Ann. Zool. Fennici 41: 117–124 ISSN 0003-455X
Helsinki 26 February 2004

Reproduction and fecundity of the Irish pollan (*Coregonus autumnalis* Pallas, 1776), a threatened lake coregonid

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Received 5 Nov. 2002, revised version received 28 July 2003, accepted 29 Aug. 2003

Harrod, C. & Griffiths, D. 2004: Reproduction and fecundity of the Irish pollan (*Coregonus autumnalis* Pallas, 1776), a threatened lake coregonid. — *Ann. Zool. Fennici* 41: 117–124.

The sex ratio, age at maturation, fecundity, and seasonal development of gonads of pollan (*Coregonus autumnalis*) in Lough Neagh are described from samples collected between November 1997 and December 1999. Pollan reproductive ecology in the 1990s was similar to that found in the 1970s. Pollan egg size and fecundity differed between years but there were no long-term trends in fecundity despite considerable subsequent eutrophication of the lough and changes in the fish community.

Introduction

The Arctic cisco *Coregonus autumnalis* is typically an anadromous fish in low productivity river and coastal systems of arctic Russia, Canada, and Alaska (McPhail 1966, Morrow 1980, Novikov *et al*. 2000). The only non-arctic populations occur in Ireland. There, *C. autumnalis* is known as pollan and occurs in four large, lowland meso-hypertrophic lakes in a temperate oceanic climate. Many authors have noted the unusual ecology of these Irish populations and pollan's elevated conservation status (Whilde 1993, Harrod *et al*. 2002) is partly due to these differences.

Unlike their arctic congeners, Lough Neagh pollan are littoral spawners, do not undertake long migrations to spawning areas, and spawn annually (Wilson 1979, Dąbrowski 1981, Wilson & Pitcher 1984, Winfield & Wood 1988). Males aggregate over spawning grounds in mid-November, and are joined by females in late November and early December. Eggs develop during winter, and larvae typically appear during March (Dąbrowski 1981, Harrod 2001). Pollan make appreciable investments in reproduction; females can invest half of their lipid reserves in ovary production (Dąbrowski 1982).

Pollan are relatively short-lived, and the populations typically consist of two to three spawning year classes (Harrod 2001). Any significant variation in reproductive ecology between ages or size classes of pollan could influence population dynamics and therefore management decisions. Lough Neagh underwent marked environmental shifts during the 1970s. Roach (*Rutilus rutilus*) were introduced and rapidly became established (Cragg-Hine 1973), while cultural eutrophication led to rapid shifts in lake productivity (Foy *et al*. 1995). The studies of pollan reproductive ecology made by Wilson and Pitcher (1984) and Dąbrowski (1981) occurred after these changes.

During the mid-1990s shifts in the size structure and behaviour of the spawning stock were thought to signal a population decline (Harrod 2001, Harrod *et al.* 2002). Spawners collected from sites on the north shore of Lough Neagh in 1996 (Harrod *et al.* 2002) were significantly smaller than those in 1977 (Dąbrowski 1981), making it likely that fewer eggs were deposited in 1996. Few 0+ pollan were caught during 1997 and 1998, suggesting that small adult size may have limited recruitment.

We describe the reproductive ecology of the Lough Neagh pollan stock: patterns of maturity and gonadal development, fecundity, and inter-population variation in reproductive investment. The possibility that recent shifts in pollan reproductive ecology were a response to environmental change is examined through comparison with earlier descriptions.

Methods

Pollan were routinely sampled in two bays between November 1997 and December 1999 with bottom and surface-set multi-panel gillnets of dimensions 1.5 × 43 m, (Modified S-Type, Lundgrens Fiskredskapsfabrik AB, Stockholm, Sweden). To investigate spawning ecology, known and suspected spawning areas were sampled by bottom-set multi-panel gillnets between mid-November and mid-December. Harrod (2001) demonstrated that this methodology did not give biased estimates of condition, fish length, sex, or age.

Sex was assessed through visual inspection of the gonads after dissection. Gonads were removed from fish and their blotted mass recorded (± 0.01 g). Gonad development was recorded by maturation score (Lagler 1978). Maturation is a continuous process and the division of gonad development into stages is somewhat arbitrary. However, Harrod (2001) demonstrated a strong sigmoidal relation between egg size and maturation class. To provide a quantitative measure of maturation, the relative mass of the gonads was calculated for each adult fish using the relative gonadosomatic index (GSI), where relative GSI = (gonad mass)/(somatic mass) × 100.

