and minnows. The extreme winter conditions experienced at Callater may also influence fecundity. In support of this view, the lower reproductive investment of pike in Loch Kinord and Loch Davan, at a lower altitude in the same Dee valley, is associated with the relatively cold winters, as these lochs are situated in the most continental part of Scotland. Also there is a restricted food supply, with a low availability of prey fish such as perch and other forage fish such as minnows and sticklebacks (Treasurer 1990). Another example is the low absolute fecundity of pike in the Vilyuy Reservoir, Russia, which is only free of ice-cover from the end of June, compared with more southern lakes (Sukhanova 1979).

Food

The food of pike in Callater was analysed by the occurrence method, i.e. the percentage of stomachs containing a particular food item. There was a narrow range of benthic organisms: Ephemeroptera larvae (75% occurrence), *Gammarus pulex* (25%), chironomid pupae (8%), Odonata (8%) and also zooplankton (8%). The two largest pike, 672 and 701 mm respectively, had eaten pike. This diet was similar to that of pike in other lakes; for example, invertebrates are the main food of small pike and larger pike are piscivores (Mills 1964). *Gammarus* was also the main food of pike in Loch Choin (Munro 1957) where, similarly, larger pike ate considerable numbers of invertebrates because suitable larger prey was absent.

Parasites

The exterior of the fish, gills, eyes and viscera were examined for protistan and metazoan parasites, with a binocular microscope at x40 magnification. No parasites were found on the skin or viscera, and only one in the eye humor, a *Diplostomum* species in one fish.

The impact of pike on pristine salmonid communities in highland lochs

There were few fishes in Scottish fresh waters following the end of the last glaciation ca. 10,000 years ago (Maitland 1977). By 1790, five additional species had colonised southern Scotland and by 1890 five more species were introduced by humans. Many of the lochs in the Cairngorm mountains retain their original simple fish communities, dominated by the salmonids - brown

trout and salmon, and also containing Arctic charr *Salvelinus alpinus* and eels (Maitland 1972). The original fish fauna of Loch Callater comprised eels and brown trout, with migratory adult salmon and salmon parr largely confined to feeder streams. Although Arctic charr are found in nearby lochs, e.g. Loch Muick, they have not been recorded from Callater as the loch is probably too small and shallow. Campbell (1979) concluded that Arctic charr were mainly, although not exclusively, present in large deep lochs. Pike and perch are common fishes in the smaller lowland east coast lochs. Although perch colonised the Dee valley, they are not found in the rivers and lochs of the Cairngorm mountains. In contrast, pike are present in many of the lochs and rivers in the Dee and Spey valleys with catchments in the Cairngorms. Pike were probably introduced into Callater by humans, as the efferent stream, the Callater Burn, is fast-flowing and has several small waterfalls.

The impact of the introduction of pike to the original indigenous salmonid-dominated fish community of Loch Callater would have been to rapidly reduce the numbers of an abundant brown trout population with a low mean weight, typically found in many small relatively shallow Scottish lochs (Campbell 1971). Pike would also prey on migrating salmon smolts in the shallow and narrow loch. For example, Mills (1964) calculated that ca. 10% of the smolt run on the River Bran catchment, Ross-shire, was eaten by pike.

Conclusions

Pike are present in Loch Callater at their highest altitude and most extreme habitat in the British Isles, with subarctic winter conditions and extended winter ice-cover. The response of pike in this environment is slower growth, due to a shorter growing season and the low availability of forage fish, giving the poorest reported length-at-age for pike in the British Isles. In some extreme environments, for example in high-altitude Alpine lakes, brown trout spawn only in each second year, as the summers are too short to permit recovery of the gonads following spawning and oogenesis (Cavalli & Chappaz 1996). This was not evident from the sample of female pike examined from Loch Callater; all were mature or had spawned in the same year, with gravid ovaries in April and normal recovering ovaries in June-July. There was an impact on reproductive potential, however, as absolute and relative fecundities were low compared with reported values. As in other lochs with few prey fishes, the larger pike ate small items such as invertebrates.

Acknowledgements

I am grateful to Invercauld Estates for permission to sample pike in Loch Callater and to the Scottish Environmental Protection Agency (East Region) for access to water chemistry data.

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