Brown *et al.* (1991) demonstrated that the number of mature oocytes in Scottish *C. lavaretus* stabilised by midsummer. Consequently, fecundity estimates were made from pollan ovaries taken in November and December. After weighing, individual ovaries were stored in Bouin's fixative. Vials were shaken monthly to enable the fixative to loosen connective tissues. After approximately six months, eggs were emptied from the vials and washed in distilled water. They were placed on laboratory tissue and allowed to air-dry prior to measurement of fecundity and egg size. Sub-samples of 100 air-dried eggs were taken at random from the ovaries of 151 pollan (aged between 1+ and 5+ and fork lengths 200–283 mm) and weighed (± 0.0001 g). Fecundity was estimated as

$$F = (M/m) \times 100$$

where M = mass of ovary; and m = mass of 100 randomly sub-sampled eggs. Wilson (1979) demonstrated that this procedure has a coefficient of variation of less than one percent. Mean egg diameter (mm) was estimated from a sub-sample of 20 eggs per female, measured using

Table 1. Relative contribution (%) by sex to age classes from multipanel gillnet catches during the study including comparison of sex ratio using the *G*-test.

Sex/Age	0+	1+	2+	3+	4+	5+	6+
Immature	95.2	6.6	0.6	0.9	0.0	0.0	0.0
Female	1.5	25.6	32.6	55.8	75.4	62.5	80.0
Male	3.3	67.8	66.8	43.3	24.6	37.5	20.0
n =	455	743	868	425	118	8	5
G_{adj} =	2.91	147.26	104.27	6.68	31.85	–	–
P	= 0.088	< 0.0001	< 0.0001	= 0.01	< 0.0001	–	–

an eyepiece graticule on a binocular microscope. Egg diameters were recorded from 358 pollan aged between 1+ and 5+ taken from December 1997–December 1999. The seasonal pattern of egg growth was investigated by plotting mean egg diameter per pooled monthly catch.

Logistic curves were fitted to estimate the length at which 50% of fish were sexually mature for 913 male and 669 female pollan. The start of spawning was taken as the first date on which females with maturation scores of VI (ripe and running) were recorded in samples. In addition, indirect evidence came from the first date when egg cannibalism was recorded during stomach analyses. To normalise the data and reduce heteroscedasticity, fecundity and fork length were $\log_{10}$-transformed. In the fecundity analyses, fish size was treated as a covariate and all means (presented back transformed) were size-adjusted least squares. Errors quoted were standard errors.

Results

Sex ratio, size, and age at maturity

The overall female:male sex ratio during the study showed that male fish dominated the catch (0.61:1, G_{adj} = 128.7; $P < 0.001$). The sex ratio varied considerably, ranging from 2.06:1 in February 1999 to 0.09:1 during December of the same year. However, sex ratios differed significantly from 1.0 in only six out of 22 months: five of these months were Novembers (1.75:1) or Decembers (0.13:1).

Length at maturity was estimated to be 211 mm for female Lough Neagh pollan and 203 mm for males, sizes attained by most fish in the second summer of life (Harrod 2001). On average, female pollan reached sexual maturity later than males; all individuals were sexually mature by age 4 (Table 1).

Spawning behaviour and date of spawning

During the spawning period, male fish dominated catches in the inshore areas (≤ 6 m) during all years and in areas offshore of spawning grounds (≥ 9 m) in two of the three years of sampling (*G* tests: $P < 0.001$). The exception was in the offshore catch in 1998 when the sex ratio was 1.0.

The start of spawning each year was generally consistent (Table 2), and fluctuated by less than two weeks between years. Unusual spawning behaviour was noted in 1996 when fish were not caught on the spawning grounds until the first week of December and ripe and running females were caught in mid-January.

The seasonal pattern of reproductive development

When sampling began in late 1997, female fish were heavily gravid and had a mean relative GSI of 25% (Fig. 1). After spawning, relative GSI rapidly fell to ca. 1% and stabilised at this level until June/July. Female gonads developed principally through the summer and autumn. The relative GSI values continued to rise until November/December, by which time females were again notably gravid with ovarian mass on average about 20% of fish somatic mass.

Table 2. Comparison of probable date of first spawning in Lough Neagh pollan 1975–1999, as the dates on which catches included females in maturation stage VI (R) and when egg-cannibalism by pollan (C) were first recorded.

Winter	Probable date of spawning	Source
1975–1976	27 Nov. 1975 (R)	Wilson (1979)
1976–1977	26 Nov. 1976 (R)	Wilson (1979)
1977–1978	28 Nov. 1977 (R)	Wilson (1979)
1987–1988	4 Dec. 1987 (R)	Winfield & Wood (1988)
1997–1998	15 Dec. 1997 (R) 21 Dec. 1997 (C)	Present study
1998–1999	2 Dec. 1998 (R) 29 Nov. 1998 (C)	Present study
1999–2000	5 Dec. 1999 (R) 11 Dec. 1999 (C)	Present study

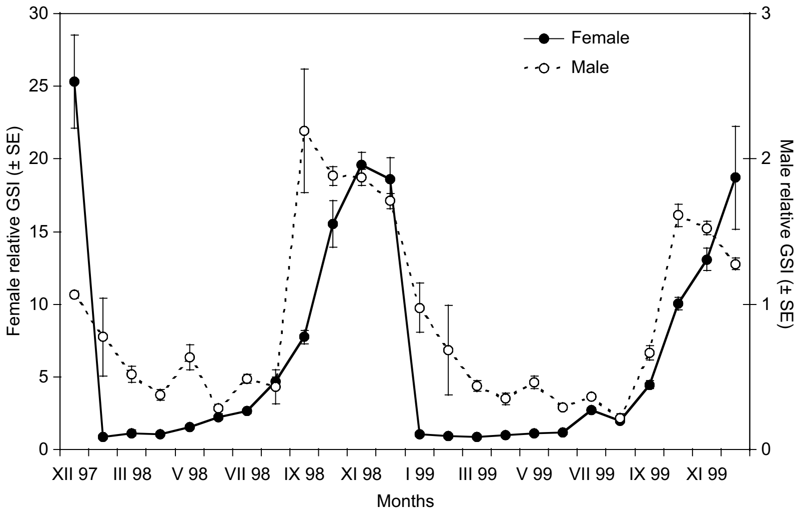

Fig. 1. Seasonal variation in mean relative GSI for females and males between December 1997–1999.

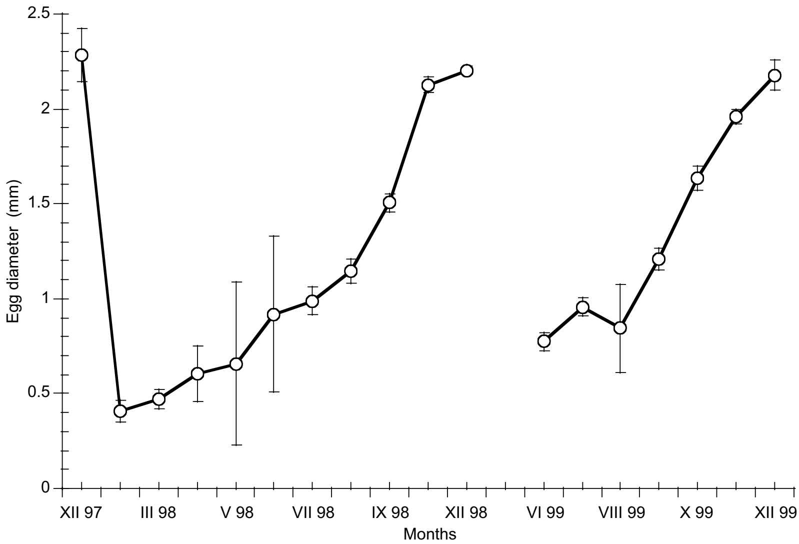

Fig. 2. Seasonal changes in mean (± 95% CI) egg diameter. Note that measurements are of preserved eggs.

Egg size increases followed an approximately sigmoidal pattern (Fig. 2). There was a general agreement between gonad growth, as shown by the relative GSI, and egg size.

Male pollan followed a similar seasonal cycle of gonad development to females but the loss of mass after spawning was slower through the winter, spring, and early summer. Testis growth did not start until late summer but relative GSI values rose rapidly towards an annual maximum of less than 2% somatic mass several months before spawning, and then declined slightly prior to spawning.

Fecundity

Fecundity of pollan ranged from 3009 to 21 130 eggs in the sample of 151 fish (200–290 mm) during 1997–1999. Although there was considerable scatter, fecundity increased with fish length (Fig. 3), mass, and age (Table 3). Within age class fecundity–length slopes of log-transformed data (2.27, 4.68, 4.03, 8.50 for ages 1–4, respectively) tended to be greater than the overall slope (b = 2.58) but only significantly so for age 4+ fish (t = 2.38, d.f. = 21, P = 0.027).

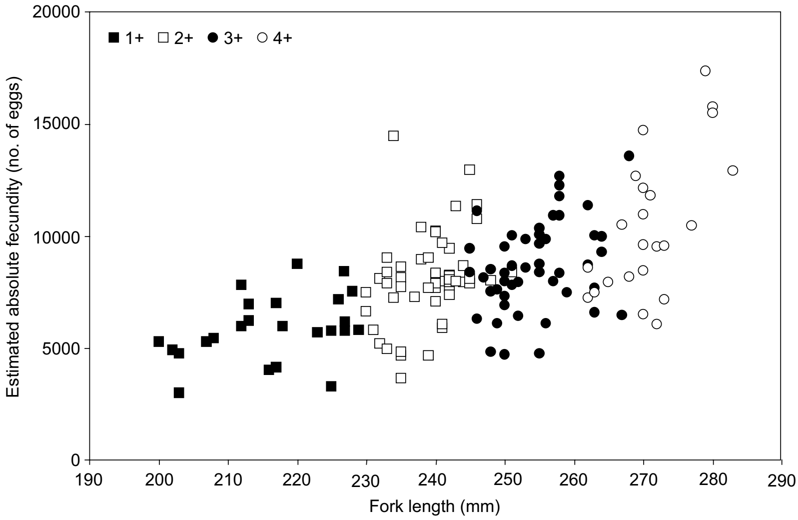

Fig. 3. Relationship between pollan length (mm), age, and absolute fecundity. Log fecundity = –2.25 + 2.58 ± 0.28log length, r^2 = 0.36, $P < 0.001$.

The mean size of stage V–VI eggs varied between 1.63 to 2.39 mm. There were significant positive correlations between fish length and fecundity, and mean egg diameter (log egg size × log length: $r = 0.39$, $n = 146$, $P < 0.001$; log egg size × log fecundity: $r = 0.25$, $n = 146$, $P < 0.01$). However, 1+ fish had significantly smaller eggs and they were significantly less fecund than older fish (egg size 1.91 *vs*. 2.13 mm, $F = 33.66$, d.f. = 1, 142, $P < 0.001$; fecundity 5585 *vs*. 8429, $F = 51.58$, d.f. = 1, 142, $P < 0.001$). When 1+ fish were removed, the relationships with age were no longer significant (length: $r = –0.002$, $n = 122$, $P = 0.984$; fecundity $r = 0.001$, $n = 122$, $P < 0.96$). Hence, the positive relationship between gonad size and pollan size resulted from increased fecundity rather than larger eggs. Size-adjusted fecundity was significantly greater in 1998 than in 1999 (8750, 7096 eggs respectively; $F = 30.35$, d.f. = 1, 140, $P < 0.001$). In addition mean egg diameter was greater in 1998 (excluding eggs from 1+ fish, 2.17 ± 0.013, $n = 71$, 2.06 ± 0.020, $n = 50$; $F = 22.46$, d.f. = 1, 119, $P < 0.001$).

Discussion

Our results show a broad agreement with those obtained in the 1970s by Wilson and Pitcher (1984) and Dąbrowski (1981). Pollan spawn on hard-bottoms (e.g. cobbles and gravel, C. Harrod, pers. obs.) in relatively shallow (≤ 3 m) areas. The earlier studies also showed that males dominated the catches on the spawning grounds though Dąbrowski found more females than males offshore (> 10 m water depth, 77 males: 88 females). We obtained a similar result in 1998 though males dominated offshore catches in 1997 and 1999. Dąbrowski (1981) and

Table 3. Lough Neagh pollan age-fecundity statistics (mean ± SE).

Age	Absolute fecundity	FL range (mm)	Relative fecundity (eggs g somatic mass^{-1})	Somatic mass range (g)	Egg diameter (mm)	*n*
1+	5816 ± 298	200–229	59.5 ± 2.64	76–123	1.97 ± 0.04	25
2+	8092 ± 279	230–251	62.1 ± 2.12	105–170	2.14 ± 0.016	52
3+	8907 ± 369	245–268	55.5 ± 2.16	121–221	2.10 ± 0.024	49
4+	10488 ± 661	262–283	55 ± 2.95	153–243	2.14 ± 0.025	23
5+	9168	285–290	39.6	226–238	2.11	2
All	8377 ± 221	200–290	58.43 ± 1.23	76–243	2.1 ± 0.013	151

Wilson and Pitcher (1984) recorded spawners in the last week of November, whereas during our study spawning was typically recorded in early December, even though known spawning grounds were regularly surveyed from mid-November onwards. Spawning may also extend longer than previously recognised. Wilson and Pitcher (1984) also found that fecundity was linearly related to length (their log-log slope = 1.37, confidence limits 0.67–2.07) while we found a much steeper slope. Such differences could be due to differences in methods of analysis, to short term changes in environment, or to longer term changes in pollan biology.

Wilson and Pitcher (1984) suggested that female pollan underwent a 14% reduction in mean relative fecundity between 1971 and 1977. The lengths of pollan examined between 1971 and 1977 were estimated by digitising fecundity–length data from Wilson (1979): we only identified 103 of the 105 data points analysed by Wilson but our slope value (1.25 ± 0.44) was close to his slope (1.37). Although not recognised by Wilson, his data showed significant heterogeneity across years with the slope of log-log transformed data being significantly different in 1975 from the other years (1975: $b = -3.37 \pm 1.49$, $n = 17$, $P < 0.05$; 1971: $b = 2.02 \pm 0.50$, $n = 39$, $P < 0.001$; 1976: $b = 2.83 \pm 0.70$, $n = 13$, $P < 0.01$; 1977: $b = 0.78 \pm 0.90$, $n = 34$, $P > 0.2$). While his sample size and size range examined in 1975 was small and the scatter in the data large, the negative trend cannot be attributed to outliers. When 1975 data were omitted, there was no significant difference across years in slopes but size-adjusted fecundity differed significantly (8810 in 1971, 7362 in 1976, and 8147 in 1977) as it did in the 1990s. Fecundity–fish size slopes differed across decades but this appeared to be due to a few large fish with low fecundities in the 1970s. When analysis was restricted to a common size range (224–282 mm fork length), the size-adjusted fecundity showed no significant difference in slopes or intercepts ($F = 1.53$, d.f. = 1, 208, $P > 0.2$) . The slope from the combined dataset of all years is significantly below 3 ($b = 2.32 \pm 0.21$, $t = 3.20$, $P < 0.05$), and hence statistical comparison of relative fecundities between different groups of pollan is invalid unless fish size is standardised (mass–fork length exponent = 3.16).

Our data show there is considerable variation in reproductive output of pollan. The size-adjusted ovary mass in 1998 was 39% greater than in 1999 (52.5 *vs*. 37.7g, $F = 105.6$, d.f. 1, 139, $P < 0.001$). Without information on egg energy content it is not possible to say if this translates to appreciable inter-annual variation in reproductive effort. Between-year variation in fecundity, egg size, and energy content has been noted also by others (Kamler 1992). Even if pollan showed similar levels of variation in energy content to that shown by *Coregonus albula,* this would be insufficient to offset the variation in ovary mass.

Considerable changes have occurred in the biotic and abiotic environments encountered by pollan since the early 1980s. By 1997, Lough Neagh had become increasingly productive due to cultural eutrophication (Foy *et al*. 1995) and is now classed as hypertrophic. Introduced roach dominated the scale-fish community, and the pollan population had recently undergone a loss of larger fish (Harrod 2001, Harrod *et al.* 2002). Eutrophication can increase mortality of developing coregonid eggs due to sedimentation on spawning grounds (Reshetnikov 1988, Müller 1992). However, eutrophication has also been associated with other shifts in reproductive ecology in coregonid fishes. Nümann (1972) reported that *C. lavaretus* matured younger and spawned later in the year following the eutrophication of the Bodensee, whilst Hartmann and Quoss (1993) suggested that relative fecundity for a standard 360 mm female increased, and then decreased with changes in this lake's productivity.

Significant changes occurred in the reproductive ecology of Lough Neagh pollan in the winter of 1996–1997. Spawning was delayed and the average size of spawners was significantly less than in previous years (Harrod *et al*. 2002). However, the reproductive ecology of pollan between 1997 and 1999 was similar to that described by earlier workers (Dąbrowski 1981, 1982, Wilson & Pitcher 1984). The seasonal pattern of gonad maturation was almost identical to that described by Wilson (1979) and Dąbrowski (1981, 1982). The gonads of male and female pollan developed rapidly during late summer and autumn, with peak GSI values for male fish recorded in the months directly before spawning, a common feature in coregonid fishes (Valtonen 1972, Pomeroy 1987, Heese 1990).

The greatest difference between studies was that Lough Neagh pollan matured at age 1+ (ca. 210 mm) in 1997–1999 whilst earlier authors concluded that the pollan matured at 2+ (ca. 245 mm; Dąbrowski 1981, Wilson & Pitcher 1984). Because pollan are short-lived (57% mean annual mortality rate; Harrod 2001), this represents a potentially significant shift in their ecology. Other lake coregonids have experienced reductions in age and size at maturity after increases in lake productivity (*C. lavaretus*; Nümann 1972) or where feeding conditions have improved due to decreases in density (*C. clupeaformis*; Jensen 1981, 1985). However, it is likely that the difference in size at first maturity described by earlier workers and our study reflects differences in the population structure during each study and not a biological shift. Early studies were conducted during a period of recruitment failure when 1+ fish were unavailable. In addition, age at maturity estimates were based on the youngest spawners in the catch and not the age at which 50% of the individuals become sexually mature.

Although the average size of spawning pollan was only 220 mm in 1996, the median length of spawners subsequently increased (Harrod 2001). Therefore, it seems that the unusual size structure and behaviour of pollan spawners in 1996 was not a result of changes in the reproductive ecology of Lough Neagh pollan, but was a consequence of the spawning stock being dominated by first-time spawners following a loss of older, larger fish. Brown (1989) noted that in Scottish populations of *C. lavaretus* first-maturing females underwent gametogenesis but failed to develop fully mature gonads and did not spawn in the first year of maturity. In Lough Neagh, first maturing females produced relatively few, small eggs. If the smaller eggs produced by 1+ pollan result in less viable larvae (Kamler & Żuromska 1979, Kamler *et al*. 1982, Miller *et al*. 1988) then the contribution made during spawning by a 1+ female to the following generation may be negligible. Intra-cohort size variation also affected fecundity, at least in older fish. This suggests that the ability of the population to replace itself is likely to vary with changes in the age structure of the spawners, and should be considered in any future management of the stock. For example, if routine monitoring shows that the stock is unusually reliant on age 1+ spawners (as in 1996), females should be protected from exploitation until they are 2+ (235 mm) when their reproductive output is greater, as suggested by Kamler and co-workers (Kamler & Żuromska 1979, Kamler *et al*. 1982) for stocks of *C. albula*. However, without considerable changes to the system of fisheries management on Lough Neagh, such protection is unlikely. If females are to be stripped to provide fertilised ova for translocations (Harrod *et al*. 2001), then only females of age ≥ 2+ (i.e. > 235 mm) should be used to maximise the viability of the trans-located eggs or larvae.

Prior to this study, the only detailed descriptions of pollan reproductive ecology were by Wilson (1979) and Dąbrowski (1981, 1982). Their data were collected in a period of considerable change in the lough and the pollan population. Cultural eutrophication was increasing (Smith 1993), roach were becoming established (Tobin 1990) and pollan reproduction had repeatedly failed, with population density falling sufficiently between 1975–1978 to disrupt the commercial fishery (Wilson 1979). This study has demonstrated that some of the conclusions drawn by these earlier workers were probably influenced by the unusual state of the pollan stock during the 1970s and the assumption that descriptions of pollan reproductive biology from the 1970s represent baseline conditions may be invalid.

Acknowledgments

Thanks to the staff and students of the former Limnology Laboratory for help and the Lough Neagh Fishermen's Co-operative and DANI for permission to fish. CH was funded through a DENI postgraduate research studentship and would like to thank JAM and EA colleagues for comments on the manuscript. Ken Mills and Eric Gyselman made many helpful suggestions which greatly improved the manuscript.

